

Comparative osteology of the North Sea flatfishes (Teleostei; Pleuronectiformes)

by

Katrien DIERICKX* (1, 2) & Wim WOUTERS (3)



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Abstract. – The identification of flatfish remains in archaeozoological studies has often been limited to higher taxonomic levels or species groups. Bones from disarticulated skeletons of eleven main commercial species of flatfish present in the North Sea were compared to define diagnostic criteria allowing species identification. Out of the thirty-four studied skeletal elements often recovered in archaeological assemblages, ten proved to be very reliable for genus and species identification and often allowed the distinction between right-eyed and left-eyed flounder. Fourteen elements have sufficient characteristics to differentiate all higher taxa but not all the genera and species. The remaining ten elements did not possess clear features to distinguish the different taxa. The diagnostic details of each element are summarised and illustrated, leading to a clear identification guide for this particular group of fishes. More precise species identifications can provide better insight in the zoogeographical distribution of flatfish and will be useful in detecting socio-economic and cultural changes throughout history.

Résumé. – Ostéologie comparée des poissons plats (Teleostei ; Pleuronectiformes) de la mer du Nord

L'identification des ossements des poissons plats est souvent limitée au niveau de la famille ou à certains groupes d'espèces dans les études archéozoologiques. Dans le cadre de la présente étude, les squelettes d'onze espèces commerciales de Mer du Nord ont été analysés. Trente-quatre éléments souvent retrouvés dans les assemblages archéologiques ont été étudiés. Dix sont très discriminants et permettent même souvent de distinguer le flet normal ou inversé. Quatorze autres éléments sont seulement utiles pour distinguer certaines espèces, et dix autres ne livrent pas de critères permettant de distinguer les différents taxons. Les critères diagnostiques sont décrits et illustrés de manière à proposer un guide d'identification pour ce groupe des poissons plats. Des identifications plus précises permettent d'obtenir plus d'informations concernant la distribution géographique de chaque espèce et seront utiles afin de détecter des changements socio-économiques et culturels à travers le temps.

INTRODUCTION

Flatfishes, or Pleuronectiformes, were and still are an important group of fish used as staple food and they had a great economic trade value through history (*e.g.*, Barrett *et al.*, 2004; Eryvynck *et al.*, 2004; Harland *et al.*, 2016; Oueslati, 2019). Despite their common occurrence, early reports from archaeological studies on North Sea material stated that bones of flatfish were difficult to identify to species level (*e.g.*, Lepiksaar and Heinrich, 1977; Heinrich, 1987). Many skeletal elements remained unidentified or were at best only identified to order, family, or species complex level. Most often, only 1 to 15% of flatfish bones are identified to species level, while the majority of remains are classified as the species complex plaice/flounder/dab (*Pleuronectes platessa* Linnaeus, 1758, *Platichthys flesus* (Linnaeus, 1758), *Limanda limanda* (Linnaeus, 1758)) or summarised as Pleuronectidae (*e.g.*, Eryvynck and Van Neer, 1992; Enghoff, 1999; Nicholson, 2009; Reynolds, 2015; Harland *et al.*, 2016; Oueslati, 2019). Several zooarchaeological reports identify some flatfish remains, but did not provide any description

of their morphology (*e.g.*, Lepiksaar and Heinrich, 1977; Brinkhuizen, 1979; Enghoff, 1986; Heinrich, 1987; Enghoff, 1989; Clavel, 1997). Within Scophthalmidae, bones were mostly assigned to family level or genus level (*e.g.*, Nicholson, 2009; Harland *et al.*, 2016). The identification of flatfish vertebrae is even more challenging, often being restricted to family level (*e.g.*, Clavel, 1997).

Comparative osteology of flatfish species or elements has been rather sporadic and hardly well-substantiated. Otoliths of flatfish and other North Sea species were described by Härkönen (1986). Roselló (1986) described the dentary and articular of six species. Dermal denticles were used in some archaeological studies to identify *P. flesus* and *Scophthalmus maximus* (Linnaeus, 1758) (Enghoff, 1986, 1999). The pteroticum and sphenoticum of *P. flesus* can easily be distinguished from other flatfish, especially *P. platessa* and *L. limanda*, by a nodose-serrated margin (Enghoff, 1989). Lepiksaar (1994) illustrated some elements, such as vertebrae and os anale, from a few species of flatfish without further comments. Watt *et al.* (1997) provided details to distinguish the premaxillae and vertebrae for 13 species of flat-

(1) University of York, Department of Archaeology, Heslington, YO10 5DD, York, United Kingdom. katrien.dierickx.icht@gmail.com

(2) Department of Archaeology and Cultural History, NTNU University Museum, NTNU, Trondheim, Norway

(3) Royal Belgian Institute of Natural Sciences, Vautierstraat 29, B-1000 Brussels, Belgium. wwouters@naturalsciences.be

* Corresponding author

fish from the North Sea. Wouters *et al.* (2007) systematically studied 38 skeletal elements from three species, *i.e.*, *P. platessa*, *P. flesus* (right- and left-eyed), and *L. limanda*. This study proved that species identification was successful for a number of elements, but not always for all the species. It further emphasised the need for a good reference collection to improve the identification rate. Pure anatomical descriptions about flatfishes in general and specifically focussed on certain species are available (*e.g.*, Gregory, 1933; Hubbs, 1945; Futch *et al.*, 1972; Cooper and Chapleau, 1998; Hoshino, 2001; Chanet, 2003; Díaz de Astarloa, 2005; Yazdani, 2009; Voronina, 2010; Märss *et al.*, 2017). However, these studies are intended for general anatomical purposes, which restricts the use for comparative osteology and zooarchaeological identification.

At least 18 species of flatfish have been reported from the North Sea area (Table I). They belong to four families: Bothidae, Pleuronectidae, Scophthalmidae, and Soleidae (Nielsen, 1986; Heessen *et al.*, 2015). Some reports attest the occasional presence of Cynoglossidae and Citharidae and other species of Soleidae and Scophthalmidae in the region (Nijssen, 1966; Nijssen and De Groot, 1974; Nielsen, 1986; Heessen *et al.*, 2015; Froese and Pauly, 2024).

The aim of this study is to provide additional osteological criteria for the identification of genera and species of flatfishes found in the North Sea, which may lead to new insights about the exploitation of these fishes through time. Improved identification rates will result in more available material for other kinds of analytical research, such as stable

isotope analysis, which can further provide insight into the historical exploitation of flatfish.

MATERIAL AND METHODS

Dry, disarticulated specimens of flatfish housed at the York Zooarchaeology Lab (YZL) at the University of York and the Royal Belgian Institute of Natural Sciences (RBINS) were used in this study. All specimens originate from European waters, with most having been caught in the North Sea area, and represent the main commercial species currently found in the North Sea: *Pleuronectes platessa*, *Limanda limanda*, *Platichthys flesus* (normal right-eyed and reversed left-eyed), *Glyptocephalus cynoglossus* (Linnaeus, 1758), *Hippoglossus hippoglossus* (Linnaeus, 1758), *Hippoglossoides platessoides* (Fabricius, 1780), *Microstomus kitt* (Walbaum, 1792), *Scophthalmus maximus* (Linnaeus, 1758), *Scophthalmus rhombus* (Linnaeus, 1758), *Lepidorhombus whiffiagonis* (Walbaum, 1792), and *Solea solea* (Linnaeus, 1758). Several common names exist for some species in English. To avoid confusion for the reader, only the scientific names will be used. Table II provides an overview of the specimens used in this study; details can be found in Table S1 in the Supplementary Information.

While *P. flesus* is known to have a variable proportion of left- versus right-eyed fishes (*e.g.*, Enghoff, 1994; Fornbacke *et al.*, 2002), other flatfish species are less prone to this feature. Cunningham (1907) described a small reversed specimen of *S. maximus*. Gudger (1935) listed all reversed

Table I. – All flatfish species commonly found in the North Sea and their maximum recorded total length (TL) (Nielsen, 1986; Heessen *et al.*, 2015).

Family	Species	Author	Common name	TL _{max}
Bothidae	<i>Arnoglossus laterna</i>	(Walbaum 1792)	scaldfish	19 cm
Pleuronectidae	<i>Glyptocephalus cynoglossus</i>	(Linnaeus, 1758)	witch	60 cm
Pleuronectidae	<i>Hippoglossoides platessoides</i>	(Fabricius, 1780)	long-rough dab	48 cm
Pleuronectidae	<i>Hippoglossus hippoglossus</i>	(Linnaeus, 1758)	halibut	254 cm
Pleuronectidae	<i>Limanda limanda</i>	(Linnaeus, 1758)	dab	42 cm
Pleuronectidae	<i>Microstomus kitt</i>	(Walbaum, 1792)	lemon sole	66 cm
Pleuronectidae	<i>Platichthys flesus</i>	(Linnaeus, 1758)	flounder	51 cm
Pleuronectidae	<i>Pleuronectes platessa</i>	Linnaeus, 1758	plaice	91 cm
Scophthalmidae	<i>Lepidorhombus whiffiagonis</i>	(Walbaum, 1792)	megrin	61 cm
Scophthalmidae	<i>Scophthalmus maximus</i>	(Linnaeus, 1758)	turbot	100 cm
Scophthalmidae	<i>Scophthalmus rhombus</i>	(Linnaeus, 1758)	brill	61 cm
Scophthalmidae	<i>Zeugopterus norvegicus</i>	(Günther, 1862)	Norwegian topknot	12 cm
Scophthalmidae	<i>Zeugopterus punctatus</i>	(Bloch, 1787)	common topknot	25 cm
Scophthalmidae	<i>Zeugopterus regius</i>	(Bonnaterre, 1788)	Ekström's topknot	20 cm
Soleidae	<i>Buglossidium luteum</i>	(Risso, 1810)	solenette	15 cm
Soleidae	<i>Microchirus variegatus</i>	(Donovan, 1808)	thickback sole	33 cm
Soleidae	<i>Pegusa lascaris</i>	(Risso, 1810)	sand sole	40 cm
Soleidae	<i>Solea solea</i>	(Linnaeus, 1758)	sole	70 cm

specimens described in older literature. His list included one Scophthalmidae (*S. maximus*), four Pleuronectidae (*P. platessa*, *L. limanda*, *P. flesus*, and *H. hippoglossus*), and one Soleidae (*S. solea*). Bruno and Fraser (1988) mentioned a very rare reversed *L. limanda*. Macdonald (2013) mentioned the single find of a reversed *L. whiffiagonis*. Recently, a reversed specimen of brill (*S. rhombus*) and four reversed *S. solea* were discovered by a fishmonger in Leuven, Belgium (Wim Wouters, unpubl. data). Archaeological traces of reversed species other than *P. flesus*, however, are unknown so far. Remains of reversed left-eyed *P. flesus* were for the first time identified by Enghoff (1994). In this study, we included only reversed specimens of *P. flesus* as these are commonly found and reported from the zooarchaeological record. Insufficient numbers of reversed specimens were available for the other species.

Several species that occur in the North Sea were excluded from this study. *Zeugopterus regius* is only an occasional guest in the North Sea. Its main habitat is found in the English Channel. *Zeugopterus punctatus* is also rare in the southern North Sea. The other four species reaching maximum sizes smaller than 20 cm total length (TL) were also excluded from this research. Fishes rarely grow to their potential full length and the bone remains of these species are too small for normal recovery, for example in a 2 mm sieved fraction, which is a common and necessary excavation technique to recover small disarticulated fish bones where soil is sieved in various size fractions. Moreover, these species were considered as fishes of low economic importance, probably due to their small size and low catch frequency. The remains of scaldfish (*Arnoglossus laterna*), Norwegian topknot (*Zeugopterus norvegicus*) and solenette (*Buglossidium luteum*) are so far absent in archaeological material from areas around the

North Sea. The sand sole (*Pegusa lascaris*) was not included either because it is a fish which prefers the English Channel. Nielsen (1986) does not mention its presence in the North Sea, while Heessen *et al.* (2015) shows how this species is moving up into the North Sea nowadays. The thickback sole (*Microchirus variegatus*) is also a smaller sized fish, up to 20 cm standard length (SL) according to Nielsen (1986). However, Heessen *et al.* (2015) considers 33 cm SL as maximum size while Fishbase (Froese and Pauly, 2024) states a maximum SL of 35 cm, but a common length of only 14 cm SL. This species is absent from the east side of the North Sea and lives only in western waters. It is considered of minor economic importance and specimens larger than 17 cm SL are not present in the reference material in York or Brussels. Therefore, the species was not included in this study.

The osteology of *P. platessa*, *P. flesus*, and *L. limanda* is already extensively described in Wouters *et al.* (2007). They are retained here and compared with the other species for consistency in the descriptions of the characteristics. Both right-eyed and left-eyed *P. flesus* are analysed and compared (Table II).

The selection of elements was based on their abundance in the material of several archaeological sites in Flanders, as the material from this region has been extensively studied by W.W. and thus allows a good insight into element representation. These elements often collectively constitute 1 to 10% of all identified flatfish bones: articular, dentary, ectopterygoid, hyomandibula, maxilla, metapterygium, palatine, premaxilla, quadrate, basioccipital, parasphenoid, vomer, basihyal, ceratohyal, epihyal, lower hypohyal, upper hypohyal, urohyal, interopercular, opercular, preopercular, pharyngeals II, III, IV, and V, basipterygium, cleithrum, coracoid, post-

Table II. – Overview of the specimens used in this study. Details can be found in Table S1 in the Supplementary Information. TL: total length; SL: standard length.

Species	Number of specimens	Min-max SL (cm)	Min-max TL (cm)	Remarks
Pleuronectidae				
<i>Glyptocephalus cynoglossus</i>	7	25-41	27-49	
<i>Hippoglossoides platessoides</i>	15	10-32	12-38.5	
<i>Hippoglossus hippoglossus</i>	14	35-240	41-270	
<i>Limanda limanda</i>	13	11-31.5	13-32	
<i>Microstomus kitt</i>	15	15-36.55	18-37.6	
<i>Platichthys flesus</i>	8	16-35.5	18.5-41.7	left-eyed
<i>Platichthys flesus</i>	6	20.6-32.9	24.7-39.3	right-eyed
<i>Pleuronectes platessa</i>	17	15-56	18-65	
Scophthalmidae				
<i>Lepidorhombus whiffiagonis</i>	8	25-35	28.5-40	
<i>Scophthalmus maximus</i>	15	18.2-48.5	22.9-57.8	
<i>Scophthalmus rhombus</i>	14	14.5-54.5	17.5-63	
Soleidae				
<i>Solea solea</i>	18	9.5-56	10.7-64	

temporal, supracleithrum, os anale, first precaudal vertebra, first caudal vertebra, and ultimate vertebra.

Although other vertebrae, fin rays, and most of the branchial elements are more commonly found, their morphology does not allow adequate species identification, so they were not described. Several head elements, used to distinguish *P. platessa*, *P. flesus*, and *L. limanda* in Wouters *et al.* (2007) were not retained here: nasal, alisphenoid, praefrontal, frontal, pteroticum, sphenoticum, and supraoccipital. These bones are very rare in the archaeological material in general, at least for the other 8 species except for *S. solea*. In some sites, complete heads of this species were recovered, but they are very characteristic and unique in shape (see Futch *et al.*, 1972).

Diagnostic characteristics are based on the presence/absence of certain morphologies as well as proportions and differences in overall shape. When describing the observed differences, the terminology of Lepiksaar (1994), complemented by Wouters *et al.* (2007), was used as much as possible. Illustrations are provided that show the observed differences. For paired elements, it is always the left bone that is illustrated, unless there are clear morphological differences between the left and right sides. In that case, a drawing of the right bone is also included. In each figure, the two top rows show the elements of Pleuronectidae, while the bottom row shows those of Scophthalmidae on the left and *S. solea* on the right. The specimens for illustrations were chosen to be of similar size (ca. 30 cm SL) where available, but other specimens were selected if elements were missing or otherwise difficult to illustrate.

RESULTS

The differentiation of the skeletal elements is summarised for each species, based on the comparison of complete bones. Only the most essential diagnostic criteria are mentioned in the text and main Figs 1-35. When identifying fragmented bones, the additional information (Tables S2-S45; Figs S1-S18) provides details about diagnostic criteria for specific characteristics of each bone part. The most diagnostic bone parts are indicated in bold in the Supplementary Information. Some criteria are sufficiently characteristic that identification is foolproof based on one single criterion. Using a combination of criteria remains recommended. Elements are described in order of their diagnostic usability. The description for each element can be seen as a kind of identification tree. Bones of those species with a unique shape (often *S. solea*, *M. kitt*, and/or *G. cynoglossus*) are clear enough to distinguish them, and therefore they are only briefly described. Following this, the characteristics which separate the Scophthalmidae from the Pleuronectidae are usually provided, and the differences between species with-

in each family are explained. However, for some elements which can only be identified for some species, this protocol was left aside. The distinction of *P. platessa*, *P. flesus* (right- and left-eyed), and *L. limanda* is mostly based on Wouters *et al.* (2007), but additional information is provided where possible. It must be emphasised that a reference collection is complementary to this identification key. Moreover, it is advised to use this identification key with caution, certainly if the researcher is not familiar with flatfish bones. The reference collection should consist of several specimens of small, medium, and large sizes for each species. It is desirable to compare bones of approximately the same size, particularly in cases when proportions are an important diagnostic feature. As noted already in Wouters *et al.* (2007), elements of small fishes are often more difficult to distinguish than elements of larger fish.

An overview of the identifiable elements is provided below (Table III). Elements with clear diagnostic features and thus allowing fast and precise identification are indicated with E (easy). Elements that can only be identified after very careful comparison and/or with an extensive reference collection are marked with D (difficult). Elements that cannot be used to identify a certain species are indicated with N (not possible).

Premaxilla

The lateral view of the left premaxilla is given in Fig. 1. Additionally, the medial and ventral views can be found in the Supplementary Information together with the detailed analysis for each species (Table S2; Fig. S1). This bone allows identification to all genera. *Solea solea* is distinct from all other species by the strongly curved corpus (1) and a very broad and semi-circular shaped tooth area (2). *Microstomus kitt* has a very high and short corpus (1), that is as long as the processus anterior (3), and no indent (4) between both processus anterior (3) and processus articularis (5). The Scophthalmidae are characterised by having 3 or more tooth rows (2), while Pleuronectidae have only 1 or 2 tooth rows (2). *Lepidorhombus whiffiagonis* can be identified from both *Scophthalmus* spp. by a relatively higher processus articularis (5) and processus anterior (3) and a more accentuated processus s. crista posterior (6) compared to both *Scophthalmus* species. No criteria were found for a reliable distinction between both *Scophthalmus* species. *Hippoglossus hippoglossus* differs from all other Pleuronectidae by the large, irregularly placed tooth alveoli (2). The corpus (1) of *H. platessoides* is very long with 39-54 small, regularly implanted tooth alveoli (2). Teeth are regularly implanted (2) but lower in number (13-30) in *P. flesus*, *P. platessa*, *L. limanda*, and *G. cynoglossus*. Left-eyed *P. flesus* can easily be distinguished from other Pleuronectidae by the straight margo symphysicus (7). The other Pleuronectidae have an anteriorly protruding ventral part of the

Table III. – Overview of the taxa able to be identified per skeletal elements. E: easy; D: difficult, requiring reference collection or prone to subjectivity; N: not possible. 1: *P. platessa* – 2: *L. limanda* – 3: *P. flesus* – 4: Right-eyed *P. flesus* – 5: Left-eyed *P. flesus* – 6: *G. cynoglossus* – 7: *H. hippoglossus* – 8: *H. platessoides* – 9: *M. kitt* – 10: Family level – 11: *Scophthalmus* spp. – 12: *S. maximus* – 13: *S. rhombus* – 14: *L. whiffiagonis* – 15: *S. solea*.

Skeletal element	Family level	Pleuronectidae										Scophthalmidae			Soletidae	
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Premaxilla	E	E			E	E	E	E	E	E	E	E	E	E	E	E
Maxilla	E	E		E	E	E	E	E	E	E	E	E	E	E	E	E
Dentary	E	E		E	E	E	E	E	E	E	E	E	E	E	E	E
Articular	E	E		E	E	E	E	E	E	E	E	E	E	E	E	E
Hyomandibula	D	E	D	N	N	E	E	E	E	E	E	E	E	E	E	E
Palatine	E	E		E	E	E	E	E	E	E	E	E	E	E	E	E
Vomer	D	D		D	E	E	E	E	E	E	E	E	E	E	E	E
Posttemporal	D	D		N	N	E	E	E	E	E	E	E	E	E	E	E
Urohyal	E	E		N	N	E	E	E	E	E	E	E	E	E	E	E
First vertebra	D	D		N	N	E	E	E	E	E	E	E	E	E	E	E
Metapterygium	N	D		N	N	E	E	E	E	E	E	E	E	E	E	E
Basioccipital	D	E		N	N	E	E	E	E	E	E	E	E	E	E	E
Cleithrum	E	D		D	D	D	D	D	D	D	D	D	D	D	D	D
Os anale	D	E		N	N	E	E	E	E	E	E	E	E	E	E	E
Quadrate	N	D		N	N	E	E	E	E	E	E	E	E	E	E	E
Ectopterygoid	D	D		D	E	E	E	E	E	E	E	E	E	E	E	E
Preopercular	N	D		N	N	E	E	E	E	E	E	E	E	E	E	E
Interopercular	D/N	D		D	D	D	D	D	D	D	D	D	D	D	D	D
Parasphenoid	N	N		N	E	N	N	N	N	N	N	N	N	N	N	N
Ceratohyal	N	D		N	N	N	N	N	N	N	N	N	N	N	N	N
Epiphyal	N	N		N	N	N	N	N	N	N	N	N	N	N	N	N
Upper hypohyal	D/N	D/N		N	N	D	N	D	D	D	D	D	D	D	D	D
Pharyngeal V	E	D/N		E	N	D/N	D/N	D/N	D/N	D/N	D/N	D/N	D/N	D/N	D/N	D/N
First caudal vertebra	D/N	D/N		D/N	D/N	D	D	D	D	D	D	D	D	D	D	D

margo symphysicus (7). The tip of the processus anterior (3) of *L. limanda* has a broad, flaglike appearance (8). The indentation (4) between the processus anterior (3) and the processus articularis (5) is usually deep in right-eyed *P. flesus* and shallow or absent in *P. platessa* and *G. cynoglossus*. The latter two species can be distinguished by the relative corpus (1) length compared to the height of the processus anterior (3), which is short and thick in *P. platessa* and long and slender in *G. cynoglossus*.

