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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 *Hymenocephalus* 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 *Hymenocephalus*, except for *H. barbatulus* (specimens of which could not be located), the two species of the related genus *Hymenogadus* 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 *Hymenocephalus* 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. striatissimus* and *H. grimaldii* Groups. *Hymenocephalus longiceps* is revised to represent a junior synonym of *H. longibarbis*. Eight species groups are defined within the genus *Hymenocephalus*. Three new species are being described in the course of this 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, *Hymenocephalus, Hymenogadus, Spicomacrurus*

Introduction

The fishes of the macrourid genus *Hymenocephalus* 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 euphasids 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 *Hymenocephalus*. 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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References

Alcock, A. (1889) Natural history notes from H.M. Indian Marine Survey Streamer 'Investigator', Commander Alfred Carpenter, R.N., D.S.O., commanding No. 13. On the bathybial fishes of the Bay of Bengal and neighboring waters, obtained during the seasons 1885-1889. *Annals and Magazine of Natural History*, Series 6, 4, 376–399. http://dx.doi.org/10.1080/00222938909460547

Alcock, A. (1891) On the deep-sea fishes collected by the 'Investigator' in 1890-1891. *Annals and Magazine of Natural History*, Series 6, 8, 119–138.
http://dx.doi.org/10.1080/00222939109460407

Alcock, A. (1899) *A Descriptive Catalogue of the Indian Deep-Sea Fishes in the Indian Museum*. Indian Museum, Calcutta, 211 pp.
http://dx.doi.org/10.5962/bhl.title.4684

Cohen, D.M., Inada, T., Iwamoto, T. & Scialabba, N. (1990) FAO species catalogue Vol. 10. Gadiform fishes of the world (Order Gadiformes). *FAO Fisheries Synopsis*, 125(10), 442 pp. [Rome]

Deng, X., Wagner, H.-J. & Popper, A.N. (2011) The inner ear and its coupling to the swim bladder in the deep-sea fish *Antimora rostrata* (Teleostei: Moridae). *Deep-Sea Research I*, 58, 27–37.
http://dx.doi.org/10.1016/j.dsr.2010.11.001

Fricke, R. & Eschmeyer, W.N. (2011) A guide to fish collections in the Catalog of Fishes. Available from: http://researcharchive.calacademy.org/research/Ichthyology/catalog/collections.asp (accessed 5 May 2014)

FishBase (2014) World Wide Web Electronic Publication. Version (04/2014), Ed. by R. Froese & Pauly, D.Available from: http://www.fishbase.org (accessed 12 November 2014)

Garman, S. (1899) The Fishes. *In*: Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U.S. Fish Commission steamer 'Albatross,' during 1891, Lieut. Commander Z.L. Tanner, U.S.N., commanding. No. XXVI. *Memoirs of the Museum of Comparative Zoology,* 24, pp. 1–431, Atlas: pls. 1–85 + A–M.

Giglioli, E.H. (1884) *Issel Pelagos. Saggi sulla vita e sui prodotti del mare.* Tipografia del R. Istituto de' Sordo-Muti, Genoa, 436 pp.
http://dx.doi.org/10.5962/bhl.title.42527

Gilbert, C.H. (1905) The deep-sea fishes of the Hawaiian Islands. *In*: Jordan & Evermann (Eds.), The aquatic resources of the Hawaiian Islands. *Bulletin of the United States Fishery Commission,* 22 (2), 575–713.
http://dx.doi.org/10.5962/bhl.title.12624

Gilbert, C.H. & Cramer, F. (1897) Report on the fishes dredged in deep water near the Hawaiian Islands, with descriptions and figures of twenty-three new species. *Proceedings of the United States National Museum,* 19 (1114), 403–448.
http://dx.doi.org/10.5479/si.00963801.19-1114.403

Gilbert, C.H. & Hubbs, C.L. (1916) Report on the Japanese macrouroid fishes collected by the United States fisheries steamer 'Albatross' in 1906, with a synopsis of the genera. *Proceedings of the United States National Museum,* 51 (2149), 135–214.
http://dx.doi.org/10.5479/si.00963801.51-2149.135

