INTERRELATIONSHIPS OF SCOPHTHALMID FISHES
(PLEURONECTIFORMES: SCOPHTHALMIDAE)

by

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ABSTRACT. - A cladistic analysis of the eight species included in the Scophthalmidae was performed using 25 morphological features, mostly osteological. The analysis resulted in a single cladogram (exhaustive search, 34 steps, consistency index = 0.735, retention index = 0.864). The monophyly of the Scophthalmidae is supported by 4 synapomorphies. Two apomorphic features confirm the genus *Scophthalmus* as monophyletic; within this genus the brill (*S. rhombus*) is more closely related to the windowpane (*S. aquosus*) than to the turbot (*S. maximus*). The genus *Lepidorhombus* is the sister group of a *Phrynorhombus+Zeugopterus* clade; within this clade, *P. regius* is closely related to *Z. punctatus*. *Phrynorhombus regius* is referred to the genus *Zeugopterus*. Analysis of the fossil record suggests that scophthalmids first appeared in the Oligocene of Europe (ca. 35 mya).

RÉSUMÉ. - Les relations de parenté entre Scophtahlmidae (Pleuronectiformes: Scophthalmidae).

Une analyse cladistique des 8 espèces appartenant à la famille des Scophthalmidae est menée ici en étudiant 25 caractères morphologiques, essentiellement ostéologiques. Cette analyse a donné un seul cladogramme (recherche exhaustive, 34 pas, indice de consistence = 0,735, indice de rétention = 0,864). L'existence des Scophthalmidae en tant que clade est soutenue par 4 synapomorphies. Deux caractères apomorphes confirment la monophylie du genre *Scophthalmus* et la barbue (*S. rhombus*) est plus étroitement apparentée au turbot de sable (*S. aquosus*) qu'au turbot (*S. maximus*). Le genre *Lepidorhombus* est le groupe frère du clade regroupant les genres *Phrynorhombus* et *Zeugopterus* et à l'intérieur de celui-ci, *P. regius* est étroitement apparenté à *Z. punctatus* et est inclus dans le genre *Zeugopterus*. Une comparaison avec les données fossiles suggère que l'apparition des Scophthalmidae s'est déroulée en Europe à l'Oligocène, il y a 35 millions d'années.

Keywords. - Scophthalmidae - Flatfishes - Phylogeny.

The Scophthalmidae is a small family of sinistral flatfishes occurring in the northern Atlantic, the Baltic, the Mediterranean and the Black Sea. Two scophthalmid species, the brill (*Scophthalmus rhombus* (Linnaeus, 1758)) and the turbot (*Scophthalmus maximus* (Linnaeus, 1758)), are valuable commercially and have been harvested since ancient times. Turbots were stored salted in the middle ages of Europe (Bauchot and Pras, 1980), and other species (such as megrims, *Lepidorhombus whiffiagonis* (Walbaum, 1792) and *L. boscii* (Risso, 1810)) have been caught regularly and help support some European fisheries (Casthilho *et al*., 1993), at least as preys for other commercial species (Du Buit, 1996). Moreover, the turbot is the first flatfish species that has been reared successfully in aquaculture farms; larvae, juveniles and adults, as well as fillets of this species are exported all around the world (Soler, 1999; Soutar, 1993).

The objectives of this work were to define the monophyletic status of the Scophthalmidae and to propose a hypothesis of relationships between its eight species.

CLASSIFICATION HISTORY
OF SCOPHTHALMIDAE

Scophthalmid fishes have been known for a long time. Linnaeus (1758) recognised two valid species: the brill (*S. rhombus*) and the turbot (*S. maximus*). Ichthyologists of the eighteenth and nineteenth centuries (Bloch, 1787; Bonaterre, 1788; Walbaum, 1792; Risso, 1810; Mitchill, 1815; Günther, 1862) identified other species of scophthalmids and placed them into a broadly defined group of sinistral flatfishes, usually united with other sinistral flounders under various subfamilial names: Rhombinae (Gill, 1893; Kyle, 1900), Pleuronectinae (Jordan and Goss, 1889), Psettinae (Jordan and Evermann, 1898). Kyle (1900) first recognised that the scophthalmid species were closely related and placed them into a turbot-like group among his Rhombinae. Regan (1910) considered these species as members of the subfamily Bothinae of an expanded Bothidae group, uniting sinistral species now considered as members

of the Bothidae and Paralichthyidae. Norman (1934) placed the scophthalmid flounders into the subfamily Scophthalminae, within the Bothidae. According to Norman, this subfamily was defined by three main features: i) anterior extension of the two pelvic fins; ii) eyes present on the left-side; iii) presence of vomerine teeth. Later, Hubbs and Hubbs (1945) and Hubbs (1945) elevated the subfamily Scophthalminae to family status. Nevertheless, in some of the literature (Russel, 1976; Martin and Drewry, 1978, among many others), scophthalmids are still considered as bothids. Lauder and Liem (1983) recognised the Scophthalmidae and placed it in a basal position among the Pleuronectiformes, between the Citharidae and the Bothidae. Ahlstrom *et al*. (1984) and Hensley and Ahlstrom (1984) recognised the Scophthalmidae as a natural group related to the Pleuronectidae, the Paralichthyidae and the Bothidae, and pointed out that more work is needed to elucidate their systematic position. Chapleau (1993) suggested two features uniting scophthalmid fishes: (i) anterior extension of the two pelvic fins; (ii) an elongated supraoccipital process in contact with the dorsal margin of the blind side frontal. However, Chapleau recommended that further studies be conducted to demonstrate the monophyly of this group. Chanet (1998) suggested that a new synapomorphy of scophthalmids was the presence of asymmetrical transverse apophyses. Chanet (1999) confirmed that the two features proposed by Chapleau (1993) also were synapomorphies of the family. Thus, three shared derived morphological features clearly establish the Scophthalmidae as comprising a natural monophyletic group among the Pleuronectiformes. Hensley and Ahlstrom (1984) considered the Scophthalmidae as a member of the bothoid group, but the interrelationships of the Scophthalmidae with the other taxa (*Brachypleura*, the Bothidae, the Pleuronectidae and the paraphyletic assemblage "Paralichthyidae") were still confused. Cooper and Chapleau (1998a) and Hoshino (2001) considered that scophthalmids form the sister group of a clade comprising the Paralichthyidae, Pleuronectidae and Bothidae (Fig. 1). However, all these authors commented on the need for corroboration of these hypotheses of relationships. In the phylogenetic analyses of flatfishes based on sequences of the 12S and 16S mitochondrial ribosomal genes by Berendzen and Dimmick (2000), the position of the Scophthalmidae differs greatly among analyses; this family being the sister group of the Poecilopsettidae or of a clade comprising Poecilopsettidae, Citharidae, Samaridae, Cynoglossidae, Achiridae and Soleidae. As Berendzen and Dimmick have indicated, the lack of resolution in their studies does not advance our understanding of the phylogenetic position of the Scophthalmidae; for now it is most parsimonious to consider scophthalmids as members of the bothoid group (Fig. 1).