The lateral view of the right premaxilla is given in Fig. 2. Additionally, the medial and ventral views can be found in the Supplementary Information together with the detailed analysis for every species (Table S3; Fig. S2). This bone allows identification to all genera. *Microstomus kitt* and *S. solea* have a characteristic corpus (1) without teeth on the toothplate (2). The right premaxilla of *M. kitt* has the typical L-shape with a distinct processus anterior (3) and corpus (1), while that of *S. solea* has an atypical shape with a large anterior section that protrudes from the processus anterior (3). The Scophthalmidae are characterised by having 3 or more tooth rows (2), while the remaining Pleuronectidae have only 1 or 2 tooth rows (2). *Lepidorhombus whiffiagonis* can be identified from both *Scophthalmus* spp. by a relatively higher processus articularis (5) and a more accentuated processus s. crista posterior (6) compared to both *Scophthalmus* species. No criteria were found for a reliable distinction between both *Scophthalmus* species. The premaxilla of *H. hippoglossus* and *H. platessoides* have a very elongated corpus (1) compared to other Pleuronectidae. *Hippoglossus hippoglossus* has very large alveoli placed irregularly with large gaps in between (2) and a broad processus anterior (3). *Hippoglossoides platessoides* has many fine tooth alveoli (2) and a slender processus anterior (3). Left-eyed *P. flesus* is easily

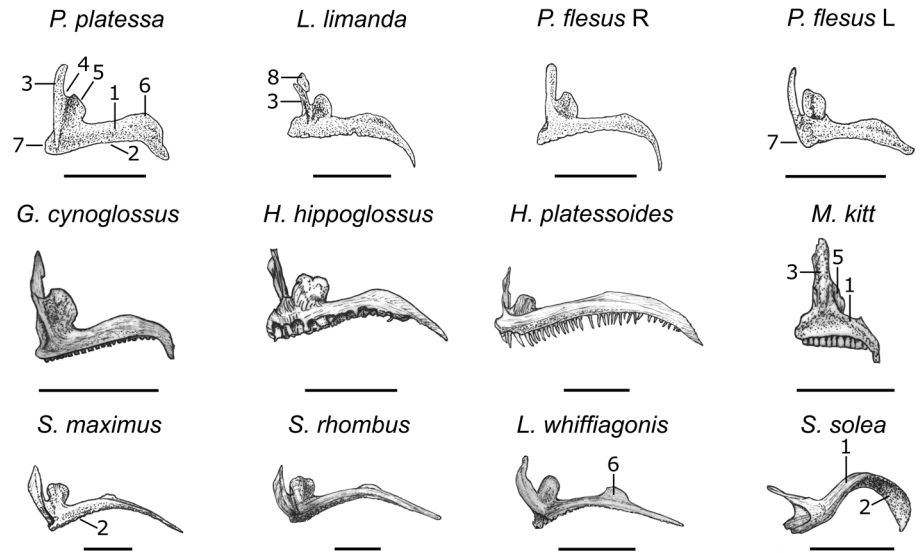


Figure 1. – Lateral view of the left premaxilla of flatfish. The black bar under each species represents 1 cm.

distinguishable by its anteriorly protruding ventral part of the margo symphysicus (7), while all other species have a straight margo symphysicus (7). The corpus (1) is shorter or about as long as the processus anterior (3) in *G. cynoglossus*, without an indentation (4) between the processus anterior (3) and processus articularis (5). In *P. platessa*, right-eyed *P. flesus* and *L. limanda*, the corpus (1) is longer than the processus anterior (3) and the indentation (4) is clearly visible. *Pleuronectes platessa* has a sturdier corpus (1) with only 3-6 teeth, while *L. limanda* and right-eyed *P. flesus* have 6-13 teeth. The indentation (4) between the processus anterior (3) and processus articularis (5) is very deep in right-eyed *P. flesus* and less deep in *L. limanda*, reaching till only halfway the processus articularis (5). Furthermore, *L. limanda* has a slightly finer corpus (1) with small tooth alveoli (2), while

right-eyed *P. flesus* has a thicker corpus (1) with large alveoli (2).

Maxilla

The lateral and medial views of the left maxilla are given in Fig. 3. Additional detailed analysis can be found in the Supplementary Information (Table S4). This bone allows identification to all species. *Solea solea* is characterised by having a highly curved pars caudalis (1), which is confluent with the collum maxillare (2). *Microstomus kitt* has a very stocky shape with a strongly protruding crista maxillaris (3). The pars caudalis (1) barely widens in *L. whiffiagonis*, and the crista maxillaris (3) is very short and protruding clearly, while in *Scophthalmus* spp. and Pleuronectidae, the pars caudalis (1) broadens over its length and the crista maxilla-

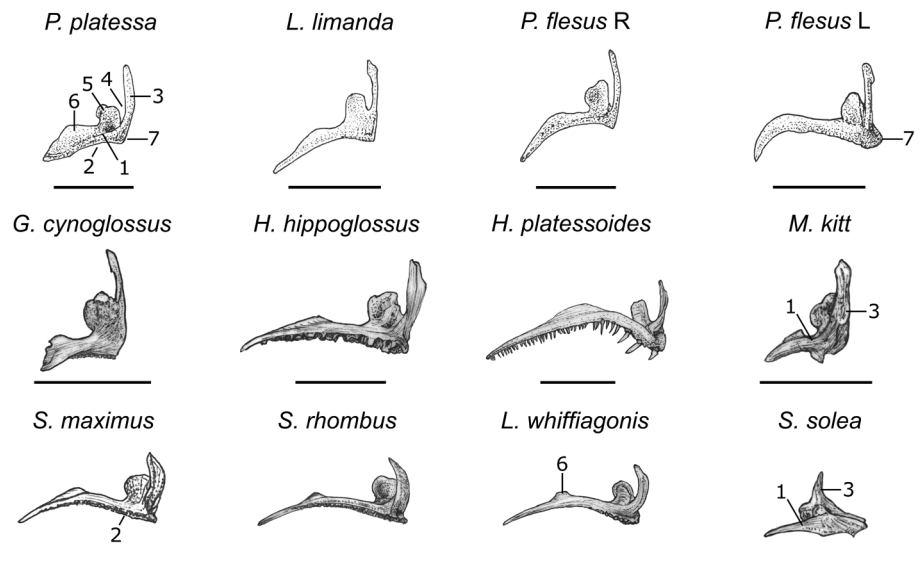


Figure 2. – Lateral view of the right premaxilla of flatfish. The black bar under each species represents 1 cm.

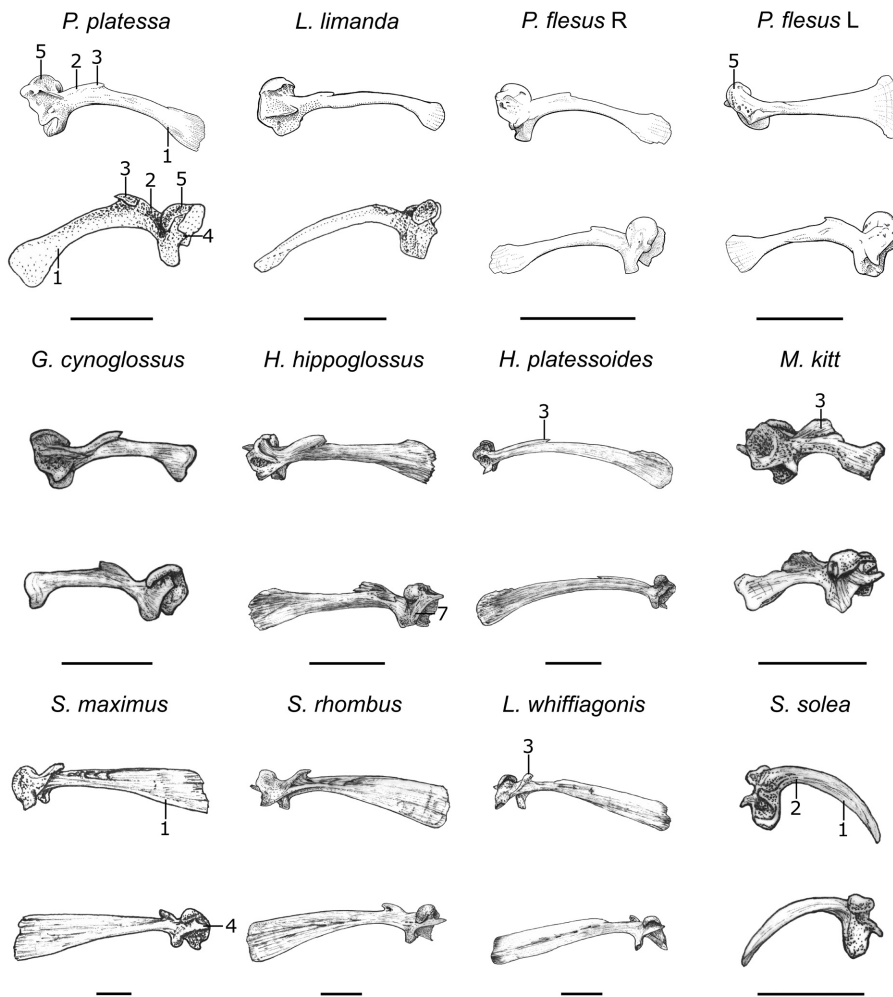


Figure 3. – Lateral (top) and medial (bottom) view of the left maxilla of flatfish. The black bar under each species represents 1 cm.

ris (3) is usually longer, lower, and less clearly protruding. In *Scophthalmus* spp. there is a gradual broadening of the pars caudalis (1) and the spina internus (4) is oriented laterally, while in Pleuronectidae the broadening of the pars caudalis (1) is clear and abrupt and the spina internus (4) is oriented anteriorly. No criteria were found for a reliable distinction between both *Scophthalmus* species. *Hippoglossoides platessoides* and *H. hippoglossus* have a very elongated maxilla in general, while *P. platessa*, *L. limanda*, *P. flesus*, and *G. cynoglossus* have a relatively shorter maxilla. *Hippoglossoides platessoides* is characterised by the very long and low crista maxillaris (3). The crista maxillaris (3) is short and strongly developed in *H. hippoglossus* and the pars caudalis (1) is hollowed out on the medial side. The crista maxillaris (3) reaches almost to midway along the maxilla and the pars caudalis (1) is well-defined in *G. cynoglossus*. Left-eyed *P. flesus* has an anteriorly bent caput maxillare (5), while right-eyed Pleuronectidae have a non-bent caput maxillare (5). In *P. platessa* the pars caudalis (1) is strongly broadened, while in right-eyed *P. flesus* and *L. limanda* this

broadening is less clear and less wide. *Limanda limanda* has in general a slenderer appearance and a less pronounced crista maxillaris (3) compared with right-eyed *P. flesus*.

The lateral and medial views of the right maxilla are given in Fig. 4. Additional detailed analysis can be found in the Supplementary Information (Table S5). This bone allows identification to all species. *Solea solea* is the only species with a strongly reduced processus externus (6) and a very wide and hollow caput maxillare (5). *Microstomus kitt* is the only species with a very short, stocky maxilla with a large crista maxillaris (3) and large caput maxillare (5). In *L. whiffiagonis*, the pars caudalis (1) doesn't get wider over its length and the crista maxillaris (3) is very short and protruding clearly, while in *Scophthalmus* spp. and Pleuronectidae, the pars caudalis (1) broadens over its length and the crista maxillaris (3) is usually longer, lower, and less clearly protruding. In *Scophthalmus* spp. there is a gradual widening of the pars caudalis (2), while in Pleuronectidae the broadening of the pars caudalis (2) is clear and abrupt near the posterior end of the pars caudalis. No criteria were found for a reli-

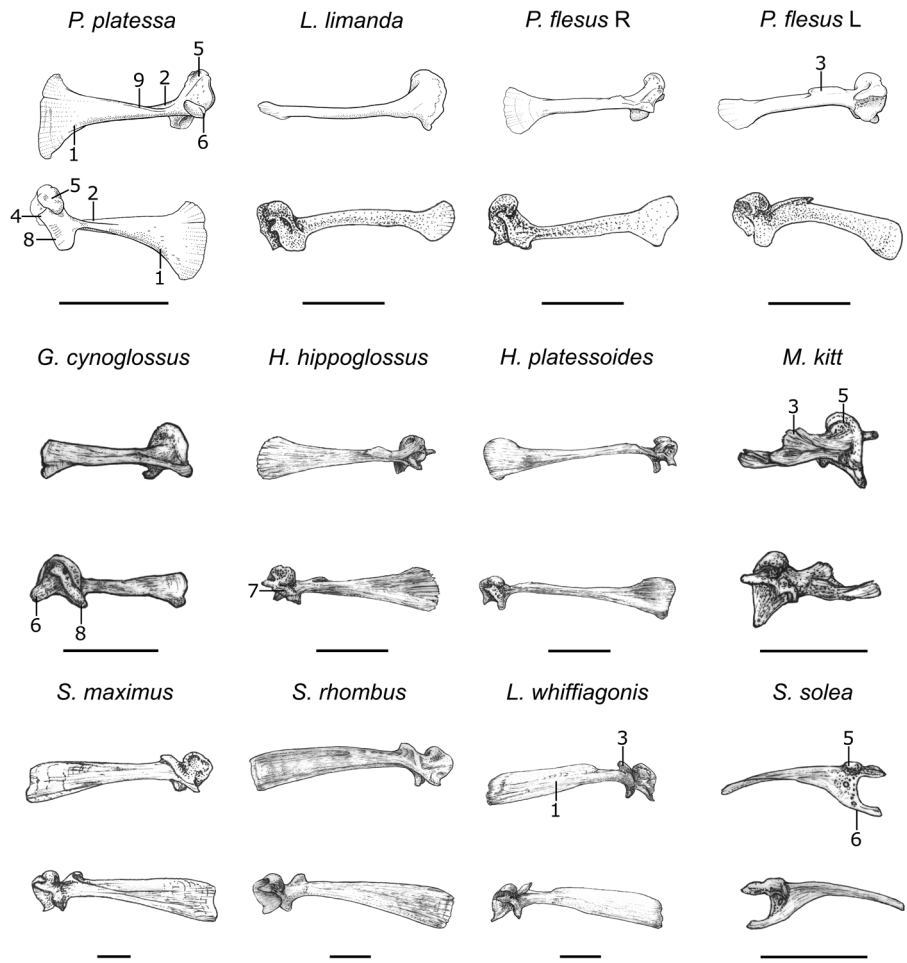


Figure 4. – Lateral (top) and medial (bottom) view of the right maxilla of flatfish. The black bar under each species represents 1 cm.

able distinction between both *Scophthalmus* species. Left-eyed *P. flesus* is the only Pleuronectidae with a strong crista maxillaris (3), which is not the case in the remaining Pleuronectidae. The crista maxillaris (3) is very low, but clearly visible in *H. hippoglossus*. Additionally, there is also a large foramen (7) on the medial side. The bone is very slender and elongated in *H. platessoides*. The processus externus (6) in *G. cynoglossus* is extending far more than the processus internus (8). The notch (9), on the collum maxillare (2) and visible in dorsal view, is usually clearly marked in *P. platessa* compared to right-eyed *P. flesus* and *L. limanda*. The collum maxillare (2) is also shorter and the pars caudalis (1) broadens more gradually over its length, becoming very broad at the end in *P. platessa*. The collum maxillare (2) is relatively longer and the pars caudalis (1) widens only near the end and is less wide in *L. limanda* and right-eyed *P. flesus*. The maxilla is slenderer and the pars caudalis (1) is only slightly curved around its axis in *L. limanda*, while in right-eyed *P. flesus* the maxilla is thicker and the pars caudalis (1) is strongly curved around its axis.

Dentary

The lateral view of the left dentary is given in Fig. 5. Additionally, the medial and ventral views can be found in the Supplementary Information together with the detailed analysis for every species (Table S6; Fig. S3). This bone allows identification to all species. *Solea solea* and *M. kitt* are easily distinguished from all other flatfish species by their unique and short shape combined with the fine dentition in *S. solea* and the very large teeth in *M. kitt*. The large orificia lineae lateralis (1) on the processus aboralis inferior (2) distinguish *G. cynoglossus* from all other species. The Scophthalmidae have 3 or more tooth rows (3) at the anterior part, while Pleuronectidae only have 1 or 2 rows (3). Midway along the corpus (4), there is also a clear depression (5) in Scophthalmidae that is absent in Pleuronectidae. The margo dorsalis (6) of *L. whiffiagonis* is curved, while straight in *Scophthalmus* spp. A thin, translucent bone combined with a huge hole at the depression (5) typifies *L. whiffiagonis*. A dense bone with an open depression (5) is most likely *S. rhombus*. When this depression (5) is closed, it is most likely *S. maximus*. If this last criterium is less clearly

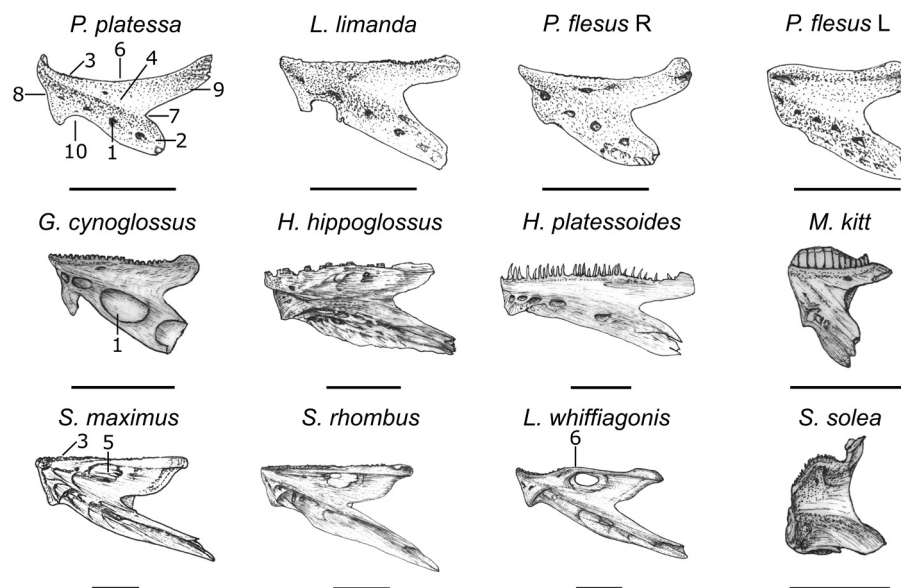


Figure 5. – Lateral view of the left dentary of flatfish. The black bar under each species represents 1 cm.

visible, it is advised to restrict identification to *Scophthalmus* spp. *Hippoglossus hippoglossus* differs from all other Pleuronectidae by having large teeth and alveoli which are placed irregularly (3). *Hippoglossoides platessoides* is characterised by the combination of an elongated dentary with 30-48 small teeth. A flat dentary is typical for left-eyed *P. flesus*, while in right-eyed *P. flesus*, *L. limanda*, and *P. platessa*, the corpus (4) of the bone is heavily curved. The tooth area (3) also extends till the incisura posterior externa (7) between both processus in left-eyed *P. flesus*, while beyond this point in right-eyed *P. flesus*, *L. limanda*, and *P. platessa*. Left-eyed *P. flesus* also has a higher symphysis (8) than right-eyed *P. flesus*, *L. limanda*, and *P. platessa*. The processus aboralis superior (9) ends at the same level as the processus aboralis inferior (2) in *L. limanda*, while it extends beyond the level of the processus aboralis inferior (2) in *P. platessa* and right-eyed *P. flesus*. The semi-circular and well-defined incisura inferior (10) characterises *L. limanda* as well. The incisura inferior (10) is wide and deep in *P. platessa* while almost absent in right-eyed *P. flesus*. *Pleuronectes platessa* also has a straight symphysis (8) and a strongly laterally curved processus aboralis superior (9), while *P. flesus* has an inclined symphysis (8) and only a slightly laterally curved processus aboralis superior (9).

The lateral view of the right dentary is given in Fig. 6. Additionally, the medial and ventral views can be found in the Supplementary Information together with the detailed analysis for every species (Table S7; Fig. S4). This bone allows identification to all species. The compact shape with a very short corpus (4) is characteristic for *M. kitt*. The rounded symphysis (8) and curved right dentary of *S. solea* is also very characteristic. The large size of the elongated officina lineae lateralis (1) distinguishes *G. cynoglossus* from

the other species. In Scophthalmidae, the processus aboralis inferior (2) is much longer than the processus aboralis superior (9) and there is a clear depression (5) midway along the corpus, which is absent in Pleuronectidae. The translucent bone and the convex margo dorsalis (6) around the open depression (5) are characteristic for *L. whiffiagonis*. Both *Scophthalmus* spp. have dense bone and a straight margo dorsalis (6). When this depression (5) is open, it is most likely *S. rhombus*. When this depression (5) is closed, it is most likely *S. maximus*. If this last criterium is less clearly visible, it is advised to restrict identification to *Scophthalmus* spp. Left-eyed *P. flesus* can easily be distinguished from the other Pleuronectidae by having a processus aboralis superior (9) that extends beyond the level of the processus aboralis inferior (2) and a strong latero-medially curved shape of the bone. In the other Pleuronectidae, the processus aboralis superior (9) extends to about the same level or less than the processus aboralis inferior (2), and the bone is flat. The dentary of *H. hippoglossus* and *H. platessoides* have an elongated appearance compared to *P. platessa*, *L. limanda*, and right-eyed *P. flesus*. *Hippoglossus hippoglossus* differs from all other Pleuronectidae by having large teeth and irregularly placed alveoli (3). *Hippoglossoides platessoides* is characterised by the irregularly implanted small teeth (3) and has a convex margo dorsalis (6), which is straight or slightly concave in *P. platessa*, *L. limanda* and right-eyed *P. flesus*. *Pleuronectes platessa* has only 4-8 teeth, while in *L. limanda* and right-eyed *P. flesus* there are more than 10 teeth. *Limanda limanda* differs from right-eyed *P. flesus* by the short and deep incisura inferior (10), which is shallow and usually longer in right-eyed *P. flesus*.

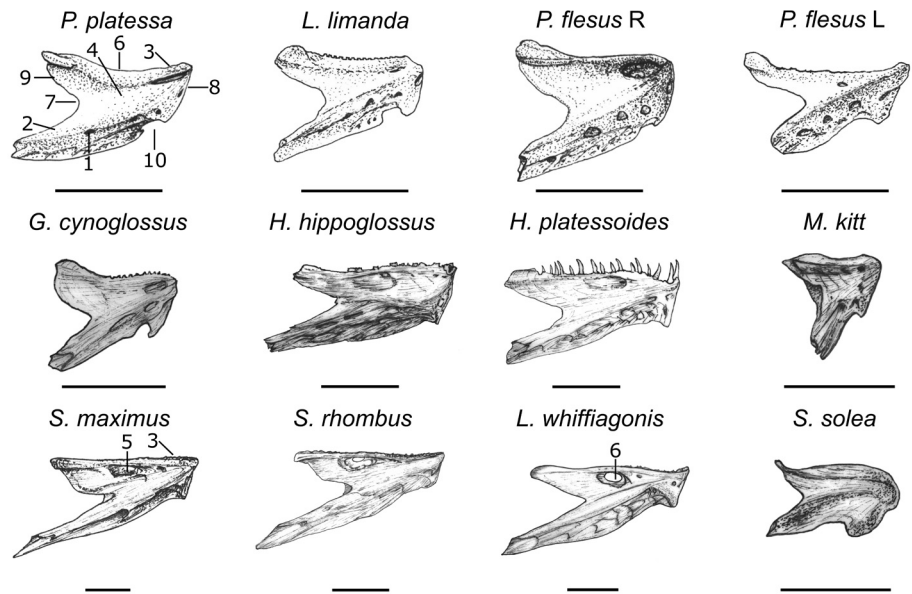


Figure 6. – Lateral view of the right dentary of flatfish. The black bar under each species represents 1 cm.

