

The distinction of isolated bones from plaice (*Pleuronectes platessa*), flounder (*Platichthys flesus*) and dab (*Limanda limanda*): a description of the diagnostic characters

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(Received *March 28, 2007*; Revised *May 10, 2007*; Accepted *May 14, 2007*)



ABSTRACT: The osteology of 38 skeletal elements is investigated in plaice, dextral and sinistral flounder, and dab with the aim of defining diagnostic characters that allow species identification of isolated bones from archaeological excavations. Five of these 38 skeletal elements have been mentioned in the literature as being diagnostic, but they appear to be unreliable for identification. All other elements allow identification, although only 23 permit the recognition of all three species. The individual bone elements and their diagnostic criteria are depicted and described in detail. Attention is paid to individual variation, and, when relevant, size-related morphological changes are also described. The keys that are developed for the various elements are finally tested on a large flatfish bone assemblage from an archaeological site. On the basis of these results, the success rate of the identifications for the various bones is discussed. Possible strategies for identification work on this group are suggested that take into account the extent of the reference collection, the time spent on the identifications and the experience needed in comparative osteology of these flatfish.

KEYWORDS: OSTEOLOGY, ARCHAEOZOOLOGY, FISH, PLEURONECTIDAE

RESUMEN: Se analiza en este trabajo la osteología de 38 huesos de platijas, sollas dextrógiras y levógiras y limandas en un intento por definir rasgos diagnósticos que permitan la identificación específica de piezas aisladas procedentes de excavaciones arqueológicas. Cinco de estos 38 huesos se mencionan en la bibliografía como con valor diagnóstico lo que no parece ser el caso. El resto tienen valor discriminante en mayor o menor medida aunque sólo 23 permiten diferenciar entre estas tres especies. Se representan en detalle todos los huesos considerados y se describen todos y cada uno de los criterios diagnósticos. Se tiene asimismo en cuenta la variación de rasgos entre individuos y, siempre que ello fuese relevante, determinados cambios morfológicos asociados con la talla. Las claves dicotómicas que se han confeccionado para los distintos huesos se ponen a prueba sobre una gran colección de restos de peces planos procedentes de un yacimiento arqueológico. Sobre la base de nuestros resultados, se valora la viabilidad de los distintos criterios. Asimismo, se apuntan posibles estrategias para la identificación de restos de este grupo teniendo en cuenta el tamaño de las colecciones de referencia, el tiempo empleado en la identificación y la experiencia requerida para abordar la osteología comparada de estos peces planos.

PALABRAS CLAVE: OSTEOLOGÍA, ARQUEOZOOLOGÍA, PECES, PLEURONECTIDAE

INTRODUCTION

The aim of this contribution is to describe the osteological differences observed on isolated bones of plaice (*Pleuronectes platessa*), flounder (*Platichthys flesus*) and dab (*Limanda limanda*). These three species, belonging to the Pleuronectidae family, occur frequently in archaeological sites, especially of countries neighbouring the North Sea and the Baltic, and have a rather similar osteomorphology. Some general osteomorphological information on the Pleuronectidae has been described by Norman (1934), but these data are of limited use when isolated skeletal elements need to be identified. Although diagnostic characters have been described for a few elements, and despite the fact that some authors seem to have undertaken comparative work during the identification of archaeological flatfish bones (see below), no systematic study has thus far been published on the osteology of isolated skeletal elements. Because of the resulting identification problems, bone remains of this group are often classified as «plaice/flounder/dab», «Pleuronectidae» or «flatfish» in faunal reports. More precise identifications would, however, enhance the possibilities of interpretation when dealing with ichthyofaunas from North-Western Europe. Nowadays, the three species are captured on different major fishing grounds, and also their spawning season and the period during which they occur in shallow, inshore, waters is different (Poll, 1947). More accurate species identifications will therefore enable a more detailed establishment of the former fishing grounds and fishing seasons. It will also provide the means to facilitate the understanding of the economic importance of the three species through time, and to verify if diachronic changes occur in the consumption patterns and the processing of plaice, flounder and dab. Our understanding of the development of fish trade will also benefit from more accurate identifications, as suggested recently on the occasion of a survey made on this issue in the U.K. (Barrett *et al.*, 2004: 621). It is vital, when dealing with inland trade, to distinguish the marine species (plaice and dab) from flounder, which is also found in estuaries and even in fresh water. It also remains to be verified to what extent the consumption patterns of coastal populations differ from those inland: previous archaeozoological research in Flanders has shown, for

instance, that export to inland markets concentrated on a limited number of taxa, and also that a selection in function of size was carried out by the fishing communities (Van Neer & Ervynck, 2006). Both the proportion of the consumed flatfish species and their sizes therefore need more attention.

From a modern fisheries point of view, proxy data on the left- or right-sidedness of flounder may be of interest. In *Platichthys flesus* the eyes are usually on the right side of the body, but up to one third of the flounders may be reversed, and it appears that the proportion of such sinistral individuals within a population shows geographic variation. Along the south-coast of England the proportion of reversed specimens is only about 5% (Duncker, 1900; Hartley, 1940) but along the coast of Holstein this is about 25% (Duncker, 1900) and in the Baltic up to 35% of the flounder are sinistral (Strodtmann, 1906). Although the possible environmental causes for reversed asymmetry are still poorly understood (Norman, 1934; Fornbacke *et al.*, 2002), inclusion of diachronic, archaeozoological data may be of interest in the future. The only archaeozoological information thus far available comes from a medieval site near Kattégat, dated between 1200 and 1300 AD, where the proportion of reversed flounder, based on the frontal bone, is 36% (Bødker Enghoff, 1994). It has been reported that hybrids between flounder and plaice can occur, especially in the western Baltic (Nielsen, 1986), but as far as we know we did not have any such specimens in our modern material. Possibly, this may affect the use of the keys presented below.

Data in the literature dealing explicitly with the distinction of isolated bones from plaice, flounder and dab are rare. They include differences described for the cleithrum (Heinrich, 1987), and for the frontal, pterotic and sphenotic (Bødker Enghoff, 1989). Heinrich (1987) mentions that the preopercular does not display consistent diagnostic characters. Brinkhuizen (1989) writes that the differences described for the os anale by Lepiksaar & Heinrich (1977) are not valid. The articular and the dentary of the three species are illustrated and described by Roselló (1986). Depictions of the dermal denticles of flounder are given in Bødker Enghoff (1986) and the same author (Bødker Enghoff, 1989, 1994) also illustrates neurocrania and frontals of normal, dextral, flounder and of reversed, sinistral, specimens.

elements analysed	recognisable species	literature	'easy' elements allowing recognition of	
			all species	some species
nasale left	none			
nasale right	dab, reversed flounder			*
alisphenoideum	dab			
praefrontale	dab, plaice, flounder, rev. flounder	7	*	
vomer	dab, reversed flounder	10		
frontale	dab, plaice, flounder, rev. flounder	6, 7, 5, 9	*	
parietale	dab, plaice, flounder, rev. flounder			
posttemporale	dab, plaice, flounder	10		
ptericum	dab, plaice, flounder	6, 9	*	
sphenoticum	dab, plaice, flounder	6, 9	*	
supraoccipitale	dab, reversed flounder	7		
basiooccipitale	dab	10		
parasphenoideum	dab, plaice, flounder, rev. flounder			
articulare	dab, plaice, flounder, rev. flounder	7, 4, 10	*	
dentale	dab, plaice, flounder, rev. flounder	1, 2, 4, 10, 8	*	
ectopterygoideum	dab, plaice, flounder, rev. flounder	10	*	
entopterygoideum left	dab, plaice, flounder, rev. flounder			
entopterygoideum right	dab, reversed flounder			
maxillare left	dab, reversed flounder	7, 10		*
maxillare right	dab, plaice, flounder, rev. flounder	7, 10	*	
palatinum	dab, plaice, flounder, rev. flounder	10		
praemaxillare	dab, plaice, flounder, rev. flounder	1, 10	*	
quadratum	dab, reversed flounder	10, 8		
ceratohyale	dab	7, 10		
hyomandibulare	dab	7, 10		*
interoperculare	dab, plaice, flounder			
praeoperculare	dab	10, 8		*
urohyale	dab, plaice, flounder	6, 9, 8	*	
pharyngobranchiale II	dab, plaice, flounder		*	
pharyngobranchiale III	dab, plaice, flounder		*	
pharyngobranchiale IV	dab, plaice, flounder		*	
pharyngobranchiale V	dab, plaice, flounder		*	
cleithrum	dab, plaice, flounder	7, 5, 10, 8	*	
postcleithrum	dab			*
supracleithrum	none	10		
os anale	dab, plaice, flounder	2, 10	*	
1st vertebra	dab, plaice, flounder	10		
2nd vertebra	none	10		
first caudal	none	10?		
penultimate vertebra	none	10?		
antepenultimate vertebra	none	10?		

TABLE 1

Overview of the studied skeletal elements of plaice, flounder and dab. For each bone, the species that can be recognised are indicated in the second column. The third column shows the authors that have described or used the skeletal elements during their analysis [1: Norman (1934); 2: Lepiksaar & Heinrich (1977); 3: Bødker Enghoff (1986); 4: Roselló (1986); 5: Heinrich (1987); 6: Bødker Enghoff (1989); 7: Brinkhuizen (1989); 8: De Jong (1994); 9: Bødker Enghoff (1994); 10: Clavel (1997)]. The elements indicated with an asterisk in the last two columns show straightforward diagnostic characters that are relatively easy to use.

Various other bones appear to have been used for the specific identification of Pleuronectidae judging from a number of archaeozoological publications, in which the intraskeletal distribution is given of the identified plaice, flounder and dab. In those cases, however, the diagnostic criteria were not described. De Jong (1994) used the dentary, quadrate, preopercular, cleithrum and urohyal, whereas Brinkhuizen (1989) made specific identifications on the basis of praefrontal, frontal, supraoccipital, articular, maxilla, ceratohyal, hyomandibular and cleithrum. Clavel (1997) made identifications on the basis of 18 different elements (Table 1). Altogether 27 different bones have thus far been used in the aforementioned archaeozoological reports. In the present contribution, these skeletal elements will be studied and, in addition, 11 other bones are retained that occur frequently in archaeological assemblages. The sagittae were not studied since these otoliths have already been described in sufficient detail in Härkönen (1986). Dab otoliths can be readily identified, but the discrimination between plaice and flounder can be precarious, especially in smaller individuals. As mentioned above, the dermal denticles, which only occur in flounder, have already been depicted by Bødker Enghoff (1986) and are therefore not retained here either.

MATERIAL AND METHODS

A large number of disarticulated, dry, flatfish skeletons are available for comparative purposes in the modern reference collection housed at the Royal Belgian Institute of Natural Sciences. These include 396 plaice skeletons measuring between 5.0 cm standard length (SL)/6.2 cm total length (TL) and 56.0 cm SL (65.0 cm TL). The 121 flounder skeletons are from individuals ranging in size from 4.2 cm SL (5.0 cm TL) to 38.0 cm SL (44.0 cm TL), and the 41 dab skeletons are from specimens measuring between 3.9 cm SL (4.8 cm TL) and 31.5 cm SL (TL unknown). All these fish are from the North Sea and were mainly obtained from commercial landings and fish shops, but the smaller specimens were collected either by ourselves or by colleagues working on research vessels. For each of the 38 analysed bone elements, modern specimens of different size classes have been considered. For plaice 15 individuals were studied and for dab, dextral flounder and sinistral flounder 12 fish skeletons were selected of each.

The smallest and the largest specimens available for each species have always been taken into account. In some cases, a particular characteristic was verified on additional specimens, for instance for the premaxilla for which the number of teeth reported in the literature deviated strongly from our own observations.

During the analysis of paired bones the first task was always to attempt to define criteria enabling the distinction between the left and right skeletal element. In the next step, the bones of the reversed flounder and the normal (i.e., dextral) flatfish were analysed for their left and right elements separately. Attention was paid to shape, proportions, minor morphological details and texture of the bones.

The terminology used in the description of the individual bone elements was mainly borrowed from Lepiksaar (1983), Rojo (1991) and Cañas (1992).

RESULTS

A summary of the results of the comparative analysis on the 38 skeletal elements is shown in Table 1. In the paragraphs below a total of 34 paired and unpaired elements are dealt with, albeit not in the traditional, anatomical order. In the case of highly diagnostic, paired bones, the distinction of species is described for left and right elements of fish that are in a normal, dextral position, and in each case, the reversed flounder is considered simultaneously. This has been done for the articular, the dentary, the ectopterygoid, the entopterygoid, the maxilla, the premaxilla, the palatine, the parasphenoid, the frontal, the prefrontal, and the parietal.

For certain skeletal elements the distinction between sinistral and dextral flounder cannot be made. In that case only one drawing is provided of flounder. This was done for the interopercular, the cleithrum, the posttemporal, the pharyngobranchials, the pterotic and the sphenotic. Unpaired elements equally allowing the recognition of the three species, but not the distinction between dextral and sinistral flounder, are the urohyal, the os anale and the first precaudal vertebra.

The next series of elements that are dealt with are those that allow the recognition of dab and of reversed flounder. Plaice and dextral flounder cannot be discriminated, however. This is the case for the quadrate, the vomer, the supraoccipital, the ethmoid, and the right nasal.

The final series includes the elements that only allow the identification of dab, i.e. the preopercular, the hyomandibular, the ceratohyal, the basioccipital, the alisphenoid, and the postcleithrum.

To facilitate identification, the users of the key are advised to concentrate on the morphology illustrated by the figures and on the position of the depicted bone as such, combined with the information provided in the text and tables. It is believed that the step-wise procedure proposed in the text for each skeletal element is more user-friendly than a dichotomous key. For most elements more than one reliable criterion is listed that can be used for identification. In a few cases characters are listed that are less clear, or that are not always observed, on all the modern specimens. Those criteria are indicated separately in the tables, in brackets.

