The anatomy of the thyroid gland among “fishes”: phylogenetic implications for the Vertebrata

by

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Abstract. – A study on the structure of the thyroid gland of 288 vertebrate species, conducted both on 99 dissections and analysis of the literature, leads to propose the following interpretations: i) the presence of this gland is a synapomorphy of Vertebrata; ii) a compact gland is a synapomorphy of Gnathostomes; iii) a diffuse gland is a possible synapomorphy of Halecostomes; iv) several independent cases of concentration in a few lobes in several groups, like Scaridae, Scombridae and some Carangimorphariae occurred and even a compact gland in Osteoglossomorphes. Moreover, the scattering of thyroidian islets in other organs (cephalic kidney, choroid,…) has occurred several times in teleost lineages and a compact thyroid gland embedded in a blood sinus appears to be a probable synapomorphy of Tetraodontiformes and Lophiiformes.

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Résumé. – L’anatomie de la glande thyroïde chez les “poissons” : implications phylogénétiques chez les vertébrés.

Une étude de la structure de la thyroïde chez 288 espèces de vertébrés, menée à partir de 99 dissections et d’analyses de la littérature, permet de proposer les interprétations suivantes: i) la présence de cette glande est une synapomorphie des vertébrés ; ii) une glande compacte est une synapomorphie des gnathostomes ; iii) une thyroïde diffuse est une synapomorphie possible des halécostomes ; iv) il existe plusieurs cas indépendants de concentration en quelques lobes chez les Scaridae, les Scombridae et certains Carangimorphariae, et même une thyroïde compacte chez les Osteoglossomorphes. Enfin, un éparpillement d’îlots thyroïdiens dans d’autres organes (rein céphalique, choroïde,…) est apparu plusieurs fois chez les téléostéens et une thyroïde compacte incluse dans un sinus sanguin est une probable synapomorphie des Tetraodontiformes et des Lophiiformes.

Key words
Vertebrata
Chondrichthyes
Actinopterygii
Thyroid gland
Anatomy
Phylogeny

The role of the thyroid gland in vertebrate physiology has been, and is still, the subject of many studies (e.g. Marine, 1913; Hoar, 1951; Geven *et al.,* 2007; Dufour *et al.,* 2012). Its importance for metabolism regulation, growth and metamorphosis has been studied in details and for a long time (Olivereau, 1954; Fontaine and Fontaine, 1957, 1962; Olivereau *et al*., 1964; Eales, 1979; Leatherland, 1982, 1988; Dufour *et al*., 2012, among many others). Moreover, the thyroidian follicles can accumulate numerous environmental chemicals (such as hydrocarbons, organochlorine and organophosphorous pesticides, cyanide compounds, methyl bromide, phenols, ammonia, metals, sex steroids, and many pharmaceutical products) (Brown *et al*., 2004a). Consequently, studying the composition of these organs can reveal to which environmental pollutants an animal has been exposed (Brown *et al.,* 2004a). In that perspective, localizing these follicles is the first and fundamental step of both physiological and toxicological investigations. However, surprisingly the anatomical structure of this endocrine gland has not really been reported among vertebrates and the question of its evolution within this group has been poorly studied. A few studies related the thyroid structure only in some subgroups without taking into account the diversity of this clade. In a few words, the thyroid is often viewed as a diffuse gland in “lower” vertebrates (i.e. “fishes”), while in “higher” vertebrates (mammals, birds and relatives) this gland presents a compact structure (Porreca, 2010; Fagman and Nilsson, 2010). Nevertheless, the anatomic diversity cannot be considered on the basis of such simple shortcuts and the diversity of the thyroid gland anatomy has to be examined in more details before suggesting possible hypotheses regarding the evolution of this organ.

The thyroid gland was first identified in vertebrates by the English physician Thomas Wharton in 1656 (Kunz, 2004) and in “fishes” by Simon (1844), even if he confused this organ with the pseudobranch in several species (Todd, 1849-1852; Owen, 1866; Gudernatsch, 1910). More than twenty years before, Retzius (1819) has described a sublingual gland in a skate: *Raja fullonica* [= *Leucoraja fullonica* (L., 1758)] (Retzius, 1819: 54, fig. 7). An examination of this figure leads us to conclude, like Todd (1849-1852) and Owen (1866), that this sublingual gland is a compact thyroid. Nevertheless, these two authors considered that the gland was a more or less compact structure in vertebrates; Owen (1866)

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studied the thyroid only in species where the gland forms a single and compact structure.

The diffuse structure of the thyroid gland in teleostean fishes was assessed later by Baber (1881), Maurer (1886) and Gudernatsch (1910). Consequently, the structural diversity of this gland within vertebrates was already pointed out at the end of the 19th century. In some species, as skates, sharks, frogs, crocodiles, birds and mammals, the gland is a compact, sometimes bilobed, encapsulated organ (Owen, 1866; Baber, 1881), while in others, as teleosteans, the gland is diffuse, not encapsulated, with scattered islets of follicles in the branchial region, close to the ventral aorta (Gudernatsch, 1910; Baker, 1958). Some ectopic thyroidian follicles may be present as well in the cephalic kidney as in the choroid of some species (Chavin, 1956; Baker, 1958; Fournie *et al*., 2005). Schlumberger and Lucke (1948) and Fournie *et al*. (2005) noticed that these highly scattered follicles have been often mistaken with invading neoplastic, tumorous structures [see Schlumberger and Lucke, 1948; Hoover, 1984; Fournie *et al*., 2005) for reports of thyroidian pathologies (tumours and goitres) in "fishes"]. Some cases of compact thyroid were described in several acanthomorphs, like scarids (Matthews and Smith, 1948), and in dipnoans (Parker, 1890; Olivereau, 1959; Chavin, 1976) and in the Comorian coelacanth (Chavin, 1972, 1976). A peculiar thyroid gland, embedded in a blood sinus, was studied in the angler, *Lophius piscatorius* Linnaeus, 1758 (Lophiidae) (Burne, 1927). This short survey shows that the thyroid gland presents a diversity of anatomical patterns within "fishes" and that the simple scheme assessing that this gland is diffuse in "lower" vertebrates and compact in "higher" vertebrates cannot be considered as valid. The purpose of the present study is to question that item in studying the structure of the thyroid gland among vertebrates, with a special focus on "fishes" that represent more than 50% of the vertebrate taxa, and to map the identified states on recent phylogenies to try to decipher the evolution of the gland and proposing possible synapomorphies for some clades regarding the structure of the thyroid gland.

MATERIAL AND METHODS

Taxonomic names have been checked in Eschmeyer and Fricke (2010). The structure of the thyroid gland has been identified by dissecting 99 animals, belonging to 65 species and 43 vertebrate families 41, of which are osteichthyan families. Animals have been fished, purchased dead at fishmongers or at fish market auctions; some of them have been provided by fishermen or by the directors of show aquariums. A few specimens have been purchased in pet shops. For each species, successive brackets indicate the number of examined specimens, the total length (TL), the standard length (SL) or the head length (HL) and the origin of the specimen. The used classification of "fishes" follows Nelson (2006) and Betancur-R *et al*. (2013b) for actinopterygian taxa.

The dissected specimens are:

CHONDRICHTHYES, Carcharhiniformes, Scyliorhinidae: *Scyliorhinus canicula* (2) (mean SL: 81 cm), purchased at fishmonger, fished off the East Atlantic Ocean coast). Torpediniformes, Torpedinidae: *Torpedo marmorata* (1) (SL: 65 cm), purchased at fishmonger, fished off the East Atlantic Ocean coast).

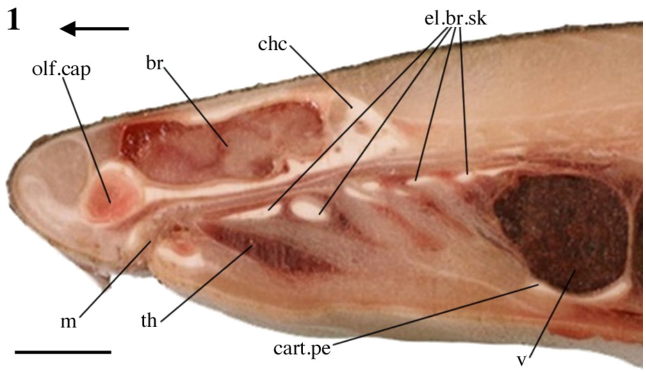
OSTEICHTHYES, Actinopterygii, Neopterygii, Lepisosteidae: *Lepisosteus osseus* (1), isolated head (HL: 23 cm, fished in the Chesapeake Bay, Virginia, USA). Teleostei, Elopomorphes, Anguillidae: *Anguilla anguilla* (1) (SL: 73 cm, purchased at fishmonger, fished off the East Atlantic Ocean coast), Congridae: *Conger conger* (1), isolated head (HL: 21 cm, purchased at fishmonger, fished off the East Atlantic Ocean coast), Megalopidae: *Megalops atlanticus* (1), isolated head (HL: 22 cm, from the Aquarium Mare Nostrum, Montpellier, France). Osteoglossomorpha, Notopteridae: *Chitala chitala* (1) (SL: 57 cm, from the Aquarium de la Porte Dorée, Paris, France), Osteoglossidae: *Osteoglossum biccirhosum* (1) (SL: 75 cm) (from the Aquarium de la Porte Dorée, Paris, France). Ostariophysii, Cypriniformes, Cyprinidae: *Abramis brama* (1) (SL: 25.8 cm, purchased at fishmonger, France), *Cyprinus carpio* (1) (SL: 42.3 cm, purchased at fishmonger, France). Salmoniformes, Salmonidae: *Salvelinus alpinus* (2) (SL: 34 cm, purchased at fishmonger, France), *Salmo trutta* (2) (SL: 25.8 cm and 26.2 cm, purchased at fishmonger, France). Acanthomorphes, Lampriformes, Lampridae: *Lampris immaculatus* (1) (SL: 60 cm, fished in the Kerguelen Islands, Indian Ocean). Gadiformes, Gadidae: *Gaidropsarus mediterraneus* (1) (SL: 9.5 cm, fished in the English Channel), *Pollachius pollachius* (1), isolated head (HL: 19 cm, purchased at fishmonger, fished off the East Atlantic Ocean coast), *Trisopterus luscus* (1) (SL: 23.2 cm, purchased at fishmonger, fished in the Atlantic Ocean). Zeiformes, Zeidae: *Zeus faber* (1) (SL: 30.5 cm, purchased at fishmonger, fished off the East Atlantic Ocean coast). Syngnathiformes, Callionymidae: *Callionymus lyra* (2) (11.7 cm and 13.2 cm, purchased at fishmonger, fished in the English Channel), Mullidae: *Mullus surmuletus* (1) (SL: 20.3 cm, purchased at fishmonger, fished off the East Atlantic Ocean coast). Scombriformes, Scombridae: *Scomber scombrus* (4) (mean SL: 30 cm, purchased at fishmonger, fished off the East Atlantic Ocean coast), Trichiuridae: *Lepidopus caudatus* (6) (SL: 70.5 cm, 73 cm, 73.5 cm, 79 cm, 91 cm and 104 cm, fished off the East Atlantic Ocean coast). Carangimorphariae, Carangiformes, Carangidae: *Trachurus trachurus* (1) (SL: 33.8 cm) (purchased at fishmonger, fished off the East Atlantic Ocean coast), Sphyraenidae: *Sphyraena afra* (1), isolated head (HL: 21.3 cm, fished off the coasts of Gabon), Pleuronectiformes, Pleuronectidae: *Microstomus kitt* (1) (SL: 24.1 cm), purchased at fishmonger, fished off the East Atlantic Ocean coast), *Pleuronectes platessa* (1) (SL: 30.5 cm, purchased at fishmonger, fished in the English Channel), Scophthalmidae: *Lepidorhombus whiffiagonis* (1) (SL: 27.4 cm, purchased at fishmonger, fished off the East Atlantic Ocean coast), *Scophthalmus maximus*