Articular

The lateral view of the left articular is given in Fig. 7. Additionally, the medial view can be found in the Supplementary Information together with the detailed analysis for every species (Table S8; Fig. S5). This bone allows identification to all species. The processus anterior (1) of *S. solea* is very short and not delineated, while it is clearly delineated and long in all other species. *Microstomus kitt* has a ventrally oriented angulus ventralis (2). An enlarged tube (3) on the angulus ventralis (2) is typical for *G. cynoglossus*. The posterior edge (4) of the angulus ventralis (2) extends more ventrally than its anterior edge (5) in both *Scophthalmus* spp., to the same height in *L. whiffiagonis*, and extends less in

Pleuronectidae. In *L. whiffiagonis*, the articular is less ossified than in *Scophthalmus* spp. In *S. maximus* the processus postarticularis (6) is much higher than in *S. rhombus*. The tip of the processus coronoideus (7) lies at the same height as the anterior tip (5) of the angulus ventralis (2) in *P. platessa*, right-eyed *P. flesus*, and *H. platessoides*, while the angulus coronoideus (7) lies anterior from the anterior tip (5) of the angulus ventralis (2) in *L. limanda*, *H. hippoglossus*, and left-eyed *P. flesus* (see dashed line showing the most anterior positioned tip). In *P. platessa*, the level of the anterior tip (5; see dashed line) of the angulus ventralis (2) is in the first half of the articular across its length, while in the second half in right-eyed *P. flesus* and *H. platessoides*. Hip-

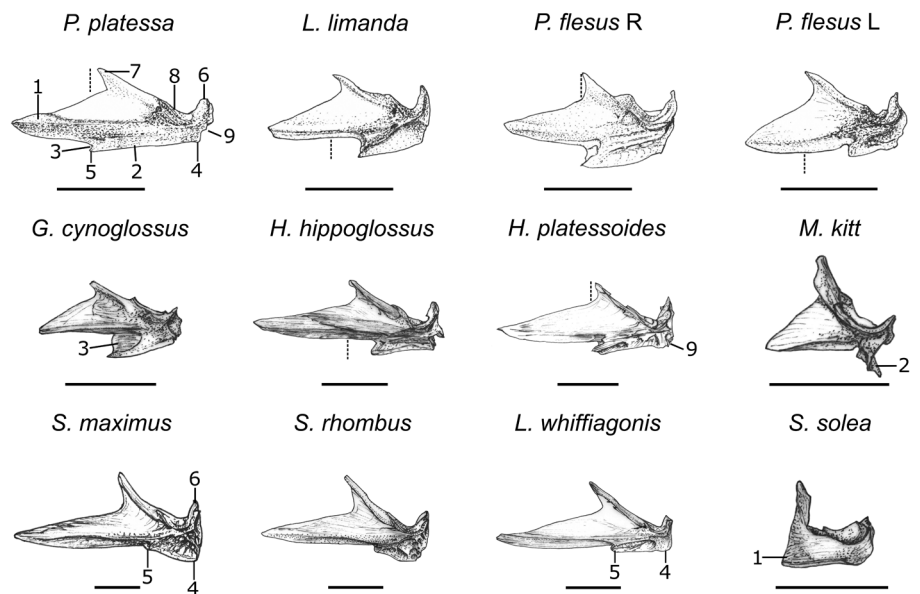


Figure 7. – Lateral view of the left articular of flatfish. The black bar under each species represents 1 cm.

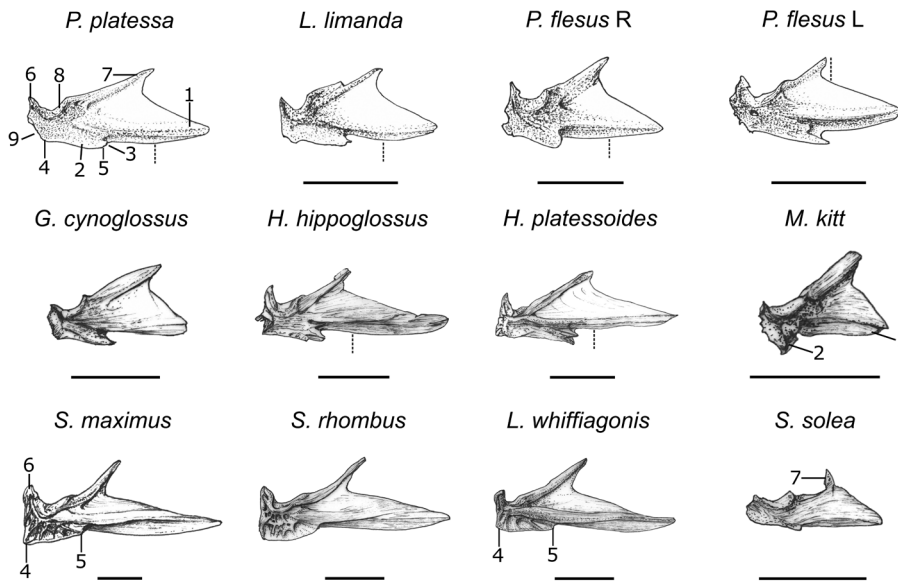


Figure 8. – Lateral view of the right articular of flatfish. The black bar under each species represents 1 cm.

poglossoides platessoides is characterised by the elongated shape of the processus anterior (1) and the rounded posterior edge (4) of the angulus ventralis (2), while these are short and angular respectively in right-eyed *P. flesus*. The shape of the articular of *H. hippoglossus* is far more elongated due to the general low shape and the long processus anterior (1) compared to those of *L. limanda*, and left-eyed *P. flesus*. The level of the anterior tip (5) of the angulus ventralis (2) lies relatively more anterior in *L. limanda* than in left-eyed *P. flesus*. Further, *L. limanda* never has a second tip on the processus postarticularis (6) on the posterior edge, while there are often two tips in left-eyed *P. flesus*.

The lateral view of the right articular is given in Fig. 8. Additionally, the medial view can be found in the Supplementary Information together with the detailed analysis for every species (Table S9; Fig. S6). This bone allows identification to all species. The processus coronoideus (7) is oriented dorsally in *S. solea*, while it is oriented anteriorly in all other species. The angulus ventralis (2) is short and doesn't reach far anteriorly and the processus anterior (1) is short in *M. kitt*. The posterior edge (5) of the angulus ventralis (2) extends more ventrally than its anterior edge (4) in both *Scophthalmus* spp., at the same height in *L. whiffiagonis*, and extends less in Pleuronectidae. In *L. whiffiagonis*, the articular is less ossified than in *Scophthalmus* spp. In *S. maximus* the processus postarticularis (6) is higher than in *S. rhombus*. In left-eyed *P. flesus*, the tip of the processus coronoideus (7) lies at the same level as the anterior tip (5) of the angulus ventralis (2), while it lies more anteriorly in the other Pleuronectidae (see dashed line). The processus anterior (1) in *H. hippoglossus* and *H. platessoides* is elongated, resulting in a general long and low articular. In *H. hippoglossus* and *H. platessoides* the tip of the process postarticularis (6) is

higher than the anterior edge of the facies articularis quadrati (8), while it is lower or similar in height in *G. cynoglossus*, *L. limanda*, *P. platessa*, and *P. flesus*. In *H. hippoglossus*, the tip of the processus coronoideus (7) lies clearly anterior to the anterior tip (5) of the angulus ventralis (2), while in *H. platessoides* these two lie almost at the same level (see dashed line). *Pleuronectes platessa* has a low processus postarticularis (6) and slightly protruding angulus ventralis (2), while *G. cynoglossus*, *L. limanda*, and *P. flesus* have a high processus postarticularis (6) and strongly protruding angulus ventralis (2). *Glyptocephalus cynoglossus* has a relatively shorter right articular compared with *L. limanda* and right-eyed *P. flesus*, with a much shorter processus anterior (1). *Limanda limanda* never has a second tip on the processus postarticularis (6) and a more angular lower posterior edge (9), while there are often two tips on the processus postarticularis (6) and a more irregular or rounded lower posterior edge (9) in right-eyed *P. flesus*.

Hyomandibula

The lateral view of the left hyomandibula is given in Fig. 9. Additionally, the medial view can be found in the Supplementary Information together with the detailed analysis for every species (Table S10; Fig. S7). This bone allows identification to all genera. *Microstomus kitt* has a short concave processus articularis (pr. a.) pteroticus (1) and a very short, non-protruding pr. a. opercularis (2). The crista anterior (3) is short, implanted halfway on the processus inferior (4), and strongly ossified in *S. solea*. In *Scophthalmus* spp. and *H. hippoglossus*, the level of the pr. a. pteroticus (1) is at the same level as the pr. a. sphenoticus (5) or slightly lower, while in *L. whiffiagonis*, *P. platessa*, *L. limanda*, *P. flesus*, and *G. cynoglossus* the pr. a. pteroticus (1) is clearly higher than

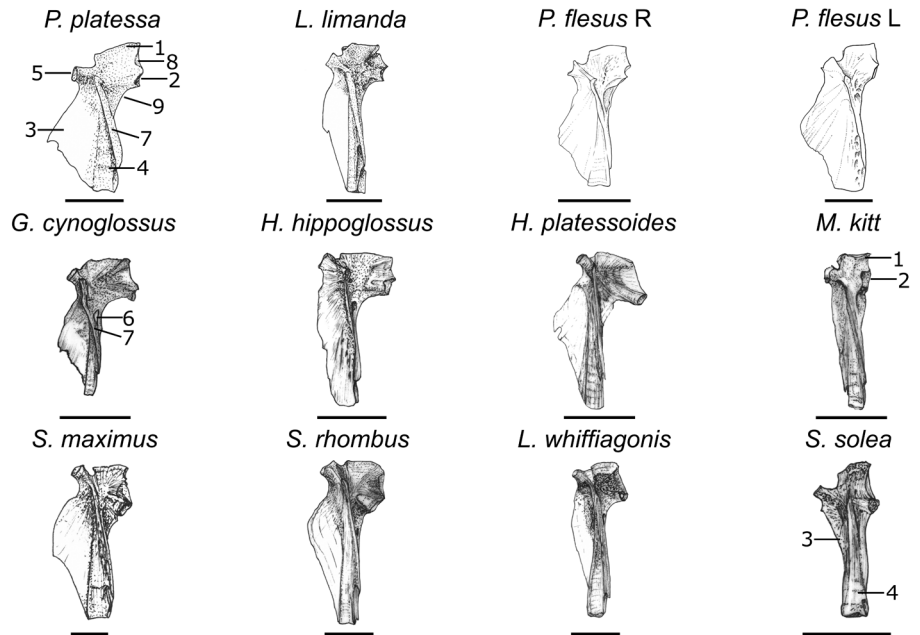


Figure 9. – Lateral view of the left hyomandibula of flatfish. The black bar under each species represents 1 cm.

the pr. a. sphenoticus (5). The level of the pr. a. pteroticus (1) is only very slightly lower than the pr. a. sphenoticus (5) in *H. platessoides*, which is not so clear. However, it is the only species with a long and clearly delineated pr. a. opercularis (2). The crista anterior (3) attaches near the tip of the pr. a. sphenoticus (5) in *H. hippoglossus*, while in both *Scophthalmus* spp., the crista anterior (3) attaches near the base. No criteria were found for a reliable distinction between both *Scophthalmus* species. *Lepidorhombus whiffiagonis*

has a slender hyomandibula, with a relatively smaller crista anterior (3). *Glyptocephalus cynoglossus* is characterised by the large foramen (6) next to the crista preopercularis (7). *Limanda limanda* has a slender appearance compared with the two latter species, due to the slender crista anterior (3), which is broad in *P. platessa* and *P. flesus*. The crista (8) between pr. a. pteroticus (1) and pr. a. opercularis (2) is also slenderer than the pr. a. pteroticus (1) in *L. limanda*, while as wide as the pr. a. pteroticus (1) in *P. platessa* and *P. fle-*

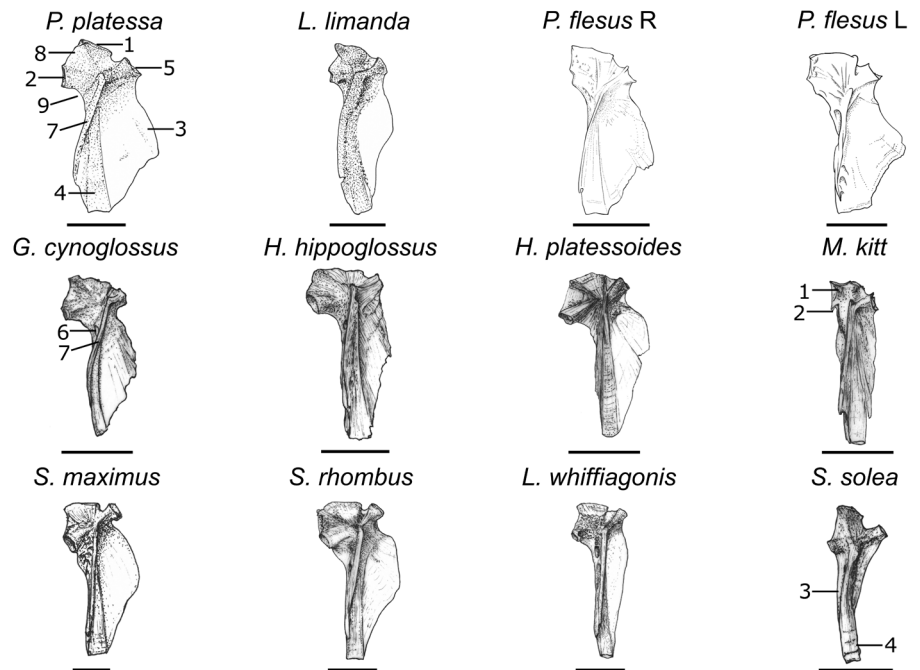


Figure 10. – Lateral view of the right hyomandibula of flatfish. The black bar under each species represents 1 cm.

pleuronectes platessa is difficult to distinguish from *P. flesus*, but the pr. a. pteroticus (1) is proportionally longer in lateral view in *P. platessa* than in *P. flesus* if bones from the same size are compared. The transition (9) between pr. a. opercularis (2) and pr. inferior (4) is somewhat deeper in *P. platessa* than in *P. flesus*. Right-eyed and left-eyed *P. flesus* cannot be confidently distinguished.

The right hyomandibula (Fig. 10) shows similar criteria as the left. Detailed analysis for each species can be found in the Supplementary Information (Table S11; Fig. S8). This bone allows identification to all genera.

Palatine

The lateral view of the left palatine is given in Fig. 11. Additionally, the medial view can be found in the Supplementary Information together with the detailed analysis for every species for the left palatine (Table S12; Fig. S9). This bone allows identification to all species. The left palatine of *S. solea* is very distinct by the very long, sharp facies articularis (f. a.) ectopterygoidalis (1), the reduced f. a. entopterygoidalis (2), and the small processus maxillaris (3). A dorsal transverse ridge (4) separates the processus maxillaris (3) from the f. a. entopterygoidalis (2) in Scopthalmidae. The processus maxillaris (3) is slender and curved in *L. whiffiagonis* and the f. a. entopterygoidalis (2) is long and slender, while both structures are stockier in *Scophthalmus* spp. The dorsal transverse ridge (4) is stronger in medial view in *S. maximus* than in *S. rhombus*. Left-eyed *P. flesus* is characterised by a short f. a. ectopterygoidalis (1), a highly reduced f. a. entopterygoidalis (2), and the smooth and gradual transition of both into the processus maxillaris (3). In *M. kitt*, the f. a. ectopterygoidalis (1) is equal in height as

the f. a. entopterygoidalis (2). The f. a. ectopterygoidalis (1) and the f. a. entopterygoidalis (2) are clearly distinct from each other in *G. cynoglossus* by a clear and deep incision (5) between them. The f. a. ectopterygoidalis (1) extends more posteriorly than the p. a. entopterygoidalis (2) in *P. platessa*, while both are at the same height in *L. limanda*, right-eyed *P. flesus*, *H. hippoglossus*, and *H. platessoides*. The general appearance of the palatine is slenderer in *H. platessoides* compared to the other species, however, this feature could be prone to subjective interpretation. Right-eyed *P. flesus* has a more distinctive processus maxillaris (3) and a longer collum (6) compared with *L. limanda* and *H. hippoglossus*. The caput (7) is clearly broader than the collum (6) with a clear separation between both in *L. limanda*, while the distinction between the caput (7) and the collum (6) is less clear in *H. hippoglossus*.

The lateral view of the right palatine is given in Fig. 12. Additionally, the medial view can be found in the Supplementary Information together with the detailed analysis for every species for the right palatine (Table S13; Fig. S10). This bone allows identification to all genera. The right palatine of *S. solea* is characterised by the very long and slender f. a. ectopterygoidalis (1), the reduced f. a. entopterygoidalis (2), and the slender processus maxillaris (3). Scopthalmidae have a clear dorsal transverse ridge (4) between the processus maxillaris (3) and the f. a. entopterygoidalis (2). The f. a. entopterygoidalis (2) is long and slender in *L. whiffiagonis*, while shorter and broader in *Scophthalmus* spp. No criteria were found for a reliable distinction between both *Scophthalmus* species. Left-eyed *P. flesus* has a distinct right palatine, which matches with the left palatine of the right-eyed *P. flesus*, but in mirror-image. The right palatine

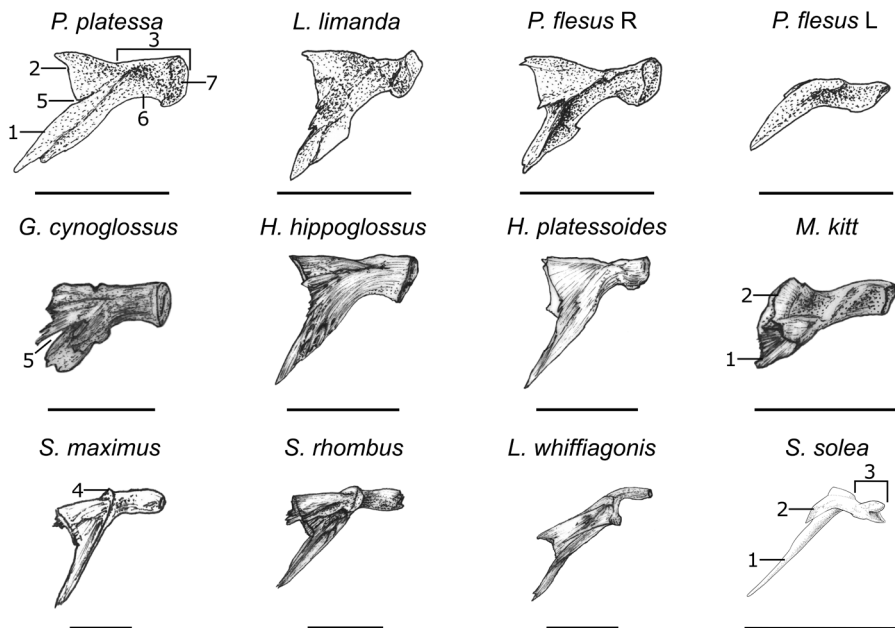


Figure 11. – Lateral view of the left palatine of flatfish. The black bar under each species represents 1 cm.

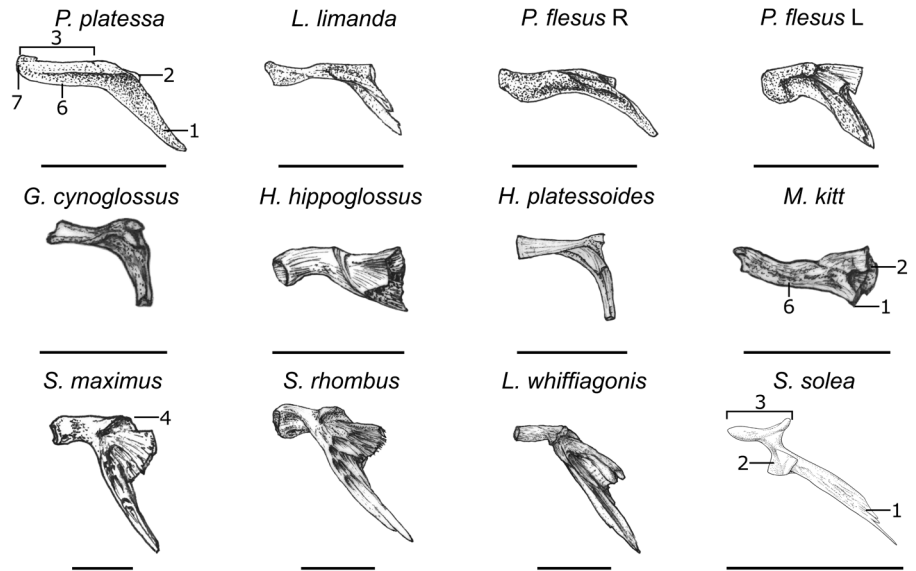


Figure 12. – Lateral view of the right palatine of flatfish. The black bar under each species represents 1 cm.

of *M. kitt* has a very long collum (6) and short f. a. ectopterygoidalis (1) and f. a. entopterygoidalis (2). In *H. hippoglossus* the f. a. ectopterygoidalis (1) is also strongly reduced, but the collum (6) is broader compared to *M. kitt*. There is a 90° transition between the processus maxillaris (3) and the f. a. ectopterygoidalis (1) in *H. platessoides* and *G. cynoglossus*, while the angle is larger in *P. platessa*, *L. limanda*, and right-eyed *P. flesus*. The palatine of *H. platessoides* is very gracile, while robust in *G. cynoglossus*. The latter species also has a large foramen at the tip of the f. a. ectopterygoidalis (1). The processus maxillaris (3) is rather straight and broad in *P. platessa*. The processus maxillaris (3) is more curved and slender in right-eyed *P. flesus* and *L. limanda*. The processus

maxillaris (3) is more developed and broader in right-eyed *P. flesus* than in *L. limanda*.

