Evidence for a close phylogenetic relationship between the teleost orders Tetraodontiformes and Lophiiformes based on an analysis of soft anatomy

by

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Key words

Lophilformes Tetraodontiformes Phylogeny Soft anatomy Abstract. – Recent phylogenetic studies based on comparisons of DNA sequences have shown that Lophiiformes (anglerfishes) and Tetraodontiformes (puffers, triggerfishes and sunfishes) were closely related, whereas no morpho-anatomical work has assessed this point. Dissections of 80 fresh specimens belonging to 49 species of 29 acanthomorph families, coupled with analyses of the literature indicate the existence of shared soft anatomy characters between Lophiiformes and Tetraodontiformes. Among acanthomorphs, anglerfishes, puffers, ocean sunfish and triggerfishes are peculiar in possessing: i) a reduced gill opening; ii) rounded and anteriorly disposed kidneys; iii) a compact thyroid included in a blood sinus; iv) an abbreviated spinal cord; v) an asymmetric liver; and vi) clusters of supramedullary neurons in the rostral part of the spinal cord. The sharing of these unusual characteristics by these two groups might be synapomorphies supporting a close relationship between Lophiiformes and Tetraodontiformes. The present study shows both the importance of comparative anatomy and the utility of confronting morpho-anatomical and molecular results.

Résumé. – Des données d'anatomie molle corroborent l'étroite parenté entre Tétraodontiformes et Lophiiformes.

Des analyses phylogénétiques récentes fondées sur la comparaison de séquences nucléotidiques ont montré que les Lophiiformes (baudroies) et les Tétraodontiformes (poissons-coffres, balistes et poissons-lunes) étaient étroitement apparentés, tandis qu'aucune donnée morpho-anatomique ne l'attestait. La dissection de 80 spécimens frais appartenant à 49 espèces de 29 familles d'acanthomorphes, associée à l'analyse de la littérature montre la présence de caractères partagés touchant l'anatomie des organes mous entre les Lophiiformes et les Tétraodontiformes. Au sein des acanthomorphes, les baudroies, poissons-coffres, balistes et poissons-lunes sont particuliers en possédant : i) une ouverture branchiale réduite ; ii) des reins arrondis et situés antérieurement dans la cavité abdominale ; iii) une thyroïde compacte incluse dans un sinus veineux ; iv) une moelle épinière courte ; v) un foie asymétrique ; et vi) des groupes de neurones supramédullaires dans la région rostrale de la moelle épinière. Le partage de ces caractères singuliers par ces groupes constitue un indice de synapomorphies probables, soutenant l'étroite parenté entre Lophiiformes et Tétraodontiformes. La présente étude montre à la fois l'importance de l'anatomie comparée et l'intérêt d'associer et confronter les résultats des travaux morpho-anatomiques et moléculaires.

Until recently, Tetraodontiformes and Lophiiformes were regarded as distinct and not closely related orders of acanthomorph fishes (Lecointre, 1994; Nelson, 2006). The Lophiiformes (anglerfishes such as goosefishes, frogfishes and sea toads) comprise 313 species in 66 genera, in which the first dorsal fin spines are modified as a luring apparatus, while the 101 genera and 357 species that comprise the Tetraodontiformes are as diverse as triggerfishes, boxfishes, puffers and ocean sunfishes (Nelson, 2006). Recently, some tetraodontiform species have become the subject of many biological studies both for their toxicity and their compact genome (Aparicio *et al.*, 2002; Jaillon *et al.*, 2004). On the basis of their respective peculiar anatomy, lophiiform and tetraodontiform species were viewed as distinctive orders that were only distantly related to one another within the acanthomorph teleosteans (Lecointre, 1994; Nelson, 2006). Lophiiformes and Tetraodontiformes were sometimes listed in close proximity (just before or after) to one another in taxonomic arrangements (Gill, 1893; Jordan and Evermann, 1900; Boulenger, 1904; Jordan, 1920, 1923; Berg, 1940), but such placements were only poorly, if at all, supported by characters and did not correspond to a documented hypothesis of relationships. Nevertheless, the anatomy of these fishes has been rarely compared. Rosen (1973) recognised two clades within the acanthomorphs: the Acanthopterygii, including the Tetraodontiformes, and the Paracanthopterygii, contain-

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ing the Lophiiformes with the Gadiformes, Batrachoidiformes, Percopsiformes, and Ophidiformes. Even if the status of these two clades has been questioned and reconsidered by several authors (Stiassny, 1986; Stiassny and Moore, 1992; Johnson and Patterson, 1993), Tetraodontiformes and Lophiiformes were still viewed as two distinctive and only distantly related orders (Lauder and Liem, 1983; Johnson and Patterson, 1993; Nelson, 2006), defined on osteological autapomorphies (Tyler, 1980; Pietsch, 1981, 1984, 2009; Pietsch and Grobecker, 1987). The absence of some bones, like ribs or nasals (Pietsch, 1981) could be viewed as synapomorphies of Tetraodontiformes and Lophiiformes, but the occurrences these absences have to be accurately examined. Miya et al. (2003) analysed the complete sequence of mitochondrial DNA for 100 higher teleostean species. Their results showed that Tetraodontiformes and Lophiiformes are two monophyletic and closely related groups: anglerfishes appear as a sister group of a clade comprising two tetraodontiform species and one caproid, Antigonia capros Lowe, 1843. The same relationships for these groups are present in Miya et al. (2005), in which the complete sequences of mitochondrial DNA were studied for 102 higher teleostean species. Dettaï and Lecointre (2004) did not find this same close relationship between Lophiiformes and Tetraodontidae in their search of notothenioid relatives on the basis of 3525 nuclear and mitochondrial characters. Dettaï and Lecointre (2005) analysed the sequences (678 + 527 base pairs) of exons of the MLL (Mixed Lineage Leukaemia-like) gene sequences for ribosomal 28S, rhodopsin gene, mitochondrial 12S and 16S in 63 acanthomorph species. In this work, Lophiiformes and Tetraodontiformes were nested in the same clade, called N by these authors, along with Caproidae, Elassomatidae, Acanthuridae, Siganidae, Pomacanthidae, Drepanidae and Chaetodontidae. While studying the sequences of the gene for the interphotoreceptor retinoid-binding protein (IRBP) in 92 acanthomorph species, Dettaï and Lecointre (2008) found again this clade. Yamanoue et al. (2007) studied 44 whole mitochondrial genomes of acanthomorph species to try to identify the phylogenetic position of tetraodontiform fishes. This group appeared as monophyletic and placed as a sistergroup of either Lophiiformes plus Caproidae or Caproidae alone. Li (2008) analysed the sequences for four nuclear genes (Rhodopsine, MLL4, IRBP and RNF213) in 200 acanthomorph species; Clade N was redefined and restricted, and Lophiiformes and Tetraodontiformes appeared (Fig. 1) in an unresolved clade with Scatophagidae, Cepolidae and Priacanthidae. The sister group of this clade was a caproid, Antigonia, and this assemblage was closely related to a clade comprising Capros, Sparidae, and Callanthiidae (Li et al., 2008). Smith and Wheeler (2006) and Smith and Craig (2007) examined the problem of the phylogenetic position of these groups. Unfortunately, one of these studies (Smith and Craig, 2007) did not include both Lophiiformes and Tetrao-