MATERIAL AND METHODS

All the scophthalmid species were studied; cleared and stained, dry skeletons and radiographs have been examined. Four outgroup taxa, chosen from the families Citharidae (*Brachypleura novaezeelandiae* Günther, 1862), Paralichthyidae (*Paralichthys squalimentus* Jordan & Gilbert, 1882), Pleuronectidae (*Hippoglossus hippoglossus* (Linnaeus, 1758)), Bothidae (*Arnoglossus laterna* (Walbaum, 1792)), were also examined. Institutional abbreviations follow Leviton *et al*. (1985). Length, in mm is standard length (SL).

Citharidae. - *Brachypleura novaezeelandiae* Günther, 1862: USNM 236122, cleared and stained, 33, 74, 94 mm.

Paralichthyidae. - *Paralichthys squalimentus* Jordan & Gilbert, 1882: ANSP 150694, cleared and stained, 49 mm.

Pleuronectidae. - *Hippoglossus hippoglossus* (Linnaeus, 1758): ARC 8808487, 148 mm.

Bothidae. - *Arnoglossus laterna* (Walbaum, 1792): MNHN 1995-608, 61, 78, 84, 86 mm; *Arnoglossus thori* (Kyle, 1913): MNHN 1962-62, 85, 90, 91, 93, 104 mm.

Scophthalmidae. - *Lepidorhombus boscii* (Risso, 1810): MNHN 1969-73, 192 mm, MNHN 1975-651, 126, 144, 146 mm, USNM
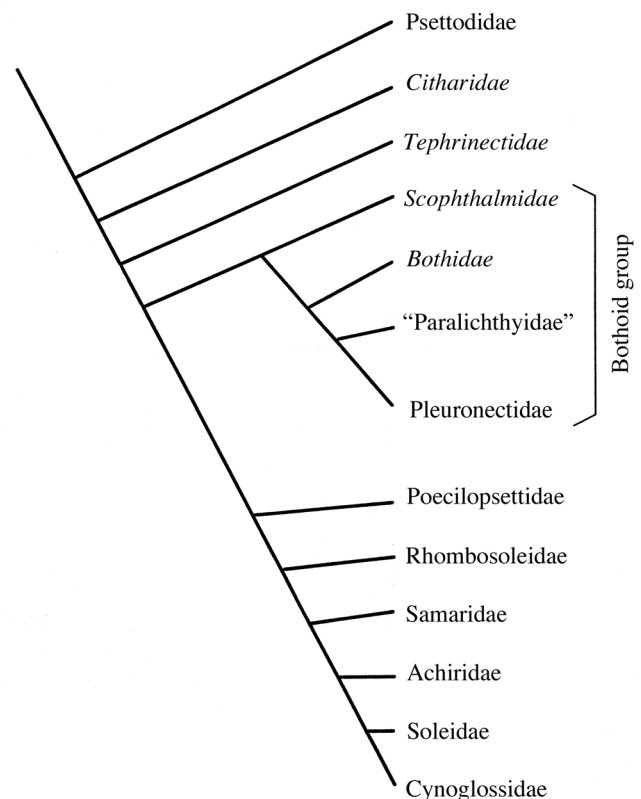

Figure 1. - Phylogenetic position of the Scophthalmidae within Pleuronectiformes (tree modified after Hoshino (2001: 401, fig. 7)).

236124, cleared and stained, 113 mm; *Lepidorhombus whiffiagonis* (Walbaum, 1792): MNHN 1997-4013, dry skeleton, 268 mm, MNHN 1998-781, dry skeleton; *Phrynorhombus norvegicus* (Günther, 1862): FMNH 35547, 66 mm, MNHN 1997-4014, dry skeleton, MNHRL, 69, 78, 89 mm, USNM 22035, 50 mm, USNM 49384, 55 mm; *Phrynorhombus regius* (Bonnaterre, 1788): ANSP 8729132, 74 mm, MNHN B-3004, 62 mm, MNHN 1999-254, 60 mm, USNM 49364, 55 mm; *Scophthalmus aquosus* (Mitchill, 1814): ANSP-150131, cleared and stained, 75 mm, NMC 80-0214, cleared and stained, 61 mm, NMC 80-0223, cleared and stained, 68 mm, NMC 86-73 (1), disarticulated dry skeleton (SL not known), NMC 86-89, disarticulated dry skeleton (SL not known), NMC 86-90, disarticulated dry skeleton (SL not known), NMC 86-91, disarticulated dry skeleton, 313 mm, NMC 87-275, disarticulated dry skeleton (SL not known), NMC 87-278, disarticulated dry skeleton (SL not known), NMC 87-279, disarticulated dry skeleton (SL not known), NMC 87-280, disarticulated dry skeleton (SL not known), NMC 87-281, disarticulated dry skeleton (SL not known); *Scophthalmus maeoticus* (Pallas, 1811): MNHN 1999-248, 131 mm, MNHN 1999-58, 81, 87, 96 mm, MNHN 1999-291, 131 mm, MNSG 12717, 184 mm; *Scophthalmus maximus* (Linnaeus, 1758): CAS 10342, 207 mm, MNHN 1997-4012, disarticulated skeleton (SL not known), MNHN 1997-4179, disarticulated skeleton (SL not known), USNM 170547, 305 mm, 270 cleared and stained young individuals reared from hatching to 60 days, collections of the University of Liege (Belgium); *Scophthalmus rhombus* (Linnaeus, 1758): MNHN 1975-652, 147 mm, MNHN 1997-410, disarticulated dry skeleton (SL not known), MNHN 1999-293, 310 mm; *Zeugopterus punctatus* (Bloch, 1787): MNHN 1974-274, 61 mm, MNHN 1995-0071, 152 mm, MNHN 1996-940, 158 mm, MNHN 1997-4015, 121 mm, MNHN 1997-4016, 170 mm, MNHN 1998-393, 66, 106 mm, MNHN 1999-249, 143 mm, MNHN 1999-251, 122, 130 mm, USNM 017361, 157 mm.