Vomer

The ventral and sinistral lateral views of the vomer are given in Fig. 13. Additionally, the dorsal and dextral lateral views can be found in the Supplementary Information together with the detailed analysis for every species (Table S14; Fig. S11). This bone allows identification to all species. The ventral part (1) of the apex (2) in *S. solea* protrudes strongly, and the partes praefrontales (3) extend in a dorsal direction, while these are oriented posterior-laterally in the other species. The ventral part (1) of the apex (2) in Scophthalmidae bears some alveoli (4) for teeth, visible in ventral

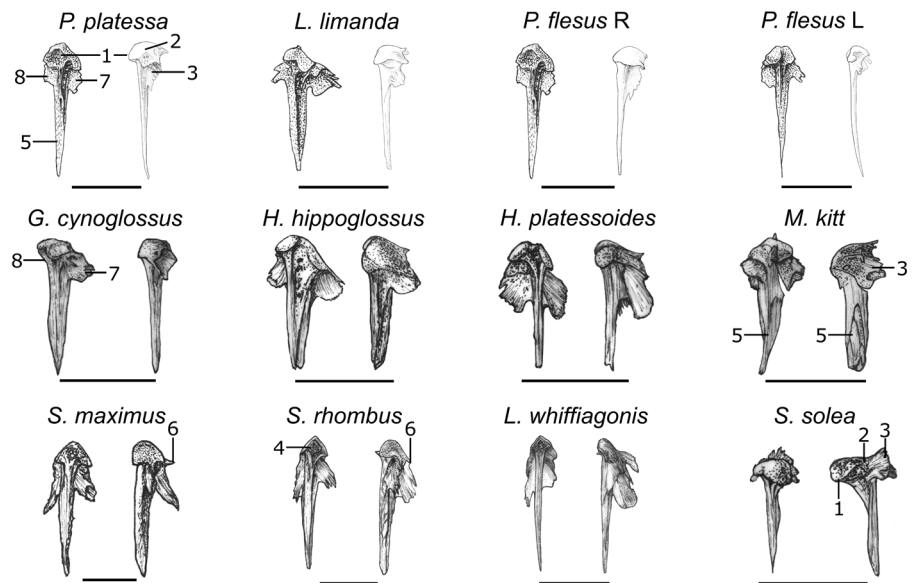


Figure 13. – Ventral (left) and sinistral lateral (right) view of the vomer of flatfish. The black bar under each species represents 1 cm.

view, which are absent in Pleuronectidae. *Scophthalmus* spp. have a wider apophysis posterior (5) than *L. whiffiagonis*, where the apophysis posterior (5) remains slender. The pars ethmoidalis (6) is laterally flat and very long in *L. whiffiagonis*. The pars ethmoidalis (6) in *S. maximus* bears a strong, hooklike ridge (6), which is much finer and pointed in *S. rhombus*, visible in lateral view. The apophysis posterior (5) is thick in lateral view in *M. kitt* and *H. hippoglossus*. The partes praefrontales (3) are small in *M. kitt* and large in *H. hippoglossus*. The partes praefrontales (3) of *H. platessoides* extend far in posterior and lateral direction, and the apophysis posterior (5) is thin. Only the left pars praefrontalis (7) is protruding laterally in *G. cynoglossus*, while the right one (8) does not. In other Pleuronectidae, both partes praefrontales (3) are well developed and extend laterally. The right pars praefrontalis (3) is more developed than the left one in left-eyed *P. flesus*, while vice versa in the remaining species. In *L. limanda*, the left pars praefrontalis (7) is far more developed compared to the right one (8) and the apex (1) is relatively small compared with the thicker apophysis posterior (5). The right half of the apex (1) can be oriented more caudally in right-eyed *P. flesus* compared to the left half of the apex. This is reversed in *P. platessa*, in which the left half of the apex (1) is more anteriorly oriented. In case both halves of the apex are on the same height, this feature should not be used.

Posttemporal

The lateral view of the left posttemporal is given in Fig. 14. Additionally, the medial view can be found in the Supplementary Information together with the detailed analy-

sis for every species (Table S15; Fig. S12). This bone allows identification to all species. The processus inferior (1) is strongly protruding in *S. solea*. The canalis lineae lateralis (2) is shaped by two large foramina (3) on the lateral side in *G. cynoglossus*. *Microstomus kitt* has a straight posttemporal with a relatively thick processus superior (4) and lacks the processus inferior (1). *Lepidorhombus whiffiagonis* has a characteristically broad processus superior (4) in combination with a very short, horizontally extending processus inferior (1). *Scophthalmus* spp. have a very flat and almost triangular posttemporal with a heavily striated lateral side. Both *Scophthalmus* spp. can only be distinguished by comparing bones of the same size. The processus inferior (1) is always longer and thinner in *S. rhombus* than in *S. maximus*. Since this difference is difficult to assess and shows some variation, confident identification of these species is rarely possible. The somewhat triangular shape is also found in the posttemporals of *H. platessoides* and *H. hippoglossus*, but the bone is much thicker compared to *Scophthalmus* spp. *Hippoglossus hippoglossus* has a more strongly curved processus superior (4) compared to *H. platessoides*. *Platichthys flesus* shows tubercles (5) along the lateral surface, which can sometimes be unclear in archaeological samples. Left and right-eyed *P. flesus* cannot be distinguished. The posttemporal of *L. limanda* is stocky and its processus superior (4) triangular in shape, while slender and more elongated respectively in *P. platessa*.

The lateral view of the right posttemporal is given in Fig. 15. Additionally, the medial view can be found in the Supplementary Information together with the detailed analysis for every species (Table S16; Fig. S13). This bone allows

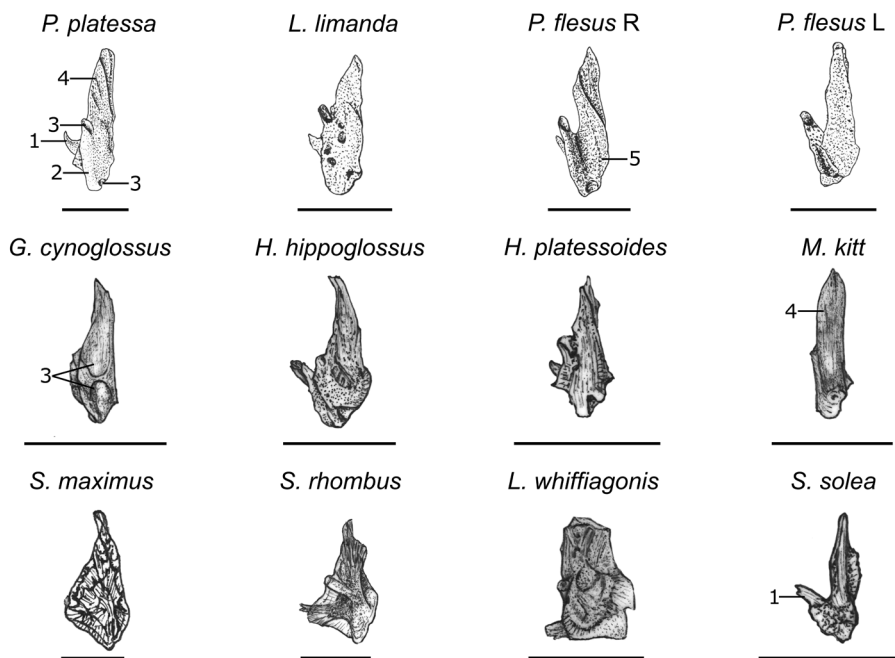


Figure 14. – Lateral view of the left posttemporal of flatfish. The black bar under each species represents 1 cm.

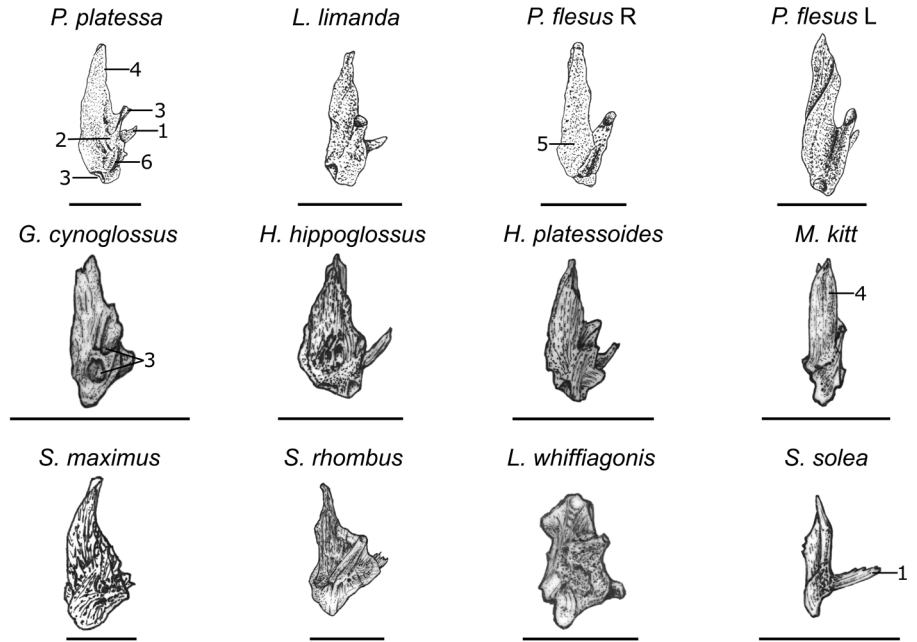


Figure 15. – Lateral view of the right posttemporal of flatfish. The black bar under each species represents 1 cm.

identification to all species. The characteristics to identify the species are similar as those for the left posttemporal, except for *H. hippoglossus*, *P. platessa*, and *L. limanda*. The right posttemporal of *P. platessa* has a large tuberosity (6) on the lateral side. The posttemporal is elongated and the canalis linea lateralis (2) is clearly visible in lateral view in *L. limanda*. The bone is rounded in the ventral part and the canalis linea lateralis (2) is invisible in *H. hippoglossus*. Right- and left-eyed *P. flesus* cannot be distinguished.

Urohyal

The dextral lateral view of the urohyal is given in Fig. 16. Additional detailed analysis can be found in the Supplementary Information (Table S17). This bone allows identification to all genera. The angulus anterior (1) and processus hypohyalis (2) are oriented perpendicular to each other in *S. solea*. *Lepidorhombus whiffiagonis* is distinct from other flatfish through the lack of a clear and deep incisura collis (3). *Scophthalmus* spp. and *M. kitt* can easily be differentiated from other flatfish by the parallel position of the angulus anterior (1) and processus hypohyalis (2). In *M. kitt*, the length of the incisura collis (3) is comparable to the height of

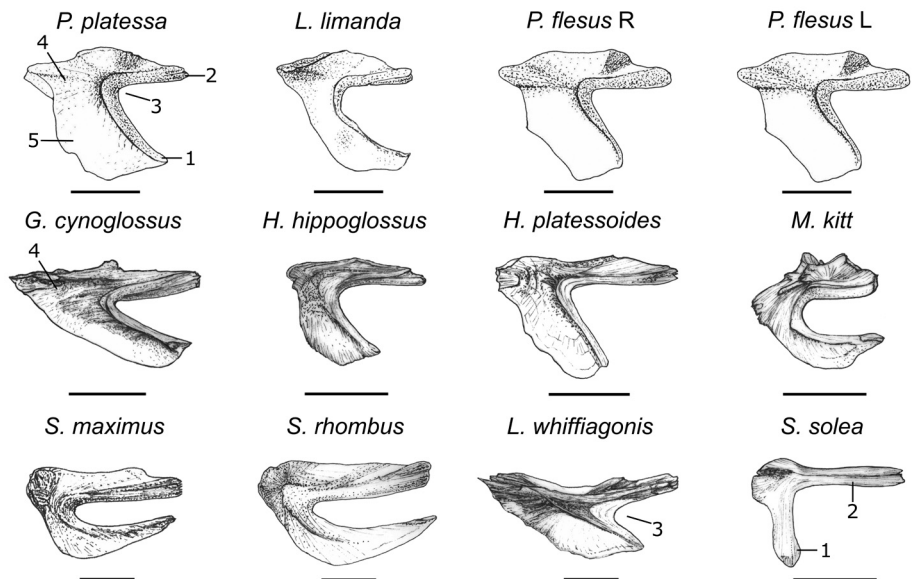


Figure 16. – Dextral lateral view of the urohyal of flatfish. The black bar under each species represents 1 cm.

the bone, while in both *Scophthalmus* spp. it is very elongated. No criteria were found for a reliable distinction between both *Scophthalmus* species. The tip of the processus hypohyalis (2) is at the same level as the tip of the angulus anterior (1) in *G. cynoglossus*, *P. platessa*, and *L. limanda*, while it lies in front of the angulus anterior (1) in *H. hippoglossus*, *H. platessoides*, and *P. flesus*, although this feature can be difficult to assess in some cases. *Glyptocephalus cynoglossus* can be distinguished from other Pleuronectidae by the long triangular lamina verticalis (4) and the narrow incisura collis (3). The shape of the incisura collis (3) is rounded and more broadly U-shaped in *L. limanda*, while more angular in *P. platessa*. *Hippoglossus hippoglossus* and *H. platessoides* have a processus hypohyalis (2) that is twice as long as the width of the lamina verticalis pars ventralis (5), while *P. pla-*

tessa and *P. flesus* have a processus hypohyalis (2) that is about as long as or slightly longer than the lamina verticalis pars ventralis (5). *Hippoglossoides platessoides* has a relatively longer and less ossified lamina verticalis pars ventralis (5) compared with *H. hippoglossus*. The tip of the angulus anterior (1) is curved ventrally in *P. flesus*, while it is straight or slightly posteriorly curved in *P. platessa*. Distinction of right and left-eyed *P. flesus* is impossible to make.

First precaudal vertebra

The anterior and lateral views of the first precaudal vertebra are given in Fig. 17 (the posterior views are given for *P. platessa*, *L. limanda*, and *P. flesus* as this was the only view available for these species). Additional detailed analysis can be found in the Supplementary Information (Table S18). This

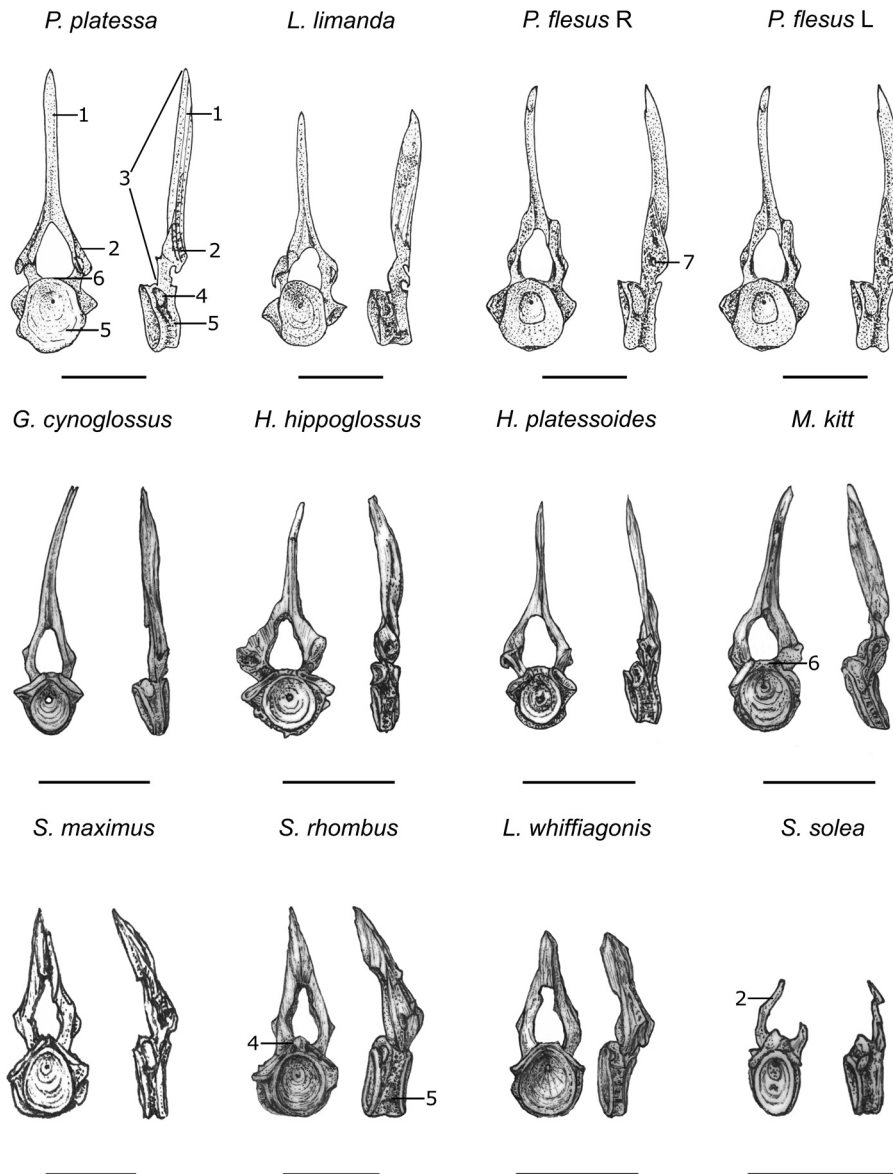


Figure 17. – Anterior (left) and sinistral lateral (right) view of the first precaudal vertebra of flatfish, with posterior view instead of anterior view for *P. platessa*, *L. limanda*, and *P. flesus*. The black bar under each species represents 1 cm.

bone allows identification to all species *Solea solea* is easily distinguished by the lack of a processus spinosus superior (1) and an incomplete neurapophysis (2) on the neural arch (3). This should not be confused with broken neural arches in other species when dealing with archaeological material. In *Scophthalmus* spp. the medial border of the condyli (4) are adjoining, while in Pleuronectidae and *L. whiffiagonis* both condyli (4) are slightly or clearly separated. The depth of the corpus (5), as seen in lateral view, is proportionally much larger in *S. rhombus* compared to *S. maximus*. Compared to Pleuronectidae, the neural arch (3) is short and very thick in *L. whiffiagonis*. The edges of the condyli (4) protrude dorsally in *H. platessoides*, but not in the other Pleuronectidae. *Microstomus kitt* has a horizontally flat dorsal edge (6) of the centre, while this is curved in the other species. *Hippoglossus hippoglossus* has condyli (4) with wide lateral borders and small medial borders and a broad neurapophysis (2), as seen in anterior view. The corpus (5) of *G. cynoglossus* is sometimes triangular in lateral view, while usually rectangular in the other species. This species also has condyli (4) that protrude more laterally than in *P. platessa*, *L. limanda*, and *P. flesus*. *Platichthys flesus* always has a foramen (7) in each neurapophysis (2) in contrast with *P. platessa* and *L. limanda*. The corpus is much deeper in *L. limanda*, as seen in lateral view, compared to *P. platessa* and *P. flesus*. No distinction between right- and left-eyed *P. flesus* is possible.

and show the same diagnostic features. The metapterygium is a very thin and fragile bone without any well-developed criteria in fish smaller than 25 cm SL. Even in larger fish, the metapterygium is mostly translucent and doesn't show many clear structures. The metapterygium of *S. solea* is triangular-shaped with a semi-circular margo quadrati (1). The margo hyomandibularis (2) is almost oriented vertically. The width and height of the bone are almost equal in Scophthalmidae, while the metapterygium tends to be much wider than high in Pleuronectidae. In both *Scophthalmus* spp., the processus dorsalis (3) is well individualised. The metapterygium of *L. whiffiagonis* is very transparent and only the margo quadrati (1) is a bit ossified, while the margo hyomandibularis (2) is semi-circular in shape. Proportionally, the metapterygium shows a more ossified texture in *S. maximus* compared to *S. rhombus*, although this characteristic is prone to subjective interpretation. The metapterygium in *L. limanda*, *G. cynoglossus*, and *H. platessoides* is very transparent, while more ossified, at least partly, in the other Pleuronectidae. The margo quadrati (1) and margo hyomandibularis (2) have about the same length in *G. cynoglossus* and *L. limanda*, while the margo hyomandibularis (2) is longer than the margo quadrati (1) in *H. platessoides*. The transition between the anterior (4) and posterior (5) lamina is marked by a small, slightly ossified canal (6), which is sometimes curved in *L. limanda* and straight and not as visible in *G. cynoglossus*. The surface of the bone in *H. hippoglossus* is strongly striated while a clear canal (6) is absent. The metapterygium of *M. kitt* is heavily ossified. *Pleuronectes platessa* and both right- and left-eyed *P. flesus* are impossible to distinguish. Differentiation between right- and left-eyed *P. flesus* seems impossible.

Metapterygium

The lateral view of the left metapterygium is given in Fig. 18. Additional detailed analysis can be found in the Supplementary Information (Table S19). This bone allows identification to most species. Only the left element is illustrated because the left and right metapterygium are similar

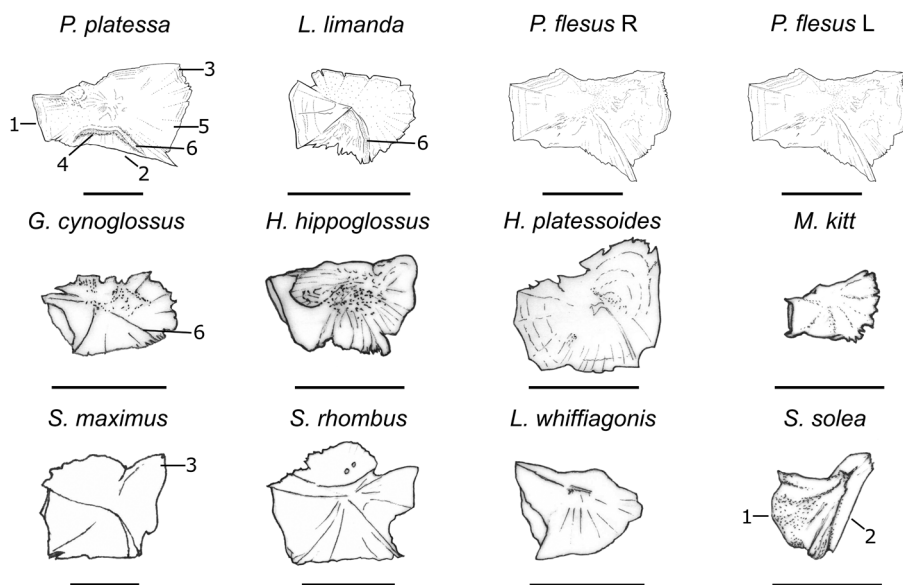


Figure 18. – Lateral view of the metapterygium of flatfish. The black bar under each species represents 1 cm.