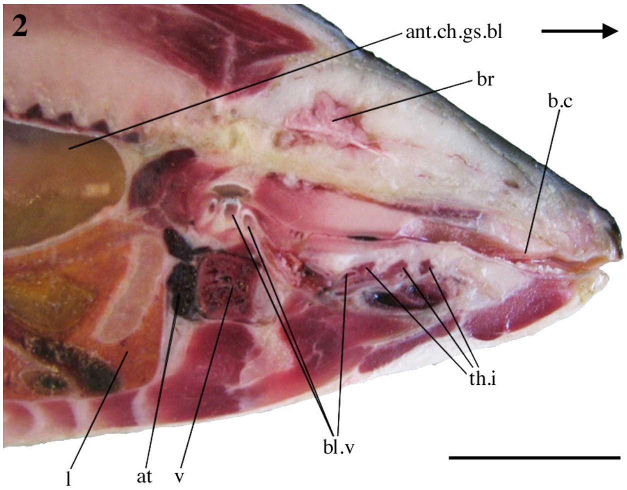
(4) (mean SL: 37.8 cm, purchased at fishmonger, fished off the East Atlantic Ocean coast), Soleidae: *Solea solea* (5) (mean SL: 24.5 cm, purchased at fishmonger, fished on the East coasts the Atlantic Ocean). Ovalentaria, Beloniformes, Belonidae: *Belone belone* (1) (76 cm, purchased at fishmonger, fished off the East Atlantic Ocean coast). Blenniiformes, Blenniidae: *Parablennius gattorugine* (1) (SL: 11.8 cm, fished in the English Channel). Percomorpharia, Pomacanthidae: *Centropyge multispinis* (1) (7.9 cm, from a private aquarium), *Pomacanthus imperator* (1) (SL: 12.6 cm, from a private aquarium). Caproidae: *Capros aper* (2) (SL: 9.4 cm; 10.5 cm, from the Aquarium Mare Nostrum, Montpellier, France), Chaetodontidae: *Chelmon rostratus* (1) (SL: 11.2 cm, from a private aquarium), Moronidae: *Dicentrarchus labrax* (4) (mean SL: 33 cm, purchased at fishmonger, fished in the Atlantic Ocean). Labriformes, Labridae: *Labrus bergylta* (2) (SL: 23.8 cm), one isolated head (HL: 11.3 cm, purchased at fishmonger, fished in the Atlantic Ocean), *Labrus mixtus* (1) (SL: 24.8 cm, fished off the East Atlantic Ocean coast), *Symphodus melops* (1) (SL: 10.6 cm, fished off the East Atlantic Ocean coast), *Ctenolabrus rupestris* (1) (SL: 11.4 cm, fished off the East Atlantic Ocean coast). Spariformes, Sparidae: *Sparus aurata* (3) (mean SL: 18 cm, purchased at fishmonger, fished off the East Atlantic Ocean coast); *Spondyliosoma cantharus* (4) (mean SL: 24 cm, purchased at fishmonger, fished off the East Atlantic Ocean coast). Lophiiformes, Lophiidae: *Lophius piscatorius* (4) (SL: 27.6 cm; 28.5 cm and 57.3 cm), one isolated head (HL: 24.2 cm, purchased at the fish auction of Concarneau, France, fished off the East Atlantic Ocean coast), Ogcocephalidae: *Ogcocephalus vespertilio* (1) (SL: 18.8 cm, from the Aquarium Mare Nostrum, Montpellier, France). Tetraodontiformes, Balistiidae: *Balistes capriscus* (1) (SL: 30 cm, fished off the East Atlantic Ocean coast), *Melichthys vidua* (1) (SL: 12.3 cm, from the Aquarium Mare Nostrum, Montpellier, France), Diodontidae: *Diodon holacanthus* (1) (SL: 23.2 cm, from the Aquarium Mare Nostrum, Montpellier, France), *Diodon liturosus* (1) (SL: 18.5 cm, from the Aquarium of Vannes, Vannes, France), Molidae: *Mola mola* (1) (TL: 142 cm, fished in the English Channel), Ostraciidae: *Lagocephalus lagocephalus* (1) (SL: 39.3 cm, fished in the Atlantic Ocean), *Ostracion cubicus* (1) (SL: 14.7 cm, from the Aquarium Mare Nostrum, Montpellier, France), *Tetrosomus gibbosus* (1) (SL: 7.4 cm, from the Aquarium of Vannes, Vannes, France), *Lactoria cornuta* (1) (SL: 28.3 cm, from the Aquarium of Vannes, Vannes, France), Tetraodontidae: *Tetraodon mbu* (1) (31.6 cm, from the Aquarium de la Porte Dorée, Paris, France), *Tetraodon palembangensis* (1) (SL: 8.8 cm, purchased alive at Europrix, Lens, France), *Canthigaster compressa* (1) (SL: 6.4 cm, from the Aquarium of Vannes, Vannes, France), *Arothron nigropunctatus* (1) (SL: 25.6 cm, from the Aquarium Mare Nostrum, Montpellier, France). Acanthuriformes, Acanthuridae: *Acanthurus achilles* (1) (SL: 8.8 cm, from a private aquarium), *Acanthurus lineatus* (1) (SL: 16.4 cm, from a private aquarium). Perciformes (= Serraniformes *sensu* Lautredou *et al*. (2013)), Percidae: *Perca fluviatilis* (2) (SL: 36.2 cm; 37.5 cm, purchased at fishmonger, France), *Sander lucioperca* (1) (SL: 59.6 cm, purchased at fishmonger, France), Sebastidae: *Sebastes norvegicus* (2) (SL: 35.1 cm; 44.9 cm, purchased at a fishmonger, France), Triglidae: *Trigla lyra* (2) (SL: 24.5 cm), one isolated head (HL: 10.4 cm, purchased at the fish auction of Concarneau, Concarneau, France, fished off the East Atlantic Ocean coast).

To complete this study, we had the opportunity to participate to the dissection of an animal that cannot be considered as “fish”. Tetrapoda, Amniota, Crocodylidae: *Alligator sinensis* (1) (TL: 145 cm, from “La Planète des crocodiles”, Civeaux, France).

For better observations and practical purposes, dissections were conducted on fresh specimens. After dissection, most of these specimens were not in a state that enables their acceptation for preservation in a systematic collection and have not been preserved. Dissections were conducted using common dissection tools (scalpels, scissors, forceps,…) and methods (Chanet, 2011). Parasagittal mechanical sections were performed using an electric meat saw (La Bovida, BG) to observe the structure of the thyroid gland on large specimens (Figs 1, 2). For some species, like the oceanic sunfish (*M. mola*, Molidae), identification of the thyroidian tissue has been confirmed through histological analyses (the slides are deposited in the Laboratoire d’Anatomie comparée at ONIRIS, Nantes). Several colleagues (D. Adriens, University of Ghent, Ghent, Belgium; T. Passos de Andrade, Universidade Estadual do Maranhão, Tirirical, São Luís, Brazil) kindly provided images of microscopic preparations of the thyroid for several species (the slides are deposited in their respective laboratories). Observations have been confirmed and completed by the description of the thyroid gland structure found in the literature for 220 species. Data are compelled in Appendix I and they represent a total of 288 species belonging to 136 families, 20 and 109 of which belong to Chondrichthyes and Actinopterygii, respectively.

The identified anatomical characters have been mapped on phylogenetic trees reconstructed from the data of Janvier (2009), Li (2008), Broughton (2010) and Betancur-R *et al*. (2013a). According to recent vertebrate phylogenies, Cyclostomota is considered as a clade (Takezaki *et al*. 2003, Shimeld and Donoghue, 2012; Osi *et al.,* 2012). As the distribution of the studied characters is not really confronted to this data, mapping of characters onto phylogenies may appear as invalid. However, there are three main reasons for using this method: i) similarities in anatomy are often overlooked until there is new evidence pointing out surprising sister-group relationships, ii) this approach is suitable for broadly defined characters, or characters for which hypotheses of homology cannot be yet confidently proposed at the beginning of a study (Grandcolas *et al.,* 2001), iii) the benefit must be extracted from inductive consilience of independent data. This method has been successfully used by many authors, like Parenti (1987), Brooks and McLennan (1991), Block *et al*. (1993), Miya and Nishida (1996), O’Toole (2002), Chanet (2003), Suzuki *et al*. (2004), Chanet





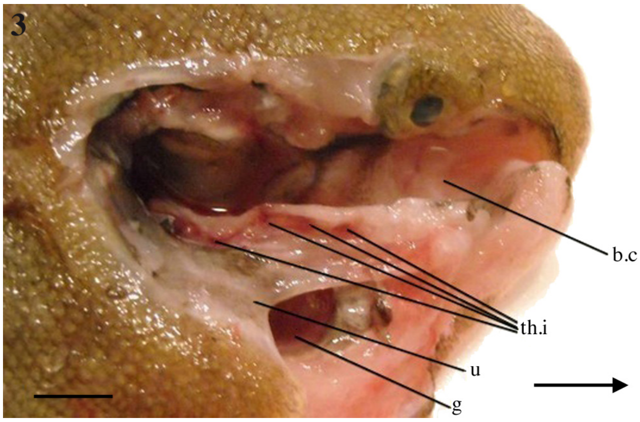


Figure 1. - Sagittal section of a frozen small-spotted catshark, *Scyliorhinus canicula* (Scyliorhinidae); left lateral view. The black arrow indicates the anterior part of the specimen. The thyroid gland is compact, pattern 1. Modified from Chanet *et al*., 2009a. br = brain; cart.pe = cartilaginous pericardium; chc = chondrocranium; el.br.sk = elements of the branchial skeleton; m = mouth; olf.cap = olfactive capsule; th = thyroid; v = ventricle. Scale bar = 10 mm.

Figure 2. - Sagittal section of a frozen common carp, *Cyprinus carpio* (Cyprinidae); right lateral view. The black arrow indicates the anterior part of the specimen. Several thyroidian islets are seen; the thyroid is diffuse, pattern 2. ant.ch.gs.bl = anterior chamber of the gas bladder; at = atrium; b.c = buccal cavity; bl.v = blood vessels; br = brain; l = liver; th.i = thyroid islets; v = ventricle; v.ao = ventral aorta. Scale bar =10 mm.

Figure 3. - Dissection of the bucco-branchial region of a common sole, *Solea solea* (Soleidae); right lateral view. The black arrow indicates the anterior part of the specimen. Several thyroidian islets are seen; the thyroid is diffuse, pattern 2. Modified from Chanet, 2011. b.c = buccal cavity; g = gills; th.i = thyroid islets; u = urohyal. Scale bar = 10 mm.