Articulare (Figure 1)

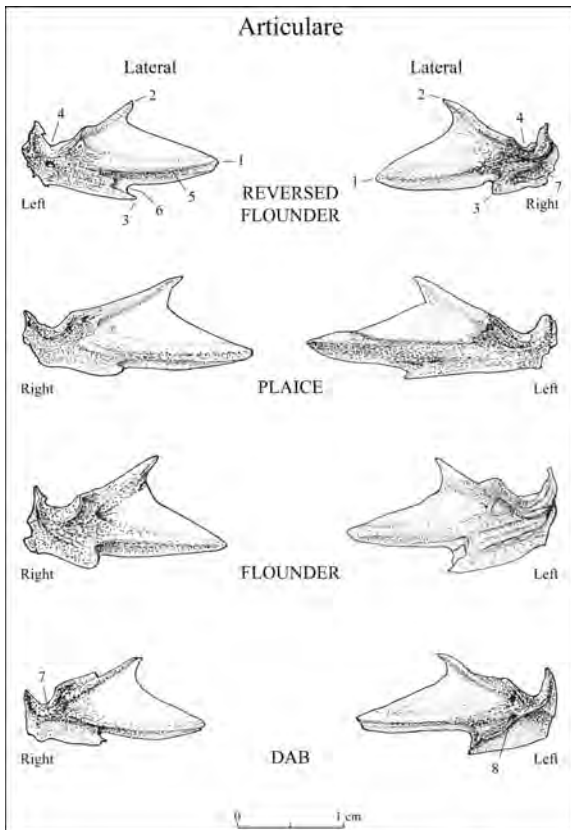


FIGURE 1

Lateral view of the articular of plaice, dab, dextral and reversed flounder.

When the *processus anterior* (1) is pointing towards the right in lateral view, the element is a right articular.

The reversed flounder can be distinguished from the three dextral species by the relative position of the *processus coronoideus* (2) and the *angulus ventralis anterior* (3). In the right articular of the reversed flounder the *angulus ventralis anterior* (3) is located below the *processus coronoideus* (2), whereas in the three other cases, the *angulus* is situated much more posteriorly. Also diagnostic for the right articular of the reversed flounder are the more deeply incised and longer *facies articularis quadrata* (4) and the very pronounced incision (6) between the *costa inferior externa* (5) and the *angulus ventralis anterior* (3).

The distinction between the right articulars of dextral plaice, flounder and dab can be made on the basis of the criteria listed in Table 2. This element cannot be brought to species when only one character is used, especially for individuals smaller than 20 cm SL. All criteria should be taken into account when dealing with small flatfish and even then identification appears to be sometimes impossible.

When the *processus anterior* (1) is pointing towards the left in lateral view, the element is a left articular.

In the next step, the relative position of the *processus coronoideus* (2) and *angulus ventralis anterior* (3) needs to be considered: when they are located more or less below each other, the element is a left articular of either dextral flounder or plaice. The distinction between the two species can be made as shown in Table 3.

When the *angulus ventralis anterior* (3) is located well behind the *processus coronoideus* (2) the element is a left articular of dab or reversed flounder. The distinction between both can be made on the basis of the criteria listed in Table 4.

It appears that the position of the *processus coronoideus* (2) relative to the *angulus ventralis anterior* (3) is a particularly constant and useful criterion to distinguish dab left articulars from those of reversed flounder. However, it is advisable to use the additional criteria as well, especially in smaller individuals.

character	plaice	flounder	dab
facies articularis quadrate (4)	shallow incision	deep incision	deep incision, short
position of the tip of the processus coronoideus (2)	situated more anteriorly than in flounder and dab	more towards the middle of the articular	more towards the middle of the articular
projection of the angulus ventralis anterior (3)	not, or poorly, pronounced	well pronounced and located more posteriorly than in plaice or dab	poorly developed, but always more pronounced than in plaice
length/height proportion of the articular	about 2.5 (2.4 – 2.9)	about 2.0 (1.8 – 2.2)	about 2.0 (1.9 – 2.2)
[density of the bone in the posterior part of the element]	large dense area in the whole posterior part	large dense area in the whole posterior part	only a small dense area in the posterior part (7)

TABLE 2

Distinction between the right articulars of dextral plaice, flounder and dab.

character	plaice	dextral flounder
projection of the angulus ventralis anterior (3)	not developed	well pronounced; more detached from body of the articular
facies articularis quadrate (4)	shallow	deep, rarely shallow
density of bone in posterior part (7)	dense over entire posterior area	dense area restricted

TABLE 3

Distinction between the left articulars of dextral flounder and plaice.

character	dab	reversed flounder
position of the processus coronoideus (2) relative to the angulus ventralis anterior (3)	relatively close to each other	angulus ventralis anterior (3) about halfway between processus coronoideus (2) and posterior edge of articular
projection of the angulus ventralis anterior (3)	pronounced	variable, mostly slight
density of bone in posterior part (7)	dense bone restricted to the ribs (8)	dense area larger

TABLE 4

Distinction between the left articular of dab and sinistral flounder.

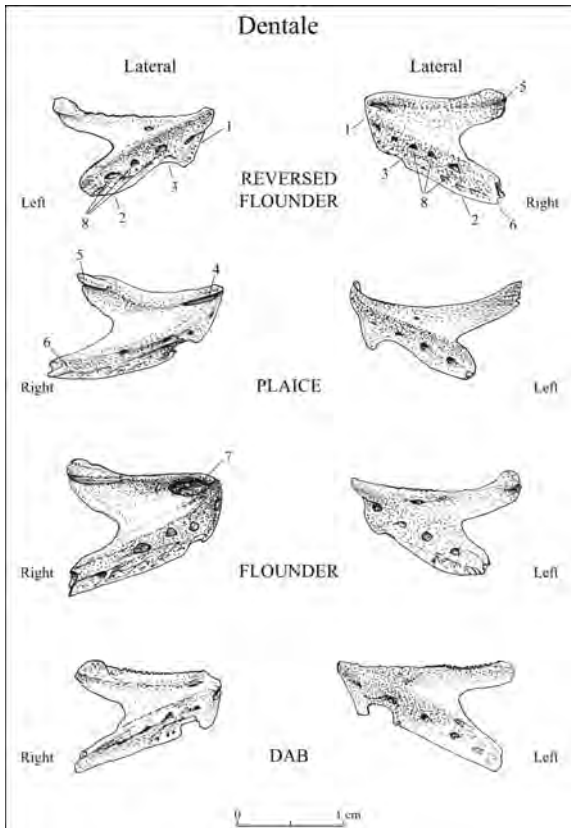
Dentale (Figure 2)

FIGURE 2

Lateral view of the dentary of plaice, dab, dextral and reversed flounder.

In lateral view the symphysis (1) is located at the right in the right dentary.

The reversed flounder can be easily distinguished from the others by the strong outward curvature of the body. In addition, the number of teeth is very high: between 15 and 24, which represents a larger variation than the 17 to 18 teeth mentioned by Norman (1934). The margo inferior (2), just posterior of the symphysis (1), shows a long and deep indentation (3). The orificiae lineae lateralis (8) are large and almost circular.

The distinction between the right dentaries of dextral plaice, flounder and dab can be made on the basis of the criteria listed in Table 5.

The characters used to identify this element are straightforward, only the distinction between sinistral and dextral flounder is sometimes unclear.

It was noticed that the outward curvature of the body was sometimes more pronounced in dextral flounder and less pronounced in reversed flounder.

In lateral view the symphysis (1) is located at the left in the left dentary.

When the body of the left dentary is strongly curved outwards, the element is from a dextral flatfish, if the bone is flat it is from a reversed flounder. The latter is also characterised by a fine ridge on the processus aboralis superior (5), and an equal posterior extension of the processus aboralis superior (5) and processus aboralis inferior (6).

The distinguishing characters of the left dentaries of dextral plaice, flounder and dab are indicated in Table 6.

The number of teeth appears to be of no use in the distinction of the left dentaries. Norman (1934) mentions the following numbers: plaice 18-32, dab 14-28, and flounder 15-26. During the present study the observations were as follows: plaice 15-31, dab 15-25, reversed flounder 12-17, and dextral flounder 20-28. It was noticed that juvenile plaice (smaller than 12 cm) have another tooth alignment. Instead of a single row along the entire dentary, the teeth form several parallel rows. In flounder and dab, such a tooth alignment was never seen. Such small specimens of plaice can have up to 32 teeth.

Ectopterygoideum (Figure 3)

When the *ectopterygoid* is viewed laterally, i.e. with the most structural details facing towards the observer, the *crus posterior* (1) is directed towards the right in the right *ectopterygoid*.

The *crus posterior* (1) and the *crus anterior* (2) are broad in the right *ectopterygoid* of reversed flounder, compared to their more slender outline in those of dextral flatfish. The distinction between the right *ectopterygoids* of dextral plaice, dab and flounder can be made on the basis of the criteria listed in Table 7.

When the *ectopterygoid* is viewed laterally, the *crus posterior* (1) is directed towards the left in the left *ectopterygoid*.

The reversed flounder can be easily distinguished from the others by its more slender general appearance. Additional characters are the hook (3) on the *crus anterior* (2), the shallow groove on the articulation (5) with the *entopterygoid* with a fine ridge (8) in the anterior part, and the fact that the *crus anterior* (2) and *crus posterior* (1) are confluent.

character	plaice	flounder	dab
indentation (3) of the margo inferior (2)	long and deep; in fish less than 25 cm rather short and deep	short and shallow	short and deep
heavy ridge on the margo superior (4)	present	absent	absent
ridge on the processus aboralis superior (5)	heavy	finer than in plaice	absent or very faint
processus aboralis inferior (6)	extending behind processus aboralis superior (5)	ending at same height as processus aboralis superior (5)	ending at same height as processus aboralis superior (5)
margo inferior (2)	curved	rather straight	straight
number of teeth (in brackets number mentioned by Norman, 1934)	2-7 (Norman: 2-7)	13-16 (Norman: 7-15)	15-20 (Norman: 9-16)
depression near symphysis (7)	absent	present	absent
[orificiae lineae lateralis (8)]	small and rather oval	larger and more rounded	very small

TABLE 5

Distinction between the right dentaries of dextral plaice, flounder and dab.

character	plaice	flounder	dab
indentation (3) of the margo inferior (2)	long and deep	shallow	short and deep
position of processus aboralis superior (5)	extends beyond processus aboralis inferior (6)	extends beyond processus aboralis inferior (6)	extends as far as processus aboralis inferior (6)
symphysis (1), processus aboralis superior (5) and processus aboralis inferior (6) in the same plane (i.e., when positioned flat the three points touch the surface)	no, the processus aboralis inferior does not touch the surface, except in some very large specimens (more than 45 cm SL)	yes	yes
margo inferior (2)	curved	curved	straight
orificiae lineae lateralis (8)	small	large and circular	hardly visible

TABLE 6

Distinction between the left dentaries of dextral plaice, flounder and dab.

character	plaice	flounder	dab
bone density	heavy built compared to dab	heavy built compared to dab	very light, transparent, bone
protrusion (3) on crus posterior (1)	present	present, but location variable along this crus	absent, more or less smooth ectopterygoid
crus posterior (1) and anterior (2)	separated by a groove (4) when viewed dorsally	confluent when viewed dorsally	confluent when viewed dorsally
articulation (5) with entopterygoid in dorsal view	heavy ridge (8) over the whole length	fine ridge (8) in anterior part	short groove (6), only present anteriorly

TABLE 7

Distinction between the right ectopterygoids of dextral plaice, flounder and dab.

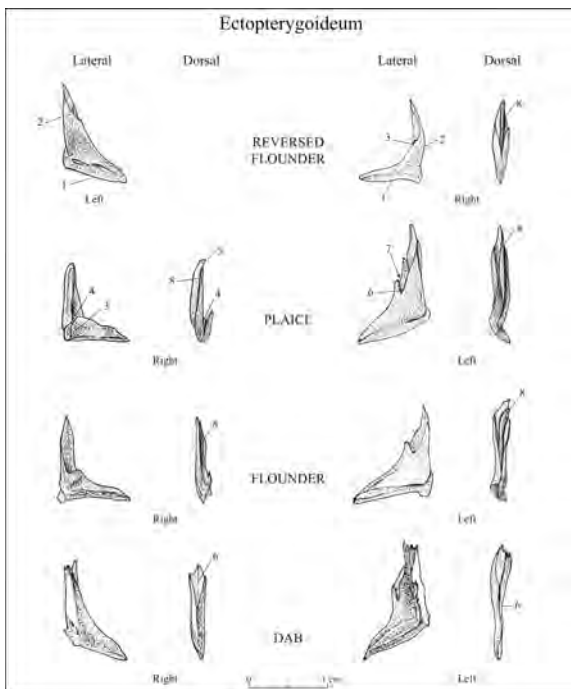


FIGURE 3

Lateral and dorsal view of the ectopterygoid of plaice, dab, dextral and reversed flounder.

When the ectopterygoid has a sturdier appearance, the element is a left ectopterygoid of a dextral plaice, flounder or dab. The distinction between the three species can be made on the basis of the characters listed in Table 8.

In small fish of 15 cm SL or less the distinction between flounder and plaice is difficult. For such

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specimens the most useful criterion seems to be the articulation with the entopterygoid.

Entopterygoideum (Figure 4)

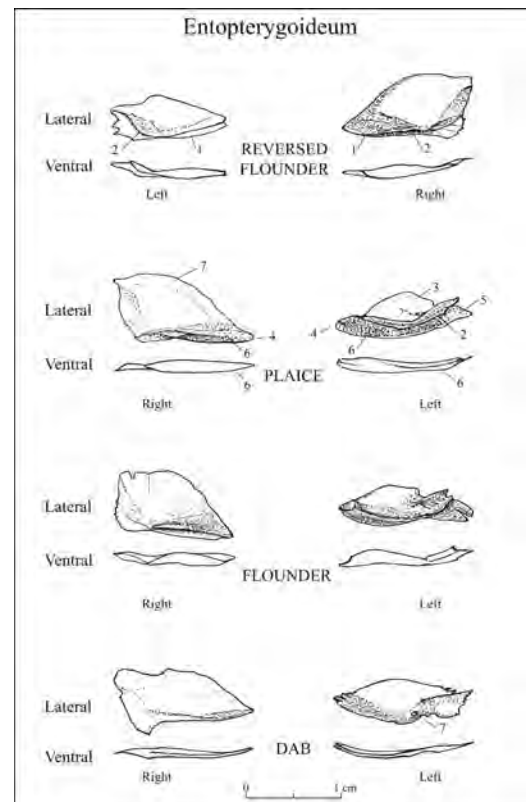


FIGURE 4

Lateral and ventral view of the entopterygoid of plaice, dab, dextral and reversed flounder.

When the *entopterygoid* is viewed laterally, with the *costa marginalis* (1) below, the element has a pointed end directed towards the right side in the right entopterygoid.