Figure 1. - Phylogenetic position of Tetraodontiformes and Lophiiformes (modified from Li (2008); note that in Dettaï and Lecointre (2008) tetraodontiforms and lophiiforms are sister-groups). Drawings from F. Dejouannet. 1: Angler (*Lophius piscatorius*, Lophiiformes, Lophiidae); 2: Puffer (*Tetraodon* sp., Tetraodontiformes, Tetraodontidae); 3: Ocean Sunfish (*Mola mola*, Tetraodontiformes, Molidae); 4: Boarfish (*Capros aper*, Caproidae); 5: Porgy (*Sparus* sp., Sparidae); 6: Perch (*Perca* sp., Percidae).

dontiformes and thus did not challenge or corroborate a close relationship between them. In the other study of Smith and Wheeler (2006), the Lophiiformes and Tetraodontiformes did not appear closely related on the basis of the analysis of five gene regions (nuclear and mitochondrial). But this result is quite unique, while 15 different studies (Miya *et al.*, 2003, 2005; Dettaï and Lecointre, 2004, 2005, 2008; Yamanoue *et al.*, 2007; Mabuchi *et al.*, 2007; Holcroft and Wiley, 2008; Li, 2008; Santini *et al.*, 2009; Yagishita *et al.*, 2009; Matschiner *et al.*, 2011; Meynard *et al.*, 2012; Near *et al.*, 2012; Wainwright *et al.*, 2012) conducted by different teams on various genes (17 nuclear genes and 36 mitochondrial genes) corroborate a close relationship between Lophiiformes and Tetraodontiformes.

Many studies of the skeletal anatomy of these two orders have not yet revealed any shared derived characters that would unite them (Tyler, 1968; Tyler, 1980; Pietsch, 1981, 2009; Matsuura and Yoneda, 1987; Pietsch and Orr, 2007; among many others). The species of each of these groups are considered as highly derived among euteleostean fishes, with many specializations, skeleton modifications and autapomorphies, which present difficulties in making osteological comparisons between them. Recently, Nakae and Sasaki (2010) noted similitude in the organization of the lateral line system and its innervation of one lophiiform species [Lophiomus setigerus (Vahl, 1797), Lophiidae] and 9 tetraodontiform species. Even if only few species were examined, these authors proposed that it may result from common ancestry. In the light of all these works, we decided to examine the soft anatomy of these animals thanks to classical dissections, literature examination and modern imaging

techniques (Chanet *et al.*, 2012). The purpose of this work is to present these data based on the study of soft anatomy, which may corroborate the close relationships between these two orders.

MATERIAL AND METHODS

Scientific names are given as in Eschmeyer and Fricke (2010) and the invalid names present in the literature were modified in the text and in the table. As the details of the soft anatomy could not be investigated on alcohol preserved specimens, the present study was conducted on the basis of literature and dissections of fresh specimens. The visceral anatomy has been investigated in dissecting 80 fresh specimens of 49 acanthomorph species. Most of them died naturally in aquariums; others were fished in the eastern Atlantic Ocean and purchased dead at fishmongers and at the fish market auction of Concarneau (France). This work was completed by a review of the literature (Annex I) and by examination of RMI images present at the Digital Fish Library (DFL), http://www.digitalfishlibrary.org.

These examined specimens are:

Acanthomorphs, Blenniidae: Parablennius gattorugine (Linnaeus, 1758) (1) (SL: 11.8 cm), fished in the English Channel; Gadidae: Gaidropsarus mediterraneus (Linnaeus, 1758) (1) (SL: 9.5 cm), fished in the English Channel, Pollachius pollachius (Linnaeus, 1758) (1), isolated head (H: 19 cm), purchased at fishmonger, fished in the Atlantic Ocean, Trisopterus luscus (Linnaeus, 1758) (1) (SL: 23.2 cm), purchased at fishmonger, fished in the Atlantic Ocean; Zeidae: Zeus faber Linnaeus, 1758 (1) (SL: 30.5 cm), purchased at fishmonger, fished in the Atlantic Ocean: Moronidae: Dicentrarchus labrax (Linnaeus, 1758) (4) (SL: 33 cm); Mullidae: Mullus surmuletus Linnaeus, 1758 (1) (SL: 20.3 cm), purchased at fishmonger, fished in the Atlantic Ocean; Trichiuridae: Lepidopus caudatus (Euphrasen, 1788) (6) (SL: 70.5 cm, 73 cm, 73.5 cm, 79 cm, 91 cm, 104 cm); Scombridae: Scomber scombrus Linnaeus, 1758 (4) (mean SL: 30 cm); Belonidae: Belone belone (Linnaeus, 1761) (1) (76 cm), fished in the Atlantic Ocean; Callionymidae: Callionymus lyra Linnaeus, 1758 (2) (11.7 cm, 13,2 cm), purchased at fishmonger, fished in the English Channel; Chaetodontidae: Chelmon rostratus (Linnaeus, 1758) (1) (SL: 11.2 cm), from a private aquarium. Carangimorphes, Soleidae: Solea solea (Linnaeus, 1758) (5) (mean SL: 24.5 cm), purchased at fishmonger, fished in the Atlantic Ocean; Pleuronectidae: Microstomus kitt (Walbaum, 1792) (1) (SL: 24.1 cm), purchased at fishmonger, fished in the Atlantic Ocean, Pleuronectes platessa Linnaeus, 1758 (1) (SL: 30.5 cm), purchased at fishmonger, fished in the English Channel; Scophthalmidae: Lepidorhombus whiffiagonis (Walbaum, 1792) (1) (SL: 27.4 cm), purchased at fishmonger, fished in the Atlantic Ocean, Scophthalmus maximus (Linnaeus, 1758) (4) (mean SL: 37.8 cm), purchased at fishmonger, fished in the Atlantic Ocean; Sphyraenidae: Sphyraena afra Peters, 1844 (1), isolated head (H: 21.3 cm), fished on the coasts of Gabon; Carangidae: Trachurus trachurus (Linnaeus, 1758) (1) (SL: 33.8 cm), purchased at fishmonger, fished in the Atlantic Ocean; Sparidae: Sparus aurata Linnaeus, 1758 (3) (mean SL: 18 cm), purchased at fishmonger, fished in the Atlantic Ocean, Spondyliosoma cantharus (Linnaeus, 1758) (4) (mean SL: 24 cm), purchased at fishmonger, fished in the Atlantic Ocean; Labridae: Labrus bergylta Ascanius, 1767 (2) (SL: 23.8 cm), one isolated head (H: 11.3 cm), purchased at fishmonger, fished in the Atlantic Ocean, Labrus mixtus Linnaeus, 1758 (1) (SL: 24.8 cm), fished in the Atlantic Ocean, Symphodus melops (Linnaeus, 1758) (1) (SL: 10.6 cm), fished in the Atlantic Ocean, Ctenolabrus rupestris (Linnaeus, 1758) (1) (SL: 11.4 cm), purchased at fishmonger, fished in the Atlantic Ocean; Acanthuridae: Acanthurus achilles Shaw, 1803 (1) (SL: 8.8 cm), from a private aquarium, Acanthurus lineatus (Linnaeus, 1758) (1) (SL: 16.4 cm), from a private aquarium; Pomacanthidae: Centropyge multispinis (Playfair, 1867) (1) (7.9 cm), Pomacanthus imperator (Bloch, 1787) (1) (SL: 12.6 cm), from a private aquarium; Percidae: Perca fluviatilis Linnaeus, 1758 (2) (SL: 36.2 cm; 37.5 cm), purchased at fishmonger, Sander lucioperca (Linnaeus, 1758) (1) (SL: 59.6 cm), purchased at fishmonger; Caproidae: Capros aper (Linnaeus, 1758) (2) (SL: 9.4 cm; 10.5 cm), from the Aquarium Mare Nostrum (Montpellier, France). Tetraodontiformes, Balistidae: Balistes capriscus Gmelin, 1789 (1) (SL: 30 cm), fished in the Atlantic Ocean, Melichthys vidua (Richardson, 1845) (1) (SL: 12.3 cm), from the Aquarium Mare Nostrum (Montpellier, France); Diodontidae: Diodon holacanthus Linnaeus, 1758 (1) (SL: 23.2 cm), from the Aquarium Mare Nostrum (Montpellier, France), Diodon liturosus Shaw, 1804 (1) (SL: 18.5 cm), from the Aquarium of Vannes (Vannes, France); Lagocephalidae: Lagocephalus lagocephalus (Linnaeus, 1758) (1) (SL: 39.3 cm), fished in the Atlantic Ocean; Molidae: Mola mola (Linnaeus, 1758) (2) (TL: 124 and 142 cm), one fished in the English Channel, the other in the Atlantic Ocean; Ostraciidae: Ostracion cubicus Linnaeus, 1758 (1) (SL: 14.7 cm), from the Aquarium Mare Nostrum (Montpellier, France), Tetrosomus gibbosus (Linnaeus, 1758) (1) (SL: 7.4 cm), from the Aquarium of Vannes (Vannes, France), Lactoria cornuta (Linnaeus, 1758) (1) (SL: 28.3 cm), from the Aquarium of Vannes (Vannes, France); Tetraodontidae: Arothron nigropunctatus (Bloch & Schneider, 1801) (1) (SL: 25.6 cm), from the Aquarium Mare Nostrum (Montpellier, France), Canthigaster compressa (Marion de Procé, 1822) (1) (SL: 6.4 cm), from the Aquarium of Vannes (Vannes, France), Tetraodon mbu Boulenger, 1899 (1) (31.6 cm), from the Aquarium de la Porte Dorée (Paris, France), Tetraodon cutcutia Hamilton, 1822 (1) (SL: 6.6 cm), purchased

