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The long-time adaptation of coelacanths to moderate deep water: reviewing the evidences

Camila CUPELLO^{1*}, Gaël CLÉMENT², François J. MEUNIER³, Marc HERBIN⁴, Yoshitaka YABUMOTO⁵ and
Paulo M. BRITO¹

¹*Departamento de Zoologia, Instituto de Biologia, Universidade do Estado do Rio de Janeiro, R. São Francisco Xavier, 524-Maracanã, Rio de Janeiro 20550–900, Brazil*

²*UMR 7207 (MNHN–Sorbonne Université–CNRS) Centre de Recherche sur la Paléobiodiversité et les Paléoenvironnements, Département Origines & Evolution, Muséum national d'Histoire naturelle, 57 rue Cuvier, 75231 Paris cedex 05, France*

³*UMR 7208 (MNHN - Sorbonne Université - Univ. Caen Normandie - Univ. Antilles – CNRS – IRD) Biologie des Organismes et Ecosystèmes Aquatiques, Département Adaptations du Vivant, Muséum national d'Histoire naturelle, 57 rue Cuvier, Paris 75231, France*

⁴*UMR 7179 (MNHN-Sorbonne Université-CNRS) Mécanismes Adaptatifs & Evolution, Département Adaptations du Vivant, Muséum national d'Histoire naturelle, 57 rue Cuvier, 75231 Paris cedex 05, France*

⁵*Department of Natural History, Kitakyushu Museum of Natural History and Human History, 2-4-1 Higashida, Yahatahigashi-ku, Kitakyushu, Fukuoka, 805-0071, Japan*

**Corresponding author. E-mail: camila.dc@gmail.com*

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ABSTRACT — The evolutionary history of coelacanths is long and complex with indications of adaptations to different aquatic environments. Fossil coelacanths are registered in shallow brackish, fresh or marine waters, while extant coelacanths inhabit moderate deep marine environments. Here we review some evidences of this long-time adaptation to moderate deep waters, focusing mainly on the hypothesis of bimodal respiration (gas exchange through gills and lungs) in most fossil coelacanths and on the aquatic gas exchange and the presence of a non-functional lung in the extant coelacanth *Latimeria chalumnae*. Another morphological evidence is the high rate of lipid accumulation in the whole body of *L. chalumnae*.

INTRODUCTION

Coelacanths are an iconic group of sarcopterygian fishes, dating back to the Early Devonian (410 million years ago) and for long thought to have disappeared along with the non-avian dinosaurs, before the discovery in 1938 of the extant species *Latimeria chalumnae* SMITH, 1939 offshore South Africa in the Indian Ocean. In 1997 a second species, *Latimeria menadoensis* POUYAUD *et al.*, 1999 was discovered off Manado, Sulawesi Island, Indonesia (ERDMANN *et al.*, 1998). Although considered to have representatives with a conservative morphology from the Early Devonian to the present (ZHU *et al.*, 2012), fossil and extant coelacanths display important morphological differences, particularly at the head, skull, vertebral column and lung (FOREY, 1988; CASANE and LAURENTI, 2013; CUPELLO *et al.*, 2017b)

We here review and summary some morphological differences of fossil and extant coelacanths that inhabit different environments (from shallow brackish, fresh or marine waters to moderate deep marine waters), focusing mainly on the adaptation to moderate deep waters. We comment about the breathing behaviour of fossil and extant coelacanths, based

on previous studies on the gills (HUGHES, 1972, 1976, 1980, 1995, 1998; VOGEL *et al.*, 1998) and on the lung (CUPELLO *et al.*, 2015, 2017a, 2017b). Extant coelacanths inhabit moderate deep waters and make gas exchange exclusively through the gills, contrasting to the well-developed calcified organ of fossil coelacanths, considered as a functional lung (BRITO *et al.*, 2010; CUPELLO *et al.*, 2015, 2019). Some comments will be also addressed regarding the lipid accumulation in the body of the extant coelacanths, another morphological evidence of the long-time adaptation of coelacanths to moderate deep waters.