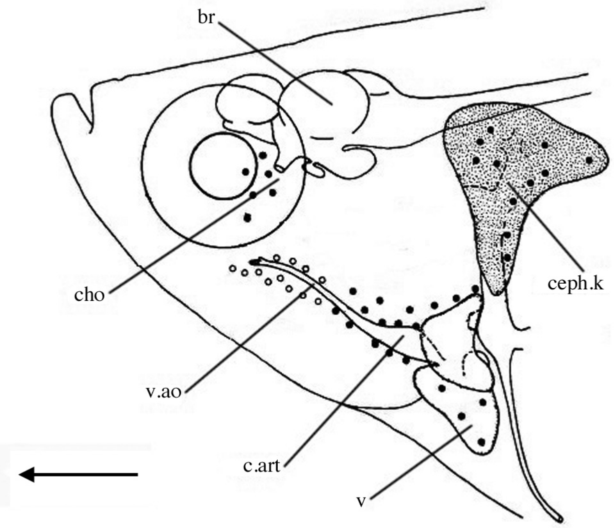


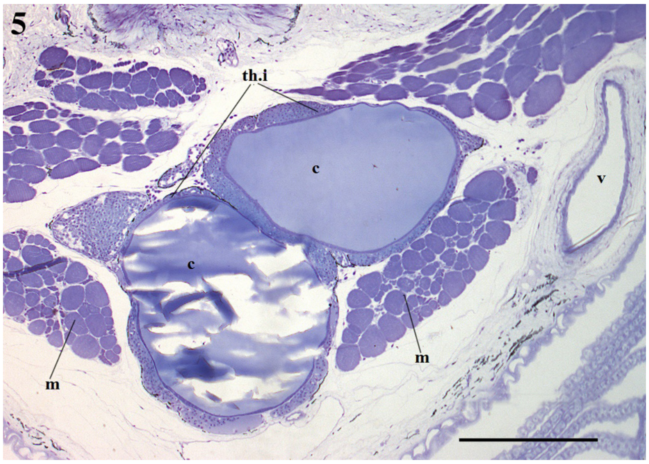
Figure 4. - Diagram of the anterior part of a platyfish, *Xiphophorus* sp. (Poecillidae), showing the distribution of thyroid islets: white circles indicate the ones in normal position while black circles indicate the ones in ectopic position, pattern 3. Modified from Baker *et al*., 1955. The black arrow indicates the anterior part. br = brain; ceph.k = cephalic kidney; cho = choroid; c.art = conus arteriosus; v = ventricle; v.ao = ventral aorta.

et al. (2013) and was discussed by Grandcolas *et al*. (2004), among many others.

RESULTS

The structure of the thyroid gland has been investigated in 288 species using dissections, histology and analysis of literature (Appendix I); five thyroidian patterns were identified [see Appendix I for references]:

i) ***Pattern 1***; the thyroid forms a compact gland. The gland is composed of a unique and large lobe, ventrally attached to the ventral aorta (Fig. 1) and often buried in a loose connective tissue. A thyroid compact gland can have various shapes, crescent-shaped or disc-shaped. In some species, as protopterids, the gland can be organised in two lobes (for examples in Appendix I) (Parker, 1890; Olivereau, 1959; Chavin, 1976). A compact thyroid was described in all studied chondrichthyans (Fig. 1), in sarcopterygians (coelacanth, lungfishes, and tetrapods), and in actinopterygians (cladistians, acipenserids, polyodontids, lepisosteids, osteoglossomorphs, and some acanthomorph families) (Appendix I). Matthews (1948) described the thyroid gland of a parrotfish (*Scarus hoefleri*, Scaridae) as being compact. But, a



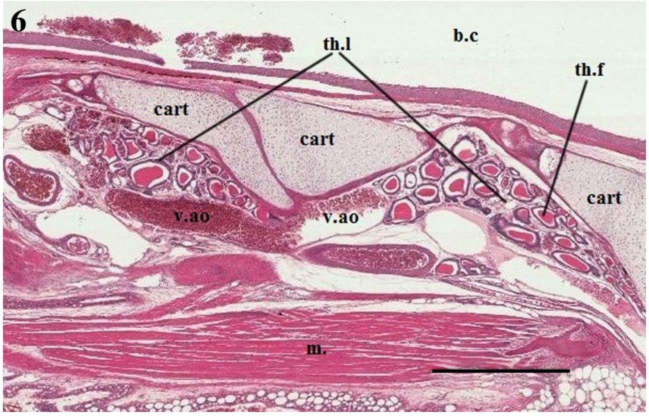


Figure 5. - Section in the branchial region of a longsnout seahorse, *Hippocampus reidi* (Syngnathidae). The thyroid is diffuse, pattern 2. c = colloid; m = muscles; th.i = thyroidian islet; v = vein. Histological preparation by Dr D. Adriens. Scale bar = 100 μm.

Figure 6. - Sagittal section of the buccal region of a cobia, *Rachycentron canadum* (Rachycentridae). The thyroid is composed of gathered lobes, pattern 4. b.c = buccal cavity; cart = cartilage; m = muscles; th.f = thyroidian follicle; th.l = thyroidian lobe; v.ao = ventral aorta. Histological preparation by Dr T. Passos de Andrade. Scale bar = 1 mm.

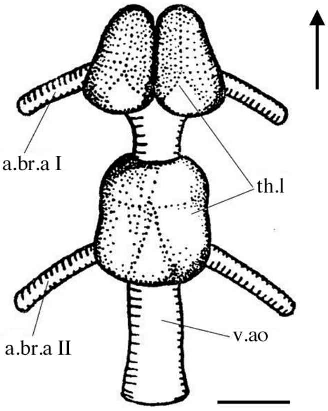


Figure 7. - Diagram of the anatomy of the thyroid gland of a yellowfin tuna, *Thunnus albacares* (Scombridae); ventral view. The thyroid is composed of gathered lobes, pattern 4. The black arrow indicates the anterior part. a.br.a = afferent branchial artery; th.l = thyroidian lobe; v.ao = ventral aorta. Modified from Honma, 1957. Scale bar = 5 mm.

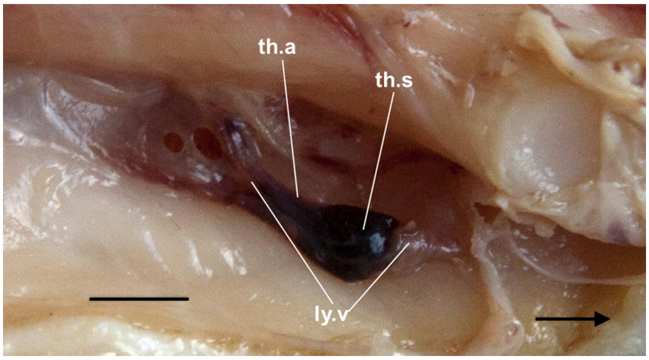


Figure 8. - Close-up of the thyroid gland of an angler, *Lophius piscatorius* (Lophiidae); right lateral view. The thyroid is embedded in a blood sinus, pattern 5. The black arrow indicates the anterior part of the specimen. ly.v = lymphatic vessels; th.a = thyroidian artery; th.s = thyroidian sinus. Modified from Chanet *et al.*, 2013. Scale bar = 3 mm.

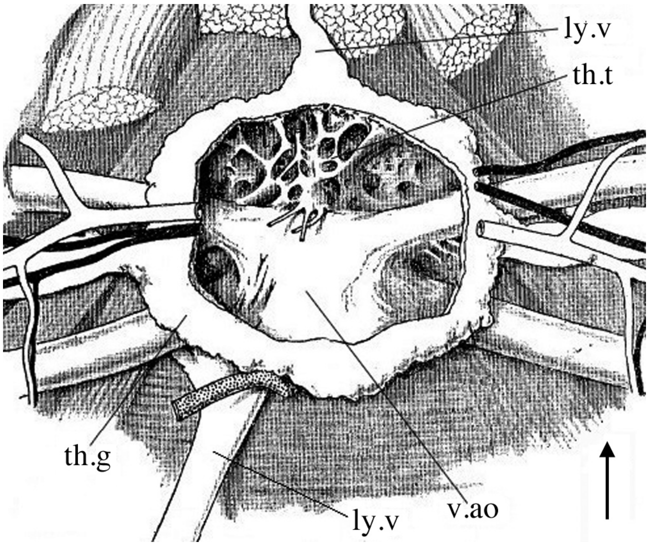


Figure 9. - Detail of the anatomy of the thyroid gland of an angler, *Lophius piscatorius* (Lophiidae); ventral view. The black arrow indicates the anterior part. Modified from Burne, 1927. ly.v = lymphatic vessel; th.g = thyroid gland; th.t = thyroidian tissue; v.ao = ventral aorta.

reexamination of his figure 1 (p. 254) shows that the shape of the various lobes is clearly visible. The gland corresponds rather to a gathering of thyroidian lobes (pattern 4).

ii) ***Pattern 2***; the thyroid gland is diffuse with scattered islets of follicles in the branchial region close to the ventral aorta (Figs 2, 3, 4, 5). This pattern is present in cyclostomes, in *Amia calva*, and in the majority of teleosteans, including elopomorphs (Appendix I).

iii) ***Pattern 3***; the thyroid gland is composed of islets of follicles disseminated in the branchial region and ectopic thyroidian follicles in the cephalic kidney, in the choroid region and along large blood vessels (Fig. 4). This type of follicle organisation was described in the literature in Engraulidae, in most of the Cyprinidae, in Siluriformes, in one salmonid (*Oncorhynchus mykiss*) and in several acanthomorph families [Atherinopsidae, Synbranchidae, two families of the

Cyprinodontiformes (Notobranchiidae and Poecillidae), and in a polynemid (*Polynemus sexfilis*)] (Appendix I).

iv) ***Pattern 4***; the thyroidian follicles form lobes, which are more or less gathered and attached to the ventral aorta (Figs 6, 7). Such organised lobes are present in: one cyprinid (*Tribolodon ezoe*), Scombridae, Trichiuridae, Scaridae, one labrid (*Semicossyphus reticulatus*), Oplegnathidae, Carangidae, Coryphaenidae, Rachycentridae, Echeneidae, Sphyraenidae, Istiophoridae and Xiphiidae (Appendix I).

v) ***Pattern 5***; The thyroid gland forms a compact gland included in a blood sinus that is dorsal to the ventral aorta (Figs 8, 9). Among vertebrates, this pattern was observed only in Lophiiformes and Tetraodontiformes (Appendix I).

As cited in the literature, the identification of the five thyroidian patterns described above could be problematic. The anatomy of the thyroid gland of *Echeneis naucrates* (Carangidae) is mentioned by Honma and Yoshie (1974). These authors wrote (p. 268) "*the main part of the thyroid gland located on the dorsal surface of the ventral aorta*", suggesting, without assessing it, that this gland is composed of more or less gathered lobes (pattern 4), as observed in other carangid species (Appendix I). Nussbaum-Hilarowicz (1923) described superficially the thyroid gland of the eurypharyngid fish, *Eurypharynx* sp., as a more or less compact gland. Tchernavin (1947: 384) wrote that "*to the naked eye the gland appears as a compact organ, light orange in colour*" in *Eurypharynx* sp. But, a few lines further, he indicated that "*the follicles are loosely connected with each other*" and that, in this species, this gland could be considered as diffuse, pattern 2, like in the other anguilliform species (Appendix I). Consequently, pending new evidence the thyroidian patterns for these species are cautiously indicated between commas in Appendix I.

If the study of the thyroid gland reveals an anatomical diversity, the histology of the gland does not differ among vertebrates (Porreca, 2010). Our analyses of both literature and histological preparations confirm this statement. Either compact or more or less dispersed, the thyroid gland is constituted of follicles (Figs 5, 6). Each follicle is lined by a layer of cubic epithelial cells the size of which varies according to species and the functional state of the gland. These cells release an acidophilic secretion in the lumen of the follicle: the colloid that stores the active thyroidian molecules (Eales, 1979; Geven, 2009).

As in tetrapods, in fish, when the thyroid gland is active, the thyroidian cells are cuboidal and the follicles show few colloid with numerous vacuoles; reversely, when the gland is underactive the epithelial cells are flat and the lumen is filled with colloid. The active molecules are released into the blood where they fulfil needs owing to the numerous capillaries that surround the follicles.

The thyroid gland was recognised to play a role in the growth and the reproduction and during the metamorphosis of Elopomorphes and Pleuronectiformes larvae (Evans and Clairborne, 2006; Dufour *et al.*, 2012). Hyperactivity was also observed before and during downstream migration of eels and salmons (Callamand and Fontaine, 1942). From a genetic perspective, the same genes (Pax2.1, Pax8 and Hhex) are expressed in the differentiation of the gland among all vertebrate species studied so far (Wendl *et al.*, 2002; Porreca, 2010).