at Europrix (Lens, France), *Tetraodon palembangensis* Bleeker, 1852 (1) (SL: 8.8 cm), purchased alive at Europrix (Lens, France). Lophiiformes, Lophiidae: *Lophius piscatorius* Linnaeus, 1758 (3) (SL: 27.6 cm; 28.5 cm; 57.3 cm), 1 isolated head (H: 24.2 cm), purchased at the fish auction of Concarneau (Concarneau, France) and 1 preserved specimen (A 5665) exhibited in the Galerie d'anatomie comparée (MNHN, Paris, France); Ogcocephalidae: *Ogcocephalus vespertilio* (Linnaeus, 1758) (1) (SL: 18.8 cm), from the Aquarium *Mare Nostrum* (Montpellier, France); Triglidae: *Trigla lyra* Linnaeus, 1758 (2) (SL: 24.5 cm), one isolated head (H: 10.4 cm), purchased at the fish auction of Concarneau (Concarneau, France); Scorpaenidae: *Sebastes norvegicus* (Ascanius, 1772) (2) (SL: 35.1 cm; 44.9 cm), purchased at a fishmonger.

Parasagittal mechanical sections were performed on frozen large fishes using an electric meat saw (La Bovida, BG) to observe the structure of the thyroid gland and the extension of the spinal cord. For practical purposes, the various specimens after dissection could not be deposited in systematic collections. Indeed, the state of the dissected specimens does not allow for suitable re-examination. We consider that the characters we describe have already been often mentioned in the literature or can be further investigated through new dissections.

The distribution of the examined anatomical characters was analysed according to the taxonomic content of clade "N" (Li *et al.*, 2008), as this work is actually the sole one presenting the interrelationships of Tetraodontiformes and Lophiiformes with a large sample of taxa, from Scatophagidae to Cepolidae, Priacanthidae, *Antigonia*, Callanthiidae,

Capros and Sparidae. As the distribution of the here studied characters is not really confronted to those of other data, in a data matrix for instance, this mapping of characters onto phylogenies may appear as illegitimate. But, there is three main reasons to apply that method: i) similarities in anatomy are often overlooked until there is some new evidence pointing out surprising sister-group relationships; ii) this approach is suitable for characters for which hypotheses of homology cannot be yet confidently proposed at the beginning of a study (Grandcolas et al., 2001); iii) it provides a strong indication of reliability and applies the principle of consilience defined as the convergence of evidence, or concordance of evidence (Whewell, 1840). This method has been successfully applied by many authors like Brooks and McLennan (1991), Block et al. (1993), Miya and Nishida (1996), O'Toole (2002), Chanet (2003), Suzuki et al. (2004) and discussed (Grandcolas et al., 2004, among many others). This approach leaves open the possibility to construct a morphological character matrix; and better, it can be seen as a first step to do it.

RESULTS

The present dissections and analyses of characters from the literature have revealed six soft anatomy characters as putative synapomorphies for the Lophiiformes and Tetraodontiformes, as follows:

1) A reduced gill opening

In teleostean fishes, each gill opening forms a dorsov-



Figure 2. - The restricted gill opening (black arrow) in a few lophiiform and tetraodontiform species. A: Lophius piscatorius (Lophiiformes, Lophiidae); B: Microlophichthys microlophus (Lophiiformes, Oneirodidae); C: Tetraodon sp., (Tetraodontiformes, Tetraodontidae); D: Mola mola (Tetraodontiformes, Molidae). All drawings from F. Dejouannet, excepted drawing B modified after Trewavas and Regan (1932). entrally elongated and curved slit. In Lophiiformes (Pietsch and Orr, 2007; Pietsch, 2009) and Tetraodontiformes (Tyler, 1980; Tyler and Sorbini, 1996), the gill openings are restricted to small, narrow and elongated tube-like orifices (Fig. 2). Similar small gill openings are present in Anguilliformes, Syngnathoidei and Callionymidae (Nelson, 2006). But, regarding teleostean interrelationship hypotheses, this character can be considered as a convergence with, on the one hand, Anguilliformes, Syngnathoidei and Callionymidae and Lophiiformes and Tetraodontiformes, on the other hand, while it can be considered as a probable synapomorphy of these two clades within the restricted clade N (Li, 2008) (Fig. 1). Nevertheless, these gill slits differ by their position: they are situated dorsal to, posterior to or ventral to (rarely partly anterior to) the pectoral-fin base (Pietsch, 2009), while they are generally anterior to the pectoral fin base and extend ventrally no further than slightly below that base in Tetraodontiformes (Tyler, 1968; Tyler, 1980). Even if more work on the structure of the endoskeleton of the opercular region of these animals is needed, this similarity in the shape of the gill openings can be hypothesised to be a synapomorphy of Lophiiformes and Tetraodontiformes. We note that the restricted gill opening of tetraodontiforms is present in both extant taxa and in fossils dating back to the Upper Cretaceous origins of the order (Tyler and Sorbini, 1996).