Gilbert, C.H. & Hubbs, C.L. (1917) Description of *Hymenocephalus tenuis*, a new macrouroid fish from the Hawaiian Islands. *Proceedings of the United States National Museum,* 54 (2231), 173–175.
http://dx.doi.org/10.5479/si.00963801.54-2231.173

Gilbert, C.H. & Hubbs, C.L. (1920) The macrouroid fishes of the Philippine Islands and the East Indies. *United States National Museum Bulletin,* 100 (1), 369–588.
http://dx.doi.org/10.5962/bhl.title.13637

Goode, G.B. & Bean, T.H. (1885) Descriptions of new fishes obtained by the United States Commission mainly from deep water off the Atlantic and Gulf coasts. *Proceedings of the United States National Museum,* 8, 589–605.
http://dx.doi.org/10.5479/si.00963801.8-543.589

Goode, G.B. & Bean, T.H. (1896) *Oceanic ichthyology, a treatise on the deep-sea and pelagic fishes of the world. Special Bulletin 2*, Smithsonian Institution, United States National Museum, Washington, 553 pp., plus atlas.
http://dx.doi.org/10.5962/bhl.title.48521

Günther, A. (1887) Report on the deep-sea fishes collected by HMS 'Challenger' during the years 1873-1876. *Report of the scientific results of the voyage of H.M.S. Challenger during the years 1873-76, Zoology*, 22, 1–335.
http://dx.doi.org/10.5962/bhl.title.15693

Iwamoto, T. & McCosker, J.E. (2014) *Deep-water fishes of the 2011 Hearst Philippine biodiversity expedition of the California Academy of Sciences*. *In*: Williams, G.C. & Gosliner, T.M. (Eds.), *The Coral Triangle. The 2011 Hearst Philippine Biodiversity Expedition*. California Academy of Sciences, San Francisco, pp. 263–332.

Iwamoto, T. & Merrett, N.R. (1997) Pisces Gadiformes: Taxonomy of grenadiers of the New Caledonian region, southwest Pacific. *Mémoires du Muséum national d'Histoire naturelle*, 176, 473–570.

Iwamoto, T., Shao, K.-T. & Ho, H.-C. (2011) Elevation of *Spicomacrurus* (Gadiformes: Macrouridae) to generic status, with descriptions of two new species from the southwestern Pacific. *Bulletin of Marine Science*, 87 (3), 513–530.
http://dx.doi.org/10.5343/bms.2011.1004

Iwamoto, T. & Williams, A. (1999) Grenadiers (Pisces, Gadiformes) from the continental slope of Western and northwestern Australia. *Proceedings of the California Academy of Sciences,* 51 (3), 105–243.

Jordan, D.S. & Gilbert, C.H. (1904) *Macrouridae*. *In*: Jordan, D.S. & Starks, E.C. *List of fishes dredged by the streamer Albatross off the coasts of Japan in the summer of 1900, with descriptions of new species and a review of the Japanese Macrouridae*. *Bulletin of the United States Fishery Commission,* 22, 577–630.

Kamohara, T. (1938) *On the offshore bottom fishes of Prov. Tosa, Shikoku, Japan.* Tokyo, 86 pp.

Koken, E. (1884) Über Fisch-Otolithen, insbesondere über diejenigen der norddeutschen Oligocän-Ablagerungen. *Zeitschrift der deutschen Geologischen Gesellschaft*, 36, 500–565.

Lombarte, A. & Popper, A.N. (2004) Quantitative changes in the otolithic organs of the inner ear during the settlement period in European hake *Merluccius merluccius*. *Marine Ecology progress series*, 267, 233–240. http://dx.doi.org/10.3354/meps267233

Marshall, N.B. (1979) *Developments in deep-sea biology*. Blandford Press Ltd, Dorset, 566 pp.

Marshall, N.B. & Iwamoto, T. (1973) Genus *Hymenocephalus*. *In*: Cohen, D.M. (Ed.), Fishes of the Western North Atlantic. *Memoires of the Sears Foundation Marine Research*, 1 (6), 601–612.

