BRIEF COMMUNICATION

Vacchi's palatal organ: a widespread trait in Holocephali

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A palatal organ, possibly used for food sorting and processing, has previously been identified among the vomerine toothplates of the chimaeroid *Chimaera monstrosa*. In this study, the palatal organ was described in six additional species, confirming it is a widespread trait among holocephalans. It is proposed that this palatal structure, which appears to differ in shape according to each chimaeroid's degree of durophagy and is not homologous to the palatal structure described in teleosts, be hereby referred to as Vacchi's organ.

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The Holocephali is a subclass of Chondrichthyes, diverging from Elasmobranchii approximately 167 million years ago (Inoue *et al.*, 2010). Extant Holocephali, namely chimaeroid fishes, are distinguished from other chondrichthyans by a number of characteristics, including fusion of the upper jaw to the neurocranium, and dentition constituted by three pairs of continually growing, hypermineralized toothplates (one in the lower jaw and two in the upper) (Didier *et al.*, 2012). These traits are essential to chimaeroid specialization for durophagy, *i.e.* feeding on hard prey (Huber *et al.*, 2008).

In the chimaeroid rabbitfish *Chimaera monstrosa* L. 1785, a palatal organ has recently been described among the upper toothplates in the anterior of the mouth (Ferrando *et al.*, 2016). This palatal organ was found to be rich in nerve endings, taste buds, and multicellular glands, and has been hypothesized to play a part in food sorting and processing (Ferrando *et al.*, 2016). As the toothplates limit the extent of oral mucosa that reaches the anterior part of the mouth (Patterson, 1992), it is unsurprising that such a structure is found in the oral cavity of this chimaeroid.

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Bony fishes of the order Cypriniformes also possess a palatal organ, located in the caudal zone of the palate (Doosey & Bart, 2011). Described as an active surface, working in conjunction with the gill sieve during food processing, the palatal organ of cypriniforms consists of sensory and motor innervation extending from the vagus nerve (Callan & Sanderson, 2003; Finger, 2008; Doosey & Bart, 2011). Unlike the structure described in cypriniforms, the chimaeroid palatal structure is relatively small in size, and positioned in the very anterior portion of the palate, as opposed to the caudal–pharyngeal zone, away from the gill sieve (Ferrando *et al.,* 2016). Additionally, the anterior palate of chimaeroids is innervated by a palatine branch of the facial nerve (Cole, 1897; Kesteven, 1933; de Beer & Moy-Thomas, 1935), which is likely to also innervate the palatal organ.

In respect to function, shape, position, and innervation, the palatal organ of chimaeroids does not appear to be homologous to that defined in teleosts. To date, however, the palatal organ has only been described in *C. monstrosa*. The aim of this work is to present evidence that the palatal organ first described in *C. monstrosa* is a widespread characteristic across all chimaeroids. A further description on the morphology of this oral structure is presented. Given its distinctiveness, the chimaeroid palatal structure is hereby proposed as Vacchi's organ, in honour of the contemporary Italian ichthyologist M. Vacchi, whose research has contributed to greater biological knowledge of cartilaginous fishes (www.shark-references.com/ literature/listByAuthor/VACCHI-M.;www.fishbase.org/References/ReferencesList .php?Author=vacchi&Year=&Title=&Source=&RefNo=).

Specimens of longnose spookfish *Harriotta raleighana* Goode & Bean 1895, Pacific spookfish *Rhinochimaera pacifica* (Mitsukuri 1895), brown chimaera *Chimaera carophila* Kemper, Ebert, Naylor & Didier 2014, black ghost shark *Hydrolagus homonycteris* Didier 2008, pale ghost shark *Hydrolagus bemisi* Didier 2002 and dark ghost shark *Hydrolagus novaezealandiae* (Fowler 1911) were obtained from within the New Zealand exclusive economic zone (EEZ) by Ministry for Primary Industries (MPI) scientific observers aboard commercial fishing vessels during 2015. All fish caught were frozen whole at sea and brought back to the laboratory for analysis where chimaera length (L_C; tip of the snout to the posterior edge of the supracaudal fin, excluding the caudal filament, mm), total mass (M, g), sex, and maturation stage were recorded (Table I).