Mapping these different patterns on recent vertebrate phylogenies (Figs. 10, 11, 12) leads us to propose the following hypotheses:

1. the presence of a thyroid gland is a synapomorphy of vertebrates;

2. a compact thyroid gland, pattern 1, is a synapomorphy of gnathostomes;

3. a diffuse thyroid gland, pattern 2, extending in the branchial region is a synapomorphy of teleosteans, with a possible convergence in *Amia calva*. In osteoglossomorphs, the thyroid is compact; it could be interpreted as synapomorphy of the group and a reversion from pattern 2 to pattern 1. However, the anatomy of the thyroid gland is largely unknown within osteoglossomorphs;

4. the presence of ectopic thyroidian follicles, pattern 3, could be the result of both inheritance and convergence. It appears that this character-state appeared several times; first in the common ancestor of Clupeocephala, followed by a reversion in Neoteleostei, and at least three times within Acanthomorphes: in Atherinomorphes (Atherinopsidae and Synbranchidae), Cyprinodontiformes (Notobranchiidae and Poecillidae) and in a polynemid (*Polynemus sexfilis*). Nevertheless, the occurrence of ectopic thyroidian islets has to be investigated in more species to specify these still putative events;

5. the presence of thyroidian lobes more or less gathered and attached to the ventral aorta, pattern 4, (Fig. 7) is a homoplastic character occurring in several subgroups: one cyprinid (*Tribolodon ezoe*), Giganturidae, Scombridae, Trichiuridae, Scaridae, one labrid (*Semicossyphus reticulatus*), Oplegnathidae, Carangidae, Coryphaenidae, Rachycentridae, the Echeneidae, Sphyraenidae, Istiophoridae, and Xiphiidae. These different cases of a thyroid gland organised in gathered lobes can be interpreted as convergences, resulting of independent and recurrent events. Nevertheless, this character-state can support several results as the monophyly of Giganturidae and certain relationships within acantomorphs (see discussion);

6. the presence of a thyroid gland embedded in a blood sinus (Fig. 8) dorsal to the ventral aorta, pattern 5, is a pattern in which the gland tissue forms a mesh (Fig. 9) included in a blood lacuna (Burne, 1927; Chanet *et al.*, 2012, 2013). This pattern is unique to Tetraodontiformes and Lophiiformes among vertebrates. It is a probable synapomorphy of the clade formed by these two orders, an interpretation

already proposed by Chanet *et al*. (2013); see this publication for further phylogenetic discussions.

DISCUSSION

The thyroid gland, with its histological characteristics, is an endocrine gland, which is only present in vertebrates and is a derivative of the pharynx (Kunz, 2004). The homology of this organ with the endostyle of Urochordata (tunicates) and Cephalocordata (lancelets) was proposed first by Müller (1873) on the basis on the reorganization of the larval endostyle into the adult thyroid in lampreys. Then this finding was corroborated by subsequent studies (Marine, 1913; Gorbman and Creaser, 1943; Barrington, 1957; Thorpe *et al*., 1972; Thorndyke, 1978; Thorndyke and Probert, 1979; Kobayashi *et al*., 1983; Fredriksson *et al*., 1985, 1988; Kluge *et al*., 2005). More recently, this hypothesis of primary homology was confirmed by: i) the discovery of thyroidian hormones in the larvae of the sea skirt, *Ciona intestinalis,* at the metamorphosis stage (Patricolo *et al*., 2001); ii) comparative analyses of expression patterns of endostyle genes (Cañestro *et al*., 2008); and iii) sharing of the same molecular pattern in the setting up of the thyroid in vertebrates and in the endostyle in non-vertebrate chordates (Cañestro *et al*., 2008). Conservation of these molecular and genetic processes in setting up of the endostyle and the thyroid gland reveals structural homologies that support a common evolutionary origin (Hiruta *et al*., 2005; Cañestro *et al*., 2008).

Even if the development of the thyroid gland differs between extant cyclostome genera (Ota and Kuratani, 2008), only petromyzodontid larvae possess an endostyle (Marine, 1913) and the thyroid is a diffuse gland (Reese, 1902; Stockard, 1906; Marine, 1913; Waterman and Gorbman, 1963; Suzuki, 1985; Henderson, 1997; Ota and Kuratani, 2008).

Within vertebrates, a scheme of thyroid gland evolution can be proposed. Mapping of the different patterns (Figs 10, 11, 12) leads to conclude that a diffuse thyroid gland, pattern 2, is the primitive state for vertebrates and that the convergent presence of a diffuse gland is either a reversion that has occurred at least in teleosteans or a character state independently acquired in teleosts. A compact thyroid, pattern 1, appears to be the widespread character state for gnathostomes. It is present in chondrichthyans, in sarcopterygians (coelacanth, lungfishes, and tetrapods), cladistians, acipenserids, polyodontids, lepisosteids and some teleosteans (osteoglossomorphs and a few acanthomorphs). Honma (1968) pointed out the similarity of the thyroid of *Latimeria chalumnae* with the one of selachians and Griffith *et al*. (1974) wondered if this similarity was due to convergence or retention from a common ancestor. The present work supports the retention hypothesis and the status of synapomorphy for the presence of a compact thyroid for the gnathostomes. A diffuse gland, pattern 2, is known in most teleosteans (Appendix I) and in bowfin, *Amia calva* (Hill, 1935; Jaroszewska and Dabrowski, 2009). This presence could be viewed as a synapomorphy of the halecostome clade, gathering teleosts and Amiidae. However, the existence of this clade is actually controversial (Arratia, 2001; Broughton *et al*., 2013) as several studies, anatomical (Grande, 2010), molecular (e.g. Kikugawa *et al*., 2004; Li *et al*., 2008; Santini *et al*., 2009; Near *et al*., 2012; Betancur-R. *et al*., 2013a) and histological (Sire and Meunier, 1993; Meunier, 2011) present evidence to support the Holostei as a clade. In contrast, some other morphological studies plead for the paraphyly of this group (e.g. Patterson, 1973; Arratia, 1999). Consequently, the interrelationships of these groups are shown as a polytomy and a dif-

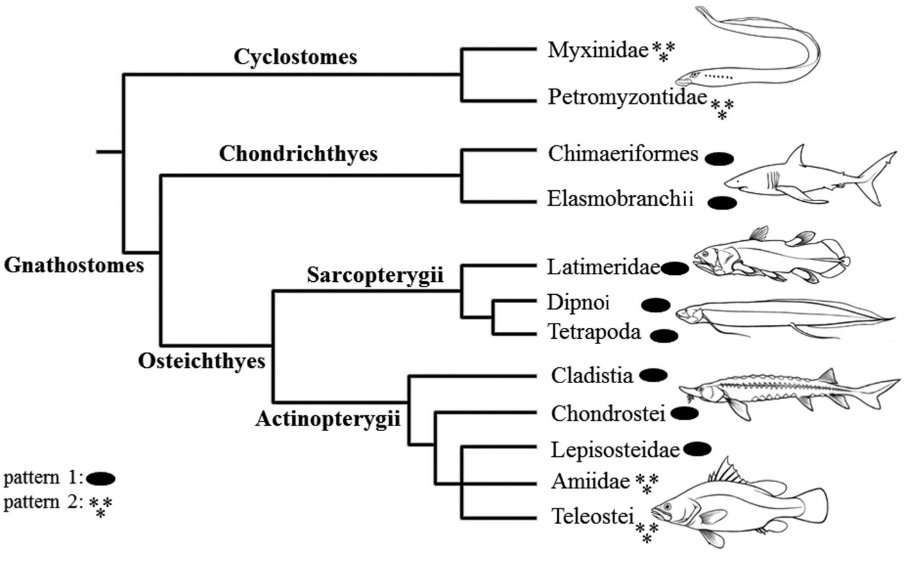


Figure 10. - Distribution of the thyroidian patterns in Vertebrates. The interrelationship tree has been reconstructed from Li (2008), Janvier (2009), Broughton (2010) and Betancur-R *et al*. (2013b). See text and Appendix I for details.

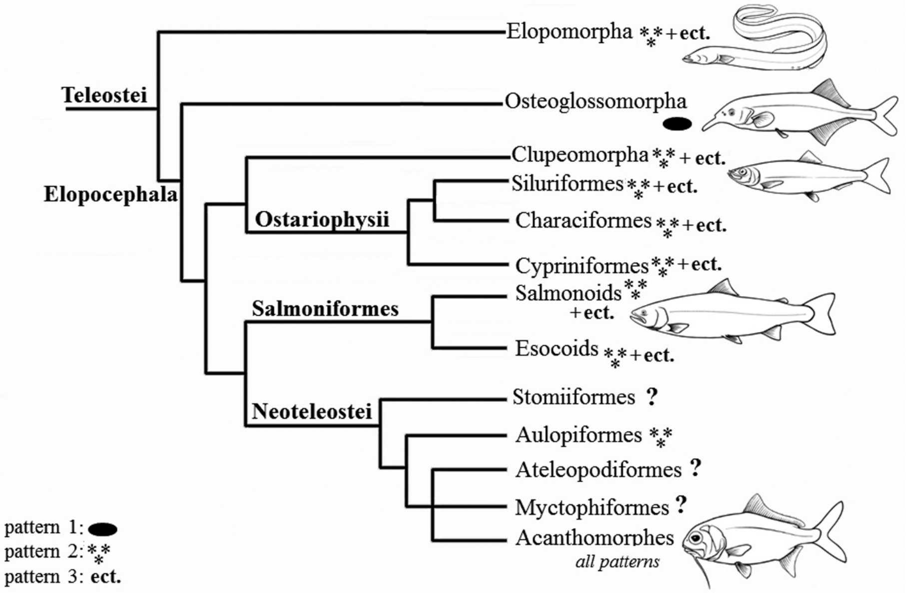


Figure 11. - Distribution of the thyroidian patterns in Teleostei. The interrelationship tree has been reconstructed from Li (2008), Broughton (2010) and Betancur-R *et al*. (2013b). See text and Appendix I for details.

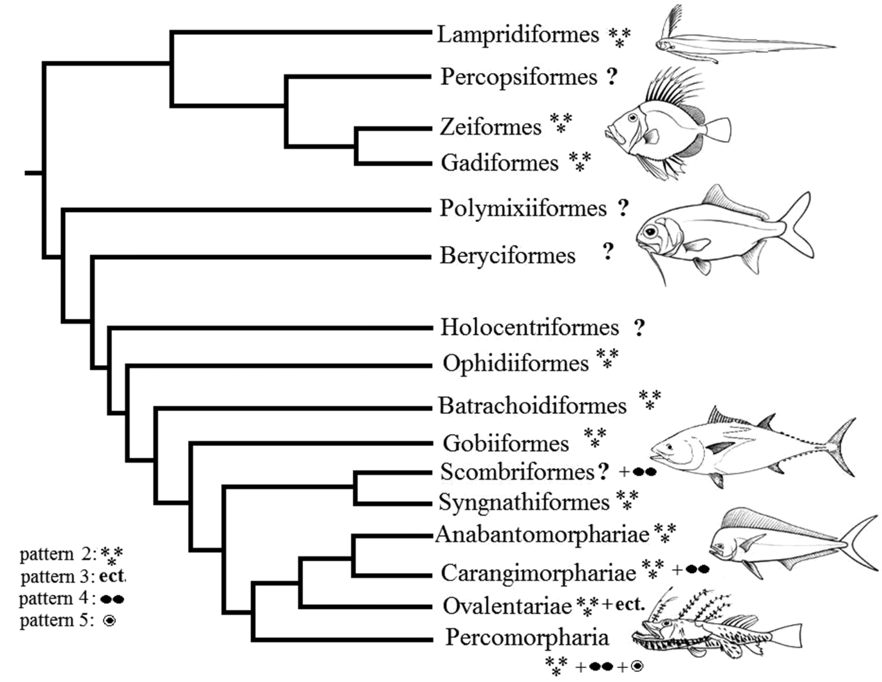


Figure 12. - Distribution of the thyroidian patterns in Acanthomorphs. The interrelationship tree have been reconstructed from Li (2008), and Betancur-R *et al*. (2013b). See text and Appendix I for details.

fuse thyroid gland is considered as a synapomorphy of teleosteans with a possible convergence in *Amia calva* (Fig. 10).

