

FIG. 4 Cladogram illustrating a hypothesis of the phylogenetic position of *Chimaerasuchus paradoxus*, derived from a numerical cladistic analysis (using PAUP) of 42 characters for 16 taxa of crocodyliforms (results in full to be presented elsewhere). Unequivocal synapomorphies for *Chimaerasuchus* and *Notosuchus*⁴ include: snout relatively broad and shorter than the remainder of the skull (determined in *Chimaerasuchus* from the length of the mandible); external nares vertical and facing directly forward; mandibular articular facet distinctly longer than wide; jaw joint in ventral position.

probably occluded in the grooves between the upper three rows. As in tritylodontids, the reversed concave cutting edges would have met during jaw closing and enclosed an ovoid space, which decreased in size during dynamic occlusion. This reversal of curvature in occluding teeth limited the area of tooth-to-tooth contact and thus served to maximize occlusal pressure between the teeth and food items at any given time. However, mandibular motion was proal (back-to-front) rather than propalinal (front-to-back), and the presence of only a single posterior cutting edge, rather than paired crests, on each cusp indicates less extensive shearing in *Chimaerasuchus* than in tritylodontid synapsids. There are also no wear facets indicative of tooth-to-tooth occlusion. The structure of the maxillary molariforms is consistent with a specialized diet including fibrous material and may indicate at least facultative herbivory in *Chimaerasuchus*. The procumbent premaxillary (and probably anterior dentary) teeth were presumably involved in seizing food items.

The proal mandibular motion in *Sphenodon* is produced by the posterior pterygoid muscle^{2,3}. In extant crocodylians, the homologous muscle pulls the mandible forward and upward^{12,13}. However, as in *Sphenodon*, the jaw joint is ventral in position in *Chimaerasuchus* and the Malawi notosuchid. Consequently, the posterior pterygoid muscle in the latter two was probably similar in its orientation to that in *Sphenodon*. As in *Sphenodon*, mandibular motion in the two crocodyliform reptiles must have been proal during jaw closing because the anterior pterygoid muscle, along with the pterygoid flange, would have restricted mandibular movements to front-to-back motion during jaw opening.

Although the skeleton of *Chimaerasuchus* is not yet fully known, characters indicating close affinities to the Notosuchidae (Fig. 4) include the articular facet of the jaw joint that is much longer than wide⁹, the ventral placement of the jaw joint, and the terminal, directly forward-facing external nares.

Notosuchid crocodyliforms have been considered endemic to the Cretaceous of Gondwana^{4,5,9}. Along with other new fossils¹⁴, the discovery of *Chimaerasuchus paradoxus* casts doubts on claims⁵ that Gondwana had a distinctly endemic tetrapod fauna during the Cretaceous. □

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Dimethyl sulphide as a foraging cue for Antarctic Procellariiform seabirds

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MANY Procellariiform seabirds make their living flying over vast expanses of seemingly featureless ocean waters in search of food. The secret of their success is a mystery, but an ability to hunt by smell has long been suspected^{1,7}. Here we present experimental evidence that Procellariiform seabirds can use a naturally occurring scented compound, dimethyl sulphide, as an orientation cue. Dimethyl sulphide has been studied intensely for its role in regulating global climate^{8,11} and is produced by phytoplankton in response to zooplankton grazing¹². Zooplankton, including Antarctic krill (*Euphausia superba*)¹³, are in turn eaten by seabirds and other animals¹⁴. Results from controlled behavioural experiments performed at sea show that many Procellariiforms can detect dimethyl sulphide, and that some species (for example, storm petrels) are highly attracted to it. To our knowledge, this constitutes the first evidence that dimethyl sulphide is part of the natural olfactory landscape overlying the southern oceans.

Experiments were conducted in sub-Antarctic waters near South Georgia during the Austral summer (January–March 1994). We chose this study area because Procellariiform species are numerous here, and the feeding habits of local species have been monitored for over two decades^{14,15}.

Our first set of experiments was designed to identify whether any Procellariiform species might be attracted to dimethyl sulphide (DMS). Our aim was to produce a down-wind DMS concentration that would be approximately the same as that which might naturally be encountered by a foraging petrel (nmol m⁻³ range)^{10,16,17}. We did this by deploying DMS-scented oil slicks on the ocean surface at ten different locations. Because surface slicks also presented visual cues to seabirds, DMS slicks were always paired with unscented ‘control’ slicks. We reasoned that if birds used DMS as a foraging cue, more birds should be attracted to DMS than to control slicks. At some locations, we also compared the response of birds to DMS with their response to cod liver oil, a well known olfactory attractant^{1,3,4,6,7}.