The palate of each specimen was isolated, fixed in 10% formalin for 24 h, and preserved in 70% ethanol. Toothplates were described following Patterson (1992), and measurements of the palatine toothplate (PT; posterior upper), vomerine toothplate (VT; anterior upper), and proposed Vacchi's organ (VO), as well as the number of tritor ridges were calculated using ImageJ software (Abramoff *et al.,* 2004). Samples were photographed on an Olympus SP-590UZ camera (www.olympus.com) and a Zeiss Stemi 2000 (www.zeiss.com) stereomicroscope equipped with a CellPad E camera (TiEsseLab S.r.l.; www.tiesselab.com). Structures identified as VO were isolated and embedded in paraffin, sectioned 5 μm thick, and stained with haematoxylin–eosin (H&E). Images were viewed on a Leica DMRB light microscope and captured with a Leica CCD camera DFC420C (Leica; www.leica.com). The palates of fishes used in this work were deposited in the Civic Museum of Natural History 'Giacomo Doria' of Genoa; the catalogue numbers are reported in Table I.

Vacchi's organ was identified in all palates, and has now been confirmed in four of the six genera of extant chimaeroids (*Chimaera* L. 1758, *Hydrolagus* Gill 1862, *Harriotta*

TABLE I. Measurements of chimaeroid specimens, including chimaera length (L_C), mass (M), number of tritors in the right vomerine toothplate (N_{TR}), and the ratio of a (the length of the Vacchi's organ plus the stalk), b (maximum width of the Vacchi's organ) and c (length of the Vacchi's organ with d, the length of the free margin of a vomerine toothplate [Fig. 1(h)]

MSNG code	Species	Sex	Maturity	L_C (mm)	M (g)	N_{TR}	a:d	b:d	c:d
MSNG 60621	*Chimaera carophila*	F	Mature	944	4829	7	1·5	0·4	0·8
MSNG 60622	*C. carophila*	F	Immature	674	1592	8	1·2	0·3	0·4
MSNG 60623	*C. carophila*	M	Mature	794	2021	6	1·3	0·2	0·6
MSNG 60624	*Harriotta raleighana*	F	Mature	840	1393	10	1·7	0·6	1·0
–	*H. raleighana*	F	Mature	853	2059	7	2·1	0·5	0·9
MSNG 60625	*H. raleighana*	I	Mature	857	1933	9	1·8	0·5	0·6
MSNG 60626	*Hydrolagus homonycteris*	M	Immature	772	2290	4	1·9	0·4	0·9
MSNG 60627	*H. homonycteris*	M	Mature	846	2544	4	1·7	0·4	0·8
MSNG 60628	*Hydrolagus bemisi*	M	Mature	623	1351	6	1·8	0·4	0·6
MSNG 60629	*H. bemisi*	F	Mature	694	2049	7	1·7	0·4	0·5
MSNG 60630	*Hydrolagus novaezealandiae*	M	Mature	567	1147	6	1·9	0·5	0·6
MSNG 60631	*H. novaezealandiae*	F	Immature	595	1244	7	2·2	0·5	0·6
MSNG 60632	*Rhinochimaera pacifica*	F	Mature	1278	4152	–	2·0	0·6	0·7
MSNG 60633	*R.pacifica*	F	Immature	1004	1573	–	2·1	0·6	0·7
MSNG 60634	*R. pacifica*	M	Mature	1110	2773	–	2·1	0·5	0·6

MSNG code: catalogue numbers of the samples deposited in the Civic Museum of Natural History 'Giacomo Doria' of Genoa. F, Female; M, male; I indeterminate.

Goode & Bean 1895, and *Rhinochimaera* Garman 1901). It is likely to be characteristic across all extant holocephalans. This fleshy organ was located between the vomerine toothplates and connected to the posterior palate by a thin band of mucosa (the stalk), between the symphysial edges of the palatine toothplates (Fig. 1). When the palatal toothplates were removed, two masses of soft tissue were visible on each side of the VO [Fig. 1(g)]. Histological analysis confirmed an abundance of nerve fibres in the connective tissue [Fig. 1(i)]. However, the epithelial structures (*e.g.* taste buds) previously observed in *C. monstrosa* were not observed, which may have been a consequence of non-optimal fixation procedures (chemical fixation after freezing and defrosting). Thus, histological descriptions of the VOs for these species were postponed at this time.