2) Rounded and anteriorly disposed kidneys

In teleostean fishes, the kidneys are usually elongated and joined organs present between the haemal arches on the dorsal margin in the abdominal cavity (Owen, 1866; Cole and Johnstone, 1902; Audigé, 1910). *Perca* (Audigé, 1910), *Capros aper, Sparus aurata* (Fig. 3) and *Spondyliosoma* (Fig. 9) have this type of kidneys. Some acanthomorph species have an asymmetric lobe extending ventrolaterally, as described in soleid species (Audigé, 1910: 403, fig. 42;



Figure 3. - Visceral anatomy of a sea bream, *Sparus aurata*, left lateral view. ep.m: epaxial musculature; k: kidney; l: liver; sb: swimbladder. The arrow indicates the anterior part of the specimen. Scale = 10 mm.



Figure 4. - Visceral anatomy of an angler, *Lophius piscatorius*, ventral view. The digestive tract has been put away. ab.cav: abdominal cavity; c.oe: cut oesophagus; k: kidneys; v: ventricle. The black arrow indicates the anterior part of the specimen. Scale = 10 mm.

Chanet *et al.*, 2005, 2007: 120, figs 3-4) and achirid species (Kobelkowsky, 2000: 55, fig. 2; Chanet *et al.*, 2007). This type of renal architecture was interpreted as a probable synapomorphy of the flatfishes of the family Soleidae by Chanet *et al.* (2005). Among the examined species and in the literature only soleid species exhibited such an asymmetry in the organization of the kidneys.

Dissections and RMI examinations (Chanet et al., 2012) show that Lophius piscatorius (Fig. 4), Balistes capriscus, Canthigaster compressa, Diodon liturosus, Melichthys vidua, Mola mola, Tetraodon cutcutia, Tetraodon mbu, Tetraodon palembangensis (Fig. 5) have two independent and rounded kidneys positioned far anteriorly on the dorsal surface of the abdominal cavity. This peculiar organisation of these organs was long ago described in Lophius piscatorius by Owen (1866) and Audigé (1910). The kidneys of Lophius piscatorius are known to be aglomerular (Beyenbach, 2004); the absence of glomeruli does not seem to have a phylogenetic value for the research of the interrelationships between the teleostean families, as it is widely spread among teleostean fishes (i.e. Saccopharyngidae, Syngnathidae, Belonidae, Gobiesocidae [Moore, 1933]). This absence does not occur in the kidney of related species such as Balistes vetula (Moore, 1933) or the genus Tetraodon (Kato et al., 2005).



Figure 5. - Visceral anatomy of a Buntal puffer, *Tetraodon palembangensis*, ventral view. The swimbladder and the digestive tract have been put away. ab.cav: abdominal cavity; c.oe: cut oesophagus; c.pc: cut pericardium; k: kidneys; v: ventricle. The black arrow indicates the anterior part of the specimen. Scale = 10 mm.

3) A compact thyroid nested in a thyroidian sinus

The structure of the thyroid gland was assessed in 135 acanthomorph species on the basis of dissections and the literature (Annex I). Among teleostean fishes, the organization of the thyroid gland is diverse: in most species the gland is diffuse, with scattered islets of follicles on the ventral margin of the basibranchials (Gudernatsch, 1910). In some species, these islets can be compact or form distinct lobes more or less gathered around the ventral aorta (Annex I). In some other groups, such as Cyprinodontiformes, some ectopic islets can spread to other organs from choroid to cephalic kidney (Fournie et al., 2005) (Annex I). Among the examined acanthomorph species (excluding Lophiiformes and Tetraodontiformes), Perca fluviatilis (Rolleston and Jackson, 1888), Solea senegalensis Kaup, 1858, Labrus bergylta, Capros aper, Sparus aurata (Campinho et al., 2006) and Spondyliosoma cantharus (Fig. 6) have a diffuse thyroid gland with separated islets in the aorta-branchial region with no visible ectopic islets in other organs (see table I for a survey of the structure of the thyroid gland among acanthomorph fishes).

The structure of the thyroid gland of *Lophius piscatorius* was described in detail by Burne (1927). In this species, this



Figure 6. - Sagittal section of a frozen of a black seabream, *Spond-yliosoma cantharus*, left lateral view. b.cav: buccal cavity; e: encephalon; s.c: spinal cord; th.i: thyroidian islets; v: ventricle. The black arrow indicates the anterior part of the specimen. Scale = 10 mm.

organ is peculiar in being embedded in a blood lacuna, forming a thyroidian sinus, closely associated with lymphatic vessels (Fig. 7). It is different from the compact thyroid gland described in Xiphias and scarid species, where the gland results from a gathering of several thyroidian lobes (Addison and Richter, 1932; Honma, 1956a, 1956b, 1956c, 1957). A compact thyroid nested in a blood lacuna was described as well in two tetraodontiform species: Cathidermis rotundatus (Balistidae) by Chiba et al. (1976) and Diodon hola*canthus* (Diodontidae). In these species, the thyroid gland is described as a compact organ closely surrounded by capillaries. A similarly organized thyroid gland has been described in L. piscatorius (Lophiidae) by Burne (1927). New dissections confirmed such a thyroid gland in this species and show the presence of a compact and highly vascularised thyroid in Ogcocephalus vespertilio (Ogcocephalidae), Balistes capriscus, Melichthys vidua (Balistidae), Ostracion cubicus, Tetrosomus gibbosus, Lactoria cornuta (Ostraciidae), Diodon holacanthus, Diodon liturosus (Diodontidae), Arothron nigropunctatus, Canthigaster compressa, Lagocephalus lagocephalus, Tetraodon cutcutia, Tetraodon palemban-



Figure 7. - The thyroid gland of an angler, *Lophius piscatorius*, right lateral view. ly.v: lymphatic vessels; th.a: thyroidian artery; th.s: thyroidian sinus. The black arrow indicates the anterior part of the specimen. Scale = 3 mm.



Figure 8. - Horizontal section in the thyroid gland of an ocean sunfish, *Mola mola*, ventral view. c.b.v: cut blood vessels; th.t: thyroidian tissue. The black arrow indicates the anterior part of the specimen. Scale = 30 mm.

gensis (Tetraodontidae), *Mola mola* (Molidae) (Annex I). In the ocean sunfish (*M. mola*), the organization of the thyroid gland has been studied both by a RMI examination (Chanet *et al.*, 2012) and by a dissection: the gland tissues form a

mesh surrounding blood vessels (Fig. 8) identical to what has been described by Burne (1927: 14, fig. 3) in *L. piscatorius*. The identification of these tissues as being thyroid in the ocean sunfish has been confirmed by histological examination.

4) An abbreviated spinal cord

In teleosts, the spinal cord extends all along the vertebral column in the medulla canal ventral to the neural arches (Serres, 1824; Owen, 1866; Kuhlenbeck, 1975). This architecture of the myelencephalon has been observed in *Capros*, *Perca, Sparus* and *Spondyliosoma* (Fig. 9).