Basioccipital

The ventral, lateral, and caudal views of the basioccipital are given in Fig. 19. Additional detailed analysis can be found in the Supplementary Information (Table S20). This bone allows identification to most genera. *Solea solea* is characterised by two round, extending styloid processus (1) in ventral view, which are absent in all other species. In *Scophthalmidae*, both *cristae exoccipitales* (2) are only about half as long as the *facies articularis parasphenoidalis* (3), which is wide over the whole length, while the *cristae* (2) are as long as the *facies articularis parasphenoidalis* (3) and the *facies articularis parasphenoidalis* (3) is slender in *Pleuronectidae*. The *cristae exoccipitales* (2) can sometimes extend much wider

in *L. whiffiagonis* than in both *Scophthalmus* species. *Scophthalmus* spp. are difficult to distinguish. *Microstomus kitt* is the only species where the borders of the *facies articularis parasphenoidalis* (3) run parallel. *Hippoglossus hippoglossus* is very recognisable by the shallow *facies articularis parasphenoidalis* (3), which widens in anterior direction, almost hiding the *cristae exoccipitales* (2). Lateral bony ridges (5) close to the *facies articularis vertebralis* (4) are typical for *G. cynoglossus*. The *facies articularis parasphenoidalis* (3) gets broader anteriorly in *L. limanda* and *H. platessoides*, while it remains the same width in *P. platessa* and *P. flesus*. In *L. limanda*, there is a distinct thin ridge (5) present on the posterior part of the corpus (6), which is absent in *H. pla-*

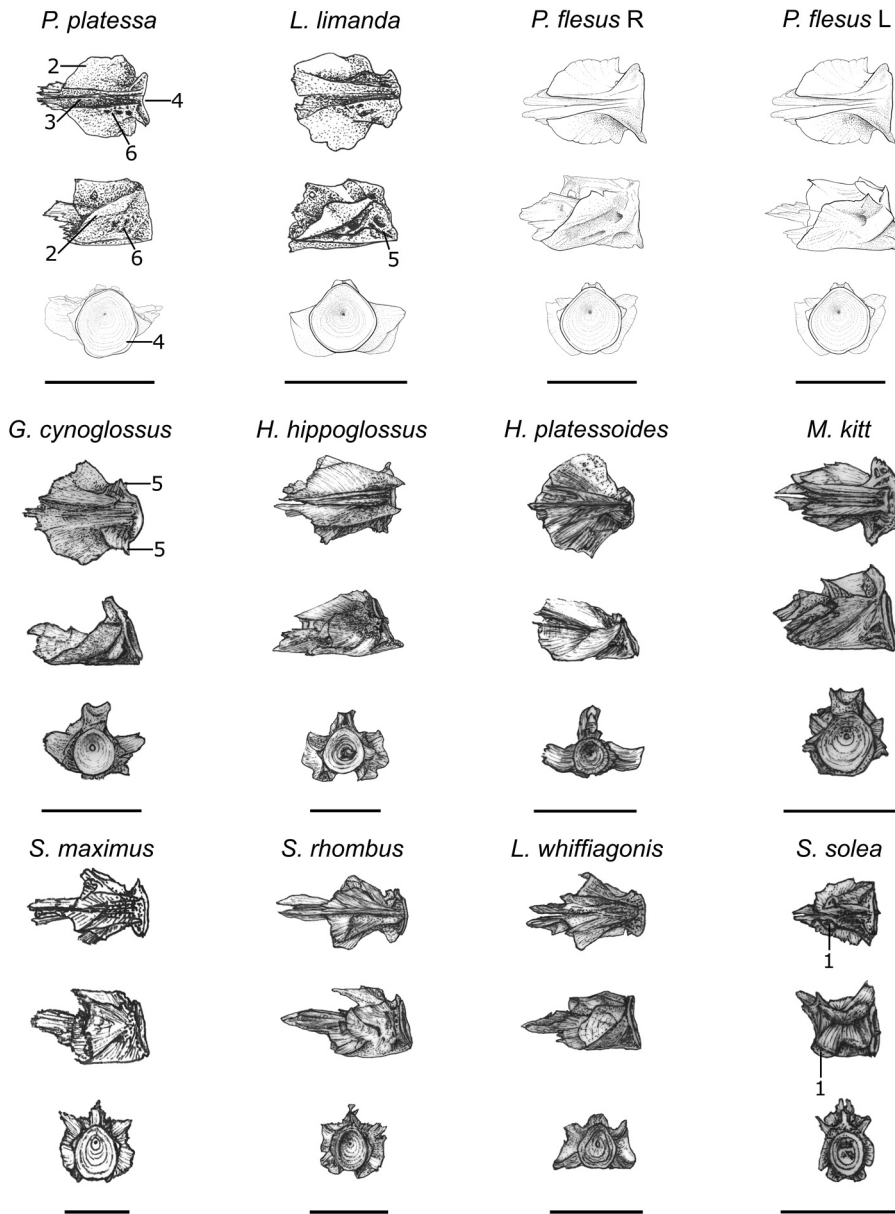


Figure 19. – Ventral (top), sinistral lateral (middle), and posterior (bottom) view of the basioccipital of flatfish. The black bar under each species represents 1 cm.

tessoides. The cristae exoccipitales (2) protrude ventrally beyond the corpus (6) of the basioccipital in *H. platessoides*. *Pleuronectes platessa* and *P. flesus* show only minor differences and cannot be distinguished with certainty. Differentiation between right- and left-eyed *P. flesus* is also impossible.

Cleithrum

The lateral and ventral views of the left cleithrum are given in Fig. 20. Additionally, the medial view can be found in the Supplementary Information together with the detailed analysis for every species (Table S21; Fig. S14). This bone allows identification to all species. The cleithrum of *S. solea* lacks a distinct crista articularis (1) and has a spina dorsalis (2) with two tips. In medial view, a well-defined costa (3),

or rib, separates the lamina anterior (4) and posterior (5) in Scopthalmidae, which is absent in Pleuronectidae. In *L. whiffiagonis*, the lamina anterior (4) is much more developed and the posterior part of the lamina dorsalis (6) is less ossified (more translucent) in very large specimens than in *Scophthalmus* spp. The depression (7) in the lamina dorsalis (6) is almost invisible or very shallow in *S. rhombus*, while clearly outlined in *S. maximus*. This characteristic needs to be checked on reference bones of the same size. *Hippoglossoides platessoides* is characterised by the very weakly developed crista articularis (1) and the rather strong bend (8) in the middle. The cleithrum of *M. kitt* has a very broad appearance and has a broad and dorsally flattened angulus anterior (9). *Hippoglossus hippoglossus*, *G. cynoglossus*, *L. limanda*, and right-eyed *P. flesus* can be

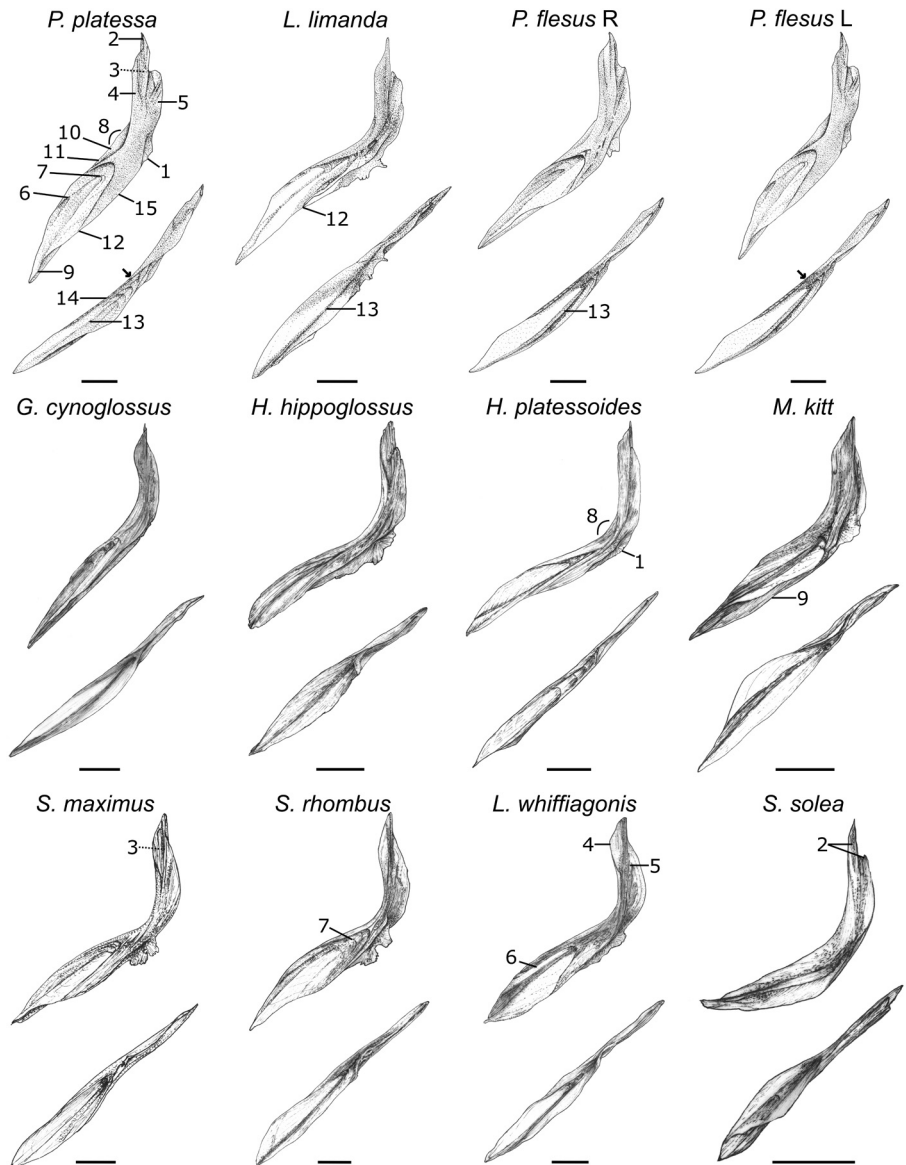


Figure 20. – Lateral (left) and ventral (right) view of the left cleithrum of flatfish. The black bar under each species represents 1 cm.

distinguished by their lack of a clear depression (10) on the crista interna (11), which is deep and broad in *P. platessa* and left-eyed *P. flesus*. *Hippoglossus hippoglossus* has a shallow depression (7) on the lamina dorsalis (6) and a typical striated lateral surface. *Limanda limanda* has a strong bend (8) midway along the bone, a translucent angulus ventralis (12) that does not reach the tip of the angulus anterior (9), and a ventral groove (13) that is positioned centrally in the angulus anterior (9) from a ventral view. Right-eyed *P. flesus* has a less pronounced bend and a ventral groove (13) that is positioned medially in the angulus anterior (9) from a ventral view. *Glyptocephalus cynoglossus* also has a less pronounced bend (8) midway along the bone, but a ventral groove (13) that is positioned centrally in the angulus ante-

rior (9) from a ventral view. *Pleuronectes platessa* and left-eyed *P. flesus* can be distinguished by the length of a shallow groove (14) in the crista externa (15). However, this groove is only clearly visible using a magnification instrument. This groove (14) is proportionally wider in *P. platessa* and ends higher up (see arrow) the bone near the crista articularis (1). In larger cleithra, this groove is often doubled in *P. platessa*, meaning that two small grooves lay parallel next to each other. The groove (14) is smaller and always single in *P. flesus* and has a clear stop lower on the bone (see arrow).

The lateral and caudal views of the right cleithrum are given in Fig. 21. Additionally, the medial view can be found in the Supplementary Information together with the detailed analysis for every species (Table S22; Fig. S15). This bone

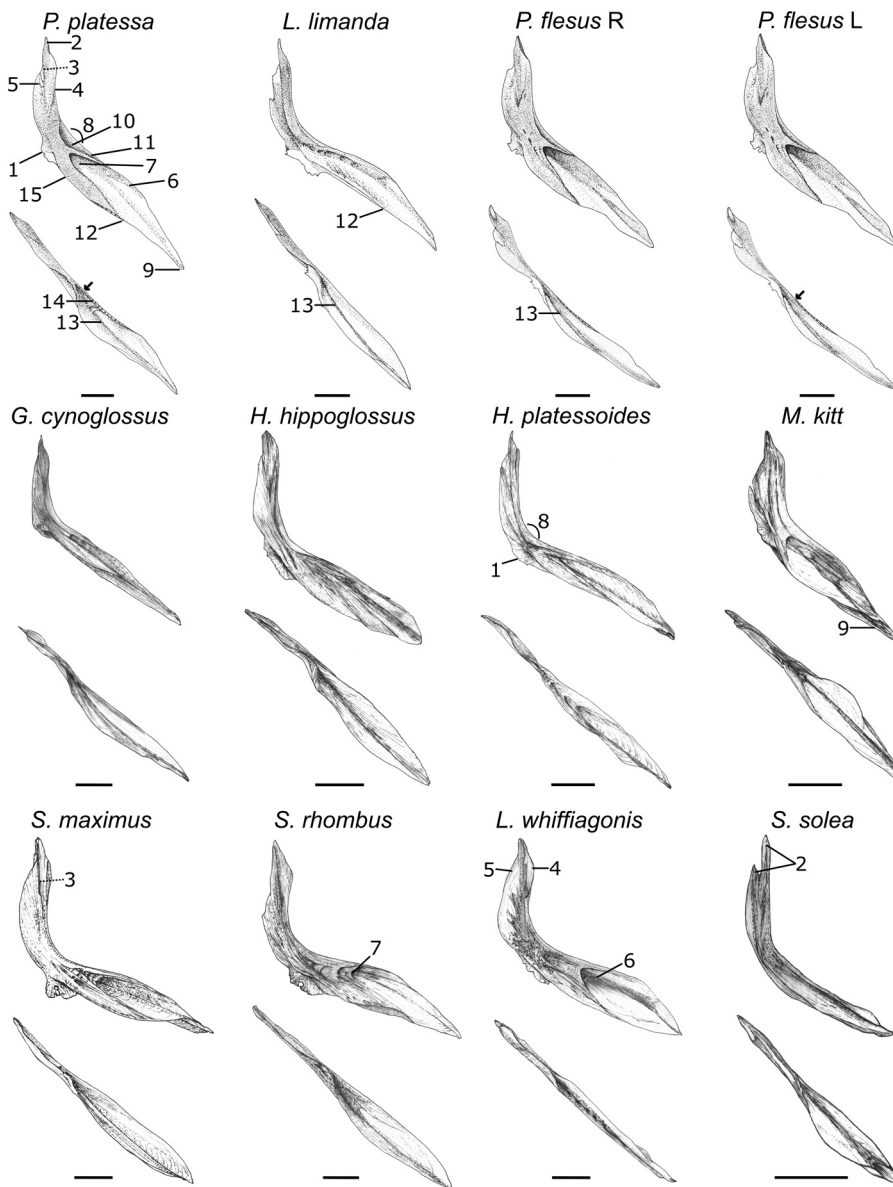


Figure 21. – Lateral (right) and ventral (left) view of the right cleithrum of flatfish. The black bar under each species represents 1 cm.

allows identification to all species. The criteria described for the left cleithrum are similar for the right in all species. Distinction between right- and left-eyed *P. flesus* is however not possible because the difference in the shallow depression (10) is far less pronounced in the cleithrum of right-eyed *P. flesus*.

Os anale

The lateral view of the os anale is given in Fig. 22. Additional detailed analysis for the os anale can be found in the Supplementary Information (Table S23). This bone allows identification to all species. The os anale of *S. solea* is only barely curved and bears just a simple outcrop, marking the ventral articulation (1) for the first anal pterygophore.

Microstomus kitt is the only species that has a dorsally flattened transition (2) between the anterior and the posterior parts. In Scopthalmidae, the articulation (1) has the shape of a long open tube on which a long anterior processus (4) is dorsally implanted. There are lateral indentations (5) of the angulus anterior (6) in *Scopthalmus* spp., which are absent in *L. whiffiagonis*. *Scopthalmus maximus* shows a high dorsal crista (7) compared to *S. rhombus*. The angulus anterior (6) shows two bumps in *L. limanda* in dorsal view. There is a ridge (8) along the angulus anterior in lateral view in *H. hippoglossus*, but a sulcus (9) is lacking in this species. This sulcus (9) is present in the other Pleuronectidae. Both lateral wings (10) break up almost directly posteriorly of the ventral articulation (1) and become rapidly broader than the

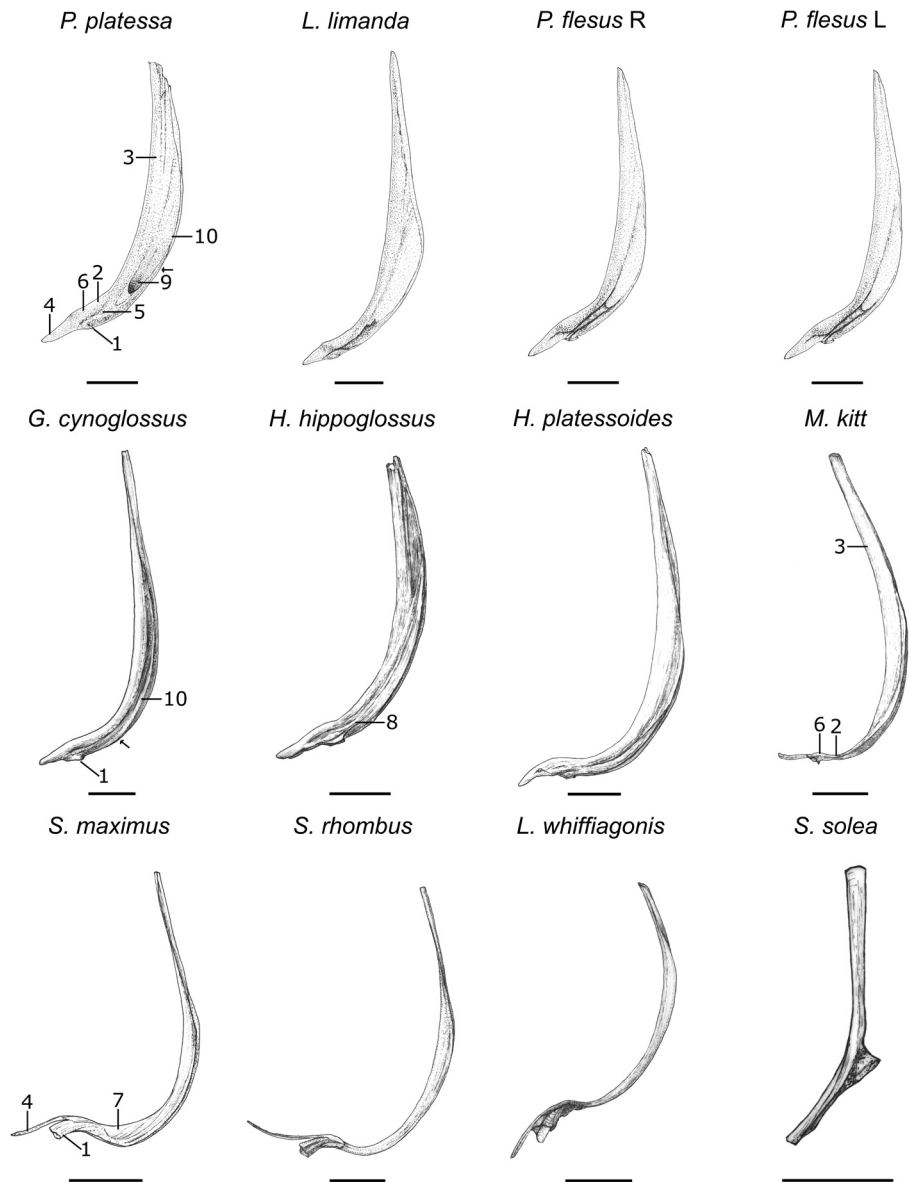


Figure 22. – Sinistral lateral view of the os anale of flatfish. The black bar under each species represents 1 cm.

anterior edge of the angulus superior (3) in *G. cynoglossus*. The sulcus (9) is clear and wide in *P. platessa* and *P. flesus*, while it is slender and less clear in *H. platessoides*. The angulus anterior (6) shows a bulbous part in dorsal view, which is typical for *P. flesus*, however this is not always 100% clear. Proportionally, the width seen halfway along the bone is always larger in *P. flesus* compared to *P. platessa*. Additionally, *P. platessa* can have relatively longer lateral indentations (5) while these are shorter in *P. flesus*. Differentiation between right-eyed and left-eyed *P. flesus* is not possible.

Quadrate

The lateral and anterior views of the left quadrate are given in Fig. 23. Additionally, the medial view can be found in the Supplementary Information together with the detailed analysis for every species (Table S24; Fig. S16). This bone allows identification to all families and most species. The margo ectopterygoidalis (1) and margo preopercularis (2) have an almost equal length in *S. solea* and the processus preopercularis (3) is very short and not protruding much. *Microstomus kitt* is characterised by the combination of a short margo superior (4), very large condyli (5), and a very broad margo ectopterygoidalis (1) in anterior view. In *Scophthalmus* spp. the margo ectopterygoidalis (1) exceeds two thirds the length of the margo preopercularis (2) and the processus preopercularis (3) is small and sharply delineated on both lateral and medial sides. There are no clear differences between *S. maximus* and *S. rhombus*, except that *S. maximus* has a proportionally more striated lateral surface of the crista (6), extending to the margo superior (4). In *S. rhombus* this striation is only visible in the lower part of the bone. This characteristic is not clear in the quadrate of fishes of less than 25–30 cm SL. *Lepidorhombus whiffiagonis* is eas-

ily distinguishable by its slender appearance in anterior view and small condyli (5). The margo preopercularis (2) is only slightly longer than the margo ectopterygoidalis (1) in *L. limanda*, *H. hippoglossus*, and *H. platessoides*. In *H. hippoglossus* the incisura symplectici (7) between the margo superior (4) and the processus preopercularis (3) is as good as absent, while present in *H. platessoides* and *L. limanda*. In anterior view, *H. hippoglossus* is short and bulky, while *H. platessoides* is long and slender. *Limanda limanda* is characterised by having large condyli (5,8,9) visible in anterior view. The margo preopercularis (2) is about twice as long as the margo ectopterygoidalis (1) in *G. cynoglossus*, *P. flesus*, and *P. platessa*. The lateral condylus (8) is larger than the medial condylus (9) in *G. cynoglossus*. Left-eyed *P. flesus* is characterised by having condyli (5) that do not extend posteriorly from the margo preopercularis (2), which is visible in lateral view. In right-eyed *P. flesus* and *P. platessa*, the condyli (5) clearly extend posteriorly beyond the margo preopercularis (2) when viewed laterally. Both species cannot be distinguished from each other due to the large variation in the bone.

The lateral and anterior views of the right quadrate are given in Fig. 24. Additionally, the medial view can be found in the Supplementary Information together with the detailed analysis for every species (Table S25; Fig. S17). This bone allows identification to all families and some species. The margo ectopterygoidalis (1) and the margo preopercularis (2) are equal in length and short in *S. solea*, with a clear incisura simplectici (7). *Microstomus kitt* is characterised by the combination of a short margo superior (4), very large condyli (5) and a very broad margo ectopterygoidalis (1) in anterior view. In *Scophthalmus* spp. the margo ectopterygoidalis (1) exceeds two thirds the length of the margo preoper-

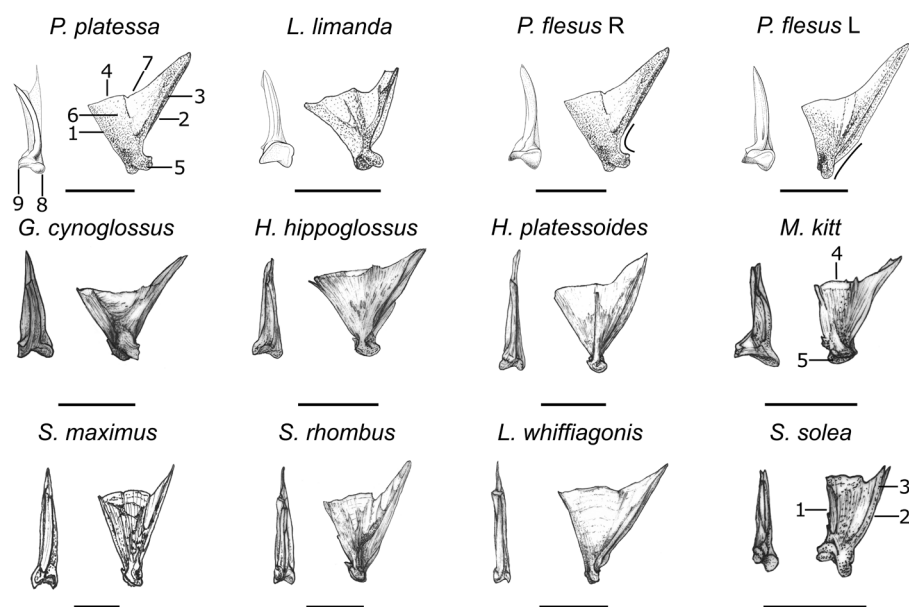


Figure 23. – Lateral (right) and anterior (left) view of the left quadrate of flatfish. The black bar under each species represents 1 cm.