Results from our paired-slick experiments indicate that DMS is a potent olfactory attractant to many Procellariiform species, including white-chinned petrels, prions and two species of storm petrels (Fig. 1)¹⁸. Wilson’s storm petrels, for example, were sighted more than twice as often flying into DMS slicks than into control slicks. Indeed, when we plot the temporal response profiles of Wilson’s storm petrels to both DMS and cod-liver oil slicks (Fig. 2), we find that the outcomes are remarkably similar suggesting that DMS is as potent an olfactory attractant

as cod liver oil to this species. Just as noteworthy, however, is the absence of any response to DMS on the part of albatrosses or cape petrels: these species arrived at both DMS slicks and control slicks with the same frequency (Fig. 1).

In a second set of experiments, we presented birds with aerosol plumes of either DMS or water and monitored their flight behaviour. This approach allowed us to test birds' responses to DMS without presenting them with visual cues. Our hypothesis was that if DMS constituted a foraging cue, then birds likely to be attracted to this odour would also increase their turning rate in an attempt to locate the source^{16,18,19}. For these experiments, either odour (DMS) or control (water) plumes were aerosoled off the ship's stern while a pair of observers monitored the flight behaviour of the birds. White-chinned petrels and black-browed albatrosses were chosen for this investigation because these species showed distinct responses to DMS-scented slicks: white-chinned petrels were attracted to DMS, whereas black-browed albatrosses were not. We therefore predicted that white-chinned petrels would increase their turning rate in response to DMS, whereas black-browed albatrosses would not.

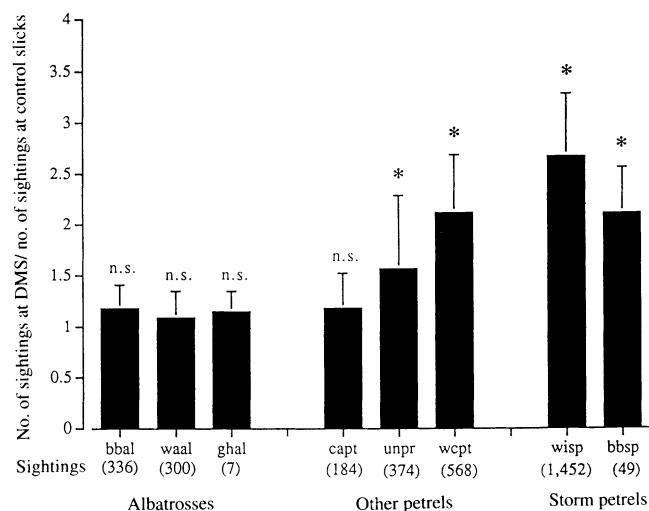


FIG. 1 Relative attraction of Procellariiform seabirds to DMS-scented oil slicks. The ratio of bird sightings at DMS slicks to sightings at control slicks was calculated for each pair of slicks. The data plotted represent means and standard errors of these 10 ratios. A value of one is expected if birds show identical responses to control and DMS-scented slicks. Significant differences (G-test, $P < 0.05$) are marked with asterisks. The total numbers of sightings during 10-min observation periods for the 10 paired slicks are listed below the species codes. Abbreviations: bbal, black-browed albatross (*Diomedea melanophrys*); waal, wandering albatross (*Diomedea exulans*); ghal, grey-headed albatross (*Diomedea chrysostoma*); capt, cape petrel (*Daption capense*); unpr, unidentified prion species; wcpt, white-chinned petrel (*Procellaria aequinoctialis*); wisp, Wilson's storm petrel (*Oceanites oceanicus*); bbsp, black-bellied storm petrel (*Fregetta tropica*).

METHODS. While the ship was positioned into the wind, a control, DMS- or cod-liver-oil-scented slick (Fig. 2 legend) was deployed, and typically drifted about 100 m from the vessel, allowing easy observation of approaching birds. Birds were counted if they (1) flew upwind over the slick within approximately 1 m of the surface, (2) alighted, or (3) pattered on the slick. Observations were made at 1-min intervals starting 2 min before deployment. Experiments were conducted as blinds: no-one involved in data collection knew the identities of the slicks, and the order of presentation was assigned randomly for each location. Data were logged on a hand-held computer so that the exact time of each event was automatically recorded. Slicks were tested one at a time and generally dissipated within 20 min; presentations were separated by at least 1 h. Experiments were conducted northwest of South Georgia (between 54°15' S, 38°00' W and 51°15' S, 41°15' W). Half (that is, 5 paired slicks for DMS and 3 paired slicks for cod-liver oil) were performed over deep water (>1,000 m), whereas the other half were performed over water ~100 m deep.

Our turning frequency results were consistent with the hypothesis we generated from our paired slick experiments (Fig. 3). White-chinned petrels turned 36% more frequently in the presence of DMS aerosol plumes than they did in response to control water plumes ($N_1 = 35$ birds, water plume; $N_2 = 34$, DMS plume; $U = 440$, $P < 0.03$, Mann-Whitney U -test)¹⁹. In contrast, turning behaviour in black-browed albatrosses was not affected by DMS ($N_1 = 20$ birds, water plume; $N_2 = 30$ birds, DMS plume; $U = 285$, $P > 0.40$), suggesting that these birds either did not detect DMS aerosols, or that they were not motivated to alter their behaviour in a fashion that would focus their activity in regions of high DMS concentrations¹⁶⁻²⁰.