In the ocean sunfish, *Mola mola* (Molidae), a reduced spinal cord was described numerous times (Serres, 1824; Vignal, 1881; Gregory and Raven, 1934; Kuhlenbeck, 1975: 110, fig. 61; Chanet *et al.*, 2012), it is a short tube-shaped organ which ends posteriorly in a cauda equina of fine nerves. Owen (1866: 272) described a similarly shortened spinal cord within the neural arch in *Diodon, Tetraodon* and *Lophius*. He emphasized this peculiarity among vertebrates. Serres (1824: 118) remarked the same thing in *Lophius*.

In L. piscatorius, the spinal cord is abbreviated; it does not extend back to the fourth or fifth abdominal vertebra (Fig. 10) (Chanet et al., 2012). Therefore, this organ is prolonged by a fairly thin filum terminale (Kuhlenbeck, 1975). An elongated spinal cord extending to the hypurals has been illustrated in the parasitic male of Haplophryne mollis (Lophiiformes, Linophrynidae) (Regan and Trewavas, 1932; Pietsch, 2009). But parasitic males retain larval and plesiomorphic characters and new examination of the specimens used by Regan and Trewavas (1932) is no longer possible as, unfortunately, the microscopical sections (specimen ZMUC P921777) have been lost (pers. com., M.A. Krag, Natural History Museum of Denmark, Copenhagen). Uehara and Ueshima (1986) described and illustrated the same organization of the spinal cord in several tetraodontiform species: two puffers, Takifugu pardalis and Takifugu poecilonotus (Tetraodontidae), two filefishes, Navodon modestus [=Thamnaconus modestus (Günther, 1877)] and Stephanolepis cirrhifer (Monacanthidae), and one triggerfish, Canthidermis maculates (Balistidae) (Uehara and Ueshima, 1986). In 2000, Uehara et al. described it too in Takifugu rubripes. Such an organization of the spinal cord could be viewed as a convergence linked to the mode of locomotion of these fishes, but the lophiiform and tetraodontiform species present a such wide range of swimming diversity from bottom-dwellers (anglerfishes, batfishes and frogfishes) to active swimmers, both pelagic (sunfishes) and benthic (puffers, filefishes, triggerfishes and boxfishes) that it negates that consideration.

5) An asymmetric liver

Owen (1866: 426) observed that "in many Fishes the two



Figure 9. - Parasagittal section on a frozen specimen of a black seabream, *Spondyliosoma cantharus*, left lateral view. k: kidney; ov: ovary; sb: swimbladder; s.c: spinal cord. The black arrow indicates the anterior part of the specimen. Scale = 20 mm.

lobes are subequal", but, on the same page, he mentioned that the liver of Lophius piscatorius has a strong asymmetry, with a far better developed left hepatic lobe. This organization has been recently observed by dissection (Fig. 11) and RMI examinations (Chanet et al., 2012) of an angler, by dissection of Ogcocephalus verpestilio and by dissections of the following tetraodontiform species: Arothron nigropunctatus, Balistes capriscus Canthigaster compressa, Diodon liturosus, Lactoria cornuta, Lagocephalus lagocephalus, Mola mola and Tetraodon mbu, and an MRI examination of an ocean sunfish (Chanet et al., 2012). Pietsch (2009: 16, fig. 16) showed the visceral organisation of a lophiiform species: a female Dolopichthys allector (Oneirodidae), from drawings of A.M. Westergren in Garman (1899). The liver appears to be voluminous in this species, but the figures do not permit observation of any hepatic asymmetry. On the DFL, this asymmetry is clearly visible in the MRI images of several lophiiform species: Lophiodes caulinaris (Lophiidae), Ogcocephalus darwini (Ogcocephalidae) and Chaenophryne draco (Oneirodidae). Unfortunately, it was not possible to determine asymmetry with confidence on the MRI images of the tetraodontiform species present in the DFL.

6) Clusters of supramedullary neurons in the rostral part of the spinal cord

Supramedullary neurons are peculiar giant neurons which are located mediodorsally on the spinal cord in teleostean species (Mola et al., 2001; Mola and Cuoghi, 2004). The function of these neurons is uncertain (Cuoghi et al., 2002); among several hypotheses, a role in the autonomic control of epidermal mucous glands has been proposed (Funakoshi et al., 1998). In Salmonidae, Syngnathidae, Cottidae, Labridae, Percidae and some Pleuronectiformes, these neurons are scattered along the spinal cord (Fig. 12A), and form a line of cells on the dorsal face of the spinal cord (Mola et al., 2001; Mola and Cuoghi, 2004). In Tetraodontiformes, Lophiiformes and Batrachoidiformes, these neurons are organized in a cluster present at the rostral extremity of the dorsal cord (Fig. 12B), between the medulla oblongata and spinal cord (Mola et al., 2001; Mola and Cuoghi, 2004; Cuoghi and Mola, 2007). These clustered cells are large, have very large nuclei, a large prominent nucleolus and small nucleoli (Mola and Cuoghi, 2004). The supramedullary neurons of Diodon and Lophius show a high DNA content from 8C in the smaller neurons to a maximum of 5000C in the larger ones (Sassi et al., 1995; Benedetti et al., 1999;



Figure 10. - The central nervous system of an angler (SL = 28.8 cm), *Lophius piscatorius*, dorsal view. cr.n.: cranial nerves; e.: encephalon; f.t.: filum terminale; op.n.: optic nerves; s.c.: spinal cord. The black arrow indicates the anterior part of the specimen. Scale = 50 mm.



Figure 11. - The asymmetric liver of an angler, *Lophius piscatorius*, dorsal view. l.h.l.: left hepatic lobe; r.h.l.: right hepatic lobe. The black arrow indicates the anterior part of the specimen. Scale = 50 mm.

Mola *et al.*, 2001; Mola and Cuoghi, 2004), a similar DNA content which is known only in the giant neurons of mollusks (Gillette, 1991; Mandrioli *et al.*, 2010). These values are interpreted as the results of endoreplication (Mola *et al.*, 2001; Mola and Cuoghi, 2004). The supramedullary neurons of *Solea ocellata* (Soleidae, Pleuronectiformes) were described by Cuoghi and Mola (2007); they differ from the above described types in being neither singularly aligned nor authentically clusterized, but instead form small groups of two or three neurons. Supramedullary neurons organized in clusters have been identified in tetraodontiform species (*Balistes capriscus* (Balistidae); *Diodon hystrix, Diodon*



Figure 12. - Schematic distribution of the supramedulary neurons among teleostean fishes [modified from Mola and Cuoghi (2004)]. A: Type I present in Salmonidae, Syngnathidae, Cottidae, Labridae, Percidae and some Pleuronectiformes; **B**: Type II present in Lophiiformes, Tetraodontiformes and Batrachoidiformes. Legend: 1: spinal cord; 2: central canal; 3: supramedulary neurons. The black arrow indicates the anterior part of the spinal cord.