BREATHING IN COELACANTHS

Lung

A well-developed calcified lung is described in almost all Palaeozoic and Mesozoic families of coelacanths, such as Hadronectoridae, Rhabdodermatidae, Laugiidae, Whiteiidae, Mawsoniidae, and Latimeriidae. This calcified organ, located in the abdominal cavity, was firstly described by MANTELL (1822) on the fossil species *Macropoma mantelli* MANTELL, 1822 (Upper Cretaceous of Sussex, England), and was later

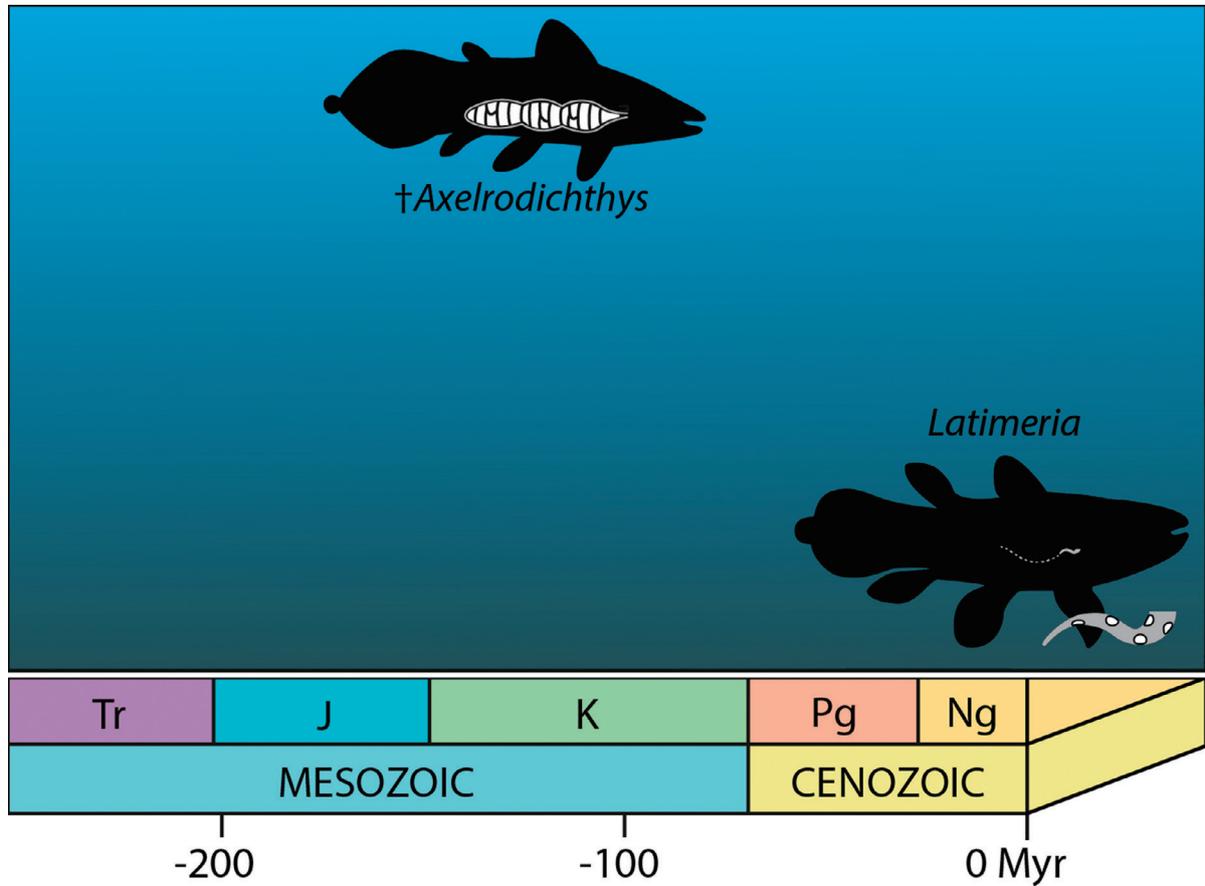


Fig. 1 Relative living water depth, size and morphology of the coelacanth lung through time. *Axelrodichthys*, a large cretaceous coelacanth from lagoonal or epicontinental shallow marine environments, exhibits a well-developed lung in the abdominal cavity, while the extant coelacanth *Latimeria*, that inhabit moderate deep-marine waters, has a vestigial lung. In white, the ossified plates of the lungs. J, Jurassic; K, Cretaceous; Myr, Million years; Ng, Neogene; Pg, Paleogene; Tr, Triassic.

identified as a bladder by WILLIAMSON (1849). Only in 2010, BRITO *et al.* identified this organ as a lung.