Data for some features of the outgroup taxa have been compiled from: Chabanaud (1933), Amaoka (1969, 1972), Hensley (1977), Sakamoto (1984) and Cooper and Chapleau (1998b).

The systematic literature on scophthalmids has been reviewed and the validity of each species has been assessed, with eight scophthalmid species being recognised.

In the literature, a ninth species is sometimes recognised: *Scophthalmus maeoticus* (Pallas, 1811) (Eschmeyer, 1998), but the available data do not permit us to consider this species as a valid taxon. The turbots present in the Black Sea and Azov Sea have been variously considered as representing a distinct species (*S. maeoticus* Pallas, 1811) related to *S. maximus* (e.g., Eschmeyer, 1998), or have been recognised as a distinct subspecies (*S. maximus maeoticus*) (Tortonese, 1971). These fish differ morphologically from other turbots in having enlarged tubercles (much larger than the diameter of the eye) present on the both sides of the body. As Norman (1934) and Nielsen (1986) noticed, it is the only morpho-anatomical difference between Black Sea

turbots and the Atlantic ones. Steindachner (1868) reported the abundance of turbots with enlarged tubercles in the Black Sea, but also mentioned the presence of specimens with large tubercles in the Mediterranean Sea, from coastal waters off Spain and in the Baltic Sea. Moreover, he indicated the presence along the Atlantic coast of Europe of turbots possessing all intermediate states of tubercle development between the two extreme forms (i.e., large tubercles on both sides of body and small tubercles present only on eyed side). Tortonese (1971) quoted the presence of a turbot with enlarged tubercles (MSNG 12717) in Baltic Sea. Populations of turbot with large tubercles are found most often in oligohaline waters (Baltic Sea: MSNG 12717, MNHN 1999-291; Black Sea: MNHN 1999-58, MNHN 1999-248; Caspian Sea: MNHN 1999-456). The latter specimens were collected in the nineteenth century, before the experimental and unsuccessful introductions of turbots during the 1930's in the former USSR (Holcík, 1991) and in Iran (Coad, 1995). The presence of individuals with large tubercles in all environments where the species is found indicates that this character alone is not informative regarding the specific status of these populations. Resolution of the status of these populations may require information derived from molecular studies. Blanquer *et al*. (1992) studied allozyme variation in brill and turbot in European seas (from Baltic Sea to Aegean Sea). Their analysis leads to the conclusion that Black Sea turbot was a valid species, but the discovered genetic diversity among all studied turbots is very low and no turbot from Black Sea was examined. This problem requires the examination of many specimens with enlarged tubercles on both sides of the body from a variety of localities (all along the coasts from the Baltic Sea to the Black Sea) and the study of more molecular data (mitochondrial or microsatellite DNA for instance). Actually, a detailed review of the features reported for various turbot populations in the literature leads us to conclude that, for now, the most conservative approach is to consider these populations as conspecific, with the senior available name being *Scophthalmus maximus*.

Phylogenetic analysis
Outgroup hypothesis for Scophthalmidae

Four outgroups were chosen for the present analysis: i) *Brachypleura novaezeelandiae*, the most basal bothoid (Cooper and Chapleau, 1998a) and a member of the Citharidae (Hoshino, 2001), ii) *Hippoglossus hippoglossus*, a basal member of the Pleuronectidae (Cooper and Chapleau, 1998b), iii) *Paralichthys squalimentus*, a member of the Paralichthyidae, iv) *Arnoglossus laterna*, a basal member of the Bothidae (Norman, 1934; Amaoka, 1969; Fukui, 1997). The four outgroups are members of the bothoid group, and the last three (*Hippoglossus hippoglossus*, *Paralichthys*

squalimentus and *Arnoglossus laterna*) are representatives of the possible sister group of the Scophthalmidae (Copper and Chapleau, 1998a; Chanet, 1999; Hoshino, 2001).

Exhaustive search method

The data matrix (Tab. I) has been analysed with PAUP 3.1.1. The four outgroups were used in the analysis and character optimisation was set for accelerated transformation (ACCTRAN).

RESULTS

The exhaustive search resulted in one tree (Fig. 2), outgroups formed a polytomy at its base. The tree had 34 steps with a consistency index (ci) of 0.735 and a retention index (ri) of 0.864. This ci value indicates that homoplasies are not important (Forey *et al*., 1992; Darlu and Tassy, 1993) and the ri value suggests that these homoplasies occur at terminal nodes and not internal nodes (Forey *et al*., 1992).

DISCUSSION

The Scophthalmidae appear to form a monophyletic group (clade I) (Fig. 2), with all the species of the genus *Scophthalmus* sharing a common ancestor and representing the most basal lineage (clade II) within the family. The brill
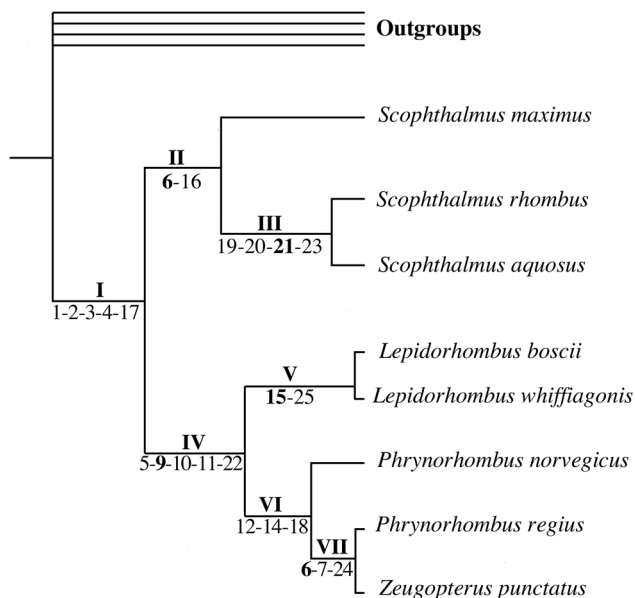

Figure 2. - Scophthalmid interrelationship tree from an exhaustive search method of an analysis of 25 features. Roman numbers above branches indicate clades. Decimal numbers indicate order of apomorphic states, bald number indicate homoplastic features (see text and appendix).