Most teleost species present a diffuse gland with some cases of compact thyroid or gathered lobes in some subgroups (Appendix I). One of the strangest thyroidian patterns is the scattering of ectopic thyroidian follicles from the branchial region to large blood vessels, the cephalic kidney and the choroid region (Fig. 4) that means far away from the ventral aortic region (Fournie *et al*., 2005). This pattern 3 is present in Engraulidae, in most Cyprinidae, at least in certain Siluriformes, in one salmonid (*Oncorhynchus mykiss*), in two atherinomorph families (Atherinopsidae and Synbranchidae), in two families of the Cyprinodontiformes (Notobranchiidae and Poecillidae) and in a polynemid species (*Polynemus sexfilis*) (Appendix I). In teleosts, this presence of ectopic follicles can be interpreted as either an inheritance from the common ancestor of the Clupeocephala with recurrent loss of this character-state in many groups or the result of independent acquisitions: one in the common ancestor of Clupeomorpha and Ostariophysii and several independent ones in Salmonidae and acanthomorphs. Within Acanthomorpha, this pattern occurs in non-related groups, such as Atherinomorphes and Cyprinodontiformes, on the one hand, and Polynemidae, on the other hand. The most parsimonious solution is to interpret this distribution as the result of independent events. It could be interesting to follow the setting-up of pattern 3 during the ontogeny of some species belonging to these groups to decipher possible homologies and point out the mechanisms of these convergences.

In most acantomorph species, the thyroid is a diffuse gland (Appendix I). A gathering of thyroidian lobes (pattern 4) is present in several groups: Scombridae, Trichiuridae, Scaridae, Oplegnathidae, a labrid species and some Carangimorphariae (= Carangimorpha *sensu* Li *et al*., 2009) like Carangidae, billfishes (= Istiophoriformes, gathering Xiphiidae and Istiophoridae), barracudas (Sphyraenidae), cobias (Rachycentridae), dolphinfishes (Coryphaenidae) and probably remoras (Echeneidae) (see comments above). This pattern seems than to have occurred several times in various groups (Fig. 12), but it may provide as well phylogenetic information supporting several previously proposed relationships. This is the case of the evolutionary relation between Scombridae and Trichiuridae, which share a common ancestor (Li, 2008; Meynard *et al*. 2012; Near *et al*. 2013) and are members of Scombriformes (*sensu* Betancur-R *et al*., 2013a; Near *et al*., 2013). In other families of this group (i.e. Arripidae, Bramidae, Centrolophidae, Chiasmodontidae, Gempylidae, Icosteidae, Nomeidae, Scombrolabracidae and Stromateidae), the anatomy of the thyroid gland is unexplored except for *Pomatomus saltatrix*, Pomatomidae, Scombriformes, where the gland is diffuse (Gudernatsch, 1910). More anatomical studies on numerous Scombriformes species are needed to specify whether this thyroidian character-state (pattern 4) provides information to decipher Scombriformes relationships.

Regarding Carangimorphariae, several studies have shown that the families Xiphiidae, Istiophoridae, Sphyraenidae, Carangidae, Rachycentridae, Echeneidae and Coryphaenidae share a common ancestor (Li, 2008; Li *et al*. 2009; Betancur-R *et al*., 2013a; Near *et al.,* 2013) and possess a thyroid gland composed of gathered lobes (pattern 4; Appendix I). We might suppose that the anatomy of their thyroid could support this relationship. However, within Carangimorphariae, numerous species, like all flatfish species, possess a diffuse thyroid gland and the anatomy of the gland is unknown for several caranginomorph families, like Centropomidae, Lactariidae, Leptobramidae, Menidae or Nematistiidae. Then, the presence of a thyroid gland composed of gathered lobes cannot be interpreted for now as an inheritance from common ancestor of all Carangimorphariae. Nevertheless, the anatomy of the thyroid gland may support two well-established phylogenetic relationships within this group: (1) for billfishes (families Istiophoridae and Xiphiidae); (2) for jacks, dolphinfishes, cobias and remoras (Carangidae, Coryphaenidae, Rachycentridae and Echeneidae, respectively). The close relationships of Istiophoridae and Xiphiidae were established using numerous anatomical and molecular studies (e.g. Collette *et al*., 1984, 2006; Little *et al*. 2010; Meynard *et al*., 2012; Betancur-R *et al*., 2013a; Near *et al*., 2013), this thyroidian character-state (pattern 4) may support this relationship. Likewise, within Carangimorphariae, the close relationship between Carangidae, Coryphaenidae, Rachycentridae and Echeneidae was proposed, based on both anatomy (Johnson, 1984; O'Toole, 2002) and sequence comparisons (Betancur-R *et al*., 2013a; Near *et al*., 2013). The existence of this clade, Echeneoidea, may be supported by the structure of the thyroid gland as well.

Finally, Chanet *et al*. (2013) recently proposed that the presence of a thyroid gland embedded in a blood sinus dorsal to the ventral aorta is a synapomorphy of tetraodontiforms and lophiiforms. This disposition, first described by Burne (1927), observed by MRI in oceanic sunfish, *Mola mola* (Chanet *et al*., 2012) and confirmed by Chanet *et al*. (2013), is unique within vertebrates and is an important anatomical character corroborating a close phylogenetic relationship between anglers (Lophiiformes) and plectognaths (Tetraodontiformes). This phylogenetic hypothesis of relationships was first assessed by analysis of gene sequences (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, 2013).

The present study provides hypotheses about the thyroid gland history in vertebrates, and leads us to propose the following scenario for the evolution of this organ. The thyroid gland originated from the endostyle, still present in extant Urochordata (tunicates), Cephalocordata (lancelets), and lamprey embryos. Regarding the distribution of the different thyroidian patterns within vertebrates, it is possible to specify that the thyroid gland was diffuse in the common ancestor of vertebrates, became compact in the common ancestor of gnathostomes, and diffuse again in, at least, the common ancestor of Teleostei. Then, in non-teleostean groups [Sarcopterygii (coelacanth, lungfishes and tetrapods), Cladistia, Acipenseridae, Polyodontidae and Lepisosteidae], the gland remained compact while in most teleostean species, it became diffuse. Within Teleostei, the structure of the gland was modified several times; from a reversion to compact gland in Osteoglossomorphes to independent scatterings of thyroidian islets into other organs (from heart, to cephalic kidney and choroid) in some groups. Moreover, several recurrent cases of gathering of thyroidian lobes occurred in some of them (Istiophoridae and Xiphiidae, on the one hand, Carangidae, Coryphaenidae, Rachycentridae and Echeneidae, on the other hand) can support the existence of these groups as clades. A peculiar organisation of the gland, embedded in a blood lacuna, appeared in the common ancestor of Lophiiformes and Tetraodontiformes.

CONCLUSION

This work is the first to report on thyroid gland structure among vertebrates and especially in "fishes" (cyclostomes, sharks, skates, dipnoans, salmons and dolphinfishes). We provide numerous original observations and gathers data about the thyroid gland structure in 288 "fish" species, and propose some phylogenetic interpretations. The latter seem promising, but we have to bear in mind that they are only tentative, as more than 32800 extant species of this grade are known (Fishbase, May 2014), while data for only several hundred species have been examined until now. The hypotheses and conclusions presented here have to be corroborated or infirmed by the examination of the thyroid gland structure in more species representative of more families, and possibly by the study of thyroid gland development in more species with inputs on the genetic control of the setting up of the thyroidian function. The observation of thyroid gland anatomy requires fine dissections of unpreserved specimens and can be a challenge. The details of thyroid gland organization can be identified by histological studies, but for large sample of species, investigations using medical imaging, like magnetic resonance imaging (MRI), could be promising. Chanet *et al*. (2012) had the chance to observe by RMI the large thyroid gland of the huge oceanic sunfish (*M. mola*, Molidae) but could not detect it by MRI on an angler (*Lophius piscatorius*, Lophiidae) (Chanet *et al.,* 2012) or smaller specimens, like common carp (*C. carpio*, Cyprinidae) (Chanet *et al*., 2009b) and common mackerel (*S. scombrus*, Scombridae) (Chanet and Guintard, 2012). On the site of the Digital Fish Library (http://www.digitalfishlibrary.org), the compact thyroid gland can be detected for large shark species. However, the observation of the gland structure is not yet possible for other smaller species. Null *et al*. (2008) investigated by MRI (18.8 Tesla) successfully and *in vivo* the internal anatomy of a small animal: a fruit fly, *Drosophila* sp. We hope that in a near future this kind of examination could be conducted easily on small fresh (dead or anesthetised) or alcohol-preserved vertebrates to study the anatomy of the thyroid gland. Therefore, we view the present study as an attempt to specify our present knowledge about the anatomy and evolution of the thyroid gland in vertebrates and as a cornerstone to orientate future works, encourage and promote again soft anatomy studies (using both dissections and histological examinations) and possibly non-invasive imaging techniques.

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Appendix I. - Distribution of the identified thyroidian patterns among vertebrates. Suprafamilial taxa are organized phylogenetically following data exposed in Li (2008), Janvier (2009), Broughton (2010) and Betancur-R *et al*. (2013b) while families and species are organized alphabetically in each suprafamilial taxon. Numbers refer to patterns (see text for definitions); commas indicate that these data must be cautiously considered (see text for comments).

Systematic	Species	Thyroid structure	Sources
VERTEBRATA **Cyclostomes**			
Myxinidae	*Bdellostoma stouti*, valid as *Eptatretus stoutii* (Lockington, 1878)	diffuse	Stockard (1906)
Myxinidae	*Eptatretus burgeri* (Girard, 1855)	diffuse	Suzuki (1985)
Myxinidae	*Myxine glutinosa* Linnaeus, 1758	diffuse	Waterman and Gorbman (1963), Ota and Kuratani (2008)
Petromyzontidae	*Lethenteron camtschaticum* (Tilesius, 1811)	diffuse	Suzuki (1985)
Petromyzontidae	*Petromyzon marinus* Linnaeus, 1758	diffuse	Reese (1902), Marine (1913), Henderson (1997)
GNATHOSTOMES CHONDRICHTHYES **Chimaeriformes**			
Callorhinchidae	*Callorhinchus* sp. Lacepède, 1798	compact	Stahl (1967)
Chimaeridae	*Chimaera* sp. Linnaeus, 1758	compact	Cameron and Vincent (1915)
Chimaeridae	*Hydrolagus colliei (*Lay & Bennett, 1839)	compact	Cameron and Vincent (1915), Stahl (1967)
Rhinochimaeridae	*Rhinochimaera* sp. Garman, 1901	compact	Stahl (1967)
ELASMOBRANCHES **Orectolobiformes**			
Hemiscylliidae	*Chiloscyllium* sp. Müller & Henle, 1837	compact	Morris *et al*. (2011)
Ginglymostomatidae	*Ginglymostoma cirratum* (Bonnaterre, 1788)	compact	Volkoff (1996)
Lamniformes			
Alopiidae	*Alopias vulpinus* (Bonnaterre, 1788)	compact	Borucinska and Tafur (2009)
Lamnidae	*Isurus oxyrinchus* Rafinesque, 1810	compact	Borucinska and Tafur (2009)
Odontaspididae	*Odontaspis taurus* valid as *Carcharias taurus* Rafinesque, 1810	compact	Ferguson (1911)
Carcharhiniformes			
Carcharhinidae	*Carcharhinus acronotus* (Poey, 1860)	compact	Volkoff (1996)
Carcharhinidae	*Carcharhinus brevipinna* (Müller & Henle, 1839)	compact	Volkoff (1996)
Carcharhinidae	*Carcharhinus isodon* (Müller & Henle, 1839)	compact	Volkoff (1996)
Carcharhinidae	*Carcharhinus limbatus* (Müller & Henle, 1839)	compact	Volkoff (1996)
Carcharhinidae	*Carcharhinus obscurus* (Lesueur, 1818)	compact	Volkoff (1996)
Carcharhinidae	*Carcharhinus plumbeus* (Nardo, 1827)	compact	Volkoff (1996)
Carcharhinidae	*Negaprion brevirostris* (Poey, 1868)	compact	Volkoff (1996)
Carcharhinidae	*Prionace glauca* (Linnaeus, 1758)	compact	Ferguson (1911), Borucinska and Tafur (2009)
Carcharhinidae	*Rhizoprionodon acutus* (Rüppell, 1837)	compact	Honma *et al*. (1987)
Carcharhinidae	*Rhizoprionodon terraenovae* (Richardson, 1836)	compact	Volkoff (1996)
Carcharhinidae	*Triaenodon obesus* (Rüppell, 1837)	compact	Crow *et al*. (1998)
Scyliorhinidae	*Cephaloscyllium umbratile* Jordan & Fowler, 1903	compact	Honma *et al*. (1987)