holacanthus and Chilomycterus sp. (Diodontidae); Mola mola (Molidae); Sphaeroides maculates, Sphaeroides spengleri, Takifugu rubripes [Uehara et al., 2000) and Tetraodon fluviatilis (Tetraodontidae)] and lophiiform species [Histrio sp. and Pterophryne histrio (Antennariidae); Lophius piscatorius (Lophiidae)] (Mola and Cuoghi, 2004). These kinds of neurons were also mentioned in a toadfish, Opsanus tau (Linnaeus, 1766) (Batrachoididae) (Barry et al., 1986; Mola and Cuoghi, 2004), a member of the order Batrachoidiformes, previously considered as related to Lophiiformes (Pietsch. 2009), but now nested in clade with the Synbranchiformes and the Indostomidae (Miya et al., 2005). Miya et al. (2010: 5) indicate that "a sister-group relationship between the Lophiiformes and Batrachoidiformes was confidently rejected by the Bayesian analyses". Nevertheless, more work is needed to confirm homologies or assess possible homoplasies for the supramedullary neurons of Batrachoidiformes, Tetraodontiformes, and Lophiiformes. Barry et al. (1986) considered that the supramedullary neurons of Opsanus tau (Batrachoididae) are homologous to those of Chilomycterus sp. and Tetraodon sp. but that the supramedullary neurons of Opsanus tau differ from the supramedullary neurons of these two tetraodontiform species by their size and number. Barry et al. (1986) mentioned that the supramedullary neurons of Chilomycterus sp. and Tetraodon sp. are much larger and fewer in number. Thus, the homology of the supramedullary neurons of the Batrachoidiformes and those of the Lophiiformes and Tetraodontiformes can be questioned and needs to be further investigated. Nevertheless, the presence of clusters of large supramedullary neurons in the rostral part of the spinal cord can be hypothesised to be a probable synapomorphy of Lophiiformes and Tetraodontiformes.

DISCUSSION

The present study shows that: i) a reduced gill opening; ii) rounded and anteriorly disposed kidneys; iii) a compact thyroid nested in a thyroidian sinus; iv) an abbreviated spinal cord; v) an asymmetric liver; vi) clusters of supramedullary neurons in the rostral part of the spinal cord are probable derived states of characters for Lophiiformes and Tetraodontiformes. This work reports possible anatomical synapomorphies of these groups, but, as the characters proposed by Nakae and Sazaki (2010), these hypotheses of primary homology have to be confirmed by a phylogenetic analysis using additional characters from a larger sample of species of both orders. However, for the present work, these putative synapomorphies could not be investigated in additional acanthomorph species, such as more species of Lophiiformes and Batrachoidiformes, nor in specimens of the following families: Scatophagidae, Cepolidae, Priacanthidae and Callanthiidae. The dissections assessing the organization of the six structures studied herein have to be conducted on fresh animals; it has not been possible for us to do so on specimens of the abovementioned groups. Using the techniques of modern imaging, such as CT-scan or MRI, could be a solution to both preserve specimens and investigate their internal anatomy (Chanet et al., 2009a; Chanet and Guintard, 2012; Chanet et al., 2012). But we doubt that it would be actually possible to identify with MRI such minute structures as thyroid islets. Recently, we had the opportunity to conduct a CT-scan examination on an alcohol preserved Scatophagus tetracanthus (specimen MNHN 1999-0202, Scatophagidae). None of the six characters studied herein could be detected. Chanet et al. (2012) mentioned that a long cystic duct opening anteriorly close to the stomach was present in Lophius piscatorius and Mola mola. Further dissections on these species and on Balistes capriscus confirmed the presence of this character. But as it could not be observed in the other examined fishes (Annex I), this character cannot be considered as a putative common character between Lophiiformes and Tetraodontiformes.

Nevertheless, the present study shows the interest of correlating anatomical and molecular works. Several anatomical structures of these taxa, like the abbreviated spinal cord or the supramedullary neurons organized in clusters, were viewed as peculiarities and autapomorphies of each group. For instance, the abbreviated spinal cord and shape of these fishes, which were regarded as having "*an enormous swimming head with a short trunk*" (Kuhlenbeck, 1975; Uehara and Ueshima, 1986). However, the present work shows for the first time that these formerly viewed peculiarities might be the result and the witness of common ancestry. Of course, these observations are preliminary and the next step will be to collect, dissect and examine more fresh specimens, especially, but not only, lophilform species. Then, these data will be incorporated in a data matrix gathering more species and more anatomical characters to try to decipher and establish the characters uniting Lophiiformes and Tetraodontiformes in a restricted clade N with the Scatophagidae, Cepolidae, Priacanthidae and Callanthiidae. It should be borne in mind that the first clue assessing this putative relationship was the result of comparative analysis on mitochondrial sequences. Molecular studies limit and propose the species to be sampled for anatomical studies, just as they provided new data to indicate relationships, which were not previously suspected.

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Order/suborder	Family	Genus/species	Structure of the thyroid gland	References
Lampridiformes	Trachipteridae	Trachipterus ishikawae Jordan & Snyder, 1901	diffuse	Honma <i>et al</i> . (2005)
Gadiformes	Gadidae	Gaidropsarus mediterraneus (Linnaeus, 1758)	diffuse	dissection
	Gadidae	Gadus morhua Linnaeus, 1758	diffuse	Woodhead (1959)
	Gadidae	Melanogrammus aeglefinus (Linnaeus, 1758)	diffuse	Zenzerov (1986)
	Gadidae	Pollachius pollachius (Linnaeus, 1758)		dissection
	Gadidae	Trisopterus luscus (Linnaeus, 1758)		dissection
Zeiformes	Zeidae	Zeus faber Linnaeus, 1758	diffuse	dissection
Batrachoidiformes	Batrachoididae	Opsanus tau (Linnaeus, 1766)	diffuse	Gudernatsch (1910)
Gobioidei	Gobiidae	<i>Gymnogobius urotaenia</i> (Hilgendorf, 1879)	diffuse	Harada <i>et al</i> . (2003)
	Gobiidae	Gobius paganellus Linnaeus, 1758	diffuse	Vivien (1941)
	Gobiidae	Leucopsarion petersii Hilgendorf, 1880	diffuse	Tamura and Honma (1970), Harada <i>et al.</i> (2003)
Synbranchiformes	Synbranchidae	Monopterus albus (Zuiew, 1793)	diffuse	Wai-Sum and Chan (1974)
	Synbranchidae	Monopterus cuchia (Hamilton, 1822)	diffuse	Srivastava and Sathyanesan (1967)
Channoïdes	Channidae	Channa punctata (Bloch, 1793)	diffuse	Ram et al. (1989)
	Channidae	Channa gachua (Hamilton, 1822)	diffuse	Roy et al. (2000)
(Percoidei)	Trichiuridae	<i>Lepidopus caudatus</i> (Euphrasen, 1788)	gathered lobes	dissection
Scombroidei	Scombridae	Auxis thazard thazard (Lacepède, 1800)	gathered lobes	Honma (1957)
	Scombridae	Scomber japonicus Houttuyn, 1782	gathered lobes	Honma (1957)
	Scombridae	Thunnus albacares (Bonnaterre, 1788)	gathered lobes	Honma (1957)
	Scombridae	Sarda sarda (Bloch, 1793)	gathered lobes	Gudernatsch (1910)
	Scombridae	Scomber scombrus Linnaeus, 1758	gathered lobes	dissection
	Scombridae	Thunnus thynnus (Linnaeus, 1758)	gathered lobes	Honma (1956a)
Syngnathoidei	Syngnathidae	<i>Phyllopteryx taeniolatus</i> (Lacepède, 1804)	diffuse	H. Schmidt-Posthaus (pers. com.)
	Syngnathidae	Syngnathus fuscus Storer, 1839	diffuse	Gudernatsch (1910)
Callionymoidei	Callionymidae	Callionymus lyra Linnaeus, 1758	diffuse	dissection
Mulloidei	Mullidae	Mullus surmuletus Linnaeus, 1758	diffuse	dissection
Cichloidei	Cichlidae	Rocio octofasciata (Regan, 1903)	diffuse	Mattheij et al. (1971)
	Cichlidae	<i>Oreochromis mossambicus</i> (Peters, 1852)	diffuse	Shukla and Pandey (1986), Geven <i>et al</i> . (2007)
	Cichlidae	Oreochromis niloticus (Linnaeus, 1758)	diffuse	Nacario (1983)
	Cichlidae	Oreochromis spilurus (Günther, 1894)	diffuse	Al-Hussaini and Rizkalla (1957)
Mugiliformes	Mugilidae	Liza parsia (Hamilton, 1822)	diffuse	Pandey et al. (1995)
	Mugilidae	Liza aurata Risso, 1810	diffuse	Leray and Febvre (1968)
	Mugilidae	Mugil cephalus Linnaeus, 1758	diffuse	Gudernatsch (1910), Weng <i>et al</i> . (2003)
(Percoidei)	Pomacentridae	Amphiprion frenatus Brevoort, 1856	diffuse	D.F. Putra (pers. com.)
	Pomatomidae	Pomatomus saltatrix (Linnaeus, 1766)	diffuse	Gudernatsch (1910)