(*S. rhombus*) and the windowpane (*S. aquosus*) share a close common ancestor (clade III). The monophyly of the megrimstopknots group (clade IV) is supported by 5 synapomorphies. Within this clade, the following relationships are evident: the megrims (clade V), *L. boscii* and *L. whiffiagonis*, are sister-taxa; the topknots form a natural group (clade VI); and the common topknot (*Zeugopterus punctatus* (Bloch, 1787)) is most closely related to the Eckstrom topknot (*Phrynorhombus regius* (Bonnaterre, 1788)) on the basis of three features (clade VII). This latter species has previously been named *Phrynorhombus regius*, but following the principles of phylogenetic systematics and the International Code of Zoological Nomenclature, it is changed here to *Zeugopterus regius* (Desoutter *et al*., 2001).

Monophyly of Scophthalmidae

Scophthalmid fishes appear to form a monophyletic group on the basis of the following features: an anterior extension of the two pelvic fins to the isthmus (feature 1) (Figs 3, 4, 5); a supraoccipital with an anterior process, often crenulated, forming a bridge with the dorsal margin of the right frontal (feature 2) (Figs 6, 7); lateral expansions, slightly asymmetric, on both pelvic bones (feature 3) (Figs 3, 4); asymmetrical transverse apophyses on the caudal vertebrae (feature 4) (Chanet, 1998) (Fig. 8); first neural spine bent at contact with the dorsal margin of the cranium (feature 17) (Figs 6, 7).

Monophyly of the genus *Scophthalmus*

Two features define this genus: a short caudal peduncle (feature 6), this character-state also being present in the species of genus *Zeugopterus*; 11 precaudal vertebrae (feature 16). Within this clade, the brill (*S. rhombus*) is more closely related to the windowpane (*S. aquosus* (Mitchill, 1814)) than to the turbot (*S. maximus*) on the base of: the deeply branched first dorsal-fin rays (feature 19); a reduced epural 2 (feature 20) (Fig. 9), in other bothoids, this bone is absent as a result of a fusion with hypural 5 (Chanet and Wagemans, 1997; 2001); a convex dorsal margin of the cranium in the orbital region (feature 21); numerous vomerine teeth (feature 23).

Monophyly of the *Lepidorhombus+Phrynorhombus+Zeugopterus* clade

This clade is supported by six features: the ventral margin of the foramen magnum is formed in part by the basioccipital (feature 5) (Figs 10, 11); two processes are present between the left frontal and the parasphenoid (feature 9) (Fig. 12); the urohyal has a postero-dorsal expansion in contact with the cleithra (feature 11) (Figs 4, 5); the skull is laterally compressed (feature 13) (Figs 10, 11); the dorsal fin extends in front of the nostrils (feature 22).

Table I. - Matrix of 25 morphological features for 4 outgroup taxa and 8 scophthalmid species. Numbers in the matrix represent character-state for each morphology as described in the Appendix. Blanks represent the hypothesised ancestral state (state 0). Question mark (?) represents an unknown state.

Feature number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Citharidae																									
Brachypleura novaezeelandiae								1				?													
Paralichthyidae																									
Paralichthys squalimentus					1			1								1									
Pleuronectidae																									
Hippoglossus hippoglossus					1			1																	
Bothidae																									
Arnoglossus laterna					1	1		1													1				
Scophthalmidae																									
Scophthalmus maximus	1	1	1	1		1										1	1								
S. rhombus	1	1	1	1		1										1	1		1	1	1		1		
S. aquosus	1	1	1	1	1	1									1	1	1		1	1	1	1	1		
Lepidorhombus whiffiagonis	1	1	1	1	1				1	1	1		1		1		1					1			1
L. boscii	1	1	1	1	1				1	1	1		1		1		1					1			1
Phrynorhombus norvegicus	1	1	1	1	1			1	1	1	1	1	1	1			1	1				1			
P. regius	1	1	1	1	1	1	1	1	1	1	1	1	1	1			1	1				1		1	
Zeugopterus punctatus	1	1	1	1	1	1	1		1	1	1	1	1	1			1	1				1		1	

Monophyly of the genus *Lepidorhombus*

Two features support the monophyly of the genus *Lepidorhombus*: the presence of a rounded keel on the ventral side of the parasphenoid (feature 25) (Fig. 7); a large supraoccipital foramen (feature 15) (Fig. 7), but this latter feature is present as well in the windowpane (*S. aquosus*).

Monophyly of the *Phrynorhombus+Zeugopterus* clade

The monophyly of the topknots is supported by three features: the absence of pyloric appendages (feature 12) (Figs 13, 14) (De Groot, 1971); the presence of rounded extensions of each median fin on the dorsal side of the caudal peduncle (feature 14) (Fig. 15); the proximal pterygiophores of the anal fin are elongated (feature 18) (Fig. 16).

Monophyly of the genus *Zeugopterus*

Three features unite the two species of the genus *Zeugopterus*: a short caudal peduncle (feature 6) (Fig. 15); the semicircular shape of the pelvic cartilage supporting the anal-fin rays (feature 7) (Fig. 5); the eyed-side scales with strong and perpendicularly orientated ctenii (feature 24) (Fig. 17).

Complementary data

Some features are possible synapomorphies for various clades within the scophthalmids, but the occurrence of these features among all scophthalmid species could not be determined and data available in the literature (for ingroup and outgroups) are too incomplete to be used in a phylogenetic analysis. Nevertheless, these characters may corroborate relationships.

1) Swimbladder in postlarval stages. According to Norman (1934), only the species belonging to the genus *Scophthalmus* possess a swimbladder in postlarval stages. In *S. maximus*, this organ disappears progressively in postlarvae, 40 to 70 days after hatching (Cousin *et al*., 1985). The presence of a swimbladder in postlarval stages seems to be a synapomorphy of the three species belonging to the genus *Scophthalmus* (clade II).

