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RESEARCH NOTE

Comparative anatomy of the caudal skeleton of lantern fishes of the genus *Triphoturus* Fraser-Brunner, 1949 (Teleostei: Myctophidae)

Anatomía comparada del complejo caudal de los peces linterna del género *Triphoturus* Fraser-Brunner, 1949 (Teleostei: Myctophidae)

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Abstract.- The caudal skeleton provides important information for the study of the systematics and ecomorphology of teleostean fish. However, studies based on the analysis of osteological traits are scarce for fishes in the order Myctophiformes. This paper describes the anatomy of the caudal bones of 3 *Triphoturus* species: *T. mexicanus* (Gilbert, 1890), *T. nigrescens* (Brauer, 1904) and *T. oculeum* (Garman, 1899). A comparative analysis was performed on cleared and stained specimens to identify the differences and similarities of bony elements and the organization of the caudal skeleton among the selected species. *Triphoturus mexicanus* differs from *T. oculeum* in the presence of medial neural plates and a foramen in the parhypural, while *T. nigrescens* differs from their congeners in a higher number of hypurals ($2 + 4 = 6$) and the separation and number of cartilaginous elements. This osteological description of the caudal region allowed updates to the nomenclature of bony and cartilaginous elements in myctophids. Further, this study allows for the recognition of structural differences between *T. mexicanus* and *T. oculeum*, as well as the major morphological distinction between *T. nigrescens* and their sister species.

Key words: Caudal fin anatomy, osteology, Mexican lantern fish, Highseas lantern fish, Myctophiformes

INTRODUCTION

Structural components in the caudal skeleton of teleosts and their variation are useful taxonomic traits for intergeneric and specific delineation (*e.g.*, Fraser 1968, Tyler 1980) as well as in the evaluation of teleostean interrelationships (Gosline 1960, Nybelin 1963, Lauder 1989, Schultze & Arratia 1989, Fujita 1990, Borden *et al.* 2013, Doosey & Wiley 2015). For this reason, most ichthyologists consider these as important sources of information for systematic, functional morphology and adaptive radiation in aquatic environments (Johnson 1975, Lauder 1989, 2000; Moriyama & Takeda 2013). However, the caudal skeleton of higher euteleosts has been studied in only a few taxa (see McDowall 1999), with studies either addressing only certain species (*e.g.*, Potthoff & Tellock 1993, Doyle 1998, Bartolino 2005), or referring to representative taxa at the generic or family level (*e.g.*, Keivany & Nelson 1998, Baldwin & Johnson 1999, Castro-Leal & Brito 2007). Hence, the descriptive study of the morphology and evolution of the caudal fin in teleosts is yet to be completed (Dunn 1983, Arratia & Schultze 1992; Schultze & Arratia 1989, 2013; Castro-Leal & Brito 2007, Moriyama & Takeda 2013, Doosey & Wiley 2015).

The family Myctophidae comprises fishes inhabiting deep, oceanic zones worldwide. This family is characterized by the presence of cephalic, lateral, and ventral photophores, the arrangement of which is an important trait for taxonomic determination (Wisner 1974). Nevertheless, photophores are commonly dislocated during collection, making the identification of species difficult (Wisner 1974).

For some myctophid genera, there are taxonomic issues not yet solved because of the lack of studies on the biology and the morphology of this family. Therefore, it is important to explore tools that can be used as potential sources of information and criteria for the taxonomic identification of species in this group, such as osteology and comparative morphology (Paxton 1972, Hulley 1986, Moser & Ahlstrom 1996).

In the family Myctophidae, osteological research has focused on establishing the phylogenetic relationships, using key bony features that are unique to the family and related groups or a general description of the skeleton for each genus (*e.g.*, Paxton 1972, Stiassny 1996). However, a detailed analysis of the distribution, shape, size and insertion point of bony structures is

important for some genera when the information required for species discrimination is missing. This lack of comparative bony studies has not allowed a clear taxonomic differentiation between the members of the genus *Triphoturus* (e.g., Paxton 1972, Hulley 1986, Moser & Ahlstrom 1996).

The anatomical information currently available for *Triphoturus* is insufficient for establishing the number of species that inhabit the Eastern Pacific Ocean. Therefore, the aim of this study was to perform the comparative analysis of the caudal skeleton in 3 species of this genus, to provide information for the taxonomic discrimination and the establishment of relationships between species in this genus.

MATERIALS AND METHODS

A total of 58 specimens were analyzed from fish collections deposited in the Centro Interdisciplinario de Ciencias Marinas (CICIMAR-CI) and the Scripps Institution of Oceanography (SIO): 13 specimens of *Triphoturus nigrescens* (Brauer, 1904) from the California Current, 16 of *T. ocaleum* (Garman, 1899) from Colombia, Ecuador and Peru, and 18 of *T. mexicanus* (Gilbert, 1890) from the Gulf of California (7 specimens) and the California Current (11 specimens).