The right entopterygoid of reversed flounder differs from the others by its more oval-shaped outline and by the presence of more structural details. The margo inferior (2) is slightly curved.

character	plaice	flounder	dab
appearance of articulation (6) with palatinum	deep groove, with fossa (7) continuing within the bone	shallow groove, fossa (7) rarely present	narrow groove, fossa (7) rarely present
articulation (5) with entopterygoid in dorsal view	heavy ridge (8) over the whole length	fine ridge (8) in anterior part	groove (6) present over the whole length; wide anteriorly
general bone structure	densely built	densely built	more fragile, less ossified

TABLE 8

Distinction between the left ectopterygoids of dextral plaice, flounder and dab.

character	plaice/flounder	dab
density of the <i>costa marginalis</i> (6)	costa thicker and denser; becoming more pronounced towards the pars anterior (4)	very thin costa; well developed only in specimens of 25 cm SL and more; not becoming more pronounced towards the pars anterior (4)
density of the bone	dense bone	transparent, except in anterior part of <i>costa marginalis</i> (6)
margo superior (7)	gently sloping in anterior direction	more or less parallel to margo inferior (2) over about two thirds of its length

TABLE 9

Distinction between the right entopterygoids of dab and dextral flounder or plaice.

character	plaice	flounder	dab
curvature of the margo inferior (2)	margo is curved	margo is rather straight in anterior part, curves slightly in posterior part	margo is straight in small specimens (10 cm SL or less); is slightly notched (7) in the posterior part in larger specimens
extent of transparent part (3) of the corpus	small surface; never reaches the anterior tip (4) or the posterior tip (5)	large surface; extends more towards anterior tip (4)	large surface; extends more towards anterior tip (4) and posterior tip (5)
density of the <i>costa marginalis</i> (6)	very dense; thickened over the almost entire length	very dense; thickened only in the anterior half or third	very lightly built, also in large individuals; almost no thickening

TABLE 10

Distinction between the left entopterygoids of dextral plaice, flounder and dab.

The right ectopterygoid of dextral plaice, flounder and dab have a more or less triangular outline, and their margo inferior (2) is nearly straight.

The right entopterygoids of dextral plaice and flounder cannot be distinguished from each other, but they differ from those of dab in the criteria listed in Table 9.

When the *entopterygoid* is viewed laterally, with the *costa marginalis* (1) below, the element has a pointed end directed towards the left side in the left entopterygoid.

The left entopterygoid of reversed flounder has a rather straight margo inferior (2), and the bone has a relatively high and short outline. The left entopterygoid of dextral plaice, flounder and dab are more elongate and have a rather oval outline.

The distinction between the left entopterygoids of dextral plaice, flounder and dab can be made with the criteria listed in Table 10.

Maxillare (Figure 5)

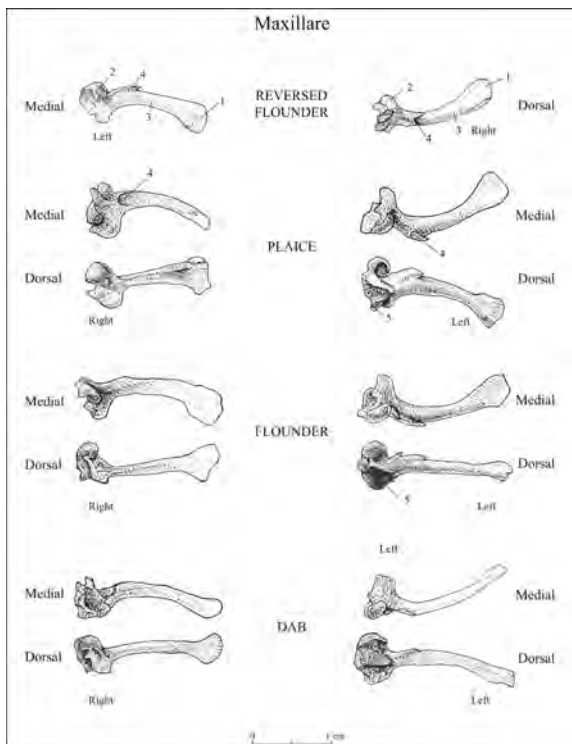


FIGURE 5

Medial and dorsal view of the maxilla of plaice, dab, dextral and reversed flounder.

When the *maxilla* is viewed medially, i.e. with the *pars caudalis* (1) located right of the *caput maxillare* (2), then the *pars caudalis* (1) is directed downwards in the right maxilla. The element is a right maxilla of a reversed flounder when the structure (4) on the collum maxillare is a clear ridge. When the structure (4) is a notch, instead of a ridge, the element is a right maxilla of a dextral plaice, flounder or dab. The listing of characters in Table 11 shows that the recognition of dab is easier than the distinction between plaice and flounder.

When the *maxilla* is viewed medially, i.e. with the *pars caudalis* (1) located right of the *caput maxillare* (2), then the *pars caudalis* (1) is directed upwards in the left maxilla. The element is a left maxilla of a reversed flounder when the structure (4) on the collum maxillare is a notch. When the structure (4) is a ridge, instead of a notch, the element is a left maxilla of a dextral plaice, flounder or dab.

It appears that dab can be easily recognised using the criteria listed in Table 12, but a distinction of plaice and flounder was not possible for dextral specimens.

character	plaice	flounder	dab
notch (4)	very clearly incised, well delineated	less clearly incised, poorly delineated	less clearly incised, poorly delineated
appearance of corpus maxillaris (3) in dorsal view	sturdy; starts broadening in a caudal direction immediately after caput maxillare (2)	more slender; more gradual broadening in a caudal direction	very slender
appearance of pars caudalis (1)	clear broadening visible in dorsal view	clear broadening visible in dorsal view	only slightly broadened posteriorly

TABLE 11

Distinction between the right maxillae of dextral plaice, flounder and dab.

character	plaice or flounder	dab
appearance of corpus maxillaris (3)	sturdy	slender
ridge (5) on processus externus	very pronounced	absent
ridge (4) on collum maxillare	very robust	slender
appearance of pars caudalis (1)	clearly broadened	only slightly broadened

TABLE 12

Distinction between the left maxillae of dab and dextral flounder or plaice.

Praemaxillare (Figure 6)

When the *premaxilla* is viewed laterally, the *processus anterior* (1) is located at the right in the right premaxilla.

The right premaxilla of reversed flounder can be distinguished from the others by the protruding lower part of the symphysis (2). Another typical feature is the shallow incision between the *processus anterior* (1) and the *processus articularis* (3). In the dextral flatfish both structures are more separated.

The distinction between the right premaxillae of dextral plaice, flounder and dab can be made with the criteria listed in Table 13.

In the right premaxilla of the reversed flounder we observed 14 to 26 teeth in our material. It was also noticed that in reversed flounder smaller than 12 cm SL more than one row of teeth could occur. On the basis of the modern material that we had at our disposal, the number of teeth seemed to be a reliable criterion, also in the smallest individuals. Despite the fact that we doubled the number of observations for this criterion, a difference in number of teeth remains if compared to the data from Norman (1934). This is no doubt due to the fact

that he lumped the data for dextral and sinistral specimens (see also below).

When the *premaxilla* is viewed laterally, the *processus anterior* (1) is located at the left in the left premaxilla.

The left premaxilla of reversed flounder can be distinguished from the others by the absence of a protrusion in the lower part of the symphysis (2). Typical for this element are also the well-separated *processus anterior* (1) and *processus articularis* (3). The number of teeth can vary between 9 and 13, and these values approach the lower part of the variation mentioned by Norman (1934).

The distinction between the left premaxillae of plaice, dextral flounder and dab can be made with the criteria listed in Table 14.

Compared to the data provided by Norman (1934), we noticed differences in the number of teeth, although less pronounced than in the dentary. In addition, it was noticed that juvenile plaice, flounder and dab (smaller than 12 cm) have another tooth alignment. Instead of a single row along the entire premaxilla in larger fish, only the anterior part has such a single row; the more posteriorly located teeth form several rows.

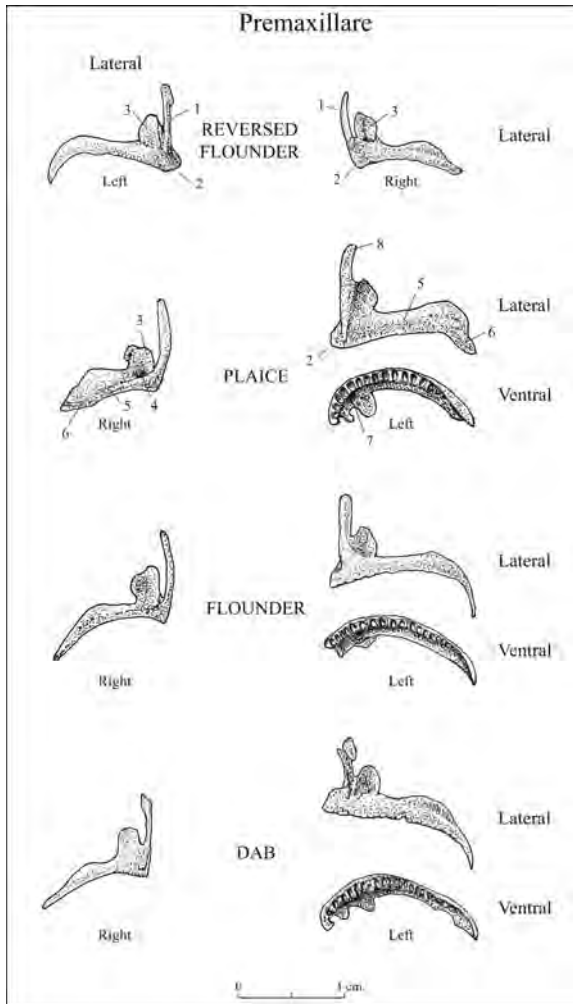


FIGURE 6

Lateral view of the premaxilla of plaice, dab, dextral and reversed flounder, and ventral view of the left premaxilla of plaice, dab and dextral flounder.

Palatinum (Figure 7)

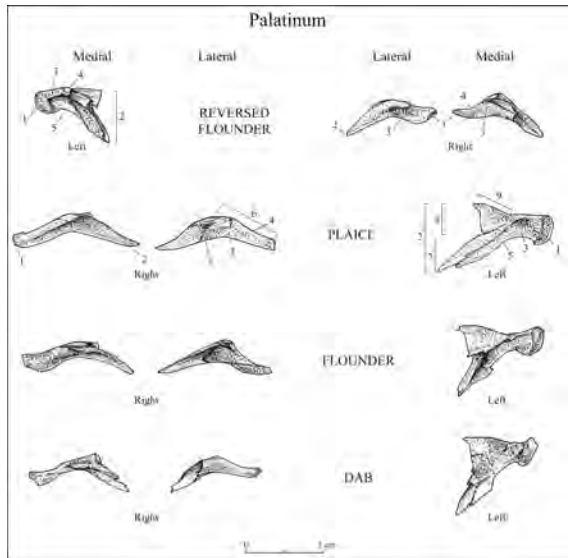


FIGURE 7

Medial and lateral view of the palatine of plaice, dab, dextral and reversed flounder.

When the *palatine* is viewed medially, the *processus maxillaris* (1) is located at the left, and the *pars subpterygoidea* (2) is pointing towards the right in the right palatine. The reversed flounder can be distinguished from the others by the sturdy appearance of the collum (3) and of the *pars subpterygoidea* (2). Typical are also the straight *margo superior* (4), the short *pars subpterygoidea* (2), the concave *margo inferior* (5), and the resulting constriction of the collum (3).

The right palatine of dextral plaice, flounder and dab are slender and show almost no structures in medial view, because the articulations are locat-

character	plaice	flounder	dab
shape of corpus (5) and its pars caudalis (6)	corpus and pars caudalis are sturdy	corpus is slender and has a long and fine pars caudalis	corpus is shorter than in flounder; corpus is slender and has a long and fine pars caudalis
foramen (4) below the processus articularis (3)	present	sometimes present	absent
number of teeth (in brackets numbers of Norman, 1934)	2-9 (Norman: 0-6)	12-15 (Norman: 7-15)	7-12 (Norman 5-13)

TABLE 13

Distinction between the right premaxillae of dextral plaice, flounder and dab.

character	plaice	flounder	dab
incision between processus anterior (1) and processus articularis (3)	absent or very slight	slight	deeper
foramen (7) on medial side, close to the symphysis	usually present	sometimes present	absent
general shape of corpus (5) in lateral view	sturdy and curved outward	slender and often rather straight	very slender and curved outward
pars caudalis (6)	sturdy	slender	very slender
tip (8) of processus anterior	no thickening	no thickening	thickening present
number of teeth (in brackets numbers of Norman, 1934)	13-32 (Norman: 18-32)	16-25 (Norman: 17-25)	16-27 (Norman 15-26)

TABLE 14

Distinction between the left premaxillae of dextral plaice, flounder and dab.

character	plaice	flounder	dab
relative length of anterior half (6) in lateral view	longest	shorter	shortest
thickness of the collum (3)	rather sturdy	rather sturdy	very slender
margo superior (4) of anterior half in lateral view	straight	always curved	almost straight
margo inferior (5) in lateral view	smoothly curved	curved, always more pronounced than in plaice	almost angular

TABLE 15

Distinction between the right palatines of dextral plaice, flounder and dab.

ed at the lateral side. The distinction between the right palatines can be made with the criteria listed in Table 15. The discrimination of dextral flounder and plaice is difficult in individuals measuring less than 20 cm SL.

When the *palatine* is viewed medially, the *processus maxillaris* (1) is located at the right, and the *pars subpterygoidea* (2) is pointing towards the left in the left palatine. The reversed flounder can be distinguished from the others by its slender and short collum (3). The margo superior (4) is very concave in lateral view.

The left palatine of dextral plaice, flounder and dab has a sturdy collum (3) and the *pars subpterygoidea* (2) clearly shows distinct articular facets

for the ectopterygoid (7) and entopterygoid (8). The distinction between the left palatines can be made with the criteria listed in Table 16. The discrimination of dextral flounder and plaice is difficult in individuals measuring less than 20 cm SL.

Parasphenoideum (Figure 8)

The prefrontal ridge (1) bordering the *facies articularis vomeris* (2) is located at the right side in the reversed flounder (on the left side in the figure) and at the left side in dextral flatfish.

