



## Complex flow in the nasal region of guitarfishes



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### ABSTRACT

Scent detection in an aquatic environment is dependent on the movement of water. We set out to determine the mechanisms for moving water through the olfactory organ of guitarfishes (Rhinobatidae, Chondrichthyes) with open nasal cavities. We found at least two. In the first mechanism, which we identified by observing dye movement in the nasal region of a life-sized physical model of the head of *Rhinobatos lentiginosus* mounted in a flume, olfactory flow is generated by the guitarfish's motion relative to water, e.g. when it swims. We suggest that the pressure difference responsible for motion-driven olfactory flow is caused by the guitarfish's nasal flaps, which create a region of high pressure at the incurrent nostril, and a region of low pressure in and behind the nasal cavity. Vortical structures in the nasal region associated with motion-driven flow may encourage passage of water through the nasal cavity and its sensory channels, and may also reduce the cost of swimming. The arrangement of vortical structures is reminiscent of aircraft wing vortices. In the second mechanism, which we identified by observing dye movement in the nasal regions of living specimens of *Glaucostegus typus*, the guitarfish's respiratory pump draws flow through the olfactory organ in a rhythmic (0.5–2 Hz), but continuous, fashion. Consequently, the respiratory pump will maintain olfactory flow whether the guitarfish is swimming or at rest. Based on our results, we propose a model for olfactory flow in guitarfishes with open nasal cavities, and suggest other neoselachians which this model might apply to.

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### 1. Introduction

A major constraint on olfaction in fishes is the very long diffusion times in water (Denny, 1993, p. 90; Cox, 2008). Consequently, to receive an olfactory signal in good time, fishes must actively draw water containing dissolved chemicals into their olfactory organs, and then circulate this water over their olfactory epithelium. Fishes may achieve the movement of water for olfactory purposes ('olfactory flow') using several different mechanisms, either alone, or in combination (Zeiske et al., 1992; Cox, 2008). For example, a fish may harness an external flow, generated either by its own movement, or by a current (the 'motion pump'). A fish may also use its respiratory pump to generate olfactory flow. In addition, if the olfactory epithelium is lined with motile, non-sensory cilia, olfactory flow may be generated by the coordinated beating of these cilia (the 'ciliary pump'). Another possibility is mechanical agitation of the olfactory organ. Understanding these mechanisms is important because the knowledge gained may lend insight

into olfaction in fishes, and may also be applied to the design of artificial aquatic sensors.

Our objective was to determine the mechanisms for generating olfactory flow in certain members of a family of rays known as the guitarfishes (Rhinobatidae, Fig. 1; Nelson, 2006, p. 74). We chose to study olfactory flow in guitarfishes (rhinobatids) for three reasons. First, such a study would complement our ongoing programme to understand olfactory flow in neoselachians (Abel et al., 2010; Rygg et al., 2013; Cox, 2013). Second, although rhinobatid nasal morphology has been depicted and described (Bigelow and Schroeder, 1953, p. 55; Kleerekoper, 1969, p. 52; Reese and Brightman, 1970; Meng and Yin, 1981; Bell, 1993; Schluessel et al., 2008; Whittington and Kearn, 2011), no one has yet undertaken a study of olfactory flow in guitarfishes, or indeed in any ray. Third, members of the two genera of guitarfishes we chose to study, *Rhinobatos* and *Glaucostegus*, have unusual nasal features: a pair of open nasal cavities and several nasal flaps on the edge of each nasal cavity (e.g. Bigelow and Schroeder, 1953, p. 55; for an overview of neoselachian nasal anatomy, see Gardiner et al., 2012, pp. 378–382 and Cox, 2013).

Rhinobatid nasal morphology suggests that olfactory flow may be generated by one or more of the following mechanisms. 1) The motion

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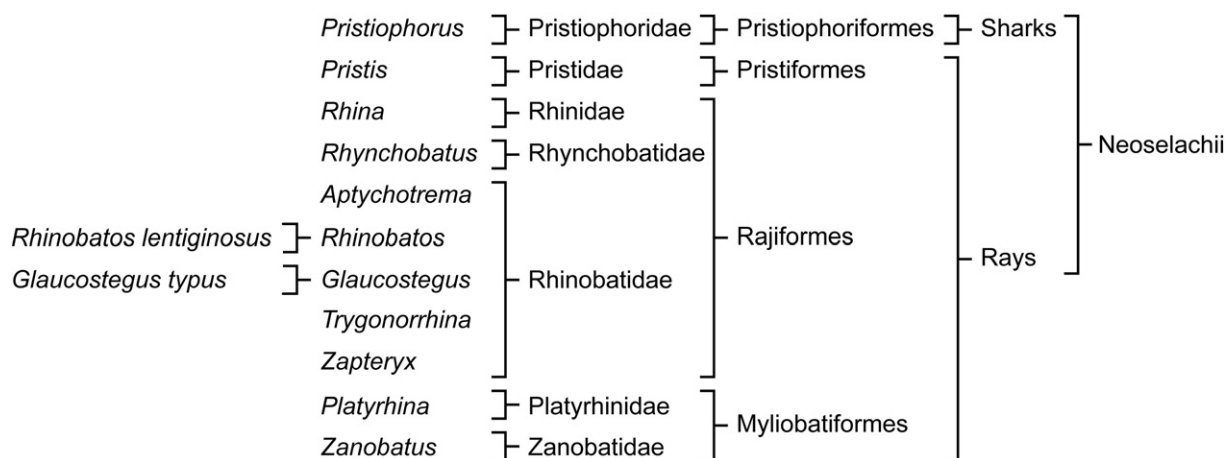