Systematic	Species	Thyroid structure	Sources
Scyliorhinidae	*Scyliorhinus canicula* (Linnaeus, 1758)	compact	Present study Parker (1907), Thompson (1911), Vivien (1941), Gridelli *et al*. (2003), Chanet *et al*. (2009a)
Scyliorhinidae	*Scyliorhinus torazame* (Tanaka, 1908)	compact	Honma *et al*. (1987)
Scyliorhinidae	*Scyliorhinus stellaris* (Linnaeus, 1758)	compact	Gridelli *et al*. (2003)
Sphyrnidae	*Sphyrna lewini* valid as *Sphyrna zygaena* (Linnaeus, 1758)	compact	Honma *et al*. (1987)
Sphyrnidae	*Sphyrna tiburo* (Linnaeus, 1758)	compact	Gash (2012)
Triakidae	*Galeus canis* valid as *Galeorhinus galeus* (Linnaeus, 1758)	compact	Balfour (1881), Ferguson (1911)
Triakidae	*Mustelus asterias* Cloquet 1819	Compact	C. Guintard (pers. com.)
Triakidae	*Mustelus canis* (Mitchill, 1815)	compact	Ferguson (1911), Thompson, (1911), Cowdry (1921), Volkoff (1996)
Triakidae	*Mustelus manazo* Bleeker, 1855	compact	Honma *et al*. (1987)
Triakidae	*Triakis scyllia* valid as *Triakis scyllium* Müller & Henle, 1839	compact	Honma *et al*. (1987) Honma and Chiba (1993)
Squaliformes			
Squalidae	*Squalus acanthias* Linnaeus, 1758	compact	Ferguson (1911), Thompson (1911), Liem and Summers (1999)
Squalidae	*Squalus suckleyi* (Girard, 1855)	compact	Cameron and Vincent (1915)
Hexanchiformes			
Chlamydoselachidae	*Chlamydoselachus anguineus* Garman, 1884	compact	Goodey (1910)
Squatiniformes			
Squatinidae	*Squatina californica* Ayres, 1859	compact	Thompson (1911)
Squatinidae	*Squatina japonica* Bleeker, 1858	compact	Honma *et al*. (1987)
Rajiformes			
Rajidae	*Raja blanda* valid as *Raja brachyura* Lafont, 1873	compact	Thompson (1911)
Rajidae	*Raja clavata* Linnaeus, 1758	compact	Ferguson (1911)
Rajidae	*Raja erinacea* valid as *Leucoraja erinacea* (Mitchill, 1825)	compact	Ferguson (1911)
Rajidae	*Raja miraletus* Linnaeus, 1758	compact	Thomson (1911)
Rajidae	*Raja porosa* valid as *Okamejei kenojei* (Müller & Henle, 1841)	compact	Honma *et al*. (1987)
Myliobatiformes			
Dasyatidae	*Dasyatis* sp. Rafinesque, 1810	compact	Ferguson (1911)
Dasyatidae	*Dasyatis akajei* (Müller & Henle, 1841)	compact	Honma *et al*. (1987)
Dasyatidae	*Dasyatis americana* Hildebrand & Schroeder, 1928	compact	Volkoff (1996)
Dasyatidae	*Dasyatis matsubarai* Miyosi, 1939	compact	Honma *et al*. (1987)
Dasyatidae	*Dasyatis sabina* (Lesueur, 1824)	compact	Jackson and Sage (1973), Volkoff *et al*. (1999)
Dasyatidae	*Dasyatis say* (Lesueur, 1817)	compact	Volkoff (1996)
Myliobatidae	*Rhinoptera bonasus* (Mitchill, 1815)	compact	Volkoff (1996)
Torpediniformes			
Narkidae	*Typhlonarke aysoni* (Hamilton, 1902)	compact	Prior and Marples (1945)
Torpedinidae	*Torpedo* sp. Houttuyn, 1764	compact	Balfour (1881), Ferguson (1911)
Torpedinidae	*Torpedo marmorata* Risso, 1810	compact	Chanet *et al*. (2009a), Present study

Systematic	Species	Thyroid structure	Sources
OSTEICHTHYES **Sarcopterygii**			
Latimeriidae	*Latimeria chalumnae* Smith, 1939	compact	Chavin (1972, 1976), Compagno (1979)
Lepidosirenidae	*Lepidosiren paradoxa* Fitzinger, 1837	compact (bilobed)	Chavin (1976)
Protopteridae	*Protopterus annectens* (Owen, 1839)	compact (bilobed)	Parker 1890, Chavin (1976)
Protopteridae	*Protopterus aethiopicus* Heckel, 1851	compact (bilobed)	Olivereau (1959), Chavin (1976)
Neoceratodontidae	*Neoceratodus forsteri* (Krefft, 1870)	compact	Chavin (1976)
Tetrapoda Amniota Archosauromorpha Crocodilia			
Crocodylidae	*Alligator sinensis* Fauvel, 1879	compact (bilobed)	Present study
ACTINOPTERYGII **Cladistia**			
Polypteridae	*Polypterus senegalus* Cuvier, 1829	compact	Thomopoulos (1969, 1975)
Chondrostei			
Acipensiridae	*Acipenser gueldenstaedtii* Brandt & Ratzeburg, 1833	compact	Ivanova (1954), Charmi *et al*. (2009, 2010)
Acipensiridae	*Acipenser stellatus* Pallas, 1771	compact	Irikhimovitch (1948)
Polyodontidae	*Polyodon spathula* (Walbaum, 1792)	compact	Modrell *et al*. (2011)
NEOPTERYGII			
Lepisosteidae	*Lepisosteus osseus* (Linnaeus, 1758)	compact	Present study
Amiidae	*Amia calva* Linnaeus, 1766	diffuse	Hill (1935)
TELEOSTEI **Elopomorpha**			
Anguillidae	*Anguilla anguilla* (Linnaeus, 1758)	diffuse	Present study, Olivereau (1971)
Anguillidae	*Anguilla japonica* Temminck & Schlegel, 1846	diffuse	Fujita *et al*. (1966)
Anguillidae	*Anguilla rostrata* (Lesueur, 1817)	diffuse	Gudernatsch (1910)
Congridae	*Conger conger* (Linnaeus, 1758)	diffuse	Present study
Congridae	*Conger myriaster* (Brevoort, 1856)	diffuse	Thompson (1911), Gudernatsch (1910)
Eurypharyngidae	*Eurypharynx pelecanoides* Vaillant, 1882	"diffuse"	Nusbaum-Hilarowicz (1923), Tchernavin (1947)
Megalopidae	*Megalops atlanticus* Valenciennes, 1847	diffuse	Present study
Osteoglossomorpha			
Gymnarchidae	*Gymnarchus niloticus* Cuvier, 1829	compact	Thomopoulos (1950)
Notopteridae	*Chitala chitala* (Hamilton, 1822)	compact	Present study
Osteoglossidae	*Osteoglossum bicirrhosum* (Cuvier, 1829)	compact	Present study
Clupeomorpha			
Clupeidae	*Alosa alosa* (Linnaeus, 1758)	diffuse	Lahaye (1966)
Clupeidae	*Brevoortia tyrannus* (Latrobe, 1802)	diffuse	Gudernatsch (1910)
Clupeidae	*Clupea harengus* Linnaeus, 1758	diffuse	Gudernatsch (1910)
Clupeidae	*Sardina pilchardus* (Walbaum, 1792)	diffuse	Buser-Lahaye and Ruivo (1952)
Clupeidae	*Tenualosa reevesii* (Richardson, 1846)	diffuse	Bingxu (1978)
Engraulidae	*Engraulis telara* valid as *Setipinna phasa* (Hamilton, 1822)	diffuse with ectopic nodules	Sathyanesan and Chary (1962)
Ostariophysii **Gonorhynchiformes**			
Chanidae	*Chanos chanos* (Forsskål, 1775)	diffuse	Tampi (1953)

Systematic	Species	Thyroid structure	Sources
Cypriniformes			
Cobitidae	*Misgurnus anguillicaudatus* (Cantor, 1842)	diffuse	Ueda (1979)
Cyprinidae	*Abramis brama* (Linnaeus, 1758)	diffuse	Irikhimovitch (1948), Chanet *et al*. (2009a), Present study
Cyprinidae	*Barbus stigma* valid as *Puntius sophore* (Hamilton, 1822)	diffuse with ectopic nodules	Sathyanesan (1963)
Cyprinidae	*Barbus titteya* valid as *Puntius titteya* Deraniyagala, 1929	diffuse with ectopic nodules	Sathyanesan (1963)
Cyprinidae	*Caecobarbus geertsii* Boulenger, 1921	diffuse	Olivereau and Francotte (1955)
Cyprinidae	*Campostoma anomalum* (Rafinesque, 1820)	diffuse	Theodorakis *et al*. (2006)
Cyprinidae	*Carassius auratus* (Linnaeus, 1758)	diffuse with ectopic nodules	Chavin (1956), Fortune (1956), Chiba *et al*. (1978), Fournie *et al*. (2005)
Cyprinidae	*Catla catla* (Hamilton, 1822)	diffuse with ectopic nodules	Ajuha and Chandy (1962)
Cyprinidae	*Cirrhinus mrigala* (Hamilton, 1822)	diffuse with ectopic nodules	Joshi and Sathyanesan (1976)
Cyprinidae	*Cyprinus carpio* Linnaeus, 1758	diffuse with ectopic nodules	Geven *et al*. (2007)
Cyprinidae	*Danio rerio* (Hamilton, 1822)	diffuse with ectopic nodules	Alt *et al*. (2006), McGonnell and Fowkes (2006)
Cyprinidae	*Esomus danricus* (Hamilton, 1822)	diffuse	Singh (1968)
Cyprinidae	*Garra congoensis* Poll, 1959	diffuse	Genten *et al*. (2009)
Cyprinidae	*Garra lamta* (Hamilton, 1822)	diffuse with ectopic nodules	Qureshi *et al*. (1978)
Cyprinidae	*Leuciscus rutilus* valid as *Rutilus rutilus* (Linnaeus, 1758)	diffuse	Kerr (1948)
Cyprinidae	*Barbus conchonius* valid as *Pethia conchonius* (Hamilton, 1822)	diffuse with ectopic nodules	Sathyanesan and Prasad (1962), Sathyanesan (1963)
Cyprinidae	*Phoxinus phoxinus* (Linnaeus, 1758)	diffuse	Fortune (1953)
Cyprinidae	*Pimephales promelas* Rafinesque, 1820	diffuse with ectopic nodules	Wabuke-Bunoti and Firling (1983), Crane *et al*. (2005)
Cyprinidae	*Puntius sophore* (Hamilton, 1822)	diffuse with ectopic nodules	Srivastava and Sathyanesan, (1971), Agrawala and Dixit (1979)
Cyprinidae	*Tanichthys albonubes* Lin, 1932	diffuse	Cheverie and Lynn (1963)
Cyprinidae	*Tribolodon ezoe* Okada & Ikeda, 1937	with gathered lobules	Honma (1958)
Cyprinidae	*Typhlogarra widdowsoni* Trewavas, 1955	diffuse with ectopic nodules	Olivereau (1960)
Characiformes			
Bryconidae	*Brycon amazonicus* (Spix & Agassiz, 1829)	diffuse	Ganeco (2007)
Characidae	*Anoptichthys jordani* valid as *Astyanax jordani* (Hubbs & Innes, 1936)	diffuse	Mattheij (1969)
Characidae	*Anoptichthys hubbsi* valid as *Astyanax jordani* (Hubbs & Innes, 1936)	diffuse	Rasquin (1949)
Characidae	*Astyanax mexicanus* (De Filippi, 1853)	diffuse	Rasquin (1949)
Siluriformes			
Bagridae	*Mystus vittatus* (Bloch, 1794)	diffuse with ectopic nodules	Singh (1968), Bose and Firoz (1978)
Clariidae	*Clarias batrachus* (Linnaeus, 1758)	diffuse with ectopic nodules	Sharma and Kumar (1982)
Clariidae	*Clarias gariepinus* (Burchell, 1822)	diffuse	Vischer and Bogerd (2003)