The finding that different species of Procellariiforms showed variable responses to DMS is consistent with many aspects of their feeding behaviour. Albatrosses, which did not respond to DMS slicks any more than to control slicks, are large, noticeable birds, and frequently hunt visually^{14,21}. Like cape petrels, they often forage by spotting and exploiting mixed-species feeding aggregations of seals, whales and other visibly conspicuous seabirds²². Storm petrels, white-chinned petrels and prions, however, were consistently attracted to DMS and their ecology¹⁴ and retinal anatomy²³ suggests that they may be less likely to exploit visual cues as readily while foraging. These species have been shown to occur at much lower frequencies than either albatrosses (black-browed and grey-heads) or cape petrels in the mixed-

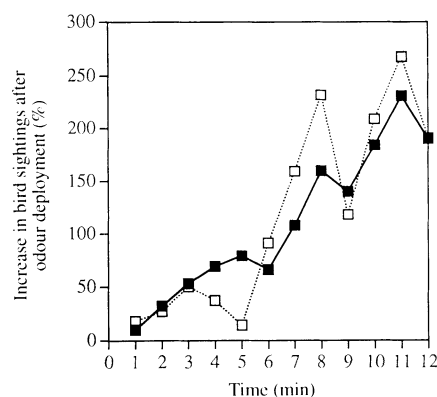
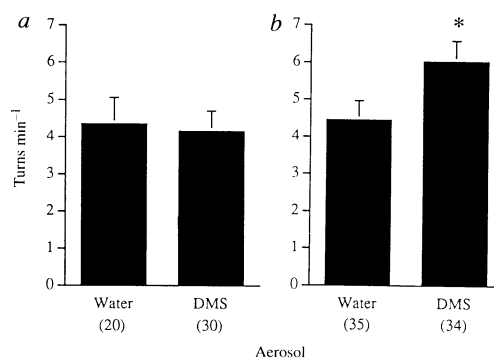


FIG. 2 Response of Wilson's storm petrels to DMS (filled squares) and cod liver oil (open squares) scented slicks. Control responses have been subtracted. Data are combined from 10 paired trials for DMS (that is, 10 DMS-control slick pairs) and six paired trials for cod liver oil. Data are normalized to the numbers of birds that were present in a visual area 200 m around the ship before each slick was deployed. Odour presentations: DMS (200 mM DMS (0.5 mol total, Aldrich Chemical) in 2.5 litres vegetable oil), cod liver oil (380 ml cod liver oil (Squib Pharmaceuticals) diluted to 2.5 l in vegetable oil) and control slicks (2.5 l vegetable oil) were prepared from stock solution ~1 h before experiments. As the ability to predict turbulent plume dynamics is poor, we adapted a simple sector model derived from empirical sampling of turbulent odour plumes to approximate average odour profiles downwind of slicks^{16,19}. This conservative approach suggests that (1) the odour disperses as a cone-shaped plume downwind of the slick with edges 20 deg from the axis; (2) the odour is dispersed continuously and rapidly (~300–600 m min⁻¹) downwind of the slick, reflecting high wind velocities during experiments (~10–20 knots; 4.6–9.4 m sec⁻¹); and that (3) this establishes an odour gradient extending kilometres downwind of the slick over the time course of the experiment (10 min). We used this model to calculate the theoretical maximum average concentration that a bird might encounter traversing a plume extending 1 km downwind of the slick. To do this we calculated what would happen if all the odour deployed was concentrated in a plume extending 1 km downwind of the slick. Although we recognize that turbulent odour plumes are not homogeneous, even this exaggerated scenario yields an average concentration of <10 nmol m⁻³, well within natural levels measured in the Antarctic (7.0–9.8 nmol m⁻³)¹⁷. Based on published estimates of flight velocity³⁰, we calculate that the maximum distance storm petrels could have travelled to reach scented slicks in the time allowed was 4 km.

FIG. 3 The influence of DMS aerosols on turning behaviour. Black bars indicate turning rates for *a*, black-browed albatrosses and *b*, white-chinned petrels, in response to water or DMS aerosols. Significant differences (Mann–Whitney *U*-test; see text) are marked with asterisks. Numbers of individual birds observed for each group are indicated in parentheses. For each observation, an individual bird was identified in a predefined visual zone set ~ 300 m at a 45-deg angle off the stern. Once a bird was spotted, the observer dictated the direction of the flight path to a partner, who entered the data into a portable computer. A new direction was entered each time the bird turned by 90 deg or more. Observers followed birds for up to 45 s, or until they entered the wake of the ship. Although treatments were always paired, the observers had no knowledge of what stimulus (DMS or water) was being presented at any given time, and were not in visual (or olfactory) contact with the person deploying the odorant. These experiments were conducted in high wind relative to slick experiments (~ 20 – 30 knots; 9.4 m sec^{-1} – 13.9 m sec^{-1}). As the ship headed upwind (6.8 – 