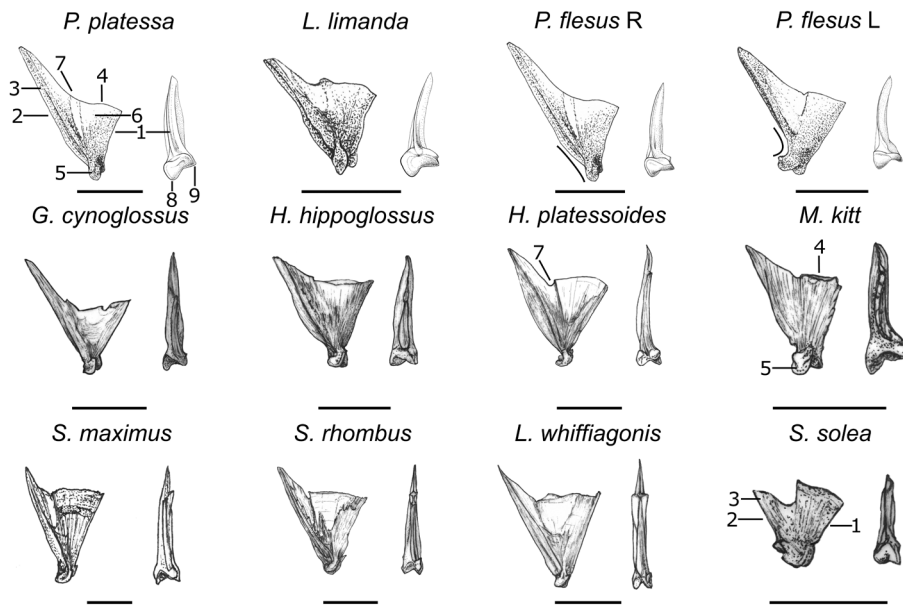


Figure 24. – Lateral (left) and anterior (right) view of the right quadrate of flatfish. The black bar under each species represents 1 cm.

cularis (2) and the processus preopercularis (3) is small and sharply delineated on both lateral and medial sides. There are no clear differences between *S. maximus* and *S. rhombus*, except that *S. maximus* has a proportionally more striated lateral surface of the crista (6), extending to the margo superior (4). In *S. rhombus* this striation is only visible in the lower part of the bone. This characteristic is not clear in the quadrate of fishes of less than 25–30 cm SL. *Lepidorhombus whiffiagonis* is easily distinguishable by its slender appearance in anterior view and small condyli (5). *Hippoglossoides platessoides* is characterised by having very small condyli (5) and the presence of a clear incisura simplectici (7). The margo ectopterygoidalis (1) is less than twice as long as the margo preopercularis (2) in *L. limanda* and *H. hippoglossus*, while it is twice as long as the margo preopercularis (2) in *P. platessa*, *P. flesus*, and *G. cynoglossus*. *Limanda limanda* is characterised by having a slight incisura simplectici (7), while *H. hippoglossus* has no incisura simplectici (7). The small condyli (5) typify *G. cynoglossus*. The condyli (5) of *P. flesus* and *P. platessa* are well developed. Left-eyed *P. flesus* has strong posteriorly protruding condyli (5) which forms a clear angle with the margo preopercularis (2) in lateral view, while these do not protrude in right-eyed *P. flesus* and *P. platessa*. Right-eyed *P. flesus* and *P. platessa* have too many overlapping criteria and cannot be distinguished from each other.

Ectopterygoid

The lateral view of the left ectopterygoid is given in Fig. 25. Additional detailed analysis can be found in the Supplementary Information (Table S26). This bone allows identification to all genera. Identification of bones of fish smaller than 15 cm SL into species is not feasible. Even with com-

plete bones of larger fish, characteristics are not always clear and great caution is advised. *Solea solea* can easily be distinguished by the robust and thick crus posterioris (1), the clear groove (2) between the medial and lateral ridge of this crus, and the dorsal extension of the angulus dorsalis (3). The crus posterioris (1) and anterioris (4) are stocky in *M. kitt*. The crus posterioris (1) and crus anterioris (4) are also shorter and bulkier in *G. cynoglossus*, compared to the other species. The fossa palatinum (5) is bigger and the angle (6) between the crura is greater in *G. cynoglossus* than in *M. kitt*. The crus posterioris (1) is only half the size of the crus anterioris (4) in *H. platessoides*, while the angulus dorsalis (3) is strongly reduced in this species. The three species of the Scopthalmidae are characterised by the fine and long crura (1,4) and the deep fossa palatinum (5) in the crus anterioris (4). Both crura (1,4) are thinner in *L. whiffiagonis* compared to those of both *Scopthalmus* spp. of the same size. No criteria were found for a reliable distinction between both *Scopthalmus* species. Left-eyed *P. flesus* can be identified from all species by the hook (7) at the base of the crus anterioris (4; not visible on illustration). The remaining species can be difficult to identify confidently, even when the ectopterygoid is complete, since many characteristics are prone to subjective interpretation. *Hippoglossus hippoglossus* has a crus anterioris (4) that is relatively longer than the crus posterioris (1). *Limanda limanda* is in general less ossified compared to *P. platessa* and right-eyed *P. flesus*. Both crura (1,4) are slightly broader and the fossa palatinum (5) runs deeper in *P. platessa* compared to right-eyed *P. flesus* and *L. limanda*.

The lateral view of the right ectopterygoid is given in Fig. 26. Additional detailed analysis can be found in the Supplementary Information (Table S27). This bone allows identification to all genera. Identification of bones of fish smaller

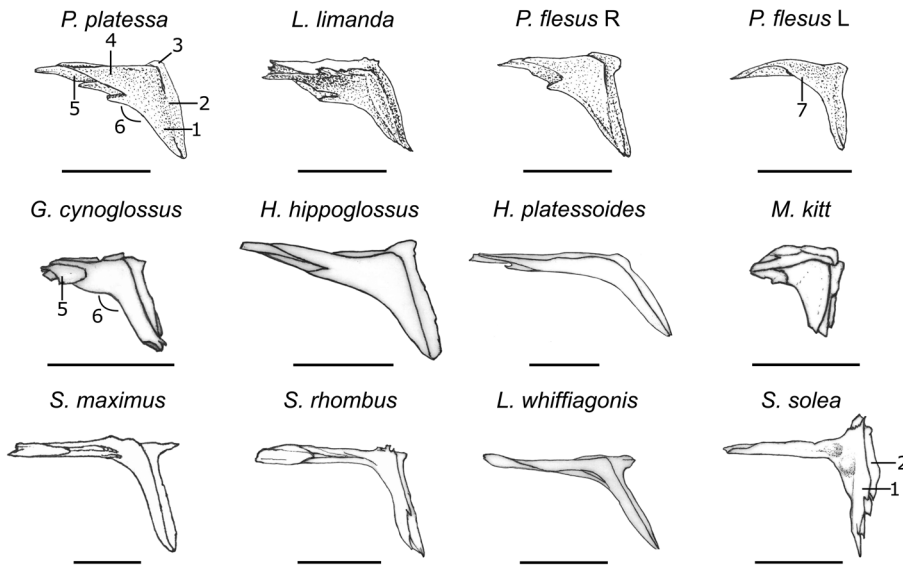


Figure 25. – Lateral view of the left ectopterygoid of flatfish. The black bar under each species represents 1 cm.

than 15 cm SL into species is not feasible. Even with complete bones of larger fish, characteristics are not always clear and great caution is advised. *Microstomus kitt* differs from all other species by the stocky and thick appearance and the strong reduction of both crura. *Solea solea* can easily be distinguished by the posterior extension (8) in the middle of the crus posterioris (1). The crus anterioris (4) in *G. cynoglossus* is very short and even less than half the length of the crus posterioris (1). Typical for the right ectopterygoid in the *Scophthalmidae* is the large angle (6) between the crura and the slender appearance. The crus anterioris (4) is only a bit longer than the crus posterioris (1) in *L. whiffiagonis*, while far longer in both *Scophthalmus* spp. No criteria were found for a reliable distinction between both *Scophthalmus* species. *Hippoglossoides platessoides* has long and slender crura (1 and

4) and resembles thus *Scophthalmidae*, but has a reduced angulus dorsalis (3). *Hippoglossus hippoglossus* differs by the lack of a clear fossa (5) and a thick appearance. The ectopterygoid of *P. platessa* and right-eyed *P. flesus* have a well-defined crus posterioris (4) separated from the crus anterioris (1), while the ectopterygoid of *L. limanda* and left-eyed *P. flesus* have a broad crus posterioris (1) and both crura seem to be indistinguishable from each other. *Pleuronectes platessa* shows a clear groove (9) between the crus posterioris (1) and anterioris (4), which is less deep in right-eyed *P. flesus*. The bone in *L. limanda* is far less ossified and the crura are thinner than in left-eyed *P. flesus*.

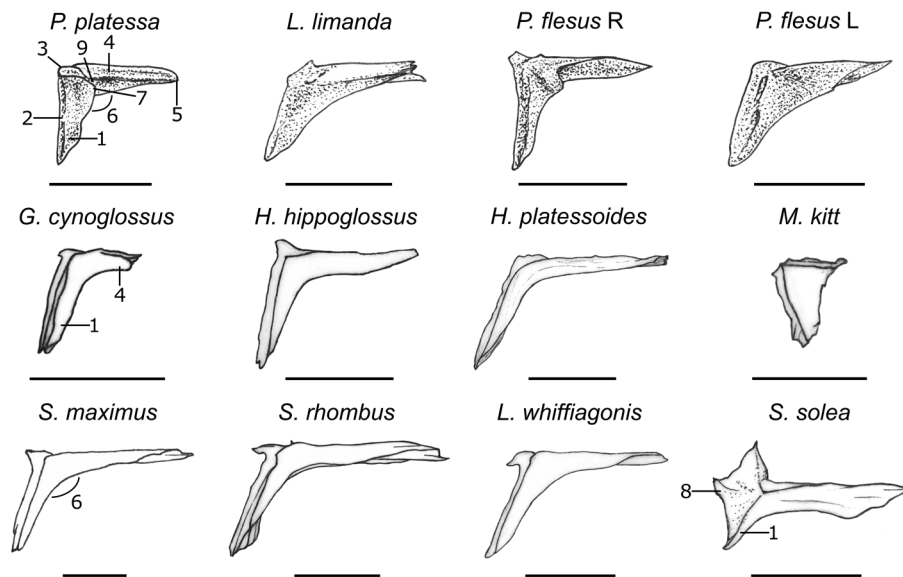


Figure 26. – Lateral view of the right ectopterygoid of flatfish. The black bar under each species represents 1 cm.

Preopercular

The lateral and medial views of the left preopercular are given in Fig. 27. Additional detailed analysis can be found in the Supplementary Information (Table S28). This bone allows identification to most species. *Glyptocephalus cynoglossus* is unique, showing four large orificia canalis lineae lateralis (1) in lateral view. These orificia canalis lineae lateralis (1) are rather small or absent in the other species. The preopercular is very thick and slender in *S. solea* and *M. kitt*. In *S. solea* the margo opercularis (2) bends smoothly into the margo interopercularis (3). In *M. kitt*, the transition between the margo opercularis (2) and the margo interopercularis (3) is sharp and makes a 90° turn. In Scophthalmidae, the crista hyomandibularis (4) is well aligned with the margo opercularis (2), running almost parallel, and the angu-

lus superior (5) is very slender. In Pleuronectidae, the margo hyomandibularis (4) and margo opercularis (2) are not parallel and the angulus superior (5) is rather broad. The angle (6) between the angulus superior (5) and angulus anterior (7) exceeds clearly 90° in *L. whiffiagonis*. This species also has a thinner bone in general than *Scophthalmus* spp. The base of the angulus anterior (7) is always smaller in width in *S. rhombus* compared with *S. maximus*. The lateral surface is proportionally always more striated in *S. maximus* than in *S. rhombus*. In *P. flesus* and *P. platessa* the angulus anterior (7) is about equal in length as the angulus superior (8), while clearly shorter in *H. hippoglossus*, *H. platessoides*, and *L. limanda*. *Hippoglossus hippoglossus* is characterised by the wide anterior part of the angulus anterior (7), and the striated lateral surface. *Limanda limanda* has few tiny ori-

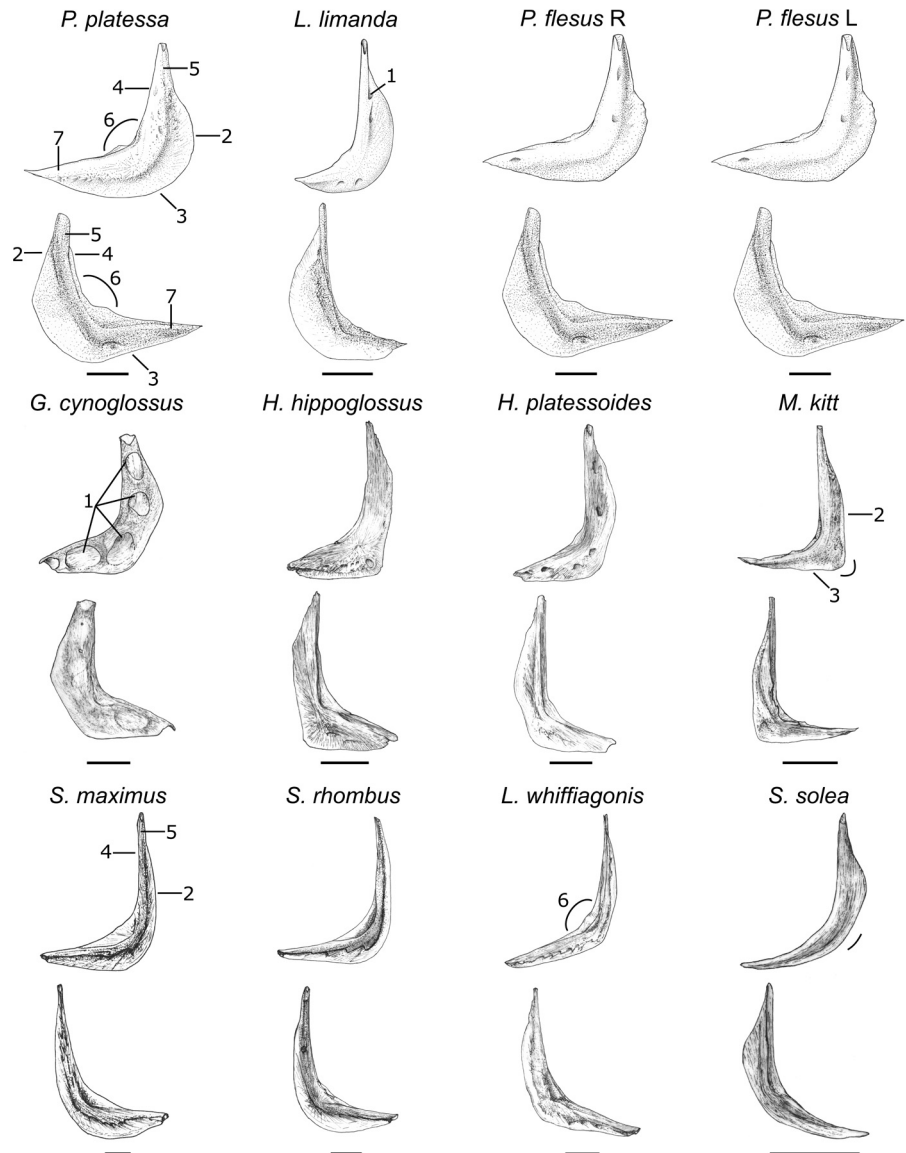


Figure 27. – Lateral (upper) and medial (bottom) view of the left preopercular of flatfish. The black bar under each species represents 1 cm.

ficia canalis lineae lateralis (1), compared to the clear orificia canalis lineae lateralis (1) in *H. platessoides*. *Limanda limanda* also has a broader preopercular compared to *H. platessoides*. No clear differences could be established to distinguish *P. platessa* from *P. flesus* nor between the right- and left-eyed forms of the latter.

The lateral and medial views of the right preopercular are given in Fig. 28. Additional detailed analysis can be found in the Supplementary Information (Table S29). This bone allows identification to most species. The criteria, described for the left preopercular are similar for the right in the following species: *S. solea*, *M. kitt*, *S. maximus*, *S. rhombus*, and *L. whiffiagonis*. The orificia canalis lineae lateralis (1) are larger in *G. cynoglossus* and *H. platessoides* than in the other species. *Glyptocephalus cynoglossus* has a concave margo interopercularis (3) and a more angular transition

between the margo opercularis (2) and the margo interopercularis (3), while *H. platessoides* has a straight margo interopercularis (3) and a more rounded transition. The L-shape of the preopercular in *H. hippoglossus* is less outspoken than in the left element, but this species is still far different from the other Pleuronectidae through the short angulus anterior (7) and the striated lateral surface. The angulus superior (5) is much longer in *L. limanda*, compared to *P. platessa* and *P. flesus*. No clear differences could be established to distinguish *P. platessa* from *P. flesus* nor between the right- and left-eyed form of the latter.

Interopercular

The medial view of the left interopercular is given in Fig. 29. Additionally, the medial view of the right interopercular can be found in the Supplementary Information

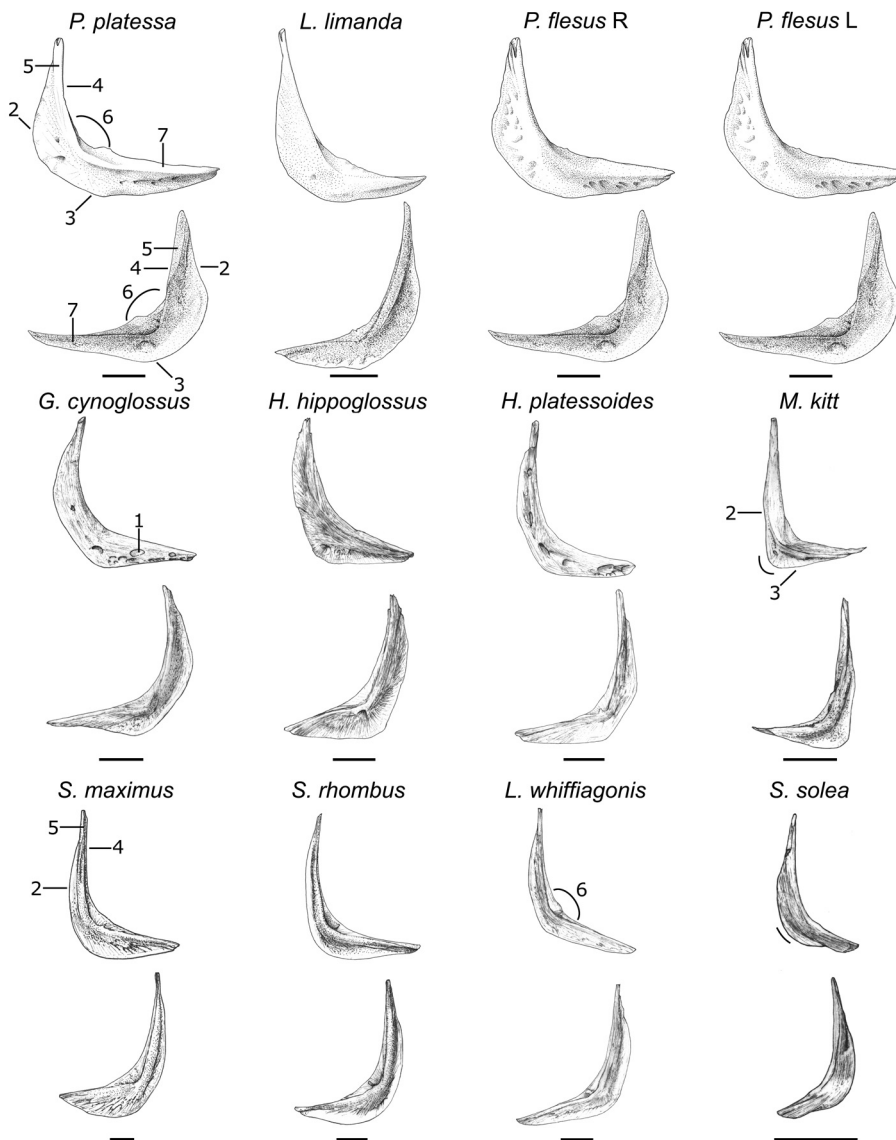


Figure 28. – Lateral (upper) and medial (bottom) view of the right preopercular of flatfish. The black bar under each species represents 1 cm.