The shape of the toothplates and the VOs were very similar across species belonging to the genera *Chimaera*, *Hydrolagus*, and *Harriotta* [Fig. 1(a)–(e)]. In these species, the palatine toothplates presented a flat, ventrally-positioned occlusal surface. Distances between the left and right palatine toothplates were modestly variable across species, with the exception of *H. homonycteris*, where the toothplates were found to be nearly touching [Fig. 1(b)]. In *R. pacifica*, the left and right palatine toothplates were relatively distant from each other and the mucosa between them had a larger surface area. Differentiation of the VO from the stalk in *R. pacifica* was difficult, as the stalk was nearly the same size as the VO [Fig. 1(f)]. Measurements of the palates as outlined in Fig. 1(h) are listed in Table I.

The consistency in toothplate and VO morphology observed across the genera *Chimaera*, *Hydrolagus*, and *Harriotta* is complemented by previous studies that have described comparable diet patterns across these groups (Dunn *et al.,* 2010; Jones, 2012; Finucci *et al.,* 2017). Diets of these species consist predominately of crustaceans, sea urchins, molluscs, and polychaetes, which would require grinder
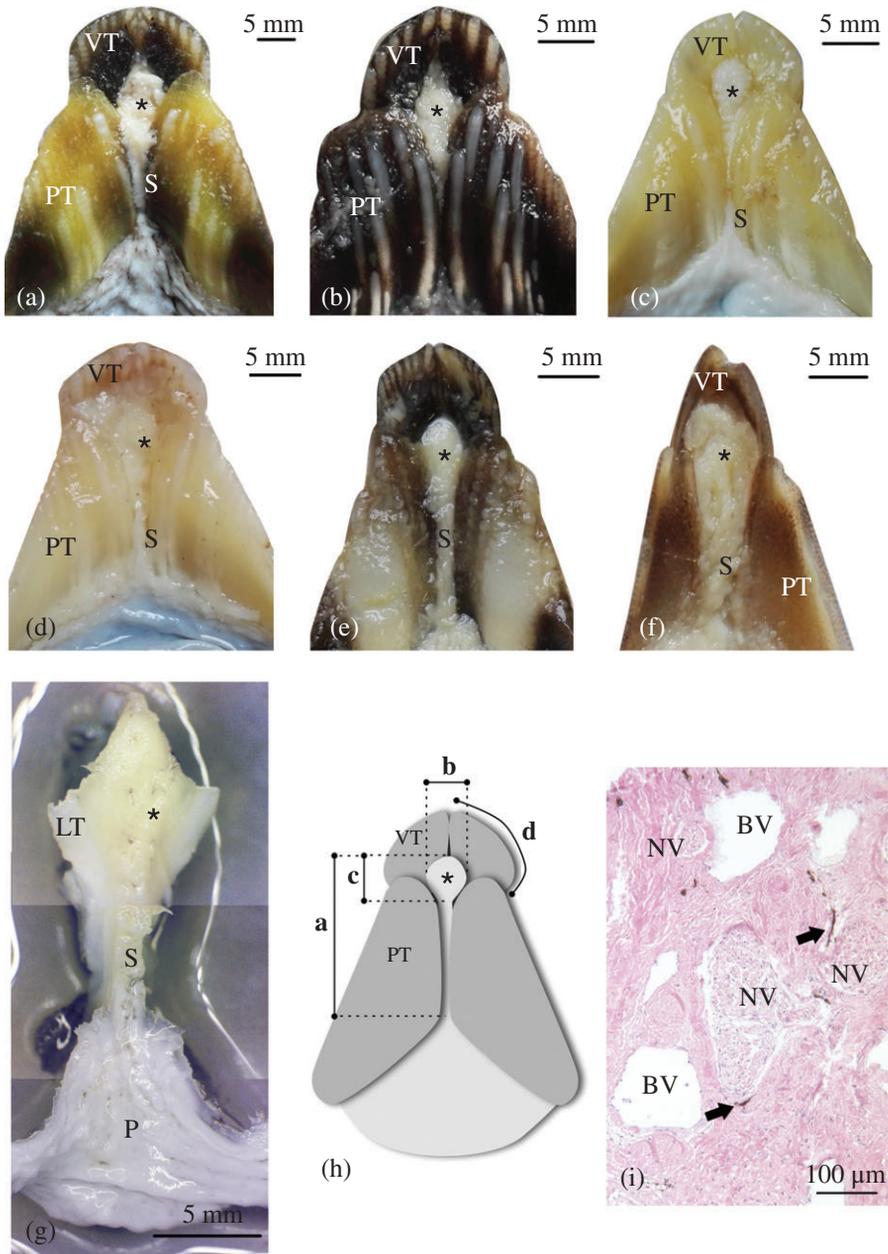
FIG. 1. Ventral view of whole palates from (a) *Chimaera carophila*, (b) *Hydrolagus homonycteris*, (c) *Hydrolagus bemisi*, (d) *Hydrolagus novaezealandiae*, (e) *Harriotta raleighana* and (f) *Rhinochimaera pacifica*. (g) Additional images of *H. raleighana* palate after the removal of the palatal and vomerine toothplates. (h) Diagram of the palate (a, length of the Vacchi's organ plus the stalk; b, maximum width of the Vacchi's organ; c, length of the Vacchi's organ; d, length of the free margin of a vomerine toothplate). (i) Histological section of the Vacchi's organ of *H. raleighana*, stained with haematoxylin–eosin. BV, blood vessel; NV, Nerve bundle; LT, lateral tissue; P, palate mucosa; PT, palatine toothplate; S, stalk; VT, vomerine toothplate; ↓, melanophore; ✱, Vacchi's organ.