The lung of fossil coelacanths is usually covered by bone plates. Recent work evidenced the presence of small bony plates surrounding the so-called oesophageal diverticulum of extant coelacanths (CUPELLO *et al.*, 2015, 2017b). The homology between the plates of extant and fossil coelacanths suggests that only the oesophageal diverticulum of the extant coelacanth *Latimeria* is the lung, questioning the fatty organ as part of the pulmonary complex (CUPELLO *et al.* 2017b). These plates in the fossil coelacanths had probably the function of regulation of volume variation, protection against hydrostatic pressure, and lung ventilation (BRITO *et al.*, 2010; CUPELLO *et al.*, 2017b).

Contrasting to the lung of fossil coelacanths, the lung of the extant coelacanth *L. chalumnae* is very reduced in size and displays an arrested differentiation in an air-breathing organ (Fig. 1), mainly evidenced by its allometric growth when compared to the growth of other organs along the ontogeny,

and the absence of pneumocytes and compartmentalization in late ontogenetic stages (CUPELLO *et al.*, 2017a). Extant coelacanths inhabit moderate deep seas (rocky environments) between 100 and 400 meters and make gas exchange only through their gills. Fossil coelacanths are usually recorded in low-depth palaeoenvironments (BRITO *et al.*, 2010). The presence of a well-developed lung may suggest that they were able to use a bimodal respiration (gas exchange from both water and air) (Fig. 1), maybe systematically or depending of the environmental conditions.

Differences between the lungs of fossil and extant coelacanths are clues for understanding which adaptations were important to live in such physiologically demanding different environments (CUPELLO *et al.*, 2019).

Gills

Although the soft tissue of the branchial apparatus is so far not described for fossil coelacanths, these forms were most

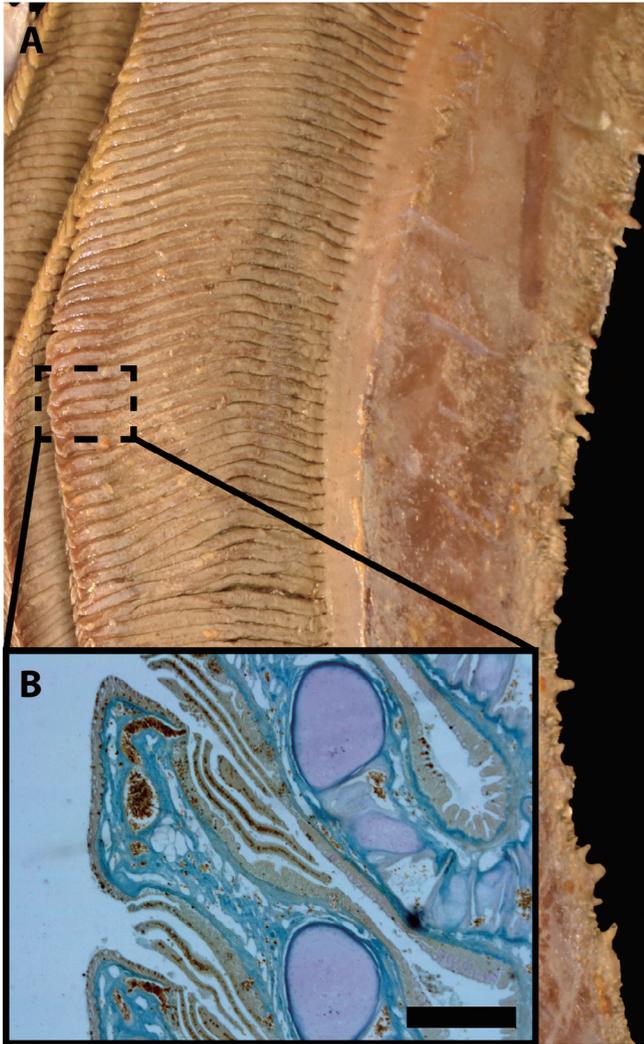


Fig. 2 The poorly developed gills of *Latimeria chalumnae*. A, General morphology of the branchial arch and gill filaments. B, Histological thin-section of the gill filaments and lamellae. Scale, 1 cm (A), 500 μ m (B).

probably bimodal breathers, making aquatic gas exchange using their gills and air-breathing through their well-developed lungs, possibly for supplementary oxygen supply in hypoxic conditions (BRITO *et al.*, 2010). Such a bimodal respiration occurs also in other taxa, such as *Neoceratodus forsteri* (KREFFT, 1870), as it increases the frequency of aquatic gas exchange, air-breathing, and pulmonary blood flow when in aquatic hypoxia (FRITSCHE *et al.*, 1993).