All specimens were processed by the clearing and staining method described by Taylor (1967) with amendments by Pothoff (1984). The dissection and identification of caudal elements was based on the bone nomenclature proposed by Gosline (1961), Nybelin (1963), Paxton (1972) and Rojo (1991),

whereas the nomenclature of cartilaginous elements followed Fujita (1989). All bony components were digitized according to Bouck & Thistle (1999).

RESULTS AND DISCUSSION

In line with the diurnal nomenclature of Arratia & Schultze (1992), we assume that the last independent vertebral centrum is the second preural centra (PU2) and the urostyle is the bone structure resulting from the (ontogenetic or phylogenetic) fusion of the first preural centrum (PU1) and the first and second ural centra (U1 and U2). This terminal vertebra (sensu Paxton 1972) that articulates with the first hypurals, was formerly known as the 'ural vertebra' or urostyle (sensu Nybelin 1963), which in accordance to Dunn (1983) corresponds to vertebral centra fused along the evolutionary history and ontogeny of fish groups like the Myctophidae. Based on the polyural interpretation (e.g., Arratia & Schultze 1992, Schultze & Arratia 2013, Wiley *et al.* 2015), the urostyle could represent the compound autocentrum of preural centrum 1 plus and unknown number of ural centra (e.g., Doosey & Wiley 2015), however, data of developmental biology studies in myctophid fishes are necessary to corroborate this statement in myctophids, a goal that it is out of the scope of this contribution.

The caudal skeleton of *T. nigrescens* have 6 hypurals bones (HY): 4 located posterodorsal and 2 in anteroventral position (Fig. 1). In contrast, *T. mexicanus* and *T. ocaleum* display HY 1 + 2 fused ventrally plus HY 3 + 4 + 5 fused dorsally in a

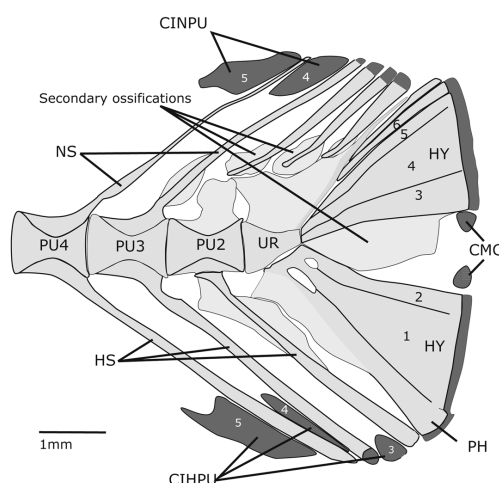


Figure 1. Lateral view of the caudal skeleton of *Triphoturus nigrescens* (Brauer, 1904) (CICIMAR-CI 2565). Hypurals (HY); median caudal cartilage (CMC); interhaemal spine cartilage (CIHPU); interneural spine cartilage (CINPU); neural spine (NS); haemal spine (HS); parahypural (PH); preural centrum (PU); urostyle (UR) / Vista lateral del esqueleto caudal de *Triphoturus nigrescens* (Brauer, 1904) (CICIMAR-CI 2565). Hipurales (HY); cartilagos medios caudales (CMC); cartilago interhemal de la espina (CIHPU); cartilago interneural de la espina (CINPU); espina neural (NS); espina hemal (HS); parahipural (PH); centro preural (PU); urostilo (UR)

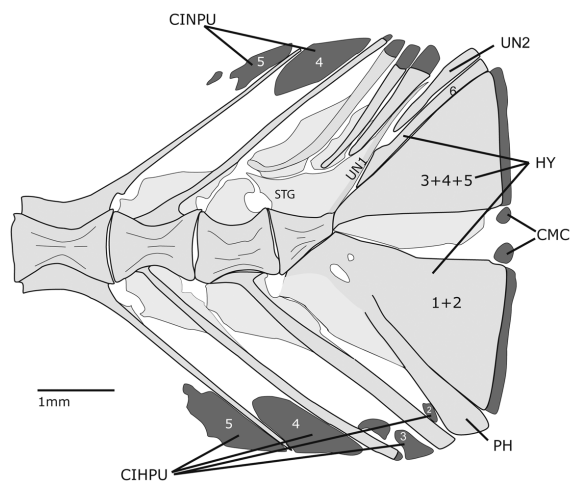


Figure 2. Lateral view of the caudal skeleton of *Triphoturus mexicanus* (Gilbert, 1890) (CICIMAR-CI 2665). Hypurals (HY); median caudal cartilage (CMC); interhaemal spine cartilage (CIHPU); interneural spine cartilage (CINPU); parhypural (PH); stegural (STG); uroneural (UN) / Vista lateral del esqueleto caudal de *Triphoturus mexicanus* (Gilbert, 1890) (CICIMAR-CI 2665). Hipurales (HY); cartílagos medios caudales (CMC); cartílago interhemal de la espina (CIHPU); cartílago interneural de la espina (CINPU); parahipural (PH); uroneural (UN)