toothplates for mastication (Huber *et al.,* 2008). In *Rhinochimaera* spp., however, the toothplates have been proposed to function as cutters based on differing characters (Garman, 1904; Didier & Nakaya, 1999). *Rhinochimaera* spp. toothplates lack calcified tritors, the occlusal surface of the palatine toothplates are oriented medioventrally (as opposed to ventrally), and have a ventrally-directed labial margin (Dean, 1904; Didier *et al.,* 2012; S. Ferrando, pers. obs.). In addition, the larger distance between the palatal toothplates observed in *R. pacifica* is compensated with a larger VO, which may host a wider range of sensory structures, such as taste buds, and overall greater sensitivity to what the individual consumes. These discrepancies may reflect different dietary preferences. At this time, the diet of *R. pacifica* is unknown, although given its morphology and distribution, it has been hypothesized that the diet of *R. pacifica* consists of infaunal prey (Dunn *et al.,* 2010). Its congener, *Rhinochimaera atlantica* Holt & Byrne 1909, was reported to feed on a diet of crustaceans, but that study was limited by a small sample size (Macpherson & Roel, 1987). More recent studies have reported empty digestive tracts for *R. pacifica* (Pethybridge *et al.,* 2011), while the remains of digested and unrecognizable fishes have been found in the stomach contents of individuals from New Zealand (Jones, 2012; B. Finucci, pers. obs.).

The morphology of chimaeroid toothplates and VOs are mutually adapted to cover the entirety of the anterior palate surface, which appears to vary in shape and size according to diet specialization. Grinder toothplates and thin-shaped VOs may be associated with those more specialized durophagous species, whilst cutter toothplates and wider VOs may be characteristic of species with a diet that includes other fishes and softer-bodied items. Further investigation is recommended to explore the morphology and functionality of the palatal organization in this group of fishes.

References

Abramoff, M. D., Magalhaes, P. J. & Ram, S. J. (2004). Image processing with ImageJ. *Biophotonics International* **11,** 36–42.

de Beer, G. R. & Moy-Thomas, J. A. (1935). On the skull of Holocephali. *Philosophical Transaction of the Royal Society B* **224,** 287–312. https://doi.org/10.1098/rstb.1935.0001

Callan, W. T. & Sanderson, S. L. (2003). Feeding mechanisms in carp: crossflow filtration, palatal protrusion and flow reversal. *Journal of Experimental Biology* **206,** 883–892. https://doi.org/10.1242/jeb.00195

Cole, F. J. (1897). XIX. – on the cranial nerves of *Chimæra monstrosa* (Linn. 1754); with a discussion on the lateral line system, and of the morphology of the chorda tympani. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **38,** 631–680. https://doi.org/10.1017/S0080456800033433

Dean, B. (1904). Notes on the long-snouted chimaeroid of Japan, *Rhinochimaera* (*Harriotta*) *pacifica* (Garman) Mitsukuri. *Journal of the College of Science, Imperial University, Tokyo* **19,** 1–26.

