Head and otolith morphology of the genera *Hymenocephalus*, *Hymenogadus* and *Spicomacrurus* (Macrouridae), with the description of three new species

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Abstract

The fishes of the genus *Hymenocепhalus* live over continental slope terrain, chiefly between 300 and 1000 m water depths, in all tropical oceans, except the eastern Pacific. They are characterized by an elongated light organ with two lenses, striations on jugular and thorax, and by an extraordinary development of sensory reception organs: strongly enlarged eyes, exceptionally large and specialized sagittal otoliths and extremely wide and deep head canals resembling caverns and housing the cephalic sensory organ for motion reception (lateral line system).

The purpose of this study is to evaluate the potential that a detailed analysis of the head and otolith morphology can offer for distinguishing the various species and assessment of their interrelationships. About 500 specimens were investigated, representing all 22 nominal species of the genus *Hymenocепhalus*, except for *H. barbatulus* (specimens of which could not be located), the two species of the related genus *Hymenogадус* and three of the four species of *Spicomacrurus*. Because of the delicate and thin nature of the head bones and head skin typical for the fishes of the genus *Hymenocепhalus* and the deteriorating effects of formalin to the aragonitic otoliths, only a fraction of the studied specimens actually contributed useful data, although that fraction represented all species studied.

Otoliths in particular and aspects of the cephalic canal system were found to contribute additional characters that help to verify the status of certain controversial species such as *H. heterolepis*, *H. nascens* and species within the *H. striatiissimus* and *H. grimaldii* Groups. *Hymenocепhalus longiceps* is revised to represent a junior synonym of *H. longibarbis*. Eight species groups are defined within the genus *Hymenocепhalus*. Three new species are being described in this course of review: *H. iwamotoi* from off northwestern Australia, *H. sazonovi* from the Sala y Gomez and Nazca Ridges, and *H. punt* from northern Somalia and the Gulf of Aden, now raising the count of valid species in the genus to a total of 24.

The specializations of the sensory reception organs show a variety of developments with well-expressed phylogenetic polarities that are discussed in the context of their evolution and interrelationships. A well-documented case of polarity reversal of certain characters in the *H. aterrimus* Group is interpreted as a functional adaptation to migration of these fishes into a deeper water environment that favors different specializations of the sensory reception.

Key words: Head morphology, otoliths, new species, *Hymenocепhalus, Hymenogадус, Spicomacrurus*

Introduction

The fishes of the macrourid genus *Hymenocепhalus* Giglioli, 1884 are found along the continental slopes of the tropical and subtropical seas of the world except for the Pacific coast of South America (but for a single specimen caught off Peru, USNM 149049). They occur predominantly at depths between 300 and 600 m where they feed mostly on planktonic euphausids and copepods (Okamura, 1970) and often seem to socialize in schools. At this water depth there is still some dim, high-frequency light and it is also within or close to the zone with highly effective long-distance sound transmission. It may have to do with their specific environment in life that evolution has favored the development of extraordinary sensory reception organs in the fishes of the genus *Hymenocепhalus*. They show strongly enlarged eyes positioned in orbits resembling parabolic mirrors and oriented perpendicular to the fish axis. The sagittal otolith (‘otolith’ in the following), which is part of the sound-receiving sensory organ in fishes, is amongst the largest found in teleosts relative to the size of the brain capsule, and it shows some very distinct specialized features. It is so big and the head bones are so translucent that very often it can be seen shining through the head from above. The orbit sizes reach up to 50% of the head length in certain species and the sagittal otolith can attain a size of about 20% of the head length. The head bones are thin and large parts of the head over the occiput, around the eyes, along the rim of the preopercle and the mandible are occupied by an extremely wide and deep cavern or canal system housing the cephalic sensory organ for motion reception (lateral-line system) with large sensory papillae or neuromasts of one mm in diameter or more. The canals are covered by a very thin integument (‘hymen’), which is almost never found fully intact on fishes brought to surface. The integument is stretched over the cephalic canals (‘caverns’) with the support of a number of bony projections from the skull (‘supporters’), not unlike the canvas of a tent stretched over its poles. As far as can be reconstructed, the canal systems do not seem to be segmented, but, where reasonably preserved, the integument does show regular linear.
(Popper, 1980), merlucciids (Lombarte & Popper, 2004) and morids (Deng et al., 2011), but no macrourid. Schwarzhans (1981) has shown the occurrence of multiple, unrelated developments of fused colliculi in the Ophidiiformes, sometimes within a genus, similar to that in Hymenocephalus. Similar observations no doubt could be made with otoliths of the Macrouridae, but in Hymenocephalus there is no indication that fusion of the colliculi has occurred more than once.

In summary, it appears that the specializations of characters associated with the visual, auditory and motion-capturing senses (eye/orbit size, sagittal otolith morphology and head canal system) have developed in parallel and along similar polarities within the genus Hymenocephalus, with the longibarbis Group the most basal and the striatissimus and grimaldii Groups the most advanced (Fig. 39). Polarity reversal is observed in two of the three main trends (visual and auditory) in the aterrimus Group, which is probably a result of adaptation to a life in deeper waters.

Conclusions

This detailed study of the head and otolith morphology of the species of Hymenocephalus has clarified the taxonomic status of several of the species, which have been under discussion in recent literature. In certain instances, however, the taxonomic status still remains poorly or tentatively resolved (H. lethonemus vs H. nascens and the three nominal species H. aeger, H. striatissimus and H. torvus). Specific large-scale statistical evaluations could contribute further to the clarification of these remaining problematic species, or DNA-analyses, when available, will yield better perspectives.

The genera Hymenocephalus and Spicomacrurus contain a number of geographically restricted species, particularly in the western Pacific, and it may well be that the recognition of individual species is still incomplete. The otoliths of two poorly preserved fishes are described under Unidentifiable Species, and probably represent two undescribed species. Also, certain regions are under-explored, particularly continental and island margins of the Indian Ocean and the tropical eastern Atlantic. Once more extensively covered we might expect not only unrecorded and possibly new species, but also recognition of wider geographical ranges of known species. A recent study on otoliths dredged from Holocene sea bottom sediments in the Gulf of Guinea and off the Azores (Schwarzhans, 2013) has already indicated the potential for the latter: the presence of at least one other previously unrecorded species of the genus Hymenocephalus in the eastern Atlantic, probably H. billsam in this case.

The value of otolith morphology in the taxonomy of the Gadiformes, and particularly the Macrouridae seems high, as has been demonstrated in this study. Therefore, I expect that studies of the otolith morphology of other macrourid genera will contribute valuable taxonomic data as demonstrated here for the genus Hymenocephalus.

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