2) Otocystic spines on larvae. Russel (1976) indicated that the larvae of *Z. punctatus* and *Z. regius* are peculiar in possessing otocystic spines, but this was not studied for all species of the family. This feature may corroborate the close relationship between *Z. punctatus* and *Z. regius* (clade VII).

3) Structure of otoliths. Within scophthalmids, the megrims (*L. bosci* and *L. whiffiagonis*) are unique in possessing otoliths with a gently curved outline, a massive rostrum and a side dimorphism (Schwarzhans, 1997: 93). These features are probable synapomorphies of the two megrim species (clade V).

4) Presence of black spots on the eyed-side. The topknots (*Phrynorhombus norvegicus* (Günther, 1862), *Z. regius* and *Z. punctatus*) have a peculiar pattern of coloration on the eyed-side of the body, with black irregular marks organised in dorso-ventral stripes (Norman, 1934). This feature seems to be a synapomorphy of the topknot group (clade VI).
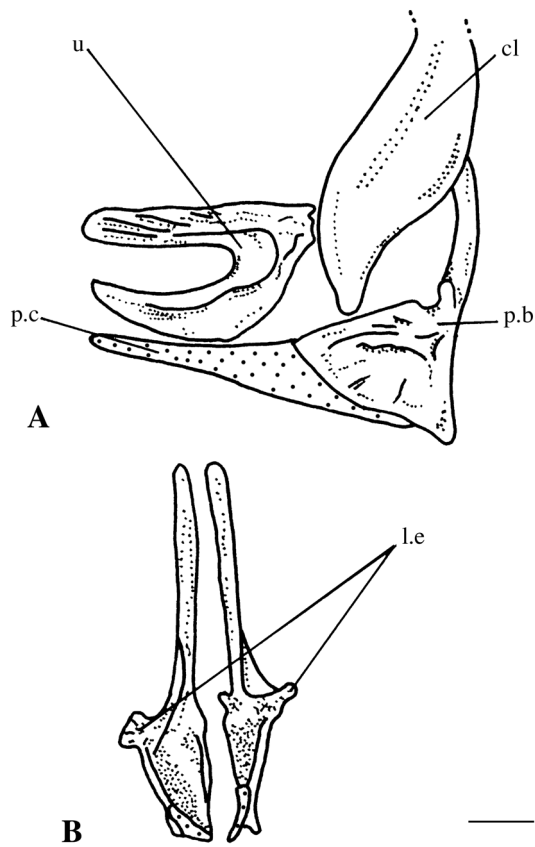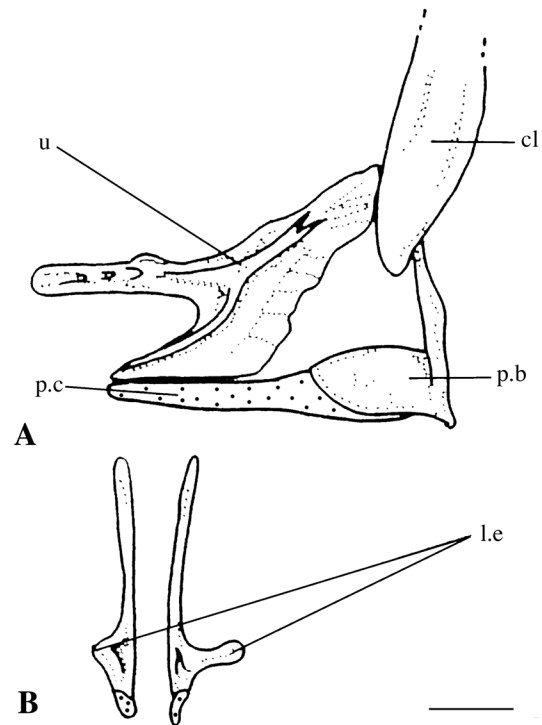
Figure 3. - **A**: Left lateral view of the skeleton of the pelvic region of a turbot (*Scophthalmus maximus*, MNHN 1997-4012). **B**: Anterior view of the pelvic bones of a turbot (*S. maximus*, MNHN 1997-4012). The areas with black circles are cartilaginous regions. cl = cleithrum; l.e = lateral expansion; p.b = pelvic bone; p.c = pelvic cartilage; u = urohyal. Scale bar = 5 mm.

5) Brewster (1987) indicated that before the metamorphosis of *Z. punctatus* and *Z. regius*, both eyes are surrounded by a tube of loose skin, while only the right eye (= migrating eye) was surrounded by such a tube in *Scophthalmus* sp. This feature may corroborate the close relationship between *Z. punctatus* and *Z. regius* (clade VII).

6) Ability to fix on vertical surfaces of rocks. The three topknots species are unique among flatfishes in being able to fix themselves on vertical surfaces of rocks and overhanging blocks (see Weinberg (1993) for *Z. regius*, Chanet (2002) for *Z. punctatus*, Hvass et Guibé (1958) for *P. norvegicus*). This feature seems to be a synapomorphy of the topknot group (clade VI). The same behaviour has been observed in Dover sole (*Solea solea* L., 1758, Soleidae) reared in tanks (pers. obs. and F. Lagardère, pers. comm.).

Classification

The present analysis leads to the following taxonomic categories of the Scophthalmidae:
Subfamily Scophthalminae

Genus *Scophthalmus* (*S. maximus*, *S. rhombus*, *S. aquosus*)

As the status of the Black sea turbot is still confused (see material and methods), no systematic change is proposed within the genus *Scophthalmus*.

Figure 4. - **A**: Left lateral view of the skeleton of the pelvic region of a megrim (*Lepidorhombus whiffiagonis*, MNHN 1997-4013). **B**: Anterior view of the pelvic bones of a megrim (*L. whiffiagonis*, MNHN 1997-4013). Legends as Fig. 1. Scale bar = 10 mm.
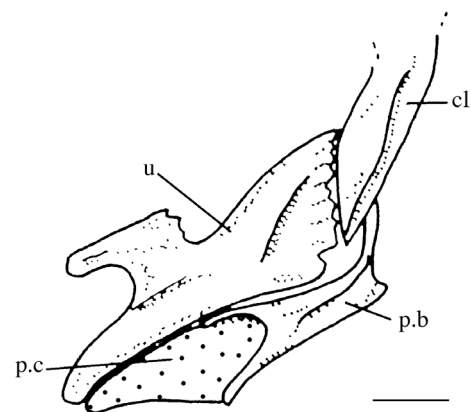
Figure 5. - Left lateral view of the skeleton of the pelvic region of a common topknot (*Zeugopterus punctatus*, USNM 017361). Legends as Fig. 1. Scale bar = 2 mm.