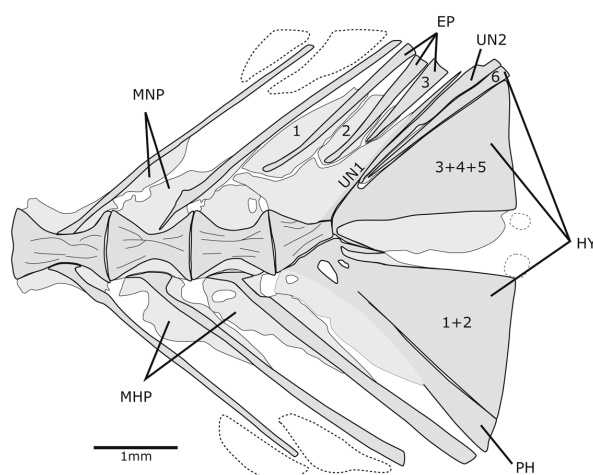


Figure 3. Lateral view of the caudal skeleton of *Triphoturus oculeum* (Garman, 1899) (SIO52-372). Epurals (EP); hypurals (HY); median haemal plates (MHP); median neural plates (MNP); parhypural (PH); uroneural (UN) / Vista lateral del esqueleto caudal de *Triphoturus oculeum* (Garman, 1899) (SIO52-372). Epurales (EP); hipurales (HY); placas medias hemales (MHP); placas medias neurales (MNP); parahipural (PH); uroneural (UN)

single plate separated from HY 6 (Figs. 2 and 3). Among these bony elements, there is a wide hypural diastema, wider in *T. nigrescens* than in its congeners.

On the other hand, the term ‘hypural flange’ used in *Triphoturus* and other myctophid genera for naming the bony extensions of ventral hypurals (*e.g.*, Paxton 1972), was here considered as a modified haemal spine of the urostyle that represents the last haemal arch spanning from the ventral aorta, based on one specimen of *T. mexicanus* with neural and haemal elements stained. For this reason, the correct terminology for this structure should be parhypural (PH), as applied in other teleost groups (Nybelin 1963, Rojo 1991). Accordingly, the members of *Triphoturus* are characterized by 2 to 4 independent or fused posterodorsal hypural elements plus one to 2 independent or fused anteroventral hypural. This updates the information reported previously by Paxton (1972), who mentions a formula of 4 dorsal + 2 – 3 ventral hypurals. The hypural fusion patterns and number of hypural observed in *Triphoturus* is a myctophiform condition similar to that established for other myctophid neoscolepids genera (Fujita 1990, Borden *et al.* 2013).

All species display two foramens: one located between the basis of the PH and HY 1; and other located between the bases of HY 1 and HY 2. A secondary ossification appears at the lower edge of HY 3 + 4 + 5 in *T. mexicanus* and *T. oculeum*, which is in HY 3 in *T. nigrescens*. This structure exhibits high intraspecific morphological variation. At the base of the urostyle, the PH develops a laminar extension thickened anteriorly that reaches beyond the midpoint of the bony axis; *T. oculeum* differs from its congeners by the presence of a foramen in this structure (Fig. 3).

In *Triphoturus*, the caudal skeleton comprises 10 dorsal and 9 ventral principal caudal rays. Procurrent rays are spine-shaped, its degree of flexibility regarding Paxton (1972) is ‘great’ as a result of the distal fusion between the two elements of each pair; *T. mexicanus* and *T. oculeum* have 6 or 7 dorsal and 6 or 7 ventral procurrent rays, while *T. nigrescens* shows 6 or 8 dorsal and 6 or 8 ventral rays.

Haemal spines (HS) of the second (PU2) and third preural centra (PU3) have at its base expanded haemal arches named median haemal plates (MHP) by Gosline (1960). In *T. nigrescens*, only the haemal spine of PU2 shows this MHP. In *T. mexicanus* and *T. oculeum*, PU2 and PU3 display MHPs; the main difference between the 2 species is the presence of a foramen in the proximal region of PU2 MHP in *T. oculeum*.

Moreover, the neural spines (NS) of PU3 are expanded at the base forming median neural plates (MNPs); *T. mexicanus* may or may not show an MNP in the PU3 neural spine. Likewise, *T. oculeum* shows an MNP in PU3, and occasionally also on the axis of the PU4 neural spine. In *T. nigrescens*, the MNP originates at the axis of the neural spine and not at its base, without exceeding the height of the anterior border of the first uroneural.