Didier, D. A. & Nakaya, K. (1999). Redescription of *Rhinochimaera pacifica* (Mitsukuri) and first record of *R. Africana* Compagno, Stehmann & Ebert from Japan (Chimaeriformes: Rhinochimaeridae). *Ichthyological Research* **46,** 139–152. https://doi.org/10.1007/BF02675432

Didier, D. A., Kemper, J. M. & Ebert, D. A. (2012). Phylogeny, biology and classification of extant holocephalans. In *Biology of Sharks and Their Relatives*, 2nd edn (Carrier, J. C.,

Musick, J. A. & Heithaus, M. R., eds), pp. 97–124. New York, NY: CRC Press. https://doi.org/10.1201/b11867-6

Doosey, M. H. & Bart, H. L. Jr. (2011). Morphological variation of the palatal organ and chewing pad of Catostomidae (Teleostei: Cypriniformes). *Journal of Morphology* **272,** 1092–1108. https://doi.org/10.1002/jmor.10966

Dunn, M. R., Griggs, L., Forman, J. & Horn, P. (2010). Feeding habits and niche separation among the deep-sea chimaeroid fishes *Harriotta raleighana*, *Hydrolagus bemisi* and *Hydrolagus novaezealandiae*. *Marine Ecology Progress Series* **407,** 209–225. https://doi.org/10.3354/meps08580

Ferrando, S., Gallus, L., Gambardella, C., Croce, D., Damiano, G., Mazzarino, C. & Vacchi, M. (2016). First description of a palatal organ in *Chimaera monstrosa* (Chondrichthyes, Holocephali). *The Anatomical Record* **299,** 118–131. https://doi.org/10.1002/ar.23280

Finger, T. (2008). Sorting food from stones: the vagal taste system in goldfish, *Carassius auratus*. *Journal of Comparative Physiology* **194,** 135–143. https://doi.org/10.1007/s00359-007-0276-0

Finucci, B., Stevens, D. W., Jones, E. G. & Dunn, M. R. (2017). Some observations on the biology of two rarely seen deep-sea chimaerids, *Chimaera carophila* and *Hydrolagus homonycteris*. *Journal of Fish Biology* **90,** 2020–2040. https://doi.org/10.1111/jfb.13284

Garman, S. (1904). The chimaeroids (Chismopnea Raf., 1815; Holocephala Müll., 1834), especially *Rhinochimaera* and its allies. *Bulletin of the Museum of Comparative Zoology at Harvard College* **41,** 245–272.

Huber, D. R., Dean, M. N. & Summers, A. P. (2008). Hard prey, soft jaws and the ontogeny of feeding mechanics in the spotted ratfish *Hydrolagus colliei*. *Journal of the Royal Society Interface* **5,** 941–952. https://doi.org/10.1098/rsif.2007.1325

Inoue, J. G., Miya, M., Lam, K., Tay, B. -H., Danks, J. A., Bell, J., Walker, T. I. & Venkatesh, B. (2010). Evolutionary origin and phylogeny of the modern holocephalans (Chondrichthyes: Chimaeriformes): a mitogenomic perspective. *Molecular Biology and Evolution* **27,** 2576–2586. https://doi.org/10.1093/molbev/msq147

Jones, M. R. L. (2012). Diets and feeding relationships of deep-sea fish from central and southern New Zealand. PhD Thesis, Auckland University of Technology. http://hdl.handle.net/10292/5765

Kesteven, H. L. (1933). The anatomy of the head of *Callorhynchhus antarcticus*. *Journal of Anatomy* **67,** 443–474.

Macpherson, E. & Roel, B. A. (1987). Trophic relationships in the demersal fish community off Namibia. *South African Journal of Marine Science* **5,** 585–596. https://doi.org/10.2989/025776187784522432

Patterson, C. (1992). Interpretation of the toothplates of chimaeroid fishes. *Zoological Journal of the Linnean Society* **106,** 33–61. https://doi.org/10.1111/j.1096-3642.1992.tb01239.x

Pethybridge, H., Daley, R. K. & Nichols, P. D. (2011). Diet of demersal shark and chimaeras inferred by fatty acid profiles and stomach content analysis. *Journal of Experimental Marine Biology and Ecology* **409,** 290–299. https://doi.org/10.1016/j.jembe.2011.09.009