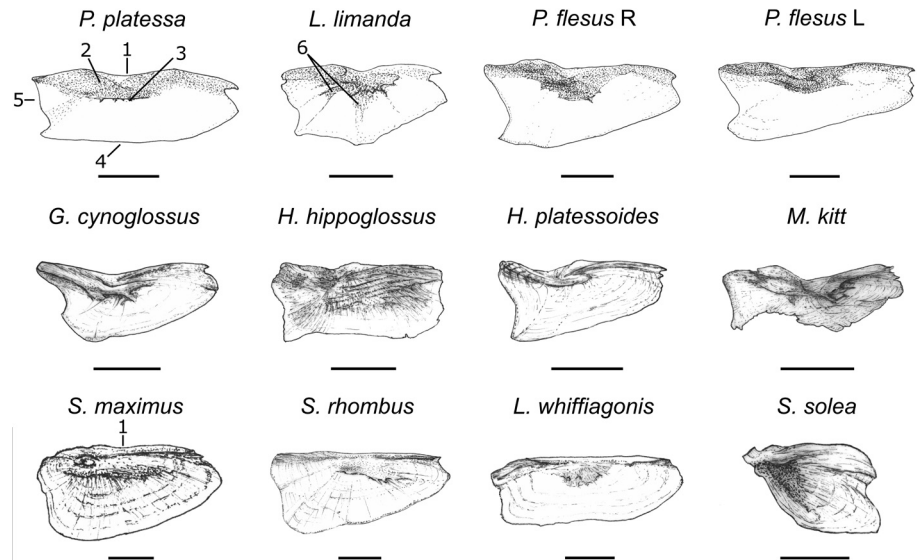


Figure 29. – Medial view of the left interopercular of flatfish. The black bar under each species represents 1 cm.

together with the detailed analysis for every species (Table S30; Fig. S18). Left and right interoperculars show the same diagnostic features per species. This bone allows identification to most species. *Solea solea* is the only species where the margo superior (1) is densely ossified and the general shape is totally different from the other species. A clear, straight rib (2) marks the margo superior (1) in the three Scophthalmidae species, while the margo superior (1) is curved and less ossified in Pleuronectidae. *Lepidorhombus whiffiagonis* differs from the *Scophthalmus* spp. by the rectangular, elongated shape with only a very limited amount of dense bone in the centre (3) that is not clearly delineated. Both *Scophthalmus* spp. can be differentiated if bones of the same size are compared. The interopercular has proportionally denser bone in the centre (3) and the ventral delineation of dense bone towards the margo inferior (4) is also stronger in *S. maximus*. These criteria should not be used in bones of fish smaller than 30 cm SL. The margo posterior (5) is deeply incised in *G. cynoglossus*. The ventral delineation of dense bone towards the margo inferior (4), reaching more than half of the height, distinguishes *H. hippoglossus* from the other species. This species also has a heavily striated lateral surface. The margo superior (1) has a dense and slightly protruding rib (2) in *M. kitt*, which is absent in the other species. The margo superior (1) of *H. platessoides* is only lightly ossified, in *L. limanda* this is more ossified with slight ventral extensions of ossification (6), and in *P. platessa* and *P. flesus* the margo superior (1) is clearly delineated. Both species are difficult to distinguish. Both *P. flesus* differ only slightly from each other and might be identified by the relative size and shape of the interopercular, for which a reference collection is advised. The left interopercular of right-eyed *P. flesus* is higher in proportion to the element in left-eyed *P. flesus*, and vice versa in the right interopercular.

Parasphenoid

The ventral and lateral views of the parasphenoid are given in Fig. 30. Additional detailed analysis can be found in the Supplementary Information (Table S31). This bone allows identification to all families and some species. The margo ventralis (1) is strongly concave in *S. solea* in lateral view. In Scophthalmidae and left-eyed *P. flesus* the facies articularis vomeris (2) curves to the left, while in the other Pleuronectidae it is curved to the right. The margo ventralis (1) has a strong curvature just above the facies articularis basioccipitalis (3) in *L. whiffiagonis* in ventral view, while it is only slightly bent in *Scophthalmus* spp., and straight in left-eyed *P. flesus*. The facies articularis basioccipitalis (3) is slender in left-eyed *P. flesus*, while broad in *Scophthalmus* spp. No criteria were found for a reliable distinction between both *Scophthalmus* species. The strongly convex margo ventralis (1) and a ridge (4) between the facies articularis basioccipitalis (3) and the lateral cristae (5) are typical for *M. kitt*. The appearance of *H. hippoglossus* is unique due to its broad and flattened facies articularis basioccipitalis (3) and vomeris (2). The anterior part of the margo ventralis (1) is curved ventrally (6) in *Glyptocephalus cynoglossus*, while in the other species this curvature is oriented dorsally or absent, being thus straight. The other species are difficult to distinguish.

Ceratohyal

The medial view of the left ceratohyal is given in Fig. 31. Additional detailed analysis can be found in the Supplementary Information (Table S32). Left and right ceratohyals have the same diagnostic features. This bone allows identification to most species. The terminology of Lepiksaar (1994) has been changed here. The margo ventralis (1) has a ridge-like structure (2) in *S. solea* and Pleuronectidae, while this struc-

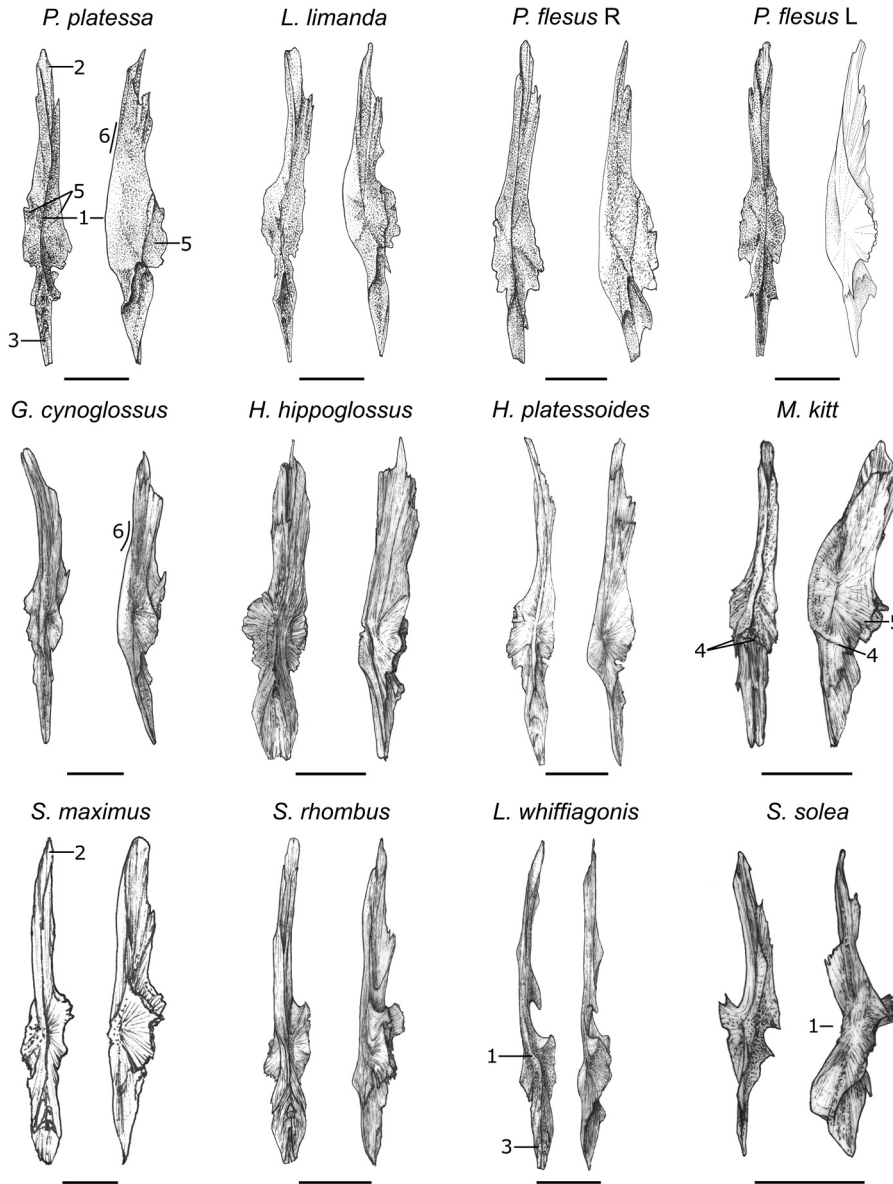


Figure 30. – Ventral (left) and sinistral lateral view (right) of the parasphenoid of flatfish. The black bar under each species represents 1 cm.

ture is absent in Scophthalmidae. *Solea solea* has a thick bulb (3) on the margo dorsalis (4). *Lepidorhombus whiffiagonis* has a slenderer appearance and is less robust than both *Scophthalmus* spp. No criteria were found for a reliable distinction between both *Scophthalmus* species. The ceratohyal of *H. platessoides* is very elongated. The margo synchondrosis (5) is less delineated and relatively large in *M. kitt*, which is distinct from the other species. The margo ventralis (1) is irregular, the ridge-like structure (2) is wide, and the margo dorsalis (4) is relatively high compared to the pedunculus ceratohyalis (6) in *H. hippoglossus*. The tip of the pedunculus ceratohyalis (6; *i.e.* processus hypohyalis ventralis 7) is broader than its base in *L. limanda* and *G. cynoglossus*, while it has the same width in *P. platessa* and *P. flesus*. The margo

dorsalis (4) starts near the tip of the pedunculus ceratohyalis (6) in *G. cynoglossus*, while far more near to the base in *L. limanda*, making the pedunculus ceratohyalis (6) visually shorter in *G. cynoglossus* than in *L. limanda*. There is no difference between *P. platessa* and *P. flesus*, nor between right-eyed and left-eyed *P. flesus*.

Epihyal

The lateral and medial views of the epihyal are given in Fig. 32. Additional detailed analysis can be found in the Supplementary Information (Table S33). This bone allows identification to only a few species. Only the left element is illustrated, as the left and right epihyal show the same diagnostic features. The apex epihyalis (1) is not individualised

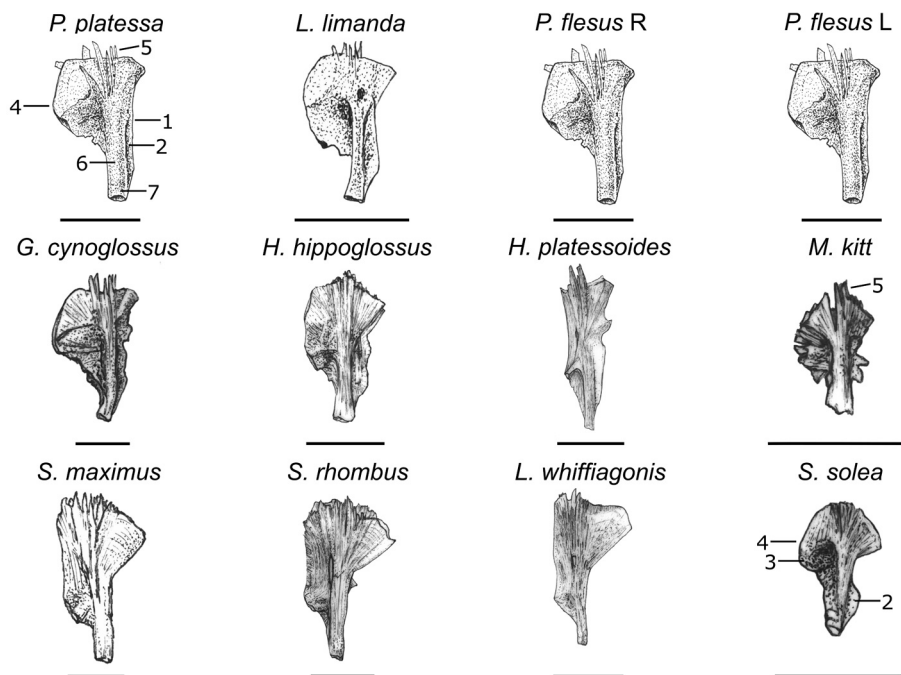


Figure 31. – Medial view of the left ceratohyal of flatfish. The black bar under each species represents 1 cm.

from the corpus (2) and widens immediately in *S. solea* and *M. kitt*. The margo synchrondrosus (3) of *S. solea* is wide, while slender in *M. kitt*. This bone is almost squarish in *S. solea* while irregular and rectangular in *M. kitt*. The epihyal has a clear triangular shape in both *Scophthalmus* spp. No criteria were found for a reliable distinction between both *Scophthalmus* species. In larger specimens of *S. rhombus*, there are ribs (4) below the apex epihyalis (1) in medial view. The margo ventralis (5) is long and the margo synchrondrosus (3) reaches till almost halfway the height of the epihyalis in *H. hippoglossus*, *H. platessoides*, and *L. whiffiagonis*. A thick rib (6) extends from the apex epihyalis (1) into the corpus (2) in lateral view in *L. whiffiagonis*. This rib (6) is slender in *H. platessoides* and extends into the margo synchrondrosus (3). The margo synchrondrosus (3) is very irregular in shape in *H. hippoglossus* and the heavy striated appearance is also characteristic. Any characteristics to distinguish *P. platessa*, *L. limanda*, *P. flesus*, and *G. cynoglossus* were not detected.

Upper hypohyal

The medial view of the left upper hypohyal is given in Fig. 33. Additional detailed analysis can be found in the Supplementary Information (Table S34). Left and right upper hypohyals show the same diagnostic features per species. This bone allows identification to all families and some species. This element is squarish in *S. solea* and *G. cynoglossus*, being about as long as high, although the margo hypohyalis inferior (1) is somewhat rounded. The foramen (2) lies close to the apex hypohyalis (3) and the corpus (4) is hollow on

both medial and lateral side in *G. cynoglossus*. In *S. solea* the foramen (2) is located centrally and the corpus (4) is not hollow. The upper hypohyals of *M. kitt* and *H. platessoides* are elongated. The margo hypohyalis inferior (1) in *M. kitt* is hollow in the middle, and the foramen (2) is only visible in medial view and doesn't pierce the bone. The margo posterior (5) shows a fine tube (6) in *H. platessoides*, and the foramen is positioned close to the apex hypohyalis (3). The apex hypohyalis (3) is as broad as the margo hypohyalis inferior (1) in the *Scophthalmidae*, while far slenderer in the remaining *Pleuronectidae*. The sulcus ceratohyalis (7) is bony in both *Scophthalmus*, while it is hollow in *Pleuronectidae* and *L. whiffiagonis*. *Scophthalmus rhombus* has a slightly more elongated upper hypohyal compared to *S. maximus*. Further differentiation within these two families is very difficult.

Infrapharyngeal V

The ventral and dorsal views of the left infrapharyngeal V are given in Fig. 34. Additional detailed analysis can be found in the Supplementary Information (Table S35). The left and right infrapharyngeal V show the same diagnostic features. This bone allows identification to all families and some species. The corpus (1) of the infrapharyngeal V of *P. platessa* and *P. flesus* is very broad and triangular in shape. All other flatfish have an elongated and slender infrapharyngeal V. *Pleuronectes platessa* has large teeth arranged in two neat rows, while *P. flesus* has fine teeth arranged in more than two, unclear rows. This can also be established with the tooth alveoli (2) even when the teeth are absent. No dis-

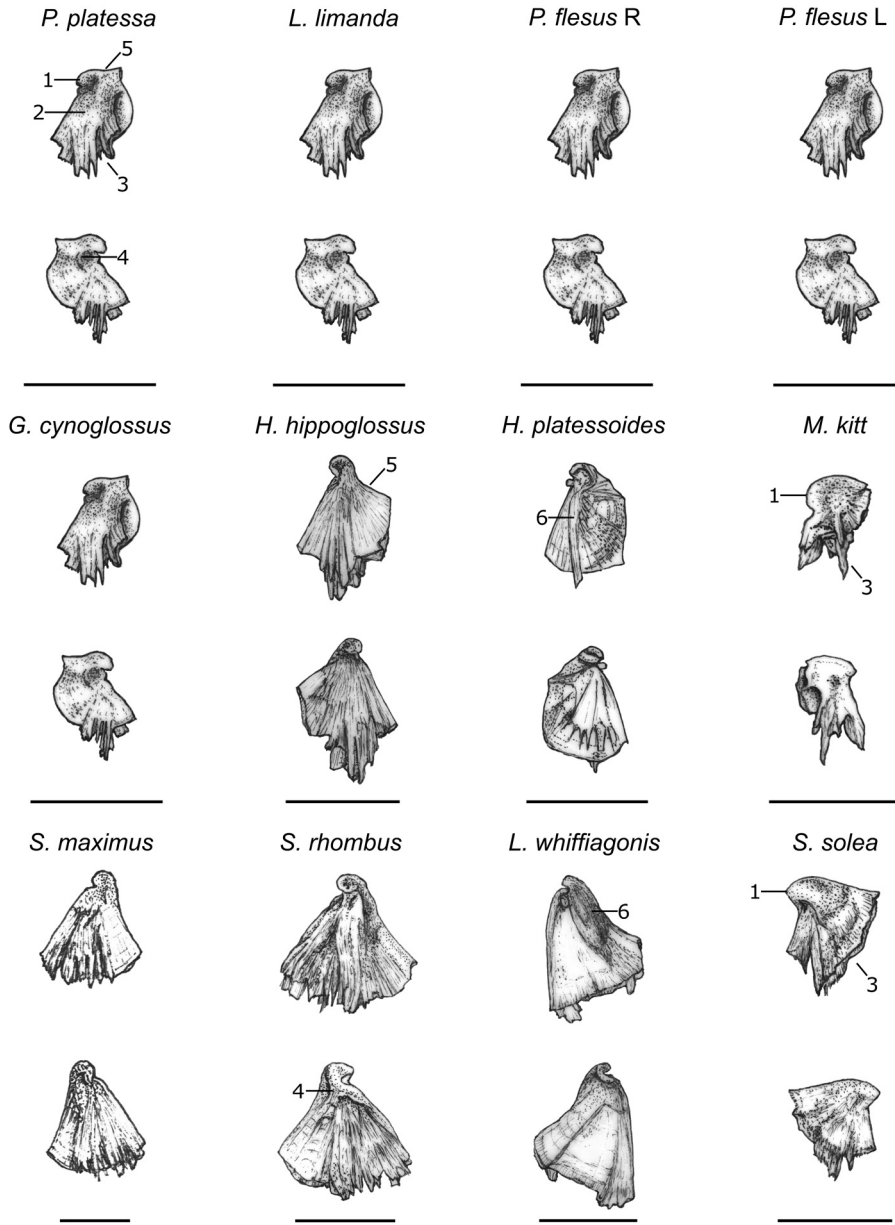


Figure 32. – Lateral (upper) and medial (bottom) view of the left epiphyal of flatfish. The black bar under each species represents 1 cm.

inction between right- and left-eyed *P. flesus* is possible. In Scophthalmidae and *S. solea*, the tooth surface (3) is broader than the corpus (1), while it is smaller in Pleuronectidae. All Scophthalmidae and *S. solea* have teeth rows, which are not neatly arranged and bear numerous minute teeth, while in Pleuronectidae there are only a few clear rows with larger teeth. The margo ventralis (4) is straight in both *Scophthalmus* spp., which are impossible to distinguish from each other. *Lepidorhombus whiffiagonis* shows only a curved part in the middle of the margo ventralis (4), while *S. solea* has a pharyngeal that is strongly curved over the whole length. The remaining Pleuronectidae are more difficult to distinguish from each other. The corpus (1) in *L. limanda*, *G. cynoglos-*

sus, and *M. kitt* is short, while in *H. hippoglossus* and *H. platessoides* it is elongated. In *M. kitt*, the margo ventralis (4) is very thin and angular, while strongly curved in *L. limanda* and *G. cynoglossus*. The tooth alveoli (2) in *G. cynoglossus* are often very regularly aligned in two rows while these are usually irregular in two (in fish up to ca. 25 cm SL) or three unclear rows in *L. limanda*. The tooth sockets (2) of the inner (5) and outer row (6) from *H. platessoides* differ clearly in size while this difference is minimal in *H. hippoglossus* (second row not visible on illustration).

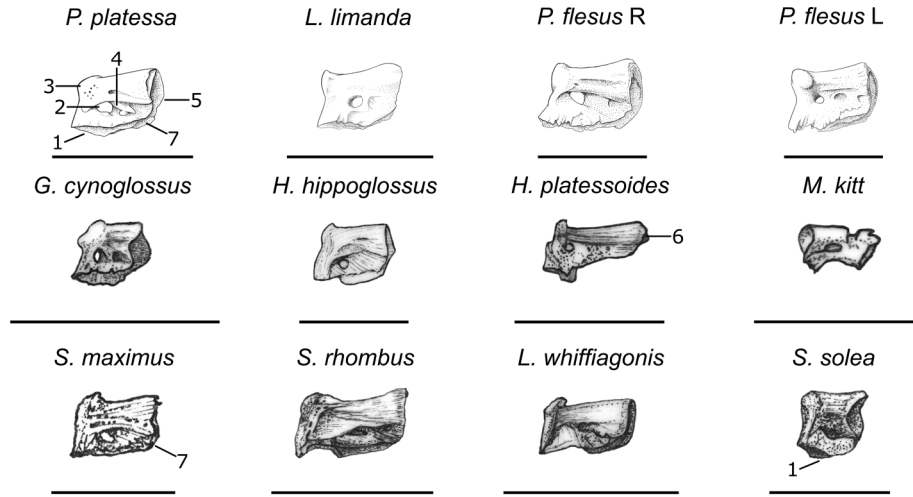


Figure 33. – Medial view of the left upper hypohyal of flatfish. The black bar under each species represents 1 cm.

First caudal vertebra

The anterior and sinistral lateral views of the first caudal vertebra are given in Fig. 35. Additional detailed analysis can be found in the Supplementary Information (Table S36). This bone allows identification to some species. This vertebra is unique in shape by the very broad ventral haemapophyses (1) which form the haemal arch (2) in Pleuronectidae and Scophthalmidae. The slender haemal arch (2) and the strongly anteriorly curved neural arch (3) typify *S. solea*. The thick lateral rib (4) is clearly delineated in this species. Pleuronectidae and *L. whiffiagonis* have a pattern of separate ribs (4) on the lateral side (5). In contrast, the lateral ribs (4) are more interwoven with pores in both *Scophthalmus* species, which cannot be distinguished from each other. *Lepidorhombus whiffiagonis* is characterised by a thick double or triple rib (4) separated by deep fossae (6). There is

no rib (4) in *H. hippoglossus* and the lateral surface (5) is smooth in smaller specimens up to 60 cm SL, while in larger specimens, the lateral surface is finely striated. The processus transversus (7) is attached on the corpus (8) of the vertebrae in *G. cynoglossus* in anterior view. In all other Pleuronectidae, the processus transversus (7) is fused with the ventral haemapophyses of the haemal arch (1). There is a large intra-species variation in the remaining species, which makes identification unreliable.

Elements which do not differentiate families or species

Some other elements frequently found in archaeological contexts were also compared, but no well-defined distinguishing criteria were found to identify flatfish species. For a few specific cases, such as opercular, supracleithrum, basipterygium, lower hypohyal, pharyngeal II, III, and IV,

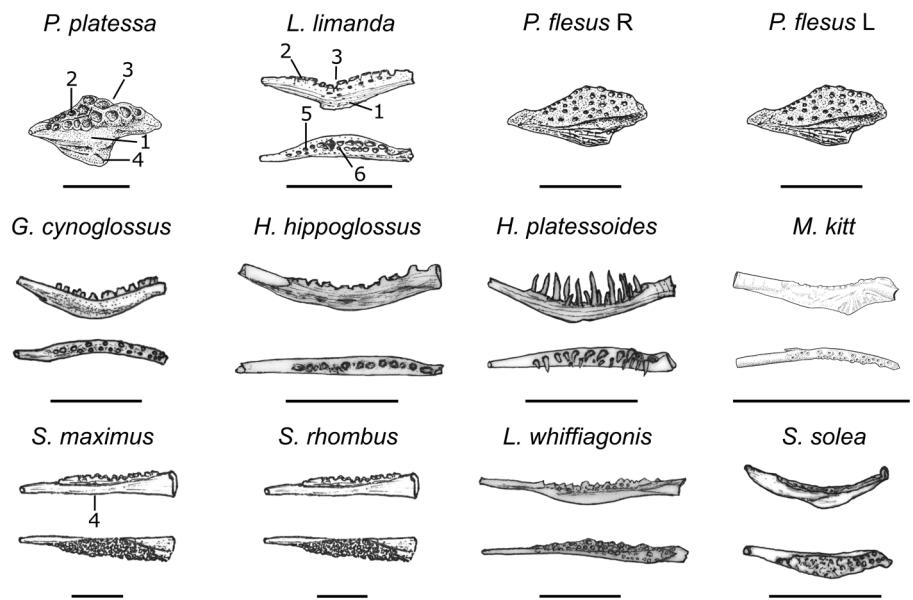


Figure 34. – Sinistral lateral (upper) and dorsal view (bottom) of the left infrapharyngeal V of flatfish. The black bar under each species represents 1 cm.