Annex I. - Structure of the thyroid gland among acanthomorph species. Systematics follow Nelson (2006), modified according to the proposals of Li *et al.* (2009). Paraphyletic groups are indicated in brackets.

Order/suborder	Family	Genus/species	Structure of the thyroid gland	References
(Percoidei)	Eleotridae	Oxyeleotris marmorata (Bleeker, 1852)	diffuse	Abol-Munafi et al. (2005)
Cyprinodontiformes	Adrianichthyidae	Oryzias latipes (Temminck & Schlegel, 1846)	diffuse	Fournie et al. (2005)
	Cyprinodontidae	<i>Cyprinodon variegatus</i> Lacepède, 1803	diffuse with ectopic renal islets	Fournie et al. (2005)
	Notobranchiidae	Nothobranchius guentheri (Pfeffer, 1893)	diffuse with ectopic renal islets	Markofsky and Milstoc (1979), Fournie <i>et al.</i> (2005)
	Poeciliidae	Xiphophorus alvarezi Rosen, 1960	diffuse	Bailey (1933)
	Poeciliidae	<i>Xiphophorus maculatus</i> (Günther, 1866)	diffuse with ectopic renal islets	Baker (1958)
	Poeciliidae	<i>Xiphophorus montezumae</i> Jordan & Snyder, 1899	diffuse with ectopic renal islets	Baker (1959)
	Rivulidae	Nematolebias whitei (Myers, 1942)	diffuse	Ruijter et al. (1987)
Blennoidei	Blenniidae	Parablennius gattorugine (Linnaeus, 1758)	diffuse	dissection
(Percoidei)	Embiotocidae	<i>Cymatogaster aggregata</i> Gibbons, 1854	diffuse	Brar (2009), Brar <i>et al</i> . (2010)
Beloniformes	Belonidae	Belone belone (Linnaeus, 1761)	diffuse	dissection
Atherinomorphes	Menidiinae	Menidia beryllina (Cope, 1867)	diffuse	Fournie et al. (2005)
	Menidiinae	Menidia menidia (Linnaeus, 1766)	diffuse	Gudernatsch (1910)
Caranginomorphes	Sphyraenidae	Sphyraena afra Peters, 1844	gathered lobes	dissection
	Xiphiidae	Xiphias gladius Linnaeus, 1758	gathered lobes	Addison and Richter (1932)
	Istiophoridae	Istiophorus platypterus (Shaw, 1792)	gathered lobes	Honma (1956b), Chiba and
				Honma (1980)
	Istiophoridae	Kajikia audax (Philippi, 1887)	gathered lobes	Honma (1957)
	Polynemidae	Polynemus sexfilis (Valenciennes, 1831)	diffuse	Qureshi et al. (1978)
	Carangidae	Echeneis naucrates Linnaeus, 1758	compact	Honma and Yoshie (1974)
	Carangidae	Seriola lalandi Valenciennes, 1833	gathered lobes	Honma (1956C)
	Carangidae	Seriola quinqueradiata Temminck & Schlegel, 1845	gathered lobes	Honma (1956C)
	Carangidae	Trachurus trachurus (Linnaeus, 1758)	gathered lobes	dissection
	Rachycentridae	Rachycentron canadum (Linnaeus, 1766)	gathered lobes	T. Passos de Andrade (pers. com.)
	Coryphaenidae	Coryphaena sp.	gathered lobes	Honma (1957)
Pleuronectiformes	Soleidae	Solea solea (Linnaeus, 1758)	diffuse	dissection
	Soleidae	Solea senegalensis Kaup, 1858	diffuse	Klarena <i>et al</i> . (2008), Ortiz- Delgado <i>et al</i> . (2006)
	Pleuronectidae	Hippoglossus hippoglossus (Linnaeus, 1758)	diffuse	Einarsdóttir et al. (2006)
	Pleuronectidae	Pseudopleuronectes americanus (Walbaum, 1792)	diffuse	Gudernatsch (1910)
	Pleuronectidae	Microstomus kitt (Walbaum, 1792)	diffuse	dissection
	Pleuronectidae	Pleuronectes platessa Linnaeus, 1758	diffuse	Cole and Johnstone (1902), dissection
	Pleuronectidae	Platichthys stellatus (Pallas, 1787)	diffuse	Hickman (1959)
	Pleuronectidae	Verasper moseri Jordan & Gilbert, 1898	diffuse	Chiba <i>et al</i> . (2004)
	Paralichthyidae	Paralichthys californicus (Ayres, 1859)	diffuse	Gisbert <i>et al.</i> (2004)