Subfamily Lepidorhombinae
    Tribe Lepidorhombini
        Genus *Lepidorhombus* (*L. whiffiagonis*, *L. boscii*)
    Tribe Phrynorhombini
        Genus *Phrynorhombus* (*P. norvegicus*)
        Genus *Zeugopterus* (*Z. regius*, *Z. punctatus*)

Information brought by fossils

    Very few fossils can be assigned to the Scophthalmidae. In his cladistic review of fossil pleuronectiformes Chanet (1997) did not mention scophthalmids. Nevertheless, Baciu and Chanet (2002) described newly discovered specimens of a fossil scophthalmid in the Oligocene of Piatra Neamt (Romania) and documented generic and family level synapomorphies in the specimens, *Scophthalmus stamatini*, which becomes the oldest known representative of the family and of the genus. Schwarzhans (1997) discussed fossil otoliths, which have been identified as scophthalmid remains. These otoliths have been found only in Europe in the deposits of Upper Oligocene to the Lower Pliocene age, and are referable to *Lepidorhombus*, *Zeugopterus* and *Phrynorhombus* (Schwarzhans, 1997). A fossil skeleton from the Upper Pliocene of Villa Potenza (Italy) as been reported to *Phrynorhombus* cf. *regius* by Sorbini (1988). Thus, it is pos-

sible to state that scophthalmids appeared and diversified at least by the Oligocene (ca. 35 mya) in what is now Europe.

Figure 8. - Anterior view of the fifth caudal vertebra in a megrim (*Lepidorhombus whiffiagonis*, MNHN 1997-4013). c = centrum; h.s = haemal spine; n.s = neural spine; t.a = transverse apophyses. Scale bar = 5 mm.
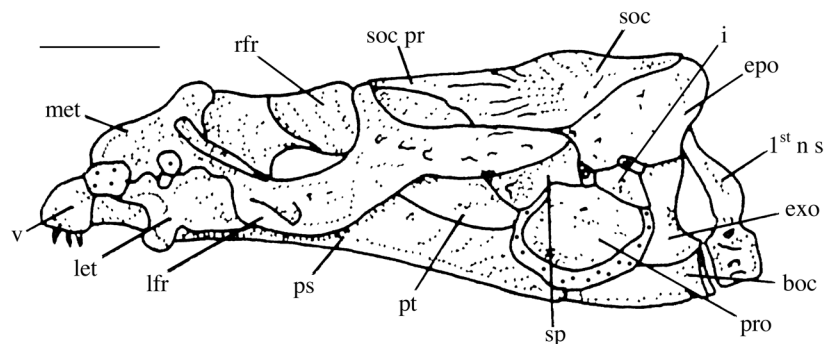
Figure 6. - Left lateral view of the neurocranium with first precaudal vertebra in a turbot (*Scophthalmus maximus*, MNHN 1997-4012). The areas with black circles are cartilaginous regions. 1st n s = first neural spine; boc = basioccipital; epo = epioccipital; exo = exoccipital; i = intercalar; let = lateral ethmoid; lfr = left frontal; met = mesethmoid; pro = prootic; ps = parasphenoid; pt = ptero-sphenoid; rfr = right frontal; sp = sphenotic; soc = supraoccipital; soc pr = supraoccipital process; v = vomer. Scale bar = 5 mm.
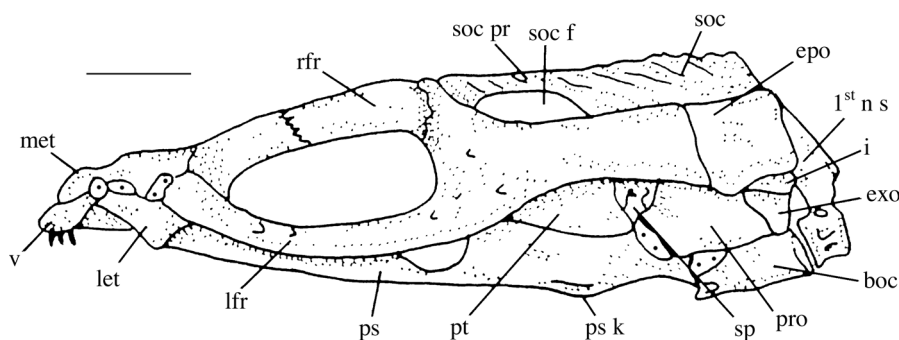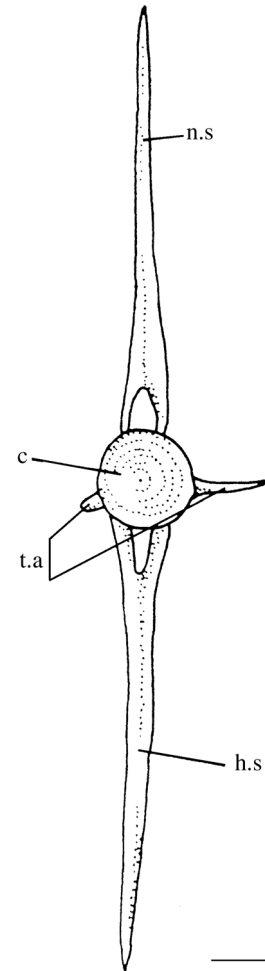