The extant coelacanth *L. chalumnae* certainly makes gas exchanges only through the gills, although these structures have a very low oxygen diffusing capacity (HUGHES, 1972, 1998) (Fig. 2). In adult specimens of *L. chalumnae* gills are poorly developed, like in deep-water fishes, with a reduced

surface area and sparse lamellae that reduce water flow resistance (HUGHES, 1998) and present: 1) a thick barrier of about 6 μ m between the water and the blood (HUGHES, 1998); 2) short gill filaments (in length), when compared to other groups of fish with more active behaviour (HUGHES, 1972; 1976; 1995); 3) non-respiratory components in the gill vessel system (VOGEL *et al.*, 1998) (Fig. 2). In embryos gill filaments are comparatively well developed (HUGHES, 1980). Although the number of filaments remains constant throughout the ontogeny, filaments decrease per centimetre in adult forms (HUGHES, 1980) and, consequently, decrease the gas exchange surface.

Besides the morphology of the gills, other evidences raise questions about the mechanism of gill ventilation and gas exchange of this taxon. With poorly developed gills and a non-functional lung, how does *Latimeria* make sufficient gas exchanges in relation with the body weight and the metabolism activity of the animal? What is the water flow pumping mechanism?

Videorecordings of *L. chalumnae* individuals in submarine caves of the Comorian Archipelago were made by Hans FRICKE and colleagues from 1986 to 2009, and the frequency of ventilatory movements were estimated in three or four per minute, with intervals of 15–20s (HUGHES, 1995; 1998). These records show that, most of the time, the mouth is slightly opened and the operculum closed (HUGHES, 1995). Ventilation cycles were inferred based on the videorecordings, describing its beginning with the mouth closure, the expansion of the opercular cavity, and the opening of the opercular valve (HUGHES, 1995).

Some data regarding the very low oxygen consumption of this taxon point out that *Latimeria* has a low activity and resting metabolism (HUGHES, 1976). The presence of short gill filaments, and the thick barrier between the water and the blood are correspondent to a lethargic behaviour for this taxon (HUGHES, 1980, 1995). Besides the correlation with the mode of life, poorly developed gills were also described for actinopterygian taxa that inhabit Comorian deep-sea (such as *Ruvettus*, *Ephinephelus* sp., and *Gempylidae*), correlating this feature also with the depth of the environment (HUGHES, 1980).

Direct observations and relatively long continue video footages in a coelacanth population of South-Africa in 2010 and 2013 have confirmed a placid behaviour most probably linked to a low metabolic activity. These observations were made during the day, when the coelacanths, which are nocturnal animals, were resting in their submarine caves. No clear ventilator movements were filmed, with no observation of mouth or operculum openings. The opercular flaps were usually tightly applied on the sides of the body and the mouth only slightly opened anteriorly (Fig. 3). It can be added that coelacanths were observed resting sometimes far in the bottom of their cave, standing in stationary position in an environment devoid of strong water currents. On the contrary of some sharks, coelacanths do not seem to benefit from sufficient