The distinction between the parasphenoids of the dextral flatfish can be made on the basis of the criteria listed in Table 17. The characteristics

character	plaice	flounder	dab
outline of the margo inferior (5)	slightly concave; no or only slight constriction of the collum (3) visible behind the processus maxillaris (1)	very concave; constriction clearly visible	very concave
pars subpterygoidea (2)	articular facet for the ectopterygoid (7) protrudes more heavily in a posterior direction than the articular facet for the entopterygoid (8)	articular facet for the ectopterygoid (7) protrudes strongly in postero-ventral direction	articular facet for the ectopterygoid (7) protrudes strongly in ventral direction
margo superior (4)	posterior part (9) clearly curved upward	straight or slightly curved upward in posterior part	straight or slightly curved upward in posterior part

TABLE 16

Distinction between the left palatines of dextral plaice, flounder and dab.

character	plaice	flounder	dab
groove (3) in the facies articularis basioccipitalis (4)	absent, or very narrow and shallow	deep, rather narrow	variable depth, always wide
width of the bone (5) in the posterior part	gradual widening of the parasphenoid in anterior direction	abrupt widening of the parasphenoid in anterior direction	in anterior direction, first widening and then narrowing
outline of the crista medialis (6) in lateral view	less pronounced, almost straight crista medialis; no clearly rounded protrusion	less pronounced, almost straight crista medialis; no clearly rounded protrusion	well pronounced and rounded protrusion (7) about mid-way the crista medialis

TABLE 17

Distinction between the parasphenoids of dextral plaice, flounder and dab.

described below for the dextral flounder are also valid for the reversed form.

Dab parasphenoids appear to be easily identifiable, but the distinction between flounder and plaice may be hampered when the bones are from fishes less than 20 cm SL.

Frontale (Figure 9)

The left frontal of reversed flounder and the right frontals of dextral flatfish have a long anteri-

or process (3). In dorsal view, this anterior process (3) is curving towards the right in the left frontal of reversed flounder. The characters described below for the right frontal of dextral flounder are also found in the reversed form.

Table 18 lists the criteria that allow distinction between the right frontals of dextral plaice, flounder and dab.

The right frontal of reversed flounder and the left frontals of dextral flatfish have a short anterior process (3). In dorsal view, this anterior process (3) is located on the left in the right frontal of

reversed flounder. The characters described below for the left frontal of dextral flounder are also found in the reversed form.

Table 19 lists the criteria that allow distinction between the left frontals of dextral plaice, flounder and dab.

The third criterion (ornamentation on the lateral margin) cannot be accurately drawn or illustrated by a photograph and should rather be examined

by palpation which allows one to feel whether the margin is almost smooth (plaice), weakly serrated (dab) or is comprised of numerous small tubercles (flounder). Despite the fact that this criterion cannot be accurately illustrated visually, it is very diagnostic. This method of examining cranial skeletal elements is also necessary in the sphenoticum and the pterotic which, as the frontal, lie along the lateral skull margins and have a species specific ornamentation.

character	plaice	flounder	dab
ornamentation on the lateral margin (1)	2, sometimes 3 well-developed tubercles	numerous small tubercles, creating a serrated margin	no ornamentation, smooth margin
length of the anterior process (3)	relatively short, compared to dab	relatively short, compared to dab	more elongate, slender
reticulate structure of dorsal side (2)	present over large part of surface; fine and regular reticulation with a few larger holes	present over large part of surface; coarse and irregular reticulation	present over small part of surface; very fine and regular reticulation

TABLE 18

Distinction between the right frontals of dextral plaice, flounder and dab.

character	plaice	flounder	dab
general shape	more elongate	shorter	shorter
texture of the bone	dense	dense	less dense
ornamentation on the lateral margin (1) (palpation necessary)	almost smooth	numerous small tubercles, creating a serrated margin	weakly serrated
appearance of dorsal side (2)	smooth	coarse and reticular structure in anterior part	coarse and reticular structure in anterior part
depression (5) below ridge (4)	filled with few, fine reticulation*	filled with dense and irregular reticulation	no reticulation
depression (7) below anterior margin (6)	deep, with reticulation	deep, with some reticulation	shallow, no reticulation

TABLE 19

Distinction between the left frontals of dextral plaice, flounder and dab. *: not visible on figure, element needs to be tilted.

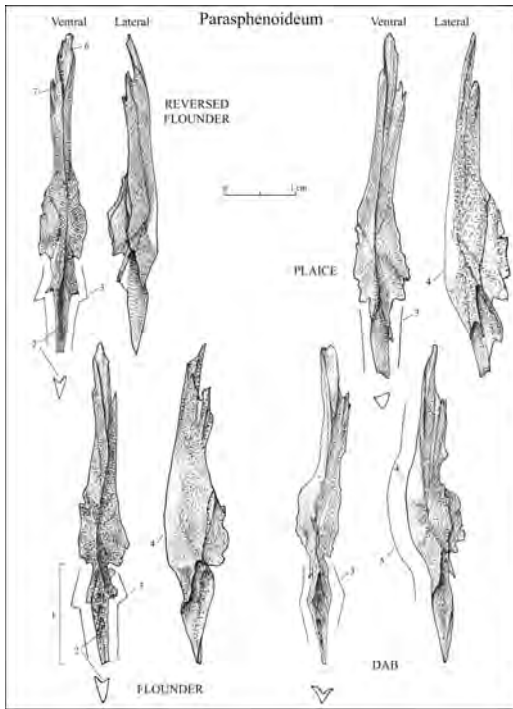


FIGURE 8

Ventral and lateral view of the parasphenoid of plaice, dab, dextral and reversed flounder.

Praefrontale (Figure 10)

The *praefrontal* is roughly triangular and has no elongate posterior extension in the left *praefrontal* of reversed flounder and in the right *praefrontal* of dextral flatfish. In reversed flounder, the foramen olfactorius (1) lies in the right part of the bone. In dextral plaice, flounder and dab, the foramen olfactorius (1) lies in the left part of the right *praefrontal*. The distinction between the three dextral flatfish can be made on the basis of the criteria listed in Table 20.

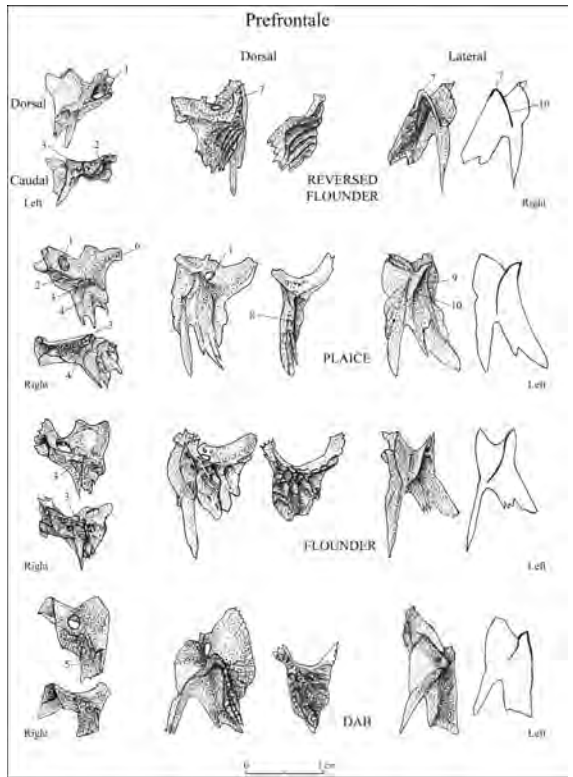


FIGURE 10

Views of the *praefrontale* of plaice, dab, dextral and reversed flounder. For the right *praefrontal* of reversed flounder and the left *praefrontals* of plaice, dab and dextral flounder, two dorsal views are provided. The left one shows the complete dorsal view, the second one is a detail of the uppermost part. For the same elements two lateral views are given as well. The second view depicts schematically the outline of the *processus lateralis* and the adjacent ridge.

The *praefrontal* is a sturdy element with elongate, posterior extensions in the right *praefrontal* of reversed flounder and in the left *praefrontal* of dextral

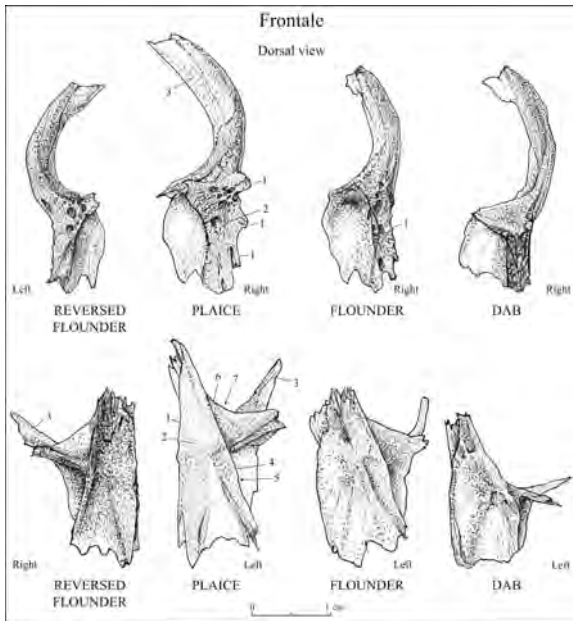


FIGURE 9

Dorsal view of the frontal of plaice, dab, dextral and reversed flounder.

flatfish. Reversed flounder can, in addition, be recognised by the position of the processus lateralis (7) which is to the right in dorsal view. In the left

prefrontals of dextral flatfish, the processus lateralis (7) lies to the left. The three species can be distinguished on the basis of the criteria given in Table 21.

character	plaice	flounder	dab
size of the foramen olfactorius (1)	small *	large	large
margō ethmoidalis (2)	very prominent, with a well developed, pointed protrusion (3)	bone is less dense; margo is prominent only in the pointed protrusion (3)	margo very faint; no protrusion visible
articulation (4) with the frontale	rather fine reticulate structure with regular design in specimens less than 40 cm SL; coarser reticulation in larger fish	always coarse reticulate structure with irregular design	very fine reticulate and regular structure; clear constriction (5) in posterior part
antero-lateral part of prefrontale (6)	protruding; made of dense bone	not protruding; bone less dense	not protruding; bone less dense

TABLE 20

Distinction between the right prefrontals of dextral plaice, flounder and dab. *: size differences are more obvious when the bone is viewed under a different angle than the one on the figure.

character	plaice	flounder	dab
tip of processus lateralis (7)	pointing in lateral direction	pointing in anterior direction	pointing in anterior direction
wing (8) lateral of articulation with frontal (dorsal view of uppermost part of the bone)	narrow and long	very wide and short	very wide
texture of bone on the wing (8) lateral of articulation with frontal	rather fine, regular reticulate structure	always coarse and irregular reticulate structure	very fine, regular reticulate structure
shape of depression (9) lateral of and below processus lateralis (7)	very narrow and shallow	very wide and deep	very wide and shallow
ridge (10)	prominent and long	very prominent and long	poorly developed and short
relative size of foramen olfactorius (1)	smaller	larger*	larger*

TABLE 21

Distinction between the left prefrontals of dextral plaice, flounder and dab. *: the foramen olfactorius of dab looks smaller on the figure, but its size depends on the position under which the element is viewed.

Parietale (Figure 11)

In dorsal view, the thin *pars medialis* (2) of the parietal is located to the left, and the thickened *pars lateralis* (1) to the right in the right parietal.

The distinction between the right parietals can be made with the criteria listed in Table 22.

In dorsal view, the thin *pars medialis* (2) of the parietal is located to the right, and the thickened *pars lateralis* (1) to the left in the left parietal. Table 23 indicates the criteria that allow a species identification.

Interoperculare (Figure 12)

For this element it was not possible to make the distinction between sinistral and dextral flounder. Hence, the characters below enable the recognition at species level only. The characters allowing species identifications are listed in Table 24. They are all related to the extent and location of denser parts within the element. Dab can be distinguished from the two other species by the lighter build of the bone. For the distinction between flounder and plaice, the criteria work well for larger individuals, but in specimens of 30 cm SL and less they are less consistent.

character	reversed flounder	plaice	flounder	dab
surface ornamentation (4) on the <i>pars lateralis</i> (1)	no clear structure visible	broad, fine and regular reticulate surface structure; covering about half the <i>pars lateralis</i>	narrow, irregular surface structure, only slightly veined; covering about 1/5 of the <i>pars lateralis</i>	narrow, fine and regular reticulate surface structure; covering about 1/3 of the <i>pars lateralis</i>
groove (5) in ventral surface	wide and shallow	wide and deep	narrow and deep	wide and deep
[thickness of <i>pars lateralis</i> in lateral view (3)]	thick	relatively thin, smooth, not pronounced	thick, serrated, very pronounced	very thick, smooth

TABLE 22

Distinction between the right parietals of plaice, flounder and dab.

character	reversed flounder	plaice	flounder	dab
surface ornamentation (4) on the <i>pars lateralis</i> (1)	thick bone with coarse reticulate structure	smooth bone with very narrow band with fine reticulate structure	thin, smooth bone	thick bone with fine reticulate structure
thickness of <i>facies articularis pteroticum</i> (6) in lateral view	thick	thin	very thin	very thick
groove (5) in ventral surface	wide and shallow	wide and deep	narrow and shallow	wide and deep

TABLE 23

Distinction between the left parietals of plaice, flounder and dab..

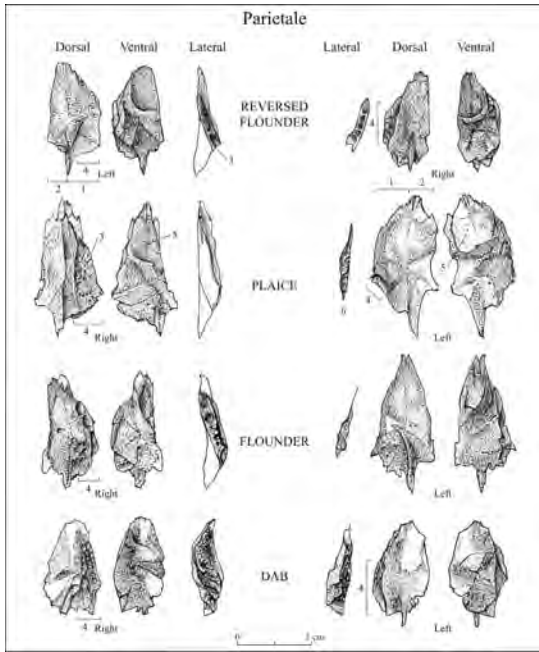


FIGURE 11

Dorsal, ventral and lateral view of the parietal of plaice, dab, dextral and reversed flounder.

Cleithrum (Figure 13)

No difference can be made between dextral and sinistral flounder. The distinguishing characters are listed in Table 25. The figures include lateral and caudal views of the left and right elements.

The groove (6) in the crista externa (7) is the most reliable criterion, but other features should be taken into account as well. For a good view of this groove, the use of a binocular microscope is necessary. The curvature of the margo anterior (9) was retained as a diagnostic character by Heinrich (1987), but this feature appears to be very variable and not very reliable, especially in small individuals.

Posttemporale (Figure 14)

For this element it was not possible to make the distinction between sinistral and dextral flounder. When the *posttemporale* is viewed medially, the *processus inferior* (1) is pointing to the right in the right element.