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	Paralichthyidae	Paralichthys olivaceus (Temminck & Schlegel, 1846)	diffuse	Tanaka et al. (1995)
	Scophthalmidae	Lepidorhombus whiffiagonis (Walbaum, 1792)	diffuse	dissection
	Scophthalmidae	Scophthalmus maximus (Linnaeus, 1758)	diffuse	Chanet et al. (2009b), dissection
	Scophthalmidae	Scophthalmus rhombus (Linnaeus, 1758)	diffuse	Hachero-Cruzado et al. (2009)
(Percoidei)	Sciaenidae	Cynoscion regalis (Bloch & Schneider, 1801)	diffuse	Gudernatsch (1910)
	Sciaenidae	Micropogon undulates (Linnaeus, 1766)	diffuse	Gudernatsch (1910)
(Percoidei)	Chaetodontidae	Chelmon rostratus (Linnaeus, 1758)	diffuse	dissection
Labroidei	Labridae	Labrus bergylta Ascanius, 1767	diffuse	Dunaevskaya (2010), dissection
	Labridae	Labrus mixtus Linnaeus, 1758	diffuse	dissection
	Labridae	Ctenolabrus rupestris (Linnaeus, 1758)	diffuse	dissection
	Labridae	Semicossyphus reticulatus (Valenciennes, 1839)	gathered lobes	Honma (1957)
	Labridae	Symphodus melops (Linnaeus, 1758)	diffuse	dissection
	Labridae	Tautoga onitis (Linnaeus, 1758)	diffuse	Gudernatsch (1910)
	Labridae	Tautogolabrus adspersus (Walbaum, 1792)	diffuse	Gudernatsch (1910)
	Scaridae	Scarus guacamaia Cuvier, 1829	gathered lobes	Matthews (1948)
	Scaridae	Scarus dubius Bennett, 1828	gathered lobes	Honma (1957), Grau <i>et al.</i> (1986)
	Scaridae	Sparisoma sp.	gathered lobes	Matthews and Smith (1948)
(Percoidei)	Moronidae	Dicentrarchus labrax (Linnaeus, 1758)	diffuse	Schnitzler <i>et al.</i> (2008), dissection
	Moronidae	Morone americana (Gmelin, 1789)	diffuse	Gudernatsch (1910)
Gasterosteiformes	Gasterosteidae	Gasterosteus aculeatus Linnaeus, 1758	diffuse	Hamada (1975), Honma <i>et al.</i> (1977)
Zoarcoidei	Anarhichadidae	Anarhichas lupus Linnaeus, 1758	diffuse	Falk-Petersen and Hansen (2001)
	Pholidae	Pholis gunnellus (Linnaeus, 1758)	diffuse	Gudernatsch (1910)
Serraniformes	Cottidae	Cottus kazika Jordan & Starks, 1904	diffuse	Mukai and Otta (1995)
	Cottidae	Leptocottus armatus Girard, 1854	diffuse	Brar (2009), Brar <i>et al</i> . (2010)
	Cottidae	Myoxocephalus scorpius (Linnaeus, 1758)	diffuse	Matishov et al. (2009)
	Cottidae	Scorpaenichthys sp.	diffuse	Burne (1927)
	Cottidae	Trachidermus fasciatus Heckel, 1837	diffuse	Bingxu et al. (2010)
	Cyclopteridae	Aptocyclus ventricosus (Pallas, 1769)	compact	Honma (1957)
	Triglidae	Trigla lyra Linnaeus, 1758	diffuse	dissection
	Scorpaenidae	Sebastes norvegicus (Ascanius, 1772)	diffuse	dissection
	Scorpaenidae	Sebastiscus marmoratus (Cuvier, 1829)	diffuse	Zhang et al. (2009)
	Scorpaenidae	Sebastes schlegelii Hilgendorf, 1880	diffuse	Kang and Chang (2005), Chin <i>et al</i> . (2010)
	Serranidae	<i>Epinephelus aeneus</i> (Geoffroy Saint- Hilaire, 1817)	diffuse	Abbas et al. (2012)

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	Serranidae	<i>Epinephelus coioides</i> (Hamilton, 1822)	diffuse	Tang <i>et al</i> . (2010)
	Serranidae	Paralabrax clathratus (Girard, 1854)	diffuse	Fournie <i>et al</i> . (2005)
	Serranidae	Serranus hepatus (Linnaeus, 1758)	diffuse	Ramos and Da Conceiçao Peleteiro (2001)
	Percidae	Perca flavescens (Mitchill, 1814)	diffuse	Levesque et al. (2003)
	Percidae	Perca fluviatilis Linnaeus, 1758	diffuse	Rolleston and Jackson (1888), dissection
	Percidae	Sander lucioperca (Linnaeus, 1758)	diffuse	dissection
Notothenioïdes	Channichthyidae	<i>Chaenocephalus aceratus</i> (Lönnberg, 1906)	diffuse	Twelves <i>et al.</i> (1975)
	Nototheniidae	Notothenia neglecta Nybelin, 1951	diffuse	Twelves et al. (1975)
	Nototheniidae	<i>Trematomus bernacchii</i> Boulenger, 1902	diffuse	Hureau (1963, 1970)
	Nototheniidae	Trematomus hansoni Boulenger, 1902	diffuse	Hureau (1963, 1970)
(Percoidei)	Oplegnathidae	<i>Oplegnathus fasciatus</i> (Temminck & Schlegel, 1844)	gathered lobes	Honma (1957)
	Pomacanthidae	Pomacanthus imperator (Bloch, 1787)	diffuse	dissection
	Pomacanthidae	<i>Centropyge multispinis</i> (Playfair, 1867)	diffuse	dissection
Acanthuroidei	Acanthuridae	Acanthurus achilles Shaw, 1803	diffuse	dissection
	Acanthuridae	Acanthurus lineatus (Linnaeus, 1758)	diffuse	dissection
Sparoidei	Sparidae	Acanthopagrus latus (Houttuyn, 1782)	diffuse	Havasi <i>et al.</i> (2010), Salamat <i>et al.</i> (2012)
	Sparidae	Dentex dentex (Linnaeus, 1758)	diffuse	Santamaria et al. (2004)
	Sparidae	Pagrus auriga Valenciennes, 1843	diffuse	Sánchez-Amaya et al. (2007)
	Sparidae	Sparus aurata Linnaeus, 1758	diffuse	Campinho <i>et al</i> . (2006), dissection
	Sparidae	Spondyliosoma cantharus (Linnaeus, 1758)	diffuse	dissection
	Sparidae	Stenotomus chrysops (Linnaeus, 1766)	diffuse	Gudernatsch (1910)
Caproidei	Caproidae	Capros aper (Linnaeus, 1758)	diffuse	dissection
Lophiiformes	Lophiidae	Lophius piscatorius Linnaeus, 1758	compact in a blood sinus	Burne (1927), dissection
	Ogcocephalidae	Ogcocephalus vespertilio (Linnaeus, 1758)	compact in a blood sinus	dissection
Tetraodontiformes	Balistiidae	Balistes capriscus Gmelin, 1789	compact in a blood sinus	dissection
	Balistiidae	<i>Canthidermis rotundatus</i> Marion de Procé, 1822	compact in a blood sinus	Chiba <i>et al</i> . (1976)
	Balistiidae	Melichthys vidua (Richardson, 1845)	compact in a blood sinus	dissection
	Diodontidae	Diodon holacanthus Linnaeus, 1758	compact in a blood sinus	Chiba and Honma (1981), dissection
	Diodontidae	Diodon liturosus Shaw, 1804	compact in a blood	dissection
	Molidae	Mola mola (Linnaeus, 1758)	compact in a blood	dissection
	Ostraciidae	Ostracion cubicus Linnaeus, 1758	compact in a blood sinus	dissection

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	Ostraciidae	Tetrosomus gibbosus (Linnaeus, 1758)	compact in a blood sinus	dissection
	Ostraciidae	Lactoria cornutal (Linnaeus, 1758)	compact in a blood sinus	dissection
	Tetraodontidae	Arothron nigropunctatus (Bloch & Schneider, 1801)	compact in a blood sinus	dissection
	Tetraodontidae	<i>Canthigaster compressa</i> (Marion de Procé, 1822)	compact in a blood sinus	dissection
	Tetraodontidae	Lagocephalus lagocephalus (Linnaeus, 1758)	compact in a blood sinus	dissection
	Tetraodontidae	Tetraodon cutcutia Hamilton, 1822	compact in a blood sinus	dissection
	Tetraodontidae	Tetraodon palembangensis Bleeker, 1852	compact in a blood sinus	dissection