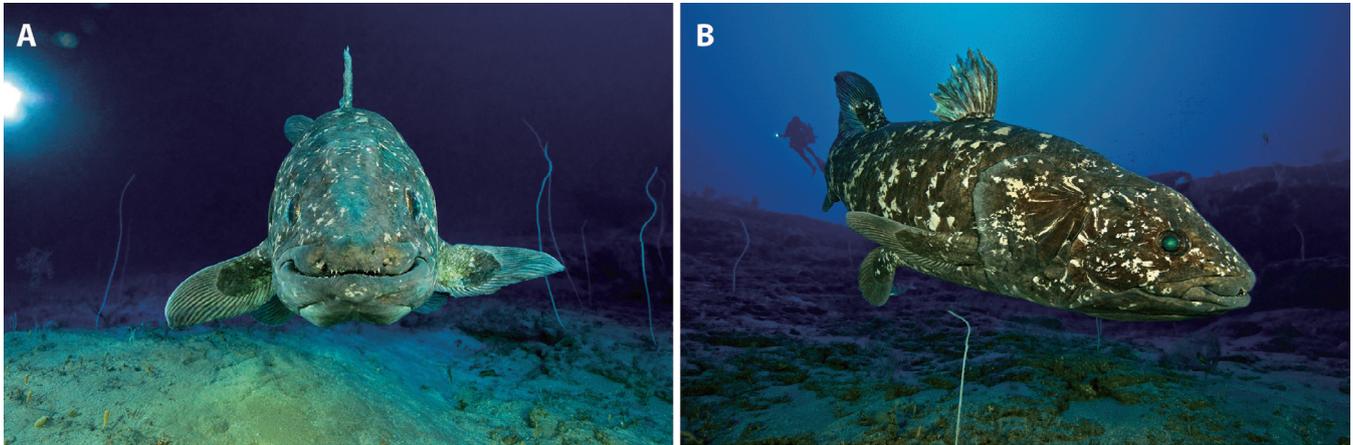


Fig. 3 Photographs of the living coelacanth *Latimeria chalumnae* in its natural environment at about 120 m of depth at Sodwana Bay, iSimangaliso Wetland Park, South Africa. A, B, The mouth is slightly opened anteriorly and the opercular flaps tightly applied along the body, as usually observed in coelacanths by deep divers or by remoted operated underwater vehicle (photographs courtesy of Laurent BALLESTA, Andromède Océanologie).

water currents to breath while resting in stationary position. Coelacanths do not have spiracles, the openings just behind the eyes that allow some bottom-dwelling sharks and rays to draw oxygenated water into the mouth cavity.

LIPID ACCUMULATION IN COELACANTHS

Soon following the discovery of a living coelacanth, SMITH (1939) highlighted the presence of high concentration of oil in *L. chalumnae* body. Indeed, high rates of lipid accumulation are distributed in different portions of the whole body of adult coelacanths: thick layers of fat that surround the nervous axis; periencephalic adipose layer (92.3% of lipid rate); fat-filled "perilymphatic cisterna" and perilymphatic sac; endocranial cavity of the anterior half of the neurocranium (90.6% of lipid rate); muscles (23.9% of lipid rate); interstitium and different cavities (including the orbits); mesenteric, peripancreatic and perihepatic deposits; liver (32,3% of lipid rate); and fatty organ (95% of lipid rate) that surrounds the vestigial lung (MILLOT, 1954; MILLOT and ANTHONY, 1965), for which the pulmonary origin has been recently questioned (CUPELLO *et al.*, 2017b). The chemical composition of this lipid accumulation in *L. chalumnae* is constituted mainly by wax esters (90%) (NEVENZEL *et al.*, 1966). High amounts of wax esters were also reported in various organs of deep-water fish taxa for buoyancy control (NEVENZEL *et al.*, 1966; CUPELLO *et al.*, 2015).

Although the presence of a fatty organ and accumulation of fat in other tissues is not described, so far, in fossil coelacanths, they probably have the function of buoyancy control in extant coelacanths (BRITO *et al.*, 2010; CUPELLO *et al.*, 2015). In *L. chalumnae*, the fatty organ, which is a large

and median sheath located in the dorsal part of the abdominal cavity, was pointed as the principal organ filled with fat, with a rate of 95% of lipids (MILLOT, 1954) (Fig. 4). This organ makes a dorsal turn-up in its middle portion in adult forms, while in embryos it presents a ventral position throughout its length in relation to the digestive tract. The dorsal turn-up in adult extant coelacanths may favor the function of buoyancy control (Fig. 4).

DISCUSSION AND CONCLUSION

The long-time adaptation of coelacanths from shallow to moderate deep marine waters is here reviewed based on the evolutionary history of the pulmonary system, branchial apparatus, and lipid distribution. Fossil and extant coelacanths effectively possess a lung with an anatomical peculiarity: it is surrounded by bony plates (BRITO *et al.*, 2010; CUPELLO *et al.*, 2017b). In fossil forms, this organ is well-developed and was most probably functional for gas-exchange, to support bimodal respiration in more intense activity and adverse conditions of shallowing or hypoxia (BRITO *et al.*, 2010; CUPELLO *et al.*, 2015). The recent description of a well-developed lung in early embryos of *L. chalumnae*, also suggest a functional lung in fossil coelacanths (CUPELLO *et al.*, 2015). However, in its marine environment, the extant coelacanth *L. chalumnae* presents a non-functional vestigial lung, and the gas exchange is made exclusively through the gills.