Two independent uroneurals (UN) are present in *Triphoturus* species. They are labeled as UN1 and UN2 because of their number and position, but not implying homology. The so-called UN1 has an anterior expansion, that is slender and tricuspid-shaped, termed stegural (Arratia & Schultze 1992, Doosey & Wiley 2015). The stegural shows slight interspecific variation in shape. The proximal tips of the epurals rest on the dorsal margin of the stegural. The anterior region of the stegural does not overlap the neural arch (spine lacking) of PU2; its base is attached to the urostyle. The paired UN2 is lanceolate-shaped.

Epurals (EP) present a secondary ossification at their proximal region (Fig. 1), which is more extended in EP2 of *T. nigrescens*, in contrast with the ossification of EP1 and EP3. In *T. mexicanus* and *T. oculeum*, EP1 displays a further development of these ossifications. EP3 is wedge-shaped in all *Triphoturus* species, and no secondary ossification is observed in most cases. Recent studies have shown the difficulty of standardizing the names of some skeletal structures as in the case of uroneurals and epurals in different groups of fishes and the importance of ontogenetic data to understand the origin and possible homologies involved (*e.g.*, Doosey & Wiley 2015).

Regarding the number of epurals in *Triphoturus*, Paxton (1972) mentioned the presence of 2 or 3 structures. All specimens analyzed here definitely show three epurals. Likewise, a comparative analysis of the morphology of epurals in other mictophids (*e.g.*, the genus *Diaphus*) revealed that adult specimens show the fusion of these bones; however, a line of suture is apparent, indicating that epurals are not truly fused (Rubio-Rodríguez 2009).

Based on the criteria of Johnson (1984), we established the caudal formula for the bony elements of *T. mexicanus* and *T. oculeum* as:

$$6/3/2/4$$

$$\text{I+II; III-V; VI}$$

In these 2 species, the caudal skeleton is composed of 6 hypurals, 3 epurals, 2 uroneurals and 4 haemal spines include a parhypural.

The caudal formula of *T. nigrescens* is:

6/3/2/4

I+II; III; IV; V; VI

In addition, 2 free cartilages appear in the dorsal region supporting the dorsal procurent rays. The first named inter-neural cartilage of the fourth preural centrum spine (CINPU4) is located between the neural spines of the third and fourth preural centra; the second cartilage of CINPU5 is located between the neural spines of the fourth and fifth preural centra.

Likewise, ventrally there are 3 or 4 free cartilages supporting the lower procurent rays: the first is located between the lateral edge of the parhypural and the haemal spine of PU2, which corresponds to the interhaemal cartilage of the second preural centrum spine (CIHPU2); this structure was observed only in *T. mexicanus*. Between the haemal spines of PU2 and PU3 there is a second free or interhaemal cartilage of the third preural centrum spine (CIHPU3). A third CIHPU4 cartilage is located between the PU3 and PU4 haemal spines, and the last CIHPU5 is located between the PU4 and PU5 haemal spines.

All species have developed a pair of median caudal cartilages (CMC; see Fig. 2). In *T. mexicanus* and *T. oculateum*, these cartilages are relatively close to one another (separated by a distance equivalent to one-third at the urostyle [UR] height); this contrasts with *T. nigrescens*, where the separation between cartilages is equivalent to more than one-half of UR height, in addition to the presence of a wider hypural diastema.

In general, the comparison between the caudal skeleton of *T. mexicanus* and *T. oculateum* revealed a similar morphology; however, a distinctive trait of *T. oculateum* is the presence of foramina in the median haemal plate of the haemal spine of PU2, as well as in the parhypural bone. In contrast, several differences on the caudal composition and external morphology of *T. nigrescens* were detected; these findings in addition to the molecular differentiation established by Rodríguez-Graña *et al.* (2004), lead us to believe *T. nigrescens* should probably be the most divergent species within the group included in this study. However, a detailed assessment based on a phylogenetic approach should be conducted in further studies.

Material examined: *Triphoturus mexicanus*: CICIMAR-CI 2627 (4 ex.) [50-54 mm SL]; CICIMAR-CI 2645 (1) [69]; CICIMAR-CI 2647 (2) [84-93]; CICIMAR-CI 2665 (3) [62-69]; CICIMAR-CI 2628 (3) [54-67]; CICIMAR-CI 2473 (5) [57-65].

T. oculateum : SIO 05-156 (2) [54-59]; SIO 52-367 (3) [64-68]; SIO 52-372 (4) [61-74]; SIO 52-404 (4) [56-66]; SIO 52-409 (3) [59-72].

T. nigrescens: CICIMAR-CI 2478 (8) [62-80]; CICIMAR-CI 2565 (3) [65-78]; CICIMAR-CI 2646 (2) [68-74].

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