Systematic	Species	Thyroid structure	Sources
Heteropneustidae	*Heteropneustes fossilis* (Bloch, 1794)	diffuse with ectopic nodules	Singh *et al*. (1974), Qureshi (1975)
Ictaluridae	*Ameiurus catus* (Linnaeus, 1758)	diffuse	McKenzie (1884), Thompson (1911)
Ictaluridae	*Ameiurus nebulosus* (Lesueur, 1819)	diffuse with ectopic nodules	Fournie *et al*. (2005)
Ictaluridae	*Ictalurus punctatus* (Rafinesque, 1818)	diffuse	Goto-Kazeto *et al*. (2003)
Esociformes			
Esocidae	*Esox lucius* Linnaeus, 1758	diffuse	Zaitsev (1955)
Salmoniformes			
Salmonidae	*Cristivomer namaycush* valid as *Salvelinus namaycush* (Walbaum, 1792)	diffuse	Gudernatsch (1910)
Salmonidae	*Coregonus lavaretus* (Linnaeus, 1758)	diffuse	Zaitsev (1971)
Salmonidae	*Oncorhynchus kisutch* (Walbaum, 1792)	diffuse	Gudernatsch (1910), Leatherland *et al*. (1978)
Salmonidae	*Oncorhynchus gorbuscha* (Walbaum, 1792)	diffuse	Maksimovich and Shevchuk (1995)
Salmonidae	*Salmo irideus* valid as *Oncorhynchus mykiss* (Walbaum, 1792)	diffuse with ectopic nodules	Gudernatsch (1910), Raine and Leatherland (2000)
Salmonidae	*Salmo salar* Linnaeus, 1758	diffuse	Olivereau (1954)
Salmonidae	*Salvelinus alpinus* (Linnaeus, 1758)	diffuse	Present study
Salmonidae	*Salvelinus fontinalis* (Mitchill, 1814)	diffuse	Gudernatsch (1910), Marine (1914)
Salmonidae	*Salvelinus namaycush* (Walbaum, 1792)	diffuse	Brown *et al*. (2004b)
Osmeriformes			
Osmeridae	*Osmerus mordax* (Mitchill, 1814)	diffuse	Gudernatsch (1910)
Salangidae	*Salangichthys microdon* (Bleeker, 1860)	diffuse	Harada *et al*. (2005)
Stomiiformes			
Stomiidae	*Stomias boa* (Risso, 1810)	diffuse	Nusbaum-Hilarowicz (1923)
Aulopiformes			
Giganturidae	*Bathypterus lisae* valid as *Gigantura indica* Brauer, 1901	with gathered lobules	Walters (1961)
Giganturidae	*Gigantura vorax* valid as *Gigantura chuni* Brauer, 1901	with gathered lobules	Walters (1961)
Ipnopidae	*Bathypterois dubius* Vaillant, 1888	diffuse	Bougis and Ruivo (1957)
ACANTHOMORPHA **Lampriformes**			
Lampridae	*Lampris immaculatus* Gilchrist, 1904	diffuse	Present study
Trachipteridae	*Trachipterus ishikawae* Jordan & Snyder, 1901	diffuse	Honma *et al*. (2005)
Gadiformes			
Gadidae	*Gadus morhua* Linnaeus, 1758	diffuse	Woodhead, 1959, Morrison (1993)
Gadidae	*Melanogrammus aeglefinus* (Linnaeus, 1758)	diffuse	Zenzerov (1986)
Gadidae	*Pollachius pollachius* (Linnaeus, 1758)	diffuse	Present study
Lotidae	*Gaidropsarus mediterraneus* (Linnaeus, 1758)	diffuse	Present study
Macrouridae	*Trachyrinchus trachyrinchus* valid as *Trachyrincus scabrus* (Rafinesque, 1810)	diffuse	Motais (1960)
Zeiformes			
Zeidae	*Zeus faber* Linnaeus, 1758	diffuse	Present study

Systematic	Species	Thyroid structure	Sources
Ophidiiformes			
Ophidiidae	*Benthocometes robustus* (Goode & Bean, 1886)	diffuse	Bougis and Ruivo (1954)
Batrachoidiformes			
Batrachoididae	*Opsanus tau* (Linnaeus, 1766)	diffuse	Gudernatsch (1910)
Gobiiformes			
Eleotridae	*Oxyeleotris marmorata* (Bleeker, 1852)	diffuse	Abol-Munafi *et al*. (2005)
Gobiidae	*Gobius paganellus* Linnaeus, 1758	diffuse	Vivien (1941)
Gobiidae	*Gymnogobius urotaenia* (Hilgendorf, 1879)	diffuse	Harada *et al*. (2003)
Gobiidae	*Leucopsarion petersii* Hilgendorf, 1880	diffuse	Tamura and Honma (1970), Harada *et al*. (2003)
Syngnathiformes			
Callionymidae	*Callionymus lyra* Linnaeus, 1758	diffuse	Present study
Mullidae	*Mullus surmuletus* Linnaeus, 1758	diffuse	Present study
Syngnathidae	*Hippocampus reidi* Ginsburg, 1933	diffuse	D. Adriens (pers. com.)
Syngnathidae	*Phycodurus eques* (Günther, 1865)	diffuse	H. Schmidt-Posthaus (pers. com.)
Syngnathidae	*Phyllopteryx taeniolatus* (Lacepède, 1804)	diffuse	H. Schmidt-Posthaus (pers. com.)
Syngnathidae	*Siphostoma fuscum* valid as *Syngnathus fuscus* Storer, 1839	diffuse	Gudernatsch (1910)
Syngnathidae	*Syngnathus acus* Linnaeus, 1758	diffuse	D. Adriaens (pers. com.)
Scombriformes			
Pomatomidae	*Pomatomus saltatrix* (Linnaeus, 1766)		Gudernatsch (1910)
Scombridae	*Auxis thazard thazard* (Lacepède, 1800)	with gathered lobes	Honma (1957)
Scombridae	*Katsuwonus pelamis* (Linnaeus, 1758)	with gathered lobes	Williams (1976)
Scombridae	*Neothunnus albacora* valid as *Thunnus albacares* (Bonnaterre, 1788)	with gathered lobes	Honma (1957)
Scombridae	*Scomber japonicus* Houttuyn, 1782	with gathered lobes	Honma (1957)
Scombridae	*Scomber scombrus* Linnaeus, 1758	with gathered lobes	Present study
Scombridae	*Thunnus thynnus* (Linnaeus, 1758)	with gathered lobes	Honma (1956a)
Trichiuridae	*Lepidopus caudatus* (Euphrasen, 1788)	with gathered lobes	Present study
Synbranchiformes			
Synbranchidae	*Monopterus albus* (Zuiew, 1793)	diffuse with ectopic nodules	Wai-Sum and Chan (1974)
Synbranchidae	*Amphipnous cuchia* valid as *Monopterus cuchia* (Hamilton, 1822)	diffuse with ectopic nodules	Srivastava and Sathyanesan (1967)
Anabantiformes			
Channidae	*Channa gachua* (Hamilton, 1822)	diffuse	Roy *et al*. (2000)
Channidae	*Channa punctatus* valid as *Channa punctata* (Bloch, 1793)	diffuse	Ram *et al*. (1989)
Carangimorphariae **Caranginomorphes**			
Polynemidae	*Polydactylus sexfilis* (Valenciennes, 1831)	diffuse with ectopic nodules	Qureshi *et al*. (1978)
Sphyraenidae	*Sphyraena afra* Peters, 1844	with gathered lobes	Present study

Systematic	Species	Thyroid structure	Sources
Istiophoriformes			
Istiophoridae	*Makaira* sp. Lacepède, 1802	with gathered lobes	Honma (1957)
Istiophoridae	*Istiophorus platypterus* (Shaw, 1792)	with gathered lobes	Honma (1956b), Chiba and Honma (1980)
Xiphiidae	*Xiphias gladius* Linnaeus, 1758	with gathered lobes	Addison and Richter (1932)
Carangiformes			
Carangidae	*Trachurus trachurus* (Linnaeus, 1758)	with gathered lobes	Present study
Carangidae	*Seriola aureovittata* valid as *Seriola lalandi* Valenciennes, 1833	with gathered lobes	Honma (1956c)
Carangidae	*Seriola quinqueradiata* Temminck & Schlegel, 1845	with gathered lobes	Honma (1956c)
Coryphaenidae	*Coryphaena* sp. Linnaeus, 1758	with gathered lobes	Honma (1957)
Rachycentridae	*Rachycentron canadum* (Linnaeus, 1766)	with gathered lobes	T. Passos de Andrade (pers. com).
Echeneidae	*Echeneis naucrates* Linnaeus, 1758	with gathered lobes	Honma and Yoshie (1974)
Pleuronectiformes			
Paralichthyidae	*Paralichthys californicus* (Ayres, 1859)	diffuse	Gisbert *et al*. (2004)
Paralichthyidae	*Paralichthys olivaceus* (Temminck & Schlegel, 1846)	diffuse	Tanaka *et al*. (1995)
Pleuronectidae	*Hippoglossus hippoglossus* (Linnaeus, 1758)	diffuse	Einarsdóttir *et al*. (2006)
Pleuronectidae	*Platichthys stellatus* (Pallas, 1787)	diffuse	Hickman (1959)
Pleuronectidae	*Pleuronectes platessa* Linnaeus, 1758	diffuse	Cole and Johnstone (1902), Present study
Pleuronectidae	*Pseudopleuronectes americanus* (Walbaum, 1792)	diffuse	Gudernatsch (1910)
Pleuronectidae	*Verasper moseri* Jordan & Gilbert, 1898	diffuse	Chiba *et al*. (2004)
Scophthalmidae	*Lepidorhombus whiffiagonis* (Walbaum, 1792)	diffuse	Present study
Scophthalmidae	*Scophthalmus maximus* (Linnaeus, 1758)	diffuse	Padros and Crespo (1996), Chanet *et al*. (2009a), Present study
Scophthalmidae	*Scophthalmus rhombus* (Linnaeus, 1758)	diffuse	Hachero-Cruzado *et al*. (2009)
Soleidae	*Solea senegalensis* Kaup, 1858	diffuse	Ortiz-Delgado *et al*. (2006), Klarena *et al*. (2008)
Soleidae	*Solea solea* (Linnaeus, 1758)	diffuse	Chanet (2011), Present study
Ovalentaria			
Embiotocidae	*Cymatogaster aggregata* Gibbons, 1854	diffuse	Brar (2009), Brar *et al*. (2010)
Pomacentridae	*Amphiprion frenatus* Brevoort, 1856	diffuse	D. Putra (pers. comm.)
Cichliformes			
Cichlidae	*Cichlasoma biocellatum* valid as *Rocio octofasciata* (Regan, 1903)	diffus	Mattheij *et al*. (1971)
Cichlidae	*Oreochromis mossambicus* (Peters, 1852)	diffus	Shukla and Pandey (1986), Geven *et al*. (2007)
Cichlidae	*Oreochromis niloticus* (Linnaeus, 1758)	diffus	Nacario (1983)
Cichlidae	*Oreochromis spilurus* (Günther, 1894)	diffus	Al-Hussaini and Bizkalla (1957)
Atherinomorphes			
Atherinopsidae	*Menidia beryllina* (Cope, 1867)	diffuse with ectopic nodules	Fournie *et al*. (2005)
Atherinopsidae	*Menidia notata* valid as *Menidia menidia* (Linnaeus, 1766)	diffuse	Gudernatsch (1910)
Beloniformes			
Adrianichthyidae	*Oryzias latipes* (Temminck & Schlegel, 1846)	diffuse	Fournie *et al*. (2005), Bauchet (2006)
Belonidae	*Belone belone* (Linnaeus, 1761)	diffuse	Present study