In lateral view, right posttemporals of plaice have a well-developed tubercle (2) on the corpus (3). This criterion alone allows a secure identification of plaice. The posttemporals of flounder and dab can be distinguished on the basis of the criteria in Table 26. In fish of less than 15 cm SL, the differences are less clear.

When the *processus inferior* (1) is pointing to the left in medial view, the posttemporale is a left element.

The criteria enabling a distinction of the three species are given in Table 27. It is advised to use all criteria since overlap can occur due to variability in shape.

Pharyngobranchiale II (Figure 15)

The distinction between left and right second pharyngobranchials of sinistral and dextral flounder could not be made. The distinguishing characters, at species level, are listed in Table 28.

The recognition of small individuals of plaice and flounder is not easy, but it is feasible especially on the basis of the outline of the margo medialis (1). An additional helpful criterion is the earlier appearance of a double tooth row in flounder, in comparison to plaice.

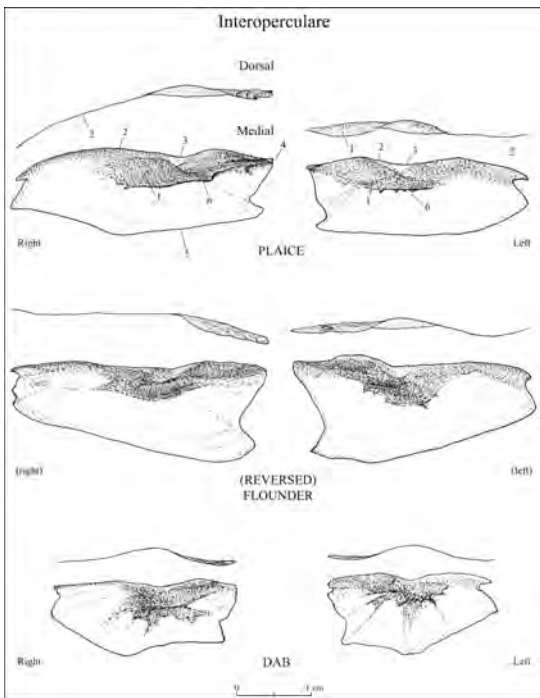


FIGURE 12

Dorsal and medial view of the interopercular of plaice, flounder and dab.

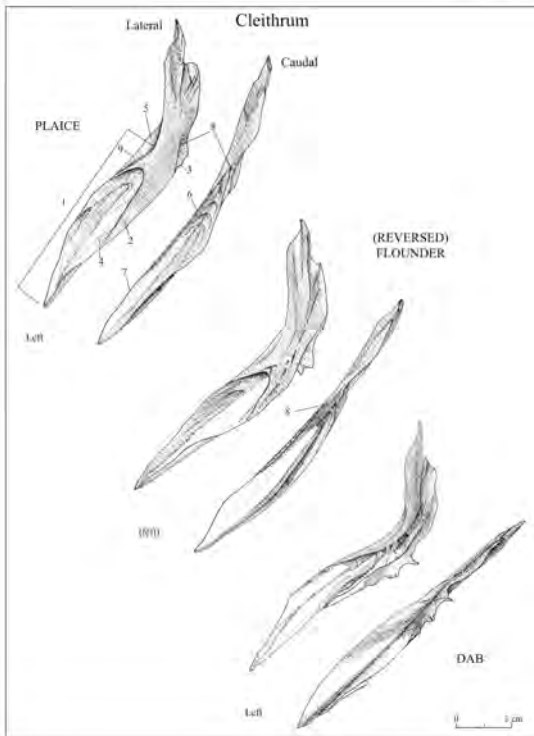
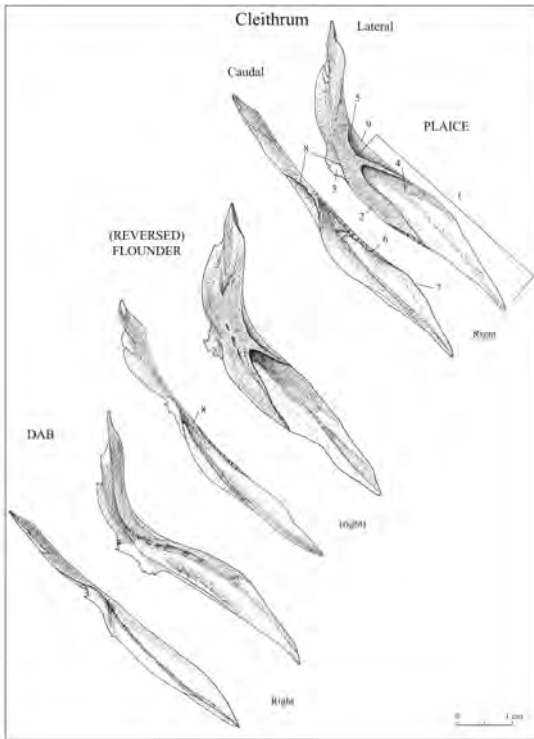


FIGURE 13a and 13b

Lateral and caudal view of the cleithrum of plaice, flounder and dab.

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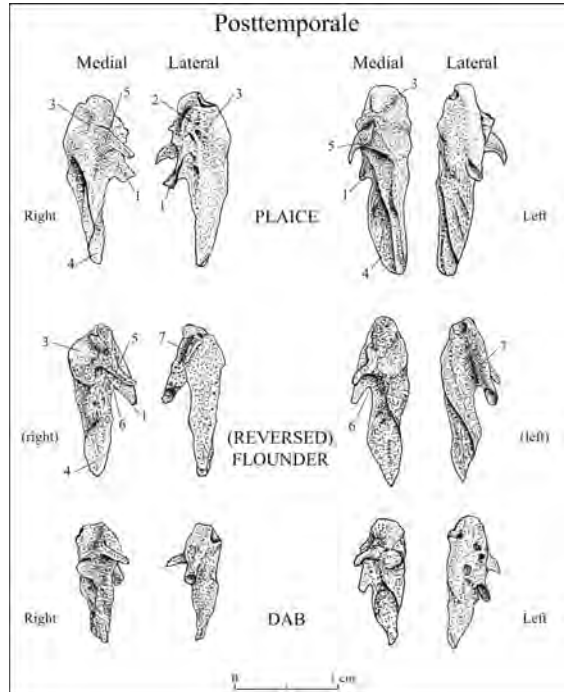


FIGURE 14

Medial and lateral view of the posttemporal of plaice, flounder and dab.

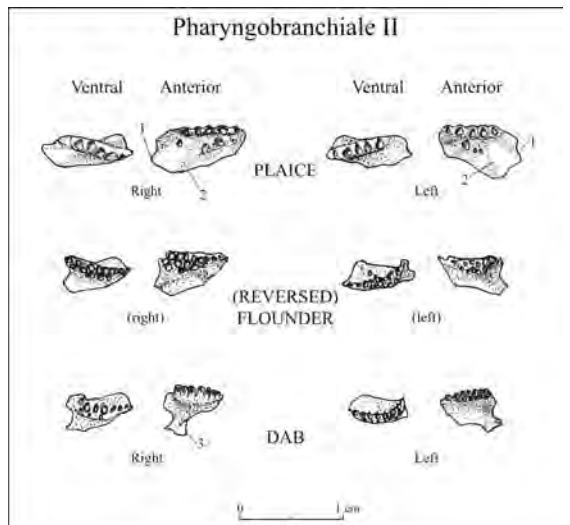


FIGURE 15

Ventral and anterior view of the second pharyngobranchials of plaice, flounder and dab.

character	plaice	flounder	dab
thickness of the bone in dorsal view	denser part (1) along the margo superior (2) is thick	denser part (1) along the margo superior (2) remains relatively thin	no, or almost no, denser bone along the margo superior (2)
[extension of the dense bone (1) along the margo superior (2) in dorsal and medial view]	from the angulus superior (4) far beyond the notch (3)	from the angulus superior (4) only to the notch (3) or slightly beyond	dense bone only near the angulus superior (4)
[ventral delineation of dense bone towards the margo inferior (5)]	very prominent line marks the delineation (6)	poorly delineated; dense bone radiating towards the margo inferior (5) extending as far as (6)	dense bone radiating towards the margo inferior (5) as far as (6); fine striae; rather vague

TABLE 24

Distinction between interoperculars of plaice, flounder and dab.

character	plaice	flounder	dab
dense bone (2) in lamina dorsalis (1)	present	present	absent
depression (4) in lamina dorsalis (1)	deep	usually wide and shallow	wide and shallow
groove (6) in crista externa (7) in the dense bone part (2)	present; groove runs beyond crista articularis (3) (stops at position (8))	present; groove does not extend beyond crista articularis (3) (stops at position (8))	absent
depression (5) lateral of the margo anterior (9)	deep and wide	absent or poorly developed; if present always narrower than in plaice	no depression

TABLE 25

Distinction between cleithra of plaice, flounder and dab.

character	flounder	dab
incision (6) near the processus inferior (1)	present	absent
proportion of corpus (3) and processus superior (4)	corpus heavily developed; much wider than processus superior	corpus less well developed; only slightly wider than processus superior
relative position of base of processus medialis (5) and processus inferior (1)	base of processus medialis (5) in contact with processus inferior (1)	no contact between base of processus medialis (5) and processus inferior (1); both are well separated
surface of canalis lineae lateralis (7)	with tubercles	smooth

TABLE 26

Distinction between the right posttemporals of flounder and dab.

character	plaice	flounder	dab
incision (6) near the processus inferior (1)	rarely present	present	absent, poorly developed in large specimens
proportion of corpus (3) and processus superior (4)	processus superior (4) almost as wide as corpus (3)	processus superior (4) narrower than corpus (3); processus superior (4) more slender than in plaice and dab	processus superior (4) almost as wide as corpus (3)
relative position of base of processus medialis (5) and processus inferior (1)	no contact between base of processus medialis (5) and processus inferior (1); both are well separated	base of processus medialis (5) in contact with processus inferior (1)	no contact between base of processus medialis (5) and processus inferior (1); both are well separated
surface of canalis lineae lateralis (7)	1 tubercle in about 50% of the cases; otherwise (as in figure) heavily ossified	usually with several tubercles; heavily ossified	smooth; less ossified

TABLE 27

Distinction between the left posttemporals of plaice, flounder and dab.

character	plaice	flounder	dab
number of teeth	4 – 9 depending on size; number can increase to 15 in specimens of 45 cm SL and more	8 – 20 depending on size	6 – 8
tooth size	large	small	small
number of tooth rows	1 row in specimens smaller than 30 cm SL; in larger individuals: additional 2 nd row with 1 or 2 teeth	1 row in specimens smaller than 20 cm SL; in larger individuals: additional 2 nd row with up to 10 teeth in 2 nd row	always 1 row
margo medialis (1)	rather straight	clearly concave	clearly concave
dorsal part of corpus (2) in anterior view	broad and high, dense bone	less broad and high than plaice, less dense	very slender with pedicle (3); light bone

TABLE 28.

Distinction between the second pharyngobranchials of plaice, flounder and dab.

Pharyngobranchiale III (Figure 16)

The distinction between left and right third pharyngobranchials of sinistral and dextral flounder could not be made. The distinguishing characters, at species level, are listed in Table 29.

Dab third pharyngobranchials are easily recognisable by the shape of the bone and by the number of teeth. For the distinction between flounder and plaice, all criteria should be taken into account. In individuals less than 25 cm SL, the differences are less clear. Occasionally deformations

of the third pharyngobranchial have been observed that hamper the use of the listed criteria.

Pharyngobranchiale IV (Figure 17)

The distinction between left and right fourth pharyngobranchials of sinistral and dextral flounder could not be made. The distinguishing characters, at species level, are listed in Table 30.

The recognition of small individuals of plaice and flounder is not easy, but it is feasible on the basis of the number of teeth.

Pharyngobranchiale V (Figure 18)

The distinction between left and right fifth pharyngobranchials of sinistral and dextral flounder could not be made. The distinguishing characters, at species level, are listed in Table 31.

Pteroticum (Figure 19)

When the *pterotic* is viewed laterally, the *margo epioticum* (1) and the *margo exoccipitalis* (2) are

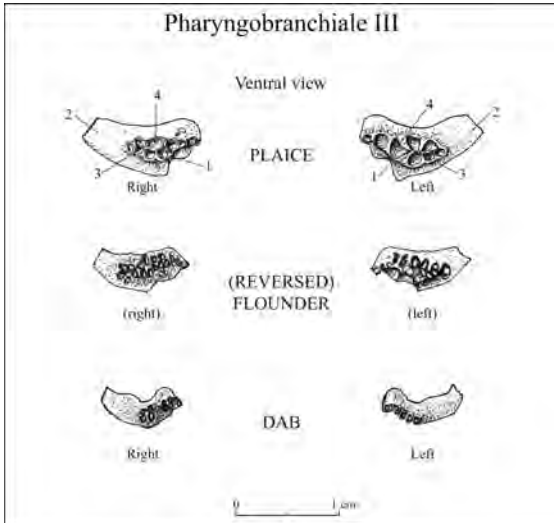


FIGURE 16

Ventral view of the third pharyngobranchials of plaice, flounder and dab.

character	plaice	flounder	dab
number of teeth	6-14 depending on size; number can increase to 25 in specimens of 45 cm SL and more	13-21 depending on size	6-8
number of tooth rows	2 rows, also in specimens of less than 10 cm SL	2 rows, also in specimens of less than 10 cm SL	1 row if 6 teeth; 2 rows if 7 or 8 teeth
size of teeth (and of sockets on tooth plate)	large	small	small
medio-posterior margin (1)	angular indentation	more or less straight; no clear indentation	rounded, no indentation
general shape	sturdy	more slender than plaice	sickle-shaped, very slender
amount of bone adjacent to tooth bearing surface (4)	tooth surface surrounded by large amount of bone in lateral (2) and posterior (3) direction	tooth surface surrounded by less bone in lateral (2) direction; almost no bone in posterior part (3)	large amount of bone in lateral part (2), no bone in posterior part

TABLE 29

Distinction between the third pharyngobranchials of plaice, flounder and dab.

character	plaice	flounder	dab
number of teeth	5-9 (depending on size)	9-22 (depending on size)	7-8
number of tooth rows	usually 1 row; occasionally 2 teeth in a second row	1 row in very small specimens, but then already 10-12 teeth; 2 full rows from 25 cm onwards	1 row
extent of tooth row	teeth only in medial part; short toothless part present in medial direction (1)	teeth along the entire length; no toothless part	teeth along the entire length; no toothless part
size of teeth (and of sockets on tooth plate)	increases along the tooth row in a medial direction	more or less constant along tooth row	more or less constant along tooth row
bone density	dense	dense	porous

TABLE 30

Distinction between the fourth pharyngobranchials of plaice, flounder and dab.

character	plaice	flounder	dab
general shape	broad corpus, triangular with deep indentation (1)	slender corpus, triangular with shallow indentation	very slender and elongate
number of teeth	14 to 32, depending on size	35 to 60, depending on size	20 to 30, depending on size
number of tooth rows	2 rows; sometimes 1 additional third row with one or a few teeth in the centre (not dependent of fish size)	more than 2 rows	2 rows
size of teeth (and of sockets on tooth plate)	large	small	very small
alignment of the teeth	regular	irregular	regular

TABLE 31

Distinction between the fifth pharyngobranchials of plaice, flounder and dab.

located to the right of the *crista lateralis* (3) in the right element. No distinction could be made between the pterotics of sinistral and dextral flounder.