Fig. 1. Classification of neoselachians considered in this report, based on Nelson (2006).

pump. The large, anteriorly-facing incurrent nostrils of some guitarfishes (Bell, 1993) suggest that these animals harness external flows for olfactory purposes, either by swimming, or by orientating themselves to an oncoming current when resting. 2) The respiratory pump. Rhinobatid olfactory organs are located close to the mouth (Bell, 1993), where the influence of the respiratory pump on olfactory flow is likely to be significant. Also, in at least one species of guitarfish, *Rhinobatos leucorhynchus*, there is a groove linking each olfactory organ to the mouth (Bell, 1993). Based on observations in other neoselachians, the rhinobatid respiratory pump is likely to draw water through the mouth, over the gills, and into the parabranial chambers, and then expel it through the gill slits (Hughes, 1960; Hughes and Ballintijn, 1965; Summers and Ferry-Graham, 2001). 3) The ciliary pump. The olfactory epithelium of neoselachians, including that of two guitarfishes, *Rhinobatos lentiginosus* (Reese and Brightman, 1970) and *Aptychotrema rostrata* (Schluessel et al., 2008), is lined by non-sensory cilia, which can potentially generate olfactory flow. In a review of ciliary function in the olfactory organs of neoselachians, Cox (2013) concluded that these cilia, which are likely to have a common function in neoselachians, propel mucus rather than water, but the evidence for this conclusion was weak. Thus, the possibility that these cilia propel water instead of (or as well as) mucus cannot be discounted. 4) Mechanical agitation of the olfactory organ by movements of a guitarfish's mouth, which lies close to the nasal regions, may also contribute to olfactory flow.

We investigated these possible mechanisms in two species of guitarfishes, *R. lentiginosus* and *Glaucostegus typus*. We used a plastic model of a preserved specimen of *R. lentiginosus* to determine whether a guitarfish can harness an external flow for olfactory purposes. We used living specimens of *G. typus* to investigate primarily the influence of the respiratory pump on olfactory flow in guitarfishes. The choice of species was governed by access to a well preserved specimen (*R. lentiginosus*) in a museum and to living specimens (*G. typus*). In both cases we used dye to visualise olfactory flow (Settles, 2005, p. 190; Lim, 2000). Experiments on the influence of external flow were informed by *in vivo* observations of *G. typus* and a wedgfish (*Rhynchobatidae*; Nelson, 2006, p. 74) in public aquaria.

## 2. Materials and methods

### 2.1. *In vivo* observations at public aquaria

Behavioural observations of single living specimens of *G. typus* (male) and *Rhynchobatus* (male, species undetermined) were made at the Oceanarium, Bournemouth, UK, and the Sea Life Aquarium, Loch Lomond, UK, respectively.

### 2.2. Visualisation of olfactory flow in *R. lentiginosus*

We investigated olfactory flow in a life-sized plastic model of the head of *R. lentiginosus*. Our strategy was as follows: 1) scan the head of a preserved specimen of *R. lentiginosus* by X-ray microcomputed tomography (micro-CT); 2) use image processing to convert the X-ray scan into a stereolithography (STL) model; 3) 3D print the STL model; 4) suspend the resultant plastic model in a flume and use dye to visualise flow in one of the model's nasal regions. The methodology underlying this strategy is described by Abel et al. (2010). Further details are given below.

#### 2.2.1. Micro-CT

The specimen of *R. lentiginosus* that we X-ray scanned (Fig. 2) belongs to the collections of the Natural History Museum, London, UK (catalogue number BMNH 1913.12.8.1). The specimen was collected in Morehead, North Carolina, USA, ca. 1913, and has since been stored in 70% industrial methylated spirits, 30% distilled water. The total length, disc length, and disc width of the specimen (Last and Stevens, 2009, p. 23) are 80, 33 and 25 cm, respectively. The wet weight of the specimen is 1.4 kg. Based on its total length and lack of claspers, the specimen is an adult female (Bigelow and Schroeder, 1953, p. 61 and p. 66).

For the X-ray scan, the specimen of *R. lentiginosus* was mounted in a polythene bag (to prevent desiccation) with the body axis (Fig. 2A, BA) vertical. The head was scanned using an HMXST 225 CT system (Nikon Metrology, Tring, UK) at the Natural History Museum, London. The X-ray beam was generated from a tungsten reflection target. The accelerating voltage and current were 180 kV and 200  $\mu$ A, respectively. A total of 3142 angular projections were collected in a single 360° rotation at 0.11458° intervals. The radial projections were transformed into a three-dimensional matrix using CT Pro (Version 2.1, Nikon Metrology, Tring, UK). The voxel size of the scan was 89  $\mu$ m  $\times$  89  $\mu$ m  $\times$  89  $\mu$ m. The scan comprises the section of the head shown in Fig. 2A. For anatomical reconstruction, the scan was converted into a set of 1998 16-bit TIFF images in the transverse plane using the software VGStudio MAX (Version 2.1, Volume Graphics GmbH, Heidelberg, Germany).

#### 2.2.2. STL model

The STL model of the head of *R. lentiginosus* (Fig. 3A, B) was generated using the image processing software ScanIP (Simpleware, Exeter, UK) as follows. The TIFF images from the X-ray scan were imported into ScanIP and segmented using the Threshold tool to create a 'mask' of the head. The Paint and Floodfill tools were used to fill internal cavities, to seal the mouth, and to remove the parts of the mask corresponding to the polythene bag that surrounded the specimen during the scan.

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