Merrett, N.R. & Iwamoto, T. (2000) Pisces Gadiformes: Grenadier fishes of the New Caledonian region, southwest Pacific Ocean. Taxonomy and distribution with ecological notes. *Mémoires du Muséum national d'Histoire naturelle*, 184, 723–781.

Nolf, D. & Steurbaut, E. (1989) Evidence from otoliths for establishing relationships within gadiforms. *Natural History Museum of Los Angeles County, science series,* 32, 89–112.

Okamura, O. (1970) *Fauna Japonica. Macrourina (Pisces).* Academic Press of Japan, Tokyo, pp. 1–216.

Okamura, O. (1984) *The Fishes of the Japanese Archipelago. Vol. 1. & 2.* Tokai University Press, 437 pp. & 370 pls. [Masuda, H., Amaoka, K., Araga, C., Uyeno, T. & Yoshino, T.]

Popper, A.N. (1980) Scanning electron microscopic study of the sacculus and lagena in several deep-sea fishes. *The American Journal of Anatomy*, 157, 115–136. http://dx.doi.org/10.1002/aja.1001570202

Prokofiev, A.M. & Kukuev, E.I. (2009) New findings of rare fish species from families Mitsukurinidae (Chondrichthyes), Muraenidae, Lophiidae, Macrouridae, and Psychrolutidae (Teleostei) on raises of the Atlantic Ocean with description of Gymnothorax walvisensis sp. nova. *Journal of Ichthyology*, 49 (3), 215–227. http://dx.doi.org/10.1134/s0032945209030023

Sazonov, Y.I. & Iwamoto, T. (1992) Grenadiers (Pisces, Gadiformes) of the Nazca and Sala y Gomez Ridges, southeastern Pacific. *Proceedings of the California Academy of Sciences*, 48 (2), 27–95.

Schwarzhans, W. (1978) Otolith-morphology and its usage for higher systematical units, with special reference to the Myctophiformes s.l. *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie,* 15, 167–185.

Schwarzhans, W. (1981) Vergleichende morphologische Untersuchungen an rezenten und fossilen Otolithen der Ordnung Ophidiiformes. *Berliner geowissenschaftliche Abhandlungen, Reihe A*, 26, 1–211.

Schwarzhans, W, (2003) Fish otoliths from the Paleocene of Denmark. *Geological Survey of Denmark and Greenland Bulletin*, 2, 1–94. http://dx.doi.org/10.13140/2.1.2532.4164

Schwarzhans, W. (2010) *The otoliths from the Miocene of the North Sea Basin*. Backhuys Publishers, Leiden; Margraf Publishers, Weikersheim, 350 pp.

Schwarzhans, W. (2013) Otoliths from dredges in the Gulf of Guinea and off the Azores - an actuo-paleontological case study. *Palaeo Ichthyologica*, 13, 7–40. http://dx.doi.org/10.13140/2.1.1299.5209

Smith, H.M. & Radcliffe, L. (1912) *in Radcliffe*. Descriptions of a new family, two new genera, and twenty-nine new species of anacanthine fishes from the Philippine Islands and contiguous waters. *Proceedings of the United States National Museum,* 43(1924), 105–140. http://dx.doi.org/10.5479/si.00963801.43-1924.105

Vaillant, L.L. (1888) *Expéditions scientifiques du TRAVAILLEUR et du TALISMAN pendant les années 1880, 1881, 1882, 1883*. Poissons, Paris, 406 pp. http://dx.doi.org/10.5962/bhl.title.13677

Weber, M. (1913) Die Fische der SIBOGA-Expedition. *Siboga Expedition*, 57, 1–179. http://dx.doi.org/10.5962/bhl.title.35825

Weiler, W. (1942) Die Otolithen des rheinischen und nordwestdeutschen Tertiärs. *Abhandlungen des Reichsamt für Bodenforschung,* 206, 1–140. [NF]

Wilson, R.R. Jr. (1985) Depth-related changes in sagitta morphology in six macrourid fishes of the Pacific and Atlantic Oceans. *Copeia*, 4, 1011–1017. http://dx.doi.org/10.2307/1445256