The criteria allowing a distinction between the three species are listed in Table 32.

When the *pterotic* is viewed laterally, the *margo epioticum* (1) and the *margo exoccipitalis* (2) are located to the left of the *crista lateralis* (3) in the left element. As for the elements mentioned Archaeofauna 16 (2007): 33-72

above, no distinction could be made between the pterotics of sinistral and dextral flounder. Apparently, as in the sphenotic, these bones from the posterior part of the skull are affected to a far lesser extent by the asymmetrical cranial deformation during the post-larval development.

The criteria allowing a distinction between the three species are listed in Table 33.

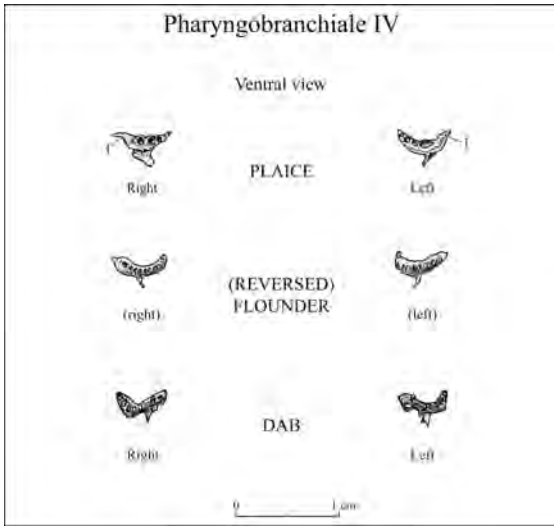


FIGURE 17

Ventral view of the fourth pharyngobranchials of plaice, flounder and dab.

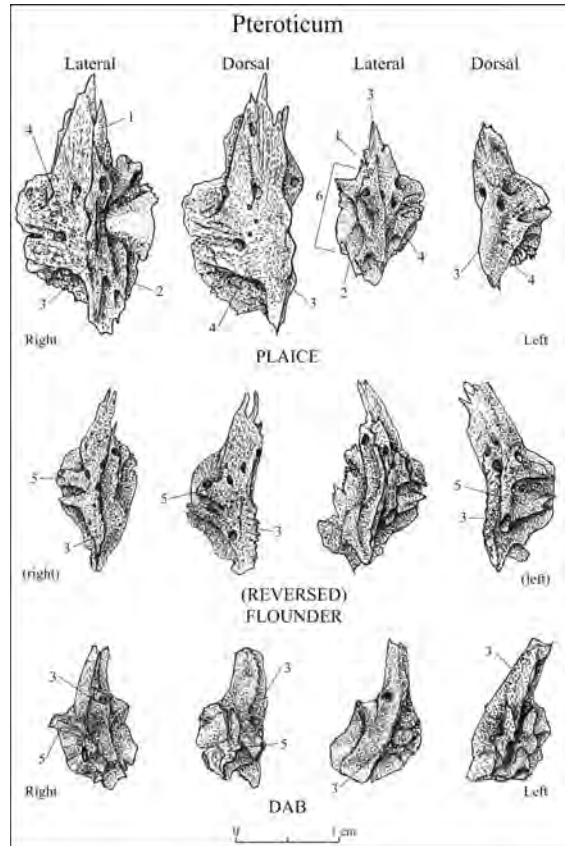


FIGURE 19

Lateral and dorsal view of the pterotic of plaice, flounder and dab.

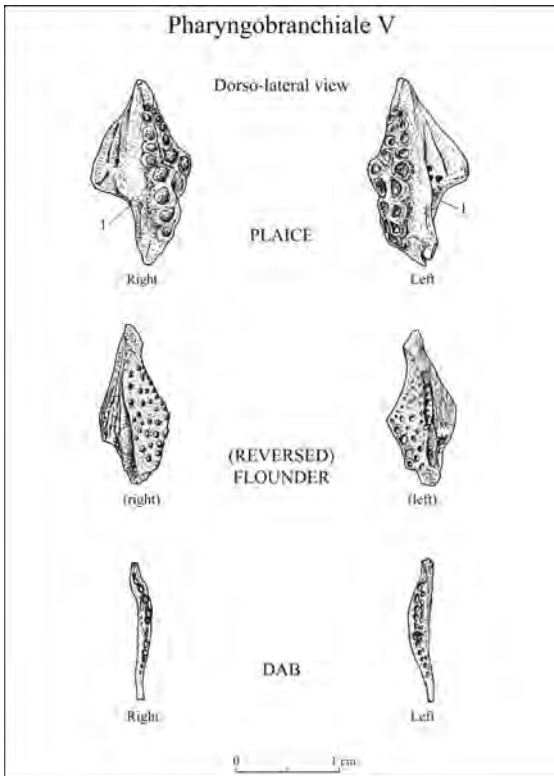


FIGURE 18

Dorso-lateral view of the fifth pharyngobranchials of plaice, flounder and dab.

Sphenoticum (Figure 20)

When the *sphenotic* is viewed laterally, the posterior part of the bone has a dorsal extension (1) that is directed to the left in the right element. No distinction could be made between the sphenotics of sinistral and dextral flounder.

The criteria allowing a distinction between the three species are listed in Table 34.

When the *sphenotic* is viewed laterally, the posterior part of the bone has a dorsal extension (1) that is directed to the right in left element. Again, no distinction could be made between the sphenotics of sinistral and dextral flounder.

The criteria allowing a distinction between the three species are listed in Table 35.

character	plaice	flounder	dab
structure of the crista lateralis (3)	presenting one or a few larger tubercles	presenting numerous small tubercles	smooth appearance, fine serration is palpable
dorsal area (4) adjacent to crista lateralis (3)	smooth, flat surface with very fine reticulation	flat surface, completely covered by tubercles	pitted surface
ossified sensory canal (5)	absent because not fused to the pterotic	always fused to the pterotic	absent because not fused to the pterotic in specimens smaller than 28 cm SL; in larger specimens often fused to the pterotic

TABLE 32

Distinction between the right pterotics of plaice, flounder and dab.

character	plaice	flounder	dab
structure of the crista lateralis (3)	thick crista, without tubercles	thick crista, presenting numerous small tubercles	thin crista, finely serrated (felt by palpation)
dorsal area (4) adjacent to crista lateralis (3)	smooth, flat surface with very fine reticulation	flat surface, completely covered by tubercles	pitted surface
ossified sensory canal (5)	absent because not fused to the pterotic	always fused to the pterotic	absent because not fused to the pterotic, even in the largest specimen available of 31.5 cm SL

TABLE 33

Distinction between the left pterotics of plaice, flounder and dab.

character	plaice	flounder	dab
structure of the crista lateralis (2)	one large tubercle (6)	many small tubercles (palpation necessary)	smooth
ridges (3) dorsal of crista lateralis (2)	one or two fine and smooth ridges	ridge absent in small fish; one heavy ridge with tubercles	one lightly built and smooth ridge
auricular lateral protrusion (4)	absent	absent	present
bone density	dense	dense	lightly built
ridge (5) ventral of crista lateralis (2)	one ridge clearly separated from the crista	one small ridge confluent with the crista	no structure visible

TABLE 34

Distinction between the right sphenotics of plaice, flounder and dab.

character	plaice	flounder	dab
crista lateralis (2)	smooth	many small tubercles	ridge very fine, denticulated
ridges (3) dorsal of crista lateralis (2)	one or two fine and smooth ridges	no clear ridge, only in very large specimens is a ridge palpable	ridge only faintly indicated by slightly denser bone
bone density	dense	dense	lightly built

TABLE 35

Distinction between the left sphenotics of plaice, flounder and dab.

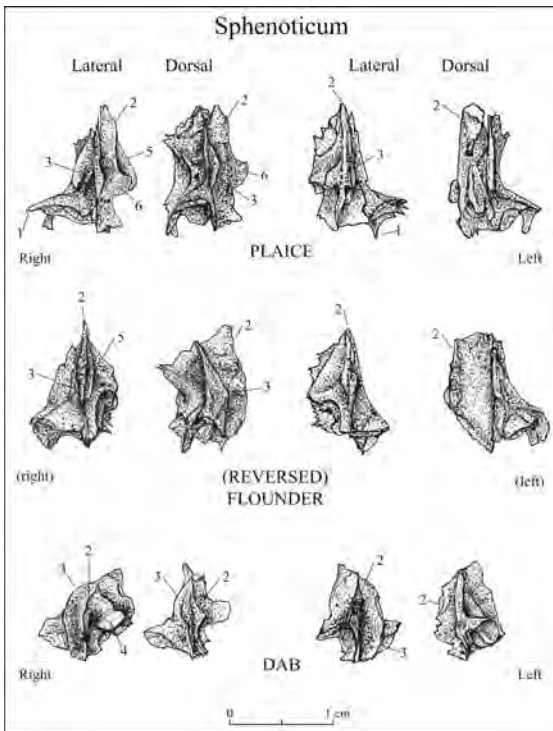


FIGURE 20

Lateral and dorsal view of the sphenotic of plaice, flounder and dab.

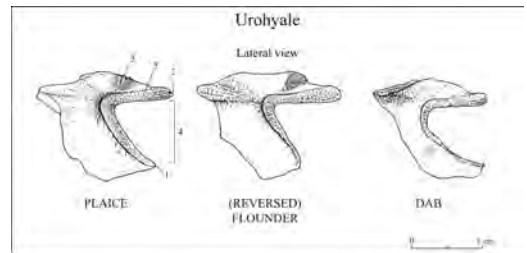


FIGURE 21

Lateral view of the urohyal of plaice, flounder and dab.

This element is very suitable for species identification, even in specimens of less than 10 cm SL. Dab is easily distinguished from the two other species by its deep incisura collis (4). Plaice and flounder can be discriminated by the position of the angulus inferior (1) relative to the processus hypohyalis (2), and by the projection of the angulus inferior (1). However, plaice larger than 35 cm SL resemble flounder for these two criteria. In that case, the thickness of the margo ventralis, measured mid-way allows discrimination of the two species: in plaice the margo ventralis is thicker than in specimens of flounder of the same size. The thickness at this level is, however, not a useful criterion for flatfish of less than 35 cm SL.

Urohyale (Figure 21)

The criteria used to distinguish the species are listed in Table 36. The bones are described as they are positioned in Figure 21, i.e. with the incisura collis (4) directed towards the right and with the margo ventralis pars horizontalis (5) horizontally aligned. It is essential that the bone is held in this position when using the last two criteria in the table. No distinction could be made between the urohyals of dextral and reversed flounder.

Os anale (Figure 22)

In this element the distinction between sinistral and dextral flounder could not be made. The criteria to distinguish the three species are listed in Table 37.

The curvature of the bone was retained as a diagnostic feature by Heinrich (1977) for the discrimination of dab, but it appears that small flounder and plaice often have a curvature similar to that seen in dab.

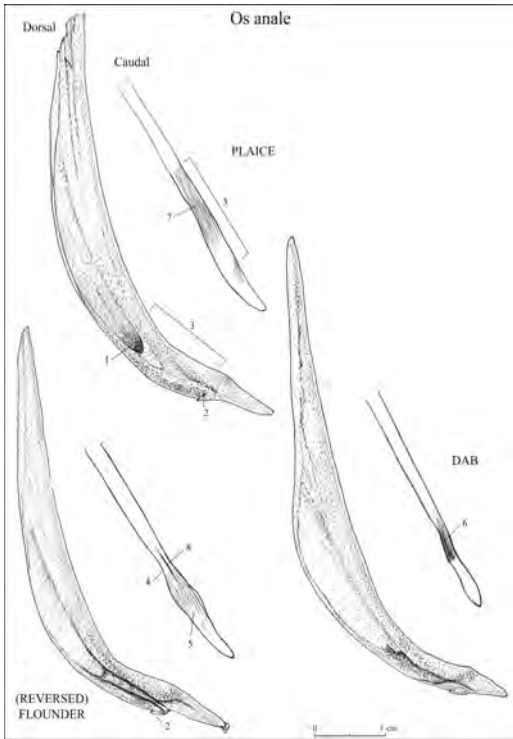


FIGURE 22

Dorsal and caudal view of the os anale of plaice, flounder and dab.

First precaudal vertebra (Figure 23)

Except for the first vertebra, no consistent distinguishing characters were found within the vertebral column. The criteria allowing species identification of the first vertebra are given in Table 38.

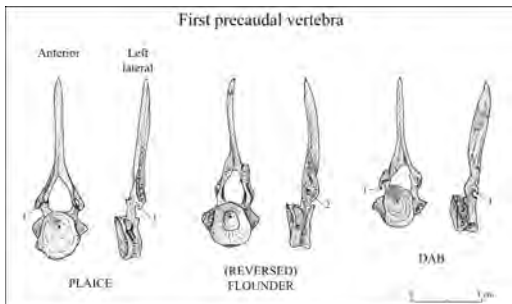


FIGURE 23

Anterior and left lateral view of the first precaudal vertebra of plaice, flounder and dab.

Identification of first vertebrae from fish of less than 15 cm SL is not recommended. Even in larger specimens, identification is not always straightforward since the postzygapophyses tend to break off.