Systematic	Species	Thyroid structure	Sources
Cyprinodontiformes			
Cyprinodontidae	*Cyprinodon variegatus* Lacepède, 1803	diffuse with ectopic nodules	Fournie *et al*. (2005)
Fundulidae	*Fundulus diaphanus* (Lesueur, 1817)	diffuse	Gudernatsch (1910)
Fundulidae	*Fundulus heteroclitus* (Linnaeus, 1766)	diffuse	Weis *et al*. (2001)
Fundulidae	*Fundulus majalis* (Walbaum, 1792)	diffuse	Gudernatsch (1910)
Notobranchiidae	*Nothobranchius guentheri* (Pfeffer, 1893)	diffuse with ectopic nodules	Markofsky and Milstoc (1979), Fournie *et al*. (2005)
Poeciliidae	*Gambusia affinis* (Baird & Girard, 1853)	diffuse	Daesik *et al*. (2004)
Poeciliidae	*Lebistes reticulatus* Schreitmüller, 1934	diffuse	Baker (1959), Fortune (1953)
Poeciliidae	*Poecilia formosa* (Girard, 1859)	diffuse with ectopic nodules	Woodhead and Scully (1977), Fournie *et al*. (2005)
Poeciliidae	*Poecilia reticulata* Peters, 1859	diffuse with ectopic nodules	Hoover (1984)
Poeciliidae	*Xiphophorus maculatus* (Günther, 1866)	diffuse with ectopic nodules	Baker *et al*. (1955)
Rivulidae	*Cynolebias whitei* valid as *Nematolebias whitei* (Myers, 1942)	diffuse	Ruijter *et al*. (1987)
Mugiliformes			
Mugilidae	*Liza parsia* valid as *Chelon parsia* (Hamilton, 1822)	diffuse	Pandey *et al*. (1995)
Mugilidae	*Mugil auratus* valid as *Liza aurata* (Risso, 1810)	diffuse	Leray and Febvre (1968)
Mugilidae	*Mugil cephalus* Linnaeus, 1758	diffuse	Gudernatsch (1910), Weng *et al*. (2003)
Blenniiformes			
Blenniidae	*Parablennius gattorugine* (Linnaeus, 1758)	diffuse	Present study
Percomorpharia			
Caproidae	*Capros aper* (Linnaeus, 1758)	diffuse	Present study
Chaetodontidae	*Chelmon rostratus* (Linnaeus, 1758)	diffuse	Present study
Moronidae	*Dicentrarchus labrax* (Linnaeus, 1758)	diffuse	Schnitzler *et al*. (2008), Present study
Moronidae	*Morone americana* (Gmelin, 1789)	diffuse	Gudernatsch (1910)
Pomacanthidae	*Pomacanthus imperator* (Bloch, 1787)	diffuse	Present study
Labriformes			
Labridae	*Labrus bergylta* Ascanius, 1767	diffuse	Dunaevskaya (2010), Dunaevskaya *et al*. (2012), Present study
Labridae	*Labrus mixtus* Linnaeus, 1758	diffuse	Present study
Labridae	*Ctenolabrus rupestris* (Linnaeus, 1758)	diffuse	Present study
Labridae	*Semicossyphus reticulatus* (Valenciennes, 1839)	with gathered lobes	Honma (1957)
Labridae	*Symphodus melops* (Linnaeus, 1758)	diffuse	Present study
Labridae	*Tautoga onitis* (Linnaeus, 1758)	diffuse	Gudernatsch (1910)
Labridae	*Tautogolabrus adspersus* (Walbaum, 1792)	diffuse	Gudernatsch (1910)
Scaridae	*Pseudoscarus guacamaia* valid as *Scarus hoefleri* (Steindachner, 1881)	with gathered lobes	Matthews (1948)
Scaridae	*Scarus dubius* Bennett, 1828	with gathered lobes	Honma (1957), Grau *et al*. (1986)
Scaridae	*Sparisoma* sp. Swainson, 1839	with gathered lobes	Matthews and Smith (1948), Matthews (1948)
Spariformes			
Sparidae	*Acanthopagrus latus* (Houttuyn, 1782)	diffuse	Havasi *et al*. (2010), Salamat *et al*. (2012)
Sparidae	*Dentex dentex* (Linnaeus, 1758)	diffuse	Santamaria *et al*. (2004)

Systematic	Species	Thyroid structure	Sources
Sparidae	*Pagrus auriga* Valenciennes, 1843	diffuse	Sánchez-Amaya *et al*. (2007)
Sparidae	*Sparus aurata* Linnaeus, 1758	diffuse	Power (2001), Campinho *et al*. (2006), Present study
Sparidae	*Spondyliosoma cantharus* (Linnaeus, 1758)	diffuse	Present study
Sparidae	*Stenotomus chrysops* (Linnaeus, 1766)	diffuse	Gudernatsch (1910)
Lophiiformes			
Lophiidae	*Lophius piscatorius* Linnaeus, 1758	compact and included in a blood sinus	Burne (1927), Present study
Ogcocephalidae	*Ogcocephalus vespertilio* (Linnaeus, 1758)	compact and included in a blood sinus	Present study
Tetraodontiformes			
Balistidae	*Balistes capriscus* Gmelin, 1789	compact and included in a blood sinus	Present study
Balistidae	*Canthidermis rotundatus* valid as *Balistes rotundatus* Marion de Procé, 1822	compact and included in a blood sinus	Chiba *et al*. (1976)
Balistidae	*Melichthys vidua* (Richardson, 1845)	compact and included in a blood sinus	Present study
Diodontidae	*Diodon holacanthus* Linnaeus, 1758	compact and included in a blood sinus	Chiba and Honma (1981), Present study
Diodontidae	*Diodon liturosus* Shaw, 1804	compact and included in a blood sinus	Present study
Molidae	*Mola mola* (Linnaeus, 1758)	compact and included in a blood sinus	Present study
Ostraciidae	*Ostracion cubicus* Linnaeus, 1758	compact and included in a blood sinus	Present study
Ostraciidae	*Tetrosomus gibbosus* (Linnaeus, 1758)	compact and included in a blood sinus	Present study
Ostraciidae	*Lactoria cornuta* (Linnaeus, 1758)	compact and included in a blood sinus	Present study
Tetraodontidae	*Arothron nigropunctatus* (Bloch & Schneider, 1801)	compact and included in a blood sinus	Present study
Tetraodontidae	*Canthigaster compressa* (Marion de Procé, 1822)	compact and included in a blood sinus	Present study
Tetraodontidae	*Lagocephalus lagocephalu*s (Linnaeus, 1758)	compact in a blood sinus	Present study
Tetraodontidae	*Tetraodon cutcutia* Hamilton, 1822	compact and included in a blood sinus	Present study
Tetraodontidae	*Tetraodon palembangensis* Bleeker, 1852	compact and included in a blood sinus	Present study
Terapontiformes			
Oplegnathidae	*Oplegnathus septemfasciatus* valid as *Oplegnathus fasciatus* (Temminck & Schlegel, 1844)	with gathered lobes	Honma (1957)
Acanthuriformes			
Acanthuridae	*Acanthurus achilles* Shaw, 1803	diffuse	Present study
Acanthuridae	*Acanthurus lineatus* (Linnaeus, 1758)	diffuse	Present study

Systematic	Species	Thyroid structure	Sources
Perciformes			
Serraniformes [= Serraniformes *sensu* Lautredou *et al.* (2013)]			
Anarhichadidae	*Anarhichas lupus* Linnaeus, 1758	diffuse	Falk-Petersen and Hansen (2001)
Cottidae	*Cottus kazika* Jordan & Starks, 1904	diffuse	Mukai and Otta (1995)
Cottidae	*Leptocottus armatus* Girard, 1854	diffuse	Brar (2009), Brar *et al*. (2010)
Cottidae	*Myoxocephalus scorpius* (Linnaeus, 1758)	diffuse	Matishov *et al*. (2009)
Cottidae	*Scorpaenichthys* sp. Girard, 1854	diffuse	Burne (1927)
Cottidae	*Trachidermus fasciatus* Heckel, 1839	diffuse	Bingxu *et al*. (2010)
Cyclopteridae	*Aptocyclus ventricosus* (Pallas, 1769)	compact	Honma (1957)
Gasterosteidae	*Gasterosteus aculeatus* Linnaeus, 1758	diffuse	Hamada (1975), Honma *et al*. (1977)
Percidae	*Perca flavescens* (Mitchill, 1814)	diffuse	Levesque *et al*. (2003)
Percidae	*Perca fluviatilis* Linnaeus, 1758	diffuse	Rolleston and Jackson (1888), Present study
Percidae	*Sander lucioperca* (Linnaeus, 1758)	diffuse	Present study
Pholidae	*Pholis gunnellus* (Linnaeus, 1758)	diffuse	Gudernatsch (1910)
Sebastidae	*Sebastes norvegicus* (Ascanius, 1772)	diffuse	Present study
Sebastidae	*Sebastes schlegeli* Hilgendorf, 1880	diffuse	Kang and Chang (2005), Chin *et al*. (2010)
Sebastidae	*Sebastiscus marmoratus* (Cuvier, 1829)	diffuse	Zhang *et al*. (2009)
Serranidae	*Epinephelus aeneus* (Geoffroy St.-Hilaire, 1817)	diffuse	Abbas *et al*. (2012)
Serranidae	*Epinephelus coioides* (Hamilton, 1822)	diffuse	Tang *et al*. (2010)
Serranidae	*Paralabrax clathratus* (Girard, 1854)	diffuse	Blasiola *et al*. (1981)
Serranidae	*Serranus hepatus* (Linnaeus, 1758)	diffuse	Ramos and da Conceiçao Peleteiro (2001)
Triglidae	*Trigla lyra* Linnaeus, 1758	diffuse	Present study
Notothenioides			
Channichthyidae	*Chaenocephalus aceratus* (Lönnberg, 1906)	diffuse	Twelves *et al*. (1975)
Nototheniidae	*Notothenia coriiceps* Richardson, 1844	diffuse	Hureau (1970)
Nototheniidae	*Notothenia cyanobrancha* valid as *Indonotothenia cyanobrancha* (Richardson, 1844)	diffuse	Hureau (1970)
Nototheniidae	*Notothenia macrocephala* valid as *Paranotothenia magellanica* (Forster, 1801)	diffuse	Hureau (1970)
Nototheniidae	*Notothenia neglecta* Nybelin, 1951	diffuse	Twelves *et al*. (1975)
Nototheniidae	*Notothenia rossii* Richardson, 1844	diffuse	Hureau (1970)
Nototheniidae	*Trematomus bernacchii* valid as *Pseudotrematomus bernacchii* (Boulenger, 1902)	diffuse	Hureau (1963, 1970)
Nototheniidae	*Trematomus hansoni* valid as *Pseudotrematomus hansoni* (Boulenger, 1902)	diffuse	Hureau (1963, 1970)