Figure 7. - Left lateral view of the neurocranium with first precaudal vertebra in a megrim (*Lepidorhombus whiffiagonis*, MNHN 1997-4013). The areas with black circles are cartilaginous regions. ps k = parasphenoid keel; soc f = supraoccipital foramen; other legends as in figure 6. Scale bar = 10 mm.
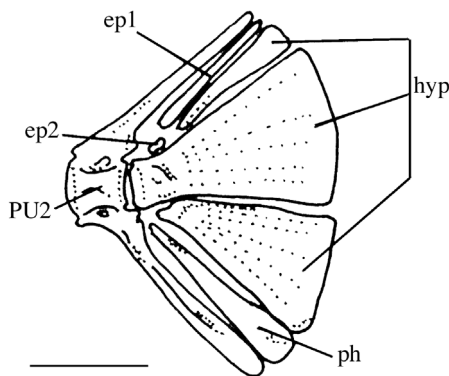
Figure 9. - Left lateral view of the caudal endoskeleton of a brill (*Scophthalmus rhombus*, MNHN 1999-293). ep = epural; hyp = hypural; ph = parhypural; PU2 = preural vertebra 2. Scale bar = 10 mm.
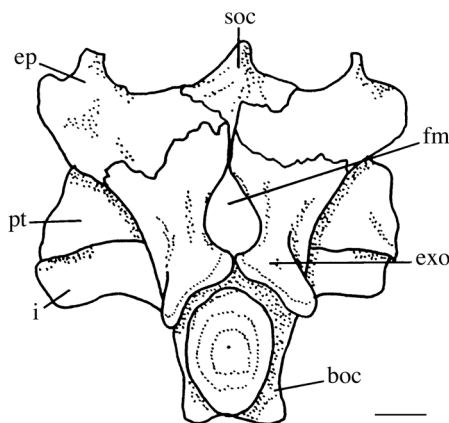

Figure 10. - Occipital view of the neurocranium of a turbot (*Scophthalmus rhombus*, MNHN 1997-410). The areas with black circles are cartilaginous regions. boc = basioccipital; ep = epioccipital; ex = exoccipital; i = intercalar; fm: foramen magnum; pt = pterotic; soc = supraoccipital. Scale bar = 5 mm.
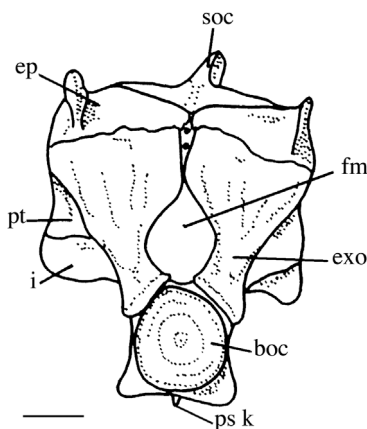
Figure 11. - Occipital view of the neurocranium of a megrim (*Lepidorhombus whiffiagonis*, MNHN 1997-4013). ps k = parasphenoid keel, other legends as in figure 10. Scale bar = 3 mm.

Biogeography

Among scophthalmids, only the windowpane (*S. aquosus*) is present on the coasts of the north-western Atlantic (Jordan and Evermann, 1889; Norman, 1934). All others species (both recent and fossil) are found on the coasts of north-eastern Atlantic and related seas (Baltic, Mediterranean and Black seas). Chanet and Desoutter (2000) mentioned two specimens of the common topknots (*Z. punctatus*) in the collections of the Muséum national d'Histoire naturelle (Paris) (specimens MNHN 1999-251) labelled as coming from Newfoundland, but this putative presence in North-American waters needs to be confirmed. Consequently, European seas seem to be the area of both the origin and diversification of the Scophthalmidae.
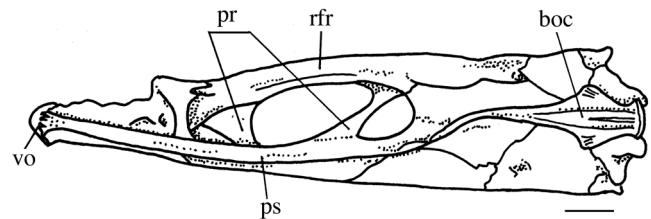

Figure 12. - Ventral view of the neurocranium of a megrim (*Lepidorhombus whiffiagonis*, MNHN 1997-4013). boc = basioccipital; l.fr = left frontal; pr = process between the parasphenoid and the left frontal; ps = parasphenoid; vo = vomer. Scale bar = 5 mm.
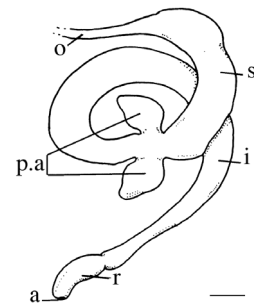

Figure 13. - Left lateral view of the digestive tract of a turbot (*Scophthalmus maximus*, MNHN 1997-4179, modified from Chanet *et al*. (2000: 29, fig. 19)). a = anus; i = intestine; o = oesophagus; p.a = pyloric appendage; r = rectum; s = stomach. Scale bar = 10 mm.
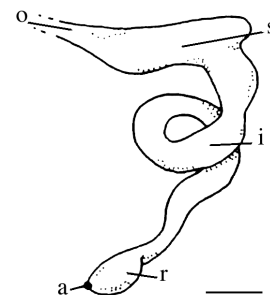

Figure 14. - Left lateral view of the digestive tract of a common topknot (*Zeugopterus punctatus*, MNHN 1997-4016). Legends as in figure 13. Scale bar = 5 mm.
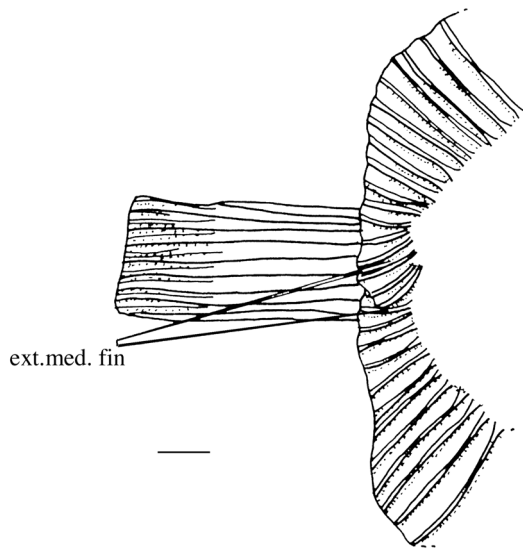
Figure 15. - Blind side view of the caudal region of a common topknot (*Zeugopterus punctatus*, MNHN 1997-4015) (modified from Chanet (2002: 5, fig. 6)). ext.med. fin = extension of median fins. Scale bar = 3 mm.
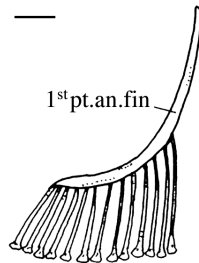
Figure 16. - Anterior part of the anal fin supporting elements in a common topknot (*Zeugopterus punctatus*, MNHN 1999-251). 1st pt.an.fin = first anal-fin pterygiophore. Scale bar = 6 mm.
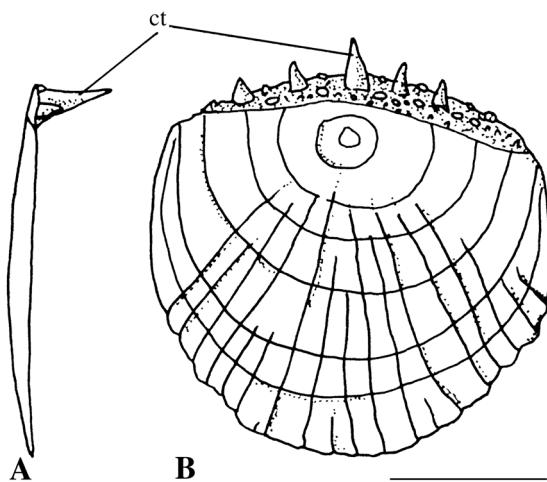