Quadratum (Figure 24)

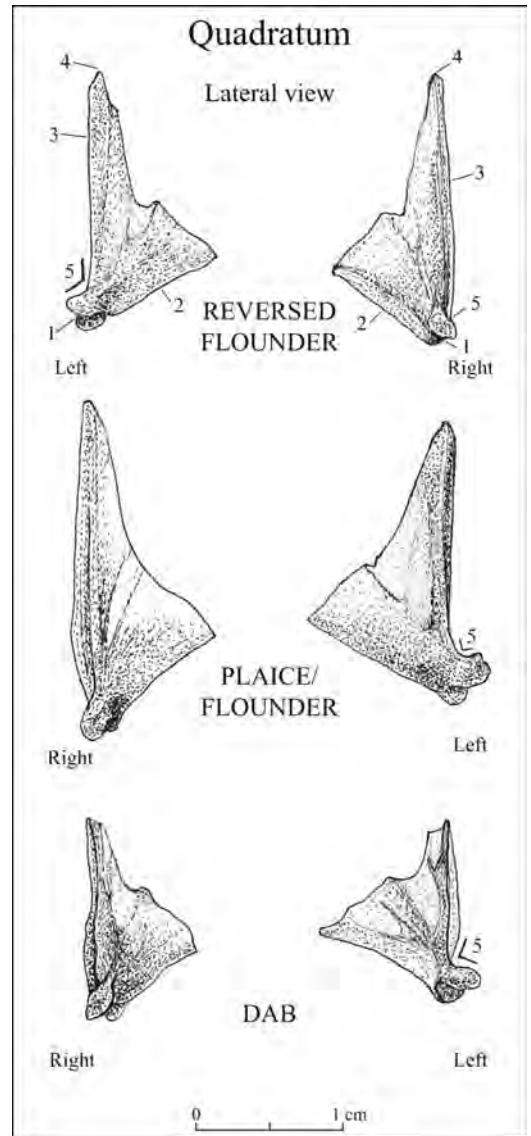


FIGURE 24

Lateral view of the quadratum of reversed flounder, dab, and plaice or dextral flounder

character	plaice	flounder	dab
area of dense bone (3) dorsal of margo ventralis pars horizontalis (5)	present	present	absent
incisura collis (4)	relatively shallow incision, V-shaped	relatively shallow incision, V-shaped	deep incision, U-shaped
projection of the angulus inferior (1)	slightly curving forward; sometimes pointing in a ventral direction in specimens larger than 45 cm SL	pointing in a ventral direction	slightly curving forward
relative position of angulus inferior (1) and processus hypohyalis (2)	angulus inferior (1) always below processus hypohyalis (2) in specimens up to 32 to 35 cm SL; in larger specimens angulus inferior (1) always posterior of processus hypohyalis (2)	angulus inferior (1) always posterior of processus hypohyalis (2)	angulus inferior (1) always below processus hypohyalis (2)

TABLE 36

Distinction between the urohyals of plaice, flounder and dab.

There seems to be a large variation in this bone resulting in an overlap of criteria that hampers the distinction between plaice and dextral flounder. Only the quadrates of dab and reversed flounder can be positively identified.

When the *quadrate* is viewed laterally, with the *condyli* (1) oriented in the inferior direction, the *margo ectopterygoidalis* (2) is located to the right in right elements. Dab and reversed flounder can be distinguished from plaice and dextral flounder using the criteria listed in Table 39. The criteria

character	plaice	flounder	dab
extent of the sulcus (1) with respect to the articulation (2) for the first fin ray	sulcus ends far behind the articulation	sulcus extends as far as the articulation	sulcus ends a little behind the articulation
outline of the neck (3) in caudal view	margins more or less parallel	margins show constriction (4), adjacent to a bulbous part (5)	margins more or less parallel; very pronounced margins result in a groove (6) in between
striation of the neck (3)	rough striation (7) over the whole neck	striae only on bulbous part with sometimes a clear groove (8) in the constricted part of the neck	striae absent

TABLE 37

Distinction between the os anale of plaice, flounder and dab.

described below are only useful in specimens of 15 cm SL and more.

When the *quadrate* is viewed laterally, with the condyli (1) oriented in the inferior direction, the margo ectopterygoidalis (2) is located to the left in

left elements. Dab and reversed flounder can be distinguished from plaice and dextral flounder using the criteria listed in Table 40. The criteria described below are only useful in specimens of 15 cm SL or larger.

character	plaice	flounder	dab
postzygapophysis (1) on neural arch	well developed	absent	present, but small
foramen (2) in neurapophysis	usually absent	present	absent
corpus in lateral view	longer	longer	short

TABLE 38

Distinction between the first precaudal vertebrae of plaice, flounder and dab.

character	reversed flounder	plaice/flounder	dab
proportion of lengths of margo ectopterygoidalis (2) and margo posterior (3)	margo ectopterygoidalis (2) is much less than half the length of the margo posterior (3)	margo ectopterygoidalis (2) is much less than half the length of the margo posterior (3)	margo ectopterygoidalis (2) is about half the length of the margo posterior (3)
[shape of processus praeopercularis (4)]	pointed and narrow	pointed and narrow	blunt and wide
[development of condyli (1)]	well developed; clear angle (5) formed with margo posterior (3)	poorly developed; no clear angle (5) formed with margo posterior (3)	poorly developed; no angle (5) formed with margo posterior (3)

TABLE 39

Distinction of the right quadrates of plaice/dextral flounder, reversed flounder and dab.

character	reversed flounder	plaice/flounder	dab
proportion of lengths of margo ectopterygoidalis (2) and margo posterior (3)	margo posterior (3) much longer than margo ectopterygoidalis (2)	margo posterior (3) much longer than margo ectopterygoidalis (2)	margo ectopterygoidalis (2) is of about same length as the margo posterior (3); the bone resembles an equilateral triangle
[shape of processus praeopercularis (4)]	pointed and narrow	pointed and narrow	blunt and wide
[development of condyli (1)]	poorly developed; no clear angle (5) formed with margo posterior (3)	well developed; clear angle (5) formed with margo posterior (3)	well developed; clear angle (5) formed with margo posterior (3)

TABLE 40

Distinction of left quadrates of plaice/dextral flounder, reversed flounder and dab.

Vomer (Figure 25)

In ventral view, vomers of plaice, dab and dextral flounder have their *pars ethmoidalis* (1) located at the left. This part is smaller than the *pars praefrontalis* (2) that is located at the right. In reversed flounder the *pars ethmoidalis* (1) lies to the right. In addition, the latter element can be recognised by its much longer apophysis posterior (3). The ventral groove (4) in the apophysis posterior (3) can be absent or poorly developed in the anterior part of the apophysis.

No criteria were found allowing a distinction between dextral flounder and plaice, but dab can be distinguished from the two other species by the features listed in Table 41.

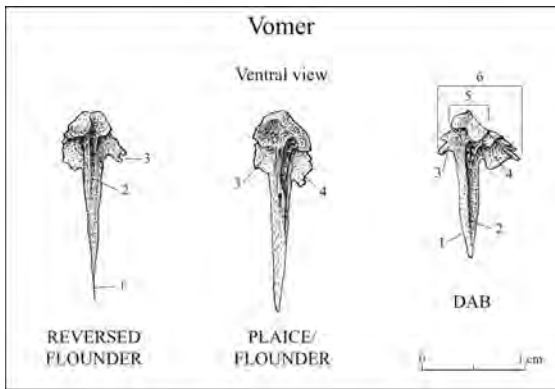


FIGURE 25

Ventral view of the vomer of reversed flounder, dab, and plaice or dextral flounder.

Supraoccipitale (Figure 26)

Identification of the supraoccipital is only possible when the element is completely preserved. The supraoccipital of reversed flounder can be distinguished from that of dextral flatfish by the location and the curvature of the crista supraoccipitalis (1): in reversed flounder this crista is situated on the right half of the bone, and it is bending towards the right. The crista can be single or double and is well developed.

The supraoccipitals of dextral flounder and plaice cannot be distinguished from each other, but dab can be identified using the criteria listed in Table 42.

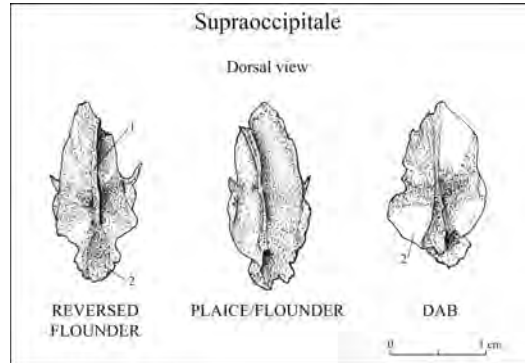


FIGURE 26

Dorsal view of the supraoccipital of reversed flounder, dab, and plaice or dextral flounder.

Ethmoid (Figure 27)

When viewed anteriorly, the ventral end (1) of the ethmoid is protruding towards the left in reversed flounder. In dextral flatfish the ventral protrusion (1) is directed towards the right side of the figure. This sole character allows the distinction of reversed flounder. The ethmoid bone of dab can also be easily recognised, but a distinction between dextral flounder and plaice seems impossible due to the large amount of variation. The ethmoid bone of dab can be distinguished from flounder and plaice using the criteria in Table 43.

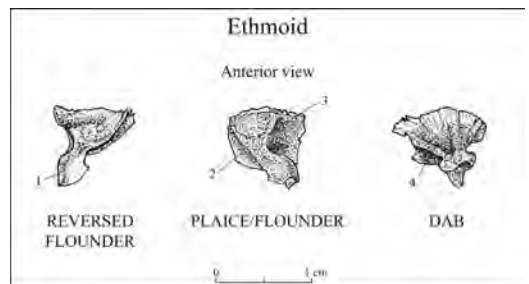


FIGURE 27

Anterior view of the ethmoid of reversed flounder, dab, and plaice or dextral flounder.

Nasale (Figure 28)

The very variable shape of the left nasals precludes species identification. In addition, they are

character	plaice/flounder	dab
length of apophysis posterior (3)	longer	shorter
ventral groove (4) in apophysis posterior (3)	no clear groove	present
lateral extension of pars ethmoidalis (1) and pars praefrontalis (2)	poorly developed	very pronounced
width of apical part (5) compared to total width (6)	apex almost equals total width	apex narrow

TABLE 41
Criteria allowing the recognition of dab vomers.

character	plaice/flounder	dab
location of the crista supraoccipitalis (1)	on left half of the bone	more or less central on the bone
bending of the crista supraoccipitalis (1)	towards the left	towards the left, but only in the anterior part
development of the crista supraoccipitalis (1)	single or double; well developed over its entire length	very thin over the entire length
outline of posterior part of the bone (2)	narrow and irregular	wide and rounded

TABLE 42
Criteria allowing the recognition of dab supraoccipitals.

character	plaice and flounder	dab
general shape	heavily ossified	transparent
presence of bony ridges	bony ridge (2) next to the margo praefrontalis dexter and another ridge (3) in the middle of the bone	ridge (4) next to the margo praefrontalis dexter

TABLE 43
Criteria allowing the recognition of dab ethmoids.

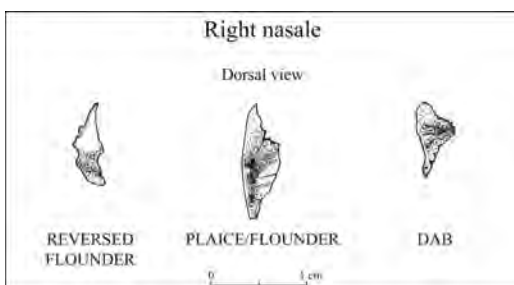


FIGURE 28

Dorsal view of the right nasale of reversed flounder, dab, and plaice or dextral flounder.

very porous, fragile, bones that almost never preserve. Of the right nasals, only those of dab and reversed flounder can be positively identified on the basis of their general shape, which is diagnostic on its own. Plaice and dextral flounder cannot be distinguished from each other.

Praeoperculare (Figure 29)

The preoperculars of dab can be easily recognised. However, the distinction between the preop-

erculars of sinistral and dextral flounder could not be made. There is, in addition, an overlap in criteria between plaice and flounder. Table 44 indicates the characters allowing the identification of dab.

flounder, and, in addition, it appeared that no discriminating characters are present allowing the distinction between plaice and flounder. The criteria listed in Table 45, hence show only how dab can be distinguished from plaice/flounder.

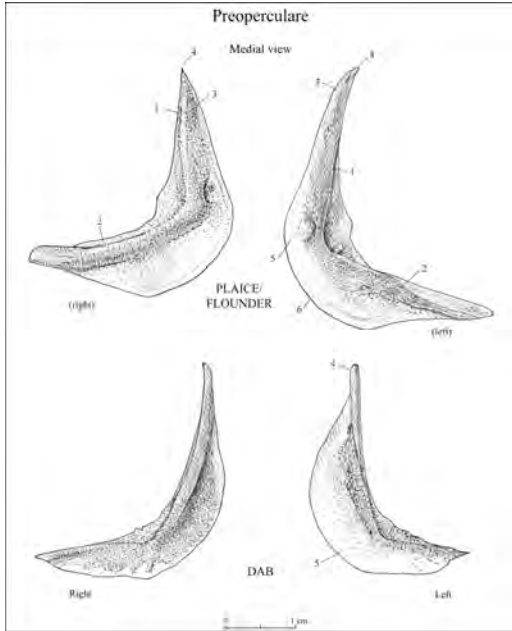


FIGURE 29

Medial view of the preopercular of dab, and plaice or flounder.

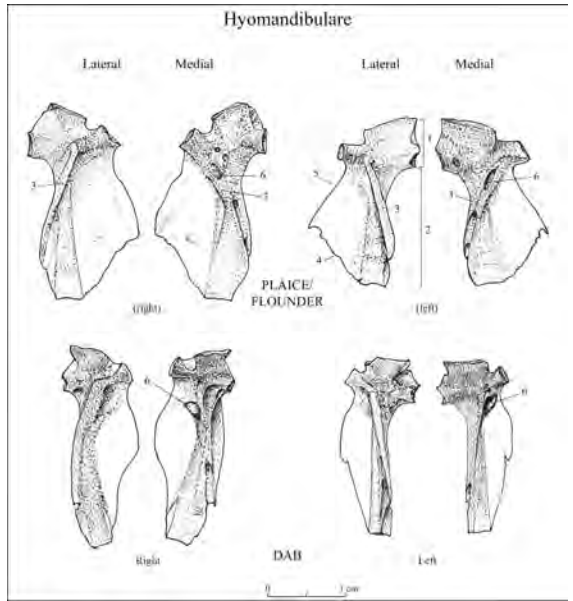


FIGURE 30

Lateral and medial view of the hyomandibular of dab, and plaice or flounder.