Although being an exclusive aquatic gas exchanger taxon, *L. chalumnae* has one of the lowest rates of gill area per unity of mass measured so far (HUGHES, 1980). This points to the long-time adaptation of this taxon to moderate deep environments. The low O₂-diffusing capacity of the gills and

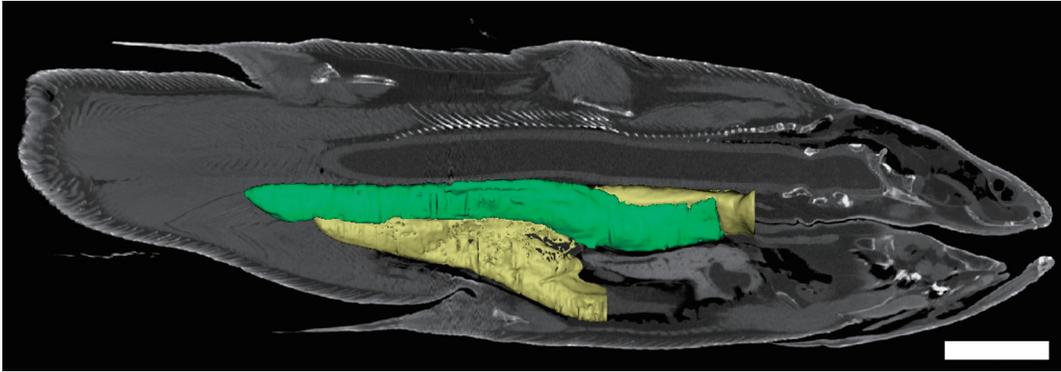


Fig. 4 The fatty organ of the extant coelacanth *Latimeria chalumnae* and its dorsal turn-up in the adult specimen CCC 22 (130cm TL). Section of a high-resolution computerized axial tomography scan and the three-dimensional reconstructions of the fatty organ, oesophagus and stomach. Yellow, oesophagus and stomach; green, fatty organ. Scale bar, 10 cm.

the non-functional lung of *L. chalumnae* may trigger on hypoxic stress or asphyxia on the water surface, which commonly reaches from 26 to 29 °C along the African east coast (FRICKE and HISSMANN, 2000). The water temperature may be one of the obstacles to the colonization of *Latimeria* in shallow waters (FRICKE and PLANTE, 1988). The resting metabolism of extant coelacanths and the very low oxygen consumption may allow this taxon to live in moderate deep-waters with moderate but constant oxygen rate and with low fish density (FRICKE and HISSMANN, 2000).

Probably in the Late Cretaceous, and possibly earlier, there were coelacanths adapted to moderate deep waters, with reduced lung and limited development of the gills, extinguishing the groups that inhabited shallow waters with little diluted oxygen. In addition, the competition in shallower waters should be more intense, favouring the colonization of new niches in deeper waters (FRICKE and HISSMANN, 2000). It is supposed that some taxa of Late Cretaceous coelacanths lived in shallow waters and could have disappeared during the Cretaceous/Palaeogene environmental crisis. However, some coelacanths already adapted to moderate deep waters, and phylogenetically close to *Latimeria*, would have survived to this crisis, due to the marine buffer zone between their living environments and the surface.

Other evidence of the adaptation of the extant coelacanth *L. chalumnae* to moderate deep-marine water is the lipid accumulation in its various organs and tissues. Such an anatomical framework seems to work analogous to 1) the liver of chondrichthyans and larval teleosts (CORNER *et al.*, 1969; NURSALL, 1989; HELFMAN *et al.*, 1997; LIEM *et al.*, 2001), that stores lipids (less dense than the glycogen, the reserve found in the liver of other vertebrates) as a reserve of energy to control buoyancy in the water column, 2) the fatty filament and the stock of extracellular fat present in some deep-water actinopterygians (NORMAN, 1975; PHLEGER, 1998), and 3) the spermaceti of some cetaceans, whose function is to promote a

system to maintain neutral buoyancy on the surface and at great depth, controlled by the variation of temperature of the oil contained in this structure (CLARKE, 1970, 1978; RIDGWAY 1971). Lipid storage, related to buoyancy control, has been reported also in different tissues and organs of various teleost taxa, such as some myctophids, gempylids, notothenioids, macrourids, and ophidiids (e.g., BONE, 1972; PHLEGER and HOLTZ, 1973; EASTMAN and DEVRIES, 1982). Besides the function of buoyancy control, fatty substance may avoid compression by the water column in deep water.

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