Figure 17. - Eyed-side scale of a common topknot (*Zeugopterus punctatus*, MNHN 1997-4016) (modified from Chanet (2002: 4, fig. 5)). **A**: Lateral view. **B**: Upper view. ct = ctenii. Scale bar = 1 mm.

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APPENDIX LIST OF CHARACTERS

1. Anterior extension of two pelvic-fin bases. 2 states, 1 step, cci = 1.00: no anterior extension of two pelvic fins (state 0), anterior extension of two pelvic fins to the isthmus (state 1) (Figs 3, 4, 5).

2. Supraoccipital process. 2 states, 1 step, cci = 1.00: supraoccipital with no anterior process joining the dorsal margin of the right frontal (state 0), supraoccipital with anterior process (often crenulated) forming a bridge with the dorsal margin of the right frontal (state 1) (Figs 6, 7).

3. Lateral wings on pelvic bones. 2 states, 1 step, cci = 1.00: no lateral expansion on pelvic bones (state 0), lateral expansions (slightly asymmetric) on both pelvic bones (state 1) (Figs 3, 4).

4. Transverse apophyses. 2 states, 1 step, cci = 1.00: symmetrical transverse apophyses on caudal vertebrae (state 0), asymmetrical transverse apophyses on caudal vertebrae (state 1) (Fig. 8).

5. Ventral margin of foramen magnum. 2 states, 1 step, cci = 0.50: exoccipitals forming ventral margin of foramen magnum (state 0) (Fig. 10), basioccipital forming part of ventral margin of foramen magnum (state 1) (Fig. 11).

6. Caudal peduncle. 2 states, 1 step, cci = 0.25: long, well individualised, caudal peduncle (state 0), short caudal peduncle (state 1) (Fig. 15).

7. Shape of the pelvic cartilage. 2 states, 1 step, cci = 1.00: slender and elongated pelvic cartilage (state 0) (Figs 3, 4), semicircular shaped pelvic cartilage (state 1) (Fig. 5).

8. Presence of vomerine teeth. 2 states, 1 step, cci = 0.50: vomerine teeth present (state 0) (Figs 6, 7, 12), vomerine teeth absent (state 1).

9. Processes between the left frontal and the parasphenoid. 2 states, 1 step, cci = 0.50: absent (state 0), present (1) (Fig. 12).

10. Cranial crests on epioccipitals and parietals. 2 states, 1 step, cci = 1.00: absent (state 0), present (1) (Fig. 11).

11. Urohyal with a developed postero-dorsal expansion in contact with the cleithra. 2 states, 1 step, cci = 1.00: absent (state 0) (Fig. 3), present (1) (Figs 4, 5).

12. Pyloric appendages. 2 states, 1 step, cci = 1.00: present (0) (Fig. 13), absent (state 1) (Fig. 14). All outgroup taxa have pyloric appendages (De Groot, 1971).

13. Laterally compressed cranium. 2 states, 1 step, cci = 0.50: cranium, in occipital view, as wide as high (state 0) (Fig. 10), cranium higher than wide (state 1) (Fig. 11).

14. Rounded extensions of each median fin on the dorsal side of caudal peduncle. 2 states, 1 step, cci = 1.00: absent (state 0), present (state 1) (Fig. 15).

15. Supraoccipital foramen. 2 states, 1 step, cci = 0.50: absent or reduced (state 0) (Fig. 6), large (state 1) (Fig. 7).

16. Number of precaudal vertebrae. 2 states, 1 step, cci = 1.00: more than 10 precaudal vertebrae (state 0), 10 precaudal vertebrae (state 1).

17. Orientation of the first neural spine. 2 states, 1 step, cci = 1.00: not in contact with the dorsal margin of the cranium (state 0), bent on the dorsal margin of the cranium (state 1) (Figs 6, 7).

18. Proximal pterygiophores of anal fin. 2 states, 1 step, cci = 1.00: short (state 0), long (state 1) (Fig. 16).

19. First dorsal-fin rays. 2 states, 1 step, cci = 1.00: unbranched (state 0), deeply branched (state 1).

20. Epural 2. 2 states, 1 step, cci = 0.50: absent (state 0), rudimentary (state 1) (Fig. 9).

21. Shape of the dorsal margin of cranium in orbital region. 2 states, 1 step, cci = 0.50: almost straight (state 0), convex (state 1).

22. Anterior extension of dorsal fin. 2 states, 1 step, cci = 0.50: behind the nostrils (state 0), in front of the nostrils (state 1).

23. Abundance of vomerine teeth. 2 states, 1 step, cci = 0.50: few vomerine teeth (state 0), a patch of vomerine teeth (state 1).

24. Eyed-side scales ctenii. 2 states, 1 step, cci = 1.00: eyed-side scales with small and posteriorly orientated ctenii (state 0), eyed-side scales with strong and perpendicular orientated (state 1) (Fig. 17).

25. Rounded keel on the ventral side of parasphenoid. 2 states, 1 step, cci = 1.00: absent (state 0), present (state 1) (Figs 7, 11).