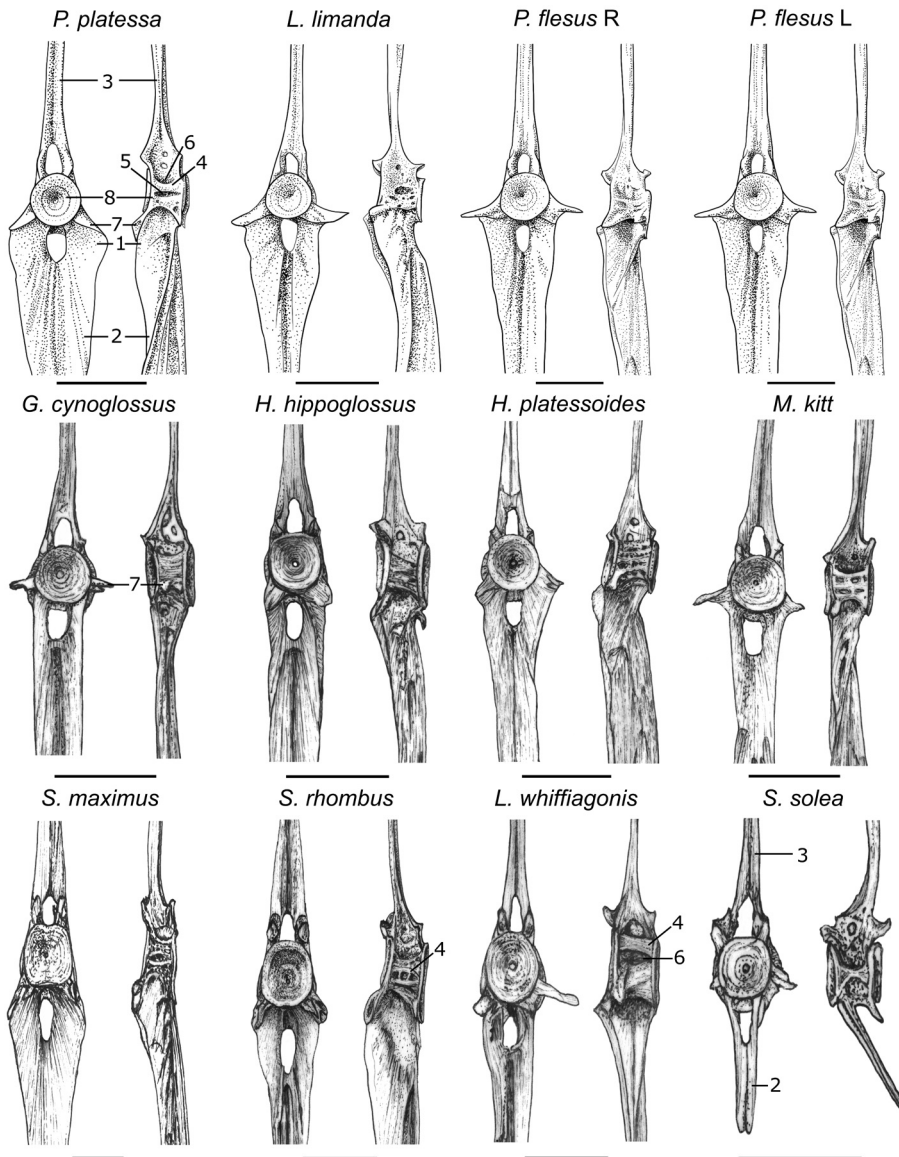


Figure 35. – Anterior (left) and sinistral lateral view (right) of the first caudal vertebra of flatfish. The black bar under each species represents 1 cm.

coracoid, basihyal, and the ultimate vertebra a species can occasionally be distinguished (see Supplementary Information, Tables S37-46).

DISCUSSION

Individual skeletal elements can be used to distinguish most of the Pleuronectiformes species from the North Sea. We studied 34 different elements. The first ten of these described in the Results, show characteristics that can identify all genera and are also easy and practical to use due to clear and objective osteological differences between all species. Fourteen other elements distinguish most of the genera, but demand also more skill and experience. The remaining

ten elements analysed are considered unreliable for species identification, allowing only identification to family level and of a few species. Compared with previous osteological studies, we provided many additional diagnostic criteria and a clear overview containing multiple families and species of flatfish found in the North Sea. Eight skeletal elements from this study had not been analysed in published studies before: metapterygium, epihyal, upper and lower hypohyal, operculum, basiptyergium, coracoid, and basihyal. Of these, the metapterygium can be used to identify most species. Two other elements, epihyal and upper hypohyal, can provide some taxonomic information. For some species, many other elements were included for the first time in an osteological comparative study.

Morphologically, flatfish split up in two main groups:

left-eyed fishes, such as Scophthalmidae and left-eyed *P. flesus*, and right-eyed, such as most Pleuronectidae and Soleidae. The two groups can easily be distinguished due to the asymmetry present in many bones. This makes family-level identification and distinction of left-eyed *P. flesus* quite straightforward in many bones. In addition to Wouters *et al.* (2007), some new diagnostic criteria were found, allowing further distinction between *P. platessa* and right-eyed *P. flesus*. This is the case for the left maxilla, the hyomandibula, and the vomer. In this study, additional criteria were described to distinguish right-eyed from left-eyed *P. flesus* using the cleithrum and the interopercular. However, none of these are easy to use and can show overlapping characteristics, making identification only possible in exceptional cases. No additional criteria were found besides those reported by Wouters *et al.* (2007) to improve the identification of *P. platessa* and *P. flesus* using the quadrate, preopercular, ceratohyal, supracleithrum, and the first caudal vertebra. The two species remain undistinguishable in these elements. The posterior part of the parasphenoid, which contained the diagnostic features according to Wouters *et al.* (2007), however, was found to be too variable in shape and too prone to subjective interpretation to be used for species identification. As noticed by Wouters *et al.* (2007), *P. platessa* and *P. flesus* of less than 20-25 cm SL show less pronounced diagnostic criteria, making it more difficult to identify juvenile fish. This issue seemed to be less relevant for the other species in this study. The remaining Pleuronectidae are generally easily distinguished with most elements. Remarkably, *M. kitt*, which is currently classified as a Pleuronectidae and genetically falls within the Pleuronectidae clade (Vinnikov *et al.*, 2018; Fricke *et al.*, 2024), shows many aberrant morphological characteristics. *Lepidorhombus whiffiagonis* distinguishes rather well from *Scophthalmus* species. *Scophthalmus maximus* and *S. rhombus* are very similar in many elements, which undermines species identification. Only seven elements can be used to confidently distinguish these congeners: articular, vomer, first vertebra, metapterygium, cleithrum, os anale, and upper hypohyal. Other elements can be difficult to use or show too many overlapping characters, which makes it impossible to distinguish these species. *Solea solea* is easily recognisable as a separate species due to clear morphological differences in its skeletal elements. However, due to the presence of other Soleidae species in the North Sea, caution is still advised. *Pegusa lascaris* differs from *S. solea* in minor but clear details (pers. obs.). If characteristics are not matching well with the descriptions of *S. solea* in this study, consultation of a reference collection is necessary, especially when dealing with bones from very small specimens. Further, it was also noticed that *S. solea* with the same standard length as a Pleuronectidae species has much smaller bones. This could potentially lead to a recovery bias of archaeological samples, with *S. solea* being less frequent-

ly found and reported because of their osteological features (*e.g.*, Struever, 1968; Von Endt and Ortner, 1984; Shaffer and Sanchez, 1994; Stahl, 1996; Smith *et al.*, 2007).

Not all described elements will be recovered equally either in archaeological contexts. Some are much smaller than others, or less sturdy. The metapterygium, for example, is very thin and can easily be broken down by biological and chemical degradation in the soil (Von Endt and Ortner, 1984; Smith *et al.*, 2007). Also, certain structures on other bones, such as cristae and thin processus and anguli, can become too degraded or broken to be used for identification, while they might otherwise be of great use (*e.g.*, preopercular, interopercular, quadrate, hyomandibula). For some elements, the described diagnostic features are prone to subjective interpretations or differences in interpretation between analysts. For example, the criteria to distinguish the parasphenoid and the use of the groove of the crista externa on the cleithrum between *P. platessa* and *P. flesus* according to Wouters *et al.* (2007), were not clear to the first author. Some subjective interpretation will always be present in any osteological key used for identification. The description of the morphology of the elements is in itself generalised and does not always reflect the possible variation. The use of a good reference collection to compare bones with, is an indispensable tool for zooarchaeological analyses.

The selection of species means that this study doesn't cover the complete species spectrum present in the North Sea. Small osteological material can contain bones of species like *P. lascaris* (Soleidae), *B. luteum* (Soleidae), *M. variegatus* (Soleidae), *Zeugopterus* sp. (Scophthalmidae) and *A. laterna* (Bothidae), the smaller flatfish species which are present in the North Sea. Fortunately, the elements of these species have the typical characteristics of the family level and are very distinctive from the species within the family. In case elements differ strongly from the species described here, it is advised to check these other species too using a reference collection.

The majority of the identified Pleuronectiformes from archaeological sites belong to the species *Pleuronectes platessa* and *Platichthys flesus*. The other species are only rarely reported from archaeological sites (*e.g.*, Nicholson, 2009; Cerón-Carrasco, 2013; Harland *et al.*, 2016). It is not clear if this phenomenon is only due to difficulties identifying the species caused by limited availability of identification guides and reference collections of these species, or if this genuinely reflects past fisheries practices. Other techniques, such as collagen peptide mass fingerprinting (Dierickx *et al.*, 2022) or DNA (*e.g.*, Espiñeira *et al.*, 2008), can close the gaps when visual identifications of flatfish remains fail.

CONCLUSION

Archaeological studies of fish remains from sites around the North Sea are still hindered by the low identification success rate of flatfish bones. With these additional diagnostic criteria for bone identification of commercially interesting species from this area, better insight into the species composition of archaeological sites is made possible. By distinguishing species with different life histories, ecologies and socio-economic values, this tool can improve the general understanding of flatfish consumption through time, adding some insight to questions such as how and where they were fished and potentially traded, and whether species preferences were linked to social status. The indications provided of which elements are easy to analyse or not, provide some directions for the novice in this kind of bone research.

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REFERENCES

- Barrett, J. H., Locker, A. M., & Roberts, C. M. (2004). The origins of intensive marine fishing in medieval Europe: The English evidence. *Proceedings of the Royal Society B Biological Sciences*, 271(1556), 2417-2421. <https://doi.org/10.1098/rspb.2004.2885>
- Brinkhuizen, D. C. (1979). Preliminary notes on fish remains from archaeological sites in the Netherlands. *Palaeohistoria*, 21, 84-90.
- Bruno, D. W., & Fraser, C. O. (1988). A case of reversal in the common dab, *Limanda limanda* (L.). *Journal of Fish Biology*, 32(3), 483-484. <https://doi.org/10.1111/j.1095-8649.1988.tb05384.x>
- Cerón-Carrasco, R. (2013). *The fish remains from the excavations at Castle Hill, Banff*. Unpublished report for Headland Archaeology Ltd, NMRS.
- Chanet, B. (2003). Interrelationships of scophthalmid fishes (Pleuronectiformes: Scophthalmidae). *Cybiuim*, 27(4), 275-286. <https://doi.org/10.26028/cybiuim/2004-274-005>
- Clavel, B. (1997). Les restes osseux animaux du Moyen Âge découverts Place de l'Hôtel de Ville à Abbeville (Somme). *Revue Archéologique de Picardie*, 3-4, 193-205. <http://dx.doi.org/10.3406/pica.1997.2258>
- Cooper, J. A., & Chapleau, F. (1998). Monophyly and intrarelationships of the family Pleuronectidae (Pleuronectiformes), with a revised classification. *Fishery Bulletin*, 96(4), 686-726.
- Cunningham, J. T. (1907). A peculiarly abnormal specimen of the Turbot. *Journal of the Marine Biological Association of the United Kingdom*, 8(1), 44-46. <https://doi.org/10.1017/S0025315400043733>
- Díaz de Astarloa, J. (2005). Osteología craneal comparada de tres especies de lenguado del género *Paralichthys* (Pleuronectiformes, Paralichthyidae) del Atlántico suroccidental. *Revista Chilena de Historia Natural*, 78(3), 343-391. <http://dx.doi.org/10.4067/S0716-078X2005000300002>
- Dierickx, K., Presslee, S., Hagan, R., Oueslati, T., Harland, J., Orton, D., Alexander, M., Hendy, J., & Harvey, V. (2022). Peptide mass fingerprinting of preserved collagen in archaeological fish bones for the identification of flatfish in European waters. *Royal Society Open Science*, 9(7), 220149. <https://doi.org/10.1098/rsos.220149>
- Enghoff, I. B. (1986). Freshwater fishing from a sea-coast settlement – the Ertebølle locus classicus revisited. *Journal of Danish Archaeology*, 5(1), 62-76. <https://doi.org/10.1080/0108464X.1986.10589958>
- Enghoff, I. B. (1989). Fishing from the Stone Age settlement Norsminde. *Journal of Danish Archaeology*, 8(1), 41-50. <https://doi.org/10.1080/0108464X.1989.10590018>
- Enghoff, I. B. (1994). Fishing from medieval Holbaek/Denmark, with notes to reversed *Platichthys flesus*. *Offa*, 51, 299-302.
- Enghoff, I. B. (1999). Fishing in the Baltic Region from the 5th century BC to the 16th century AD: Evidence from fish bones. *Archaeofauna*, 8, 41-85.
- Ervynck, A., & Van Neer, W. (1992). De voedselvoorziening in de Sint-Salvatorsabdij te Ename (stad Oudenaarde, prov. Oost-Vlaanderen) I. Beenderen onder een keukenvloer (1450-1550 AD) [The food supply in Saint Salvator's Abbey at Ename (town of Oudenaarde, prov. East Flanders) I. Bones under a kitchen floor (1450-1550 AD)]. *Archeologie in Vlaanderen*, 2, 419-434. <http://dx.doi.org/10.55465/XTQG8319>
- Ervynck, A., Van Neer, W., & Pieters, M. (2004). How the North was won (and lost again): historical and archaeological data on the exploitation of the North Atlantic by the Flemish fishery. In R. A. Housley & G. Coles (eds), *Atlantic connections and adaptations: Economies, environments and subsistence in lands bordering the North Atlantic* (p. 230-239). Oxford, Oxbow Books.
- Espiñeira, M., González-Lavin, N., Vieites, J. M., & Santaclara, F. J. (2008). Development of a method for the genetic identification of flatfish species on the basis of mitochondrial DNA sequences. *Journal of Agricultural and Food Chemistry*, 56(19), 8954-8961. <https://doi.org/10.1021/jf800570r>
- Fornbacke, M., Gombrii, M., & Lundberg, A. (2002). Sidedness frequencies in the flounder *Platichthys flesus* (Pleuronectiformes) along a biogeographical cline. *Sarsia*, 87(5), 392-395. <https://doi.org/10.1080/0036482021000155835>
- Fricke, R., Eschmeyer, W. N., & van der Laan R. (2024). *Eschmeyer's catalog of fishes: Genera, species, references*. (retrieved from <https://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>) [Accessed 2 Sep. 2022].

- Froese, R., & Pauly, D. (2024). *FishBase. World Wide Web electronic publication*. <http://www.fishbase.org>, version (02/2022).
- Futch, C. R., Topp, R. W., Houde, E. D. (1972). Developmental osteology of the lined sole, *Achirus lineatus* (Pisces: Soleidae). *Contributions in Marine Science*, 16, 33-58.
- Gregory, W. K. (1933). Fish skulls. A study of the evolution of natural mechanisms. *Transactions of The American Philosophical Society*, 23(2), 1-417. <https://doi.org/10.2307/3231917>
- Gudger, E. W. (1935). Abnormalities in flatfishes (Heterosomata). I. Reversal of sides: a comparative study of the known data. *Journal of Morphology*, 58(1), 1-39. <https://doi.org/10.1002/jmor.1050580102>
- Härkönen, T. (1986). *Guide to the otoliths of the bony fishes of the Northeast Atlantic*. Hellerup, Danbui ApS.
- Harland, J., Jones, A. K. G., Orton, D. C., & Barrett, J. H. (2016). Fishing and fish trade in Medieval York: The zooarchaeological evidence. In: J. H. Barrett & D. C. Orton (eds), *Cod and herring* (p. 172-204). Oxford, Oxbow Books. <http://dx.doi.org/10.2307/j.ctvh1dw0d.19>
- Heessen, H. J. L., Daan, N., & Ellis, J. R. (2015). *Fish atlas of the Celtic Sea, North Sea, and Baltic Sea: Based on international research-vessel surveys*. Wageningen, Wageningen Academic Publishers.
- Heinrich, D. (1987). *Untersuchungen an mittelalterlichen Fischresten aus Schleswig*. Neumünster, Wachholtz Verlag.
- Hoshino, K. (2001). Monophyly of the Citharidae (Pleuronectoidei: Pleuronectiformes: Teleostei) with considerations of pleuronectoid phylogeny. *Ichthyological Research*, 48(4), 391-404. <https://doi.org/10.1007/s10228-001-8163-0>
- Hubbs, C. (1945). Phylogenetic position of the Citharidae, a family of flatfishes. *Miscellaneous Publications – Museum of Zoology, University Of Michigan*, 63.
- Lepiksaar, J. (1994). *Introduction to osteology of fishes for paleo- and archaeozoologists*. Göteborg.
- Lepiksaar, J., & Heinrich, D. (1977). *Untersuchungen an Fischresten aus der frühmittelalterlichen Siedlung Haihabu*. Neue Ausgrabungen in Haihabu 10. Neumünster, Wachholtz Verlag.
- MacDonald, P. (2013). A rare occurrence of reversal in the common megrim *Lepidorhombus whiffiagonis* (Pleuronectiformes: Scophthalmidae) in the northern North Sea. *Journal of Fish Biology*, 83(3), 691-694. <https://doi.org/10.1111/jfb.12204>
- Märss, T., Wilson, V. H., Saat, T., & Špilev, H. (2017). Gill rakers and teeth of three pleuronectiform species (Teleostei) of the Baltic Sea: A microichthyological approach. *Proceedings of the Estonian Academy of Sciences Geology*, 66(1), 21-46. <http://dx.doi.org/10.3176/earth.2017.01>
- Nicholson, R. (2009). *Southampton French Quarter 1382 specialist report: Fish bone*. Oxford, Oxford Archaeology. Available from: http://library.thehumanjourney.net/58/1/SOU_1382_Specialist_report_download_E2.pdf
- Nielsen, J. G. (1986). Pleuronectidae. In P. J. P Whitehead, M.-L. Bauchot & J.-C. Hureau (eds), *Fishes of the North-Eastern Atlantic and Mediterranean/Poissons de l'Atlantique du Nord-Est et de la Méditerranée* (p. 1299-1307). UNESCO, Paris.
- Nijssen, H. (1966). The occurrence of *Cynoglossus browni* Chabaud, 1949, in the North Sea (Pisces, Pleuronectiformes). *Beaufortia*, 13(155), 87-90.
- Nijssen, H., & De Groot, S. J. (1974). Catalogue of fish species of the Netherlands. *Beaufortia*, 21(285), 173-207.
- Oueslati, T. (2019). A French fish event at the turn of the 10th century? Environment, economy, and ethnicity in maritime Flanders. *International Journal of Osteoarchaeology*, 29(3), 443-451. <https://doi.org/10.1002/oa.2780>
- Reynolds, R. V. (2015). *Food for the soul: The dynamics of fishing and fish consumption in Anglo-Saxon England: c. A.D. 410-1066*. Nottingham, University of Nottingham.
- Roselló, E. (1986). *Contribución al Atlas Osteológico de los Teleosteos Ibéricos*. I. Dentario y Articular. Colección de Estudios nº 14. Ediciones de la Universidad Autónoma de Madrid, Madrid.
- Shaffer, B. S., & Sanchez, J. L. J. (1994). Comparison of 1/8"- and 1/4"-mesh recovery of controlled samples of small-to-medium sized mammals. *American Antiquity*, 59(3), 525-530. <https://doi.org/10.2307/282464>
- Smith, C. I., Nielsen-Marsh, C. M., Jans, M. M. E., & Collins, M. J. (2007). Bone diagenesis in the European Holocene I: Patterns and mechanisms. *Journal of Archaeological Science*, 34(9) 1485-1493. <https://doi.org/10.1016/j.jas.2006.11.006>
- Stahl, P. W. (1996). The recovery and interpretation of microvertebrate bone assemblages from archaeological contexts. *Journal of Archaeological Method and Theory*, 3(1), 31-75. <https://doi.org/10.1007/BF02228930>
- Struever, S. (1968). Flotation techniques for the recovery of small-scale archaeological remains. *American Antiquity*, 33(3) 353-362. <https://doi.org/10.2307/278703>
- Vinnikov, K. A., Thomson, R. C., & Munroe, T. A. (2018). Revised classification of the righteye flounders (Teleostei: Pleuronectidae) based on multilocus phylogeny with complete taxon sampling. *Molecular Phylogenetics and Evolution*, 125, 147-162. <https://doi.org/10.1016/j.ympev.2018.03.014>
- Von Endt, D. W., & Ortner, D. J. (1984). Experimental effects of bone size and temperature on bone diagenesis. *Journal of Archaeological Science*, 11(3), 247-253. [https://doi.org/10.1016/0305-4403\(84\)90005-0](https://doi.org/10.1016/0305-4403(84)90005-0)
- Voronina, E.P. (2010). On morphology and taxonomy of Scophthalmids. *Journal of Ichthyology*, 50(9), 695-703. <https://doi.org/10.1134/S0032945210090018>
- Watt, J., Pierce, G. J., & Boyle, P. R. (1997). Guide to the identification of North Sea fish using premaxillae and vertebrae. *ICES Cooperative Research Report*, 220, 231.
- Wouters, W., Muylaert, L., & Van Neer, W. (2007). The distinction of isolated bones from plaice (*Pleuronectes platessa*), flounder (*Platichthys flesus*) and dab (*Limanda limanda*): a description of the diagnostic characters. *Archaeofauna*, 16, 33-72.
- Yazdani, G. M. (2009). Adaptation in the jaws of flatfish (Pleuronectiformes). *Journal of Zoology*, 159(2), 181-222. <https://doi.org/10.1111/j.1469-7998.1969.tb03078.x>