Hyomandibulare (Figure 30)

For the hyomandibular it was not possible to make the distinction between sinistral and dextral

Ceratohyale (Figure 31)

The ceratohyals of dab can be easily recognised. However, the distinction between the ceratohyals of sinistral and dextral flounder could not

character	plaice/flounder	dab
relative length of crista hyomandibularis (1) and crista quadrati (2)	about same length	crista hyomandibularis (1) much longer
dorsal onset of the lamina interna (3) relative to angulus superior (4)	lamina sometimes starts at the angulus superior (4)	always starts below angulus superior (4)
structure of bone (5) near margo opercularis (6)	always wide band of transparent bone	band of transparent bone narrow or absent in right preopercular; wider in left preopercular

TABLE 44

Criteria allowing the recognition of dab preoperculars.

character	plaice/flounder	dab
general appearance	dorsal (1) and ventral part (2) broad	more elongate appearance, with less developed dorsal part (1) and slender ventral part (2)
structure of the bone	denser bone	less dense, most of the bone with transparent appearance
crista praeopercularis (3)	straight	strongly bent in right hyomandibular; straight in left hyomandibular
outline anterior margin	angular appearance; transition between crista anterior (4) and antero-dorsal margin (5) shows clear angle	no angular appearance; smooth transition between crista anterior (4) and antero-dorsal margin (5)
[location of foramen ramus hyomandibulare (6)]	within the dense bone of the crista praeopercularis (3)	below the crista praeopercularis (3)

TABLE 45

Criteria allowing the recognition of dab hyomandibulars.

be made. There is, in addition, an overlap in criteria between plaice and flounder. Table 46 indicates the characters allowing the identification of dab.

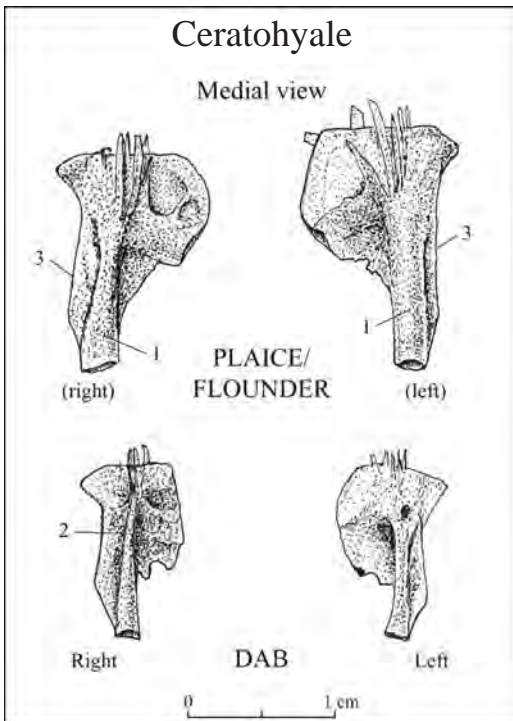


FIGURE 31

Medial view of the ceratohyal of dab, and plaice or flounder.

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Basioccipitale (Figure 32)

The basioccipitals of dab can be easily recognised (Table 47), but a distinction between flounder and plaice seems impossible due to the large variation. In addition, sinistral and dextral flounder cannot be distinguished from each other.

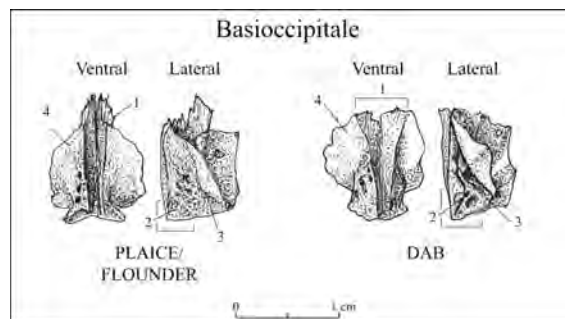


FIGURE 32

Ventral and lateral view of the basioccipital of dab, and plaice or flounder.

Alisphenoideum (Figure 33)

The alisphenoid of dab is a rather flat bone that has no protruding articulation (1) with the alisphenoid of the opposite side. In plaice and flounder this articulation (1) is well pronounced in medial view. The alisphenoids of dextral plaice and floun-

character	plaice/flounder	dab
pedunculus ceratohyalis (1)	remains wide over entire length	narrows in posterior direction (2)
margo anterior (3)	smooth	angular

TABLE 46

Criteria allowing the recognition of dab ceratohyals.

character	plaice/flounder	dab
appearance of the facies articularis parasphenoidalis (1)	narrow groove, only slightly widening in an anterior direction	wide groove, much widening in an anterior direction
ventro-lateral fossa (2)	fossa less distinct because of almost complete filling with reticular bone	fossa more distinct; filled with few trabeculae
lateral side of facies articularis parasphenoidalis (1)	very wide groove (3)	narrow groove
density of bone of the crista exoccipitalis (4)	dense	very light

TABLE 47

Criteria allowing the recognition of dab basioccipitals.

der cannot be distinguished from each other, and it is also impossible to distinguish sinistral and dextral flounder.

Postcleithrum (Figure 34)

Postcleithra with a notch (1) in the anterior margin are only seen in dab. The anterior margin is smooth in plaice and flounder. In dab of large size (25 cm SL or more) the notch seems always to be absent, while in most smaller fish it is clearly visible.

DISCUSSION

The 38 skeletal elements retained in this comparative analysis include those that have been used in the past by other researchers as well as 11 additional bones that occur frequently on archaeological sites (Table 1). When ontogenetic series are considered, it appears that the diagnostic criteria are most clearly pronounced in specimens of rather large size (25-40 cm SL in plaice and flounder, and 25-35 cm SL in dab). In fish exceeding those lengths the defined criteria can sometimes become obscure to some extent due to irregular bone development. Heavily distorted elements are very rare, however, except in the pharyngobranchials where the tooth sockets can be frequently eroded or deformed.

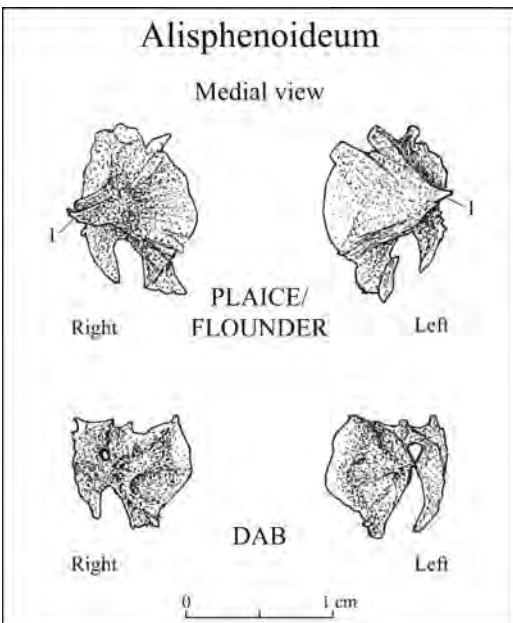


FIGURE 33

Medial view of the alisphenoid of dab, and plaice or flounder.

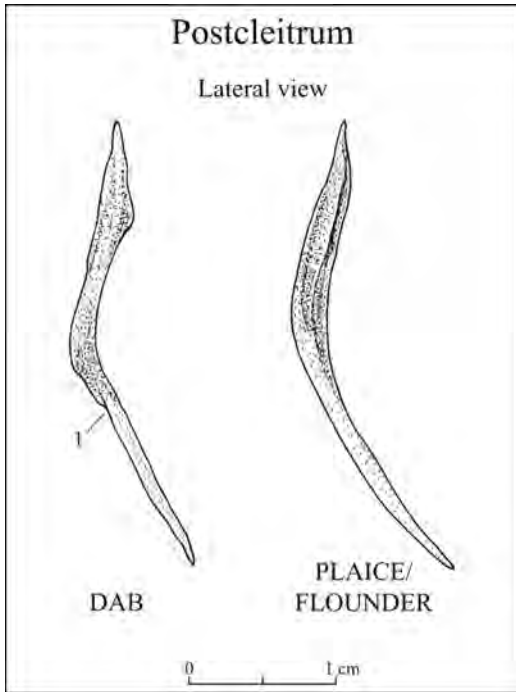


FIGURE 34

Lateral view of the postcleithrum of dab, and plaice or flounder.

Five of the selected elements proved to be unsuitable for species identification, namely the supracleithrum, the second precaudal vertebra, the first caudal vertebra, the penultimate and the antepenultimate vertebra. Of the nasal bones, only the right element allows species identification. It appears that 23 elements allow an identification of the three species, although 6 of them are harder to identify when dealing with smaller individuals. On eleven of those 23 elements the distinction between left- and right-sided flounder can be made. Six skeletal elements allow only the recognition of dab, whereas six other bones permit the identification of both dab and reversed flounder. Dab bones are indeed usually very distinct morphologically from those of plaice and flounder. The latter two species show more similarities, which often hamper identification, especially in smaller specimens. Some elements also appear to vary considerably in morphology.

The number of skeletal elements that is useful for species identification is significantly higher than that indicated in the literature, no doubt because of our more large-scale approach and the

time that was invested. Some of the results are in contradiction with the literature, i.e. concerning the use of the os anale (cf. Lepiksaar & Heinrich, 1977) or the cleithrum (Heinrich, 1987), and several other elements (cf. Table 1). Possible explanations for these conflicting results could be the limited reference samples that were used previously, which may have resulted in an underestimation of the intraspecific variation. Also size-dependent morphological changes may have escaped attention. It is also unclear from most previous publications to what extent reversed flounder has been included in the analyses.

It is realised that the diagnostic criteria described in the present contribution are sometimes very subtle and that some experience with flatfish osteology is needed for the identification of certain bones, especially small elements from the braincase and the branchial apparatus. However, at least 14 bones allow a fairly easy recognition of the three species when the criteria described here are used (see fourth column in Table 1). Identification of these bones should be done in combination with a reference collection consisting minimally of one plaice, one dab, one dextral and one sinistral flounder of medium to large size. For identification of the other skeletal elements, the key can only be used optimally when a larger collection of modern reference specimens is available. Ideally such a collection should consist of fish of different size classes (<10 cm; 10-20 cm; 20-30 cm and 30-40 cm SL), and this for plaice, dab, dextral and reversed flounder.

The applicability of the key was tested on the ichthyofauna of a late 15th- early 16th century urban site along the Belgian coast (Oostende, Mijnplein) (Pieters *et al.*, 2005). In this assemblage, that was sieved on a series of 4, 2 and 1 mm meshes, 2601 flatfish fragments were available, of which 1826 (or 70.2%) could not be identified to species (Table 48). The unidentifiable fraction consisted mainly of undiagnostic skeletal elements that were not retained in the present comparative study, i.e. fin rays, pterygiophores, branchial elements and vertebrae. Among the unidentified bones are 52 remains (or 2% of the total) of very diagnostic elements that could not be brought to species because of their fragmented state. Another 161 bones could be classified as plaice/flounder. In total, 614 bones (or 23.6%) were identifiable to species. Concerning the flounder remains, it should be noted that a high proportion of elements (44%) consisted of dermal denticles. Sixty-one

flounder bones allowed a distinction between dextral and sinistral specimens, and it appeared that 52% of them came from reversed flounders. If only the 14 skeletal elements are considered that allow the most straightforward identifications, then only 5.9% of the remains was unidentifiable (those that were too heavily fragmented). Retaining these 14 elements seems to be a good strategy when samples of the size studied here are available, but a further reduction of the number of skeletal elements considered for identification is not recommended. Table 49 shows that there is no particular bone that yields a relatively higher pro-

portion of species identifications. Inclusion of the more difficult skeletal elements in the identification work can, however, be important when only limited flatfish samples are available from a given site and will deliver the maximum of species identifications. When all 34 elements are considered, the number of identified specimens doubles (614 bones, instead of 273 when only 14 elements are retained). The success rate of the identification when dealing with the whole series of bones is significantly lower (25.8% identifiable versus 94.1% when only the 14 elements are retained).

Taxon/Group	number of fragments	%	%	%	%
plaice	115	4.4	13.9	14.8	18.7
dab	259	10.0	31.3	33.4	42.2
flounder	240	9.2	29.0	31.0	39.1
plaice or flounder	161	6.2	19.5	20.8	
unidentified, diagnostic elements	52	2.0	6.3		
unidentified, undiagnostic elements	1774	68.2			
total	2601	100.0	100.0	100.0	100.0

TABLE 48

Results of the identification of flatfish remains from the 15th-16th century AD site «Mijnplein» at Oostende.

Element	plaice/flounder/dab	dab	plaice	flounder	total
praefrontale	2	12	5	6	25
frontale		12	3	8	23
sphenoticum		10		2	12
ptericum		9	3	5	17
articulare	3	9	8	5	25
dentale	1	7	6	4	18
ectopterygoideum		12	2	7	21
maxillare right	2	4	3	2	11
praemaxillare	6	12	6	7	31
urohyale	3	3	1	4	11
pharyngobranchiale III		8	16	7	31
pharyngobranchiale V		14	7	4	25
cleithrum		16	17	4	37
os anale		1	1	1	3
Total	17	129	78	66	290

TABLE 49

Unidentified and identified flatfish bones from the 15th-16th century AD site «Mijnplein» at Oostende, for the 14 most straightforward skeletal elements.

CONCLUDING REMARKS

The diagnostic characters described in the present paper should enable a more systematic identification of flatfish bones from archaeological sites in North-Western Europe. As already indicated in the introduction, more specific identifications will make it possible to better quantify the importance of each species in the food provisioning of coastal and inland consumers. It is also likely that inferences about the season of fishing and the establishment of former fishing grounds will be facilitated. Since flounder and plaice reach larger sizes than dab, the proportion of the latter species may have an influence on the average size of a flatfish assemblage. Future interpretations may therefore benefit from an increased number of body size reconstructions for each individual species. Although size reconstructions remain possible by direct comparison with specimens of known body length, it would be preferable to use regression formulae. It remains to be verified to what extent such formulae of the 3 species will be similar to each other. For the Epinephelinae it has been established that the same formulae can be used for all the taxa included in the subfamily (Desse & Desse-Berset, 1996), but in the case of the three species considered here there are indications that such an approach may not be advisable. Norman (1934) mentions that the proportion of head length to total length is 3 ? to 4 ? in dab, 3 1/8 to 3 ? in flounder and 3 to 3 7/8 in plaice. Preliminary observations on the modern material investigated in the present study show, for instance, that the basioccipital is consistently smaller in dab than in plaice or flounder of the same body size. In addition, future size reconstructions of individual species will need to take into account the laterality of the bone, and for flounder separate regressions may be needed for dextral and sinistral individuals.

ACKNOWLEDGEMENTS

The contribution of Wim Wouters and Wim Van Neer to this paper presents research results of the Interuniversity Poles of Attraction Programme-Belgian Federal Science Policy Office. We express our sincere thanks to Anne-Marie Wittek (RBIN-Sc) for the artwork and her patience. Aude Van Driessche (RBINSc) helped with the layout of the

plates, and Sheila Hamilton-Dyer (Southampton) is acknowledged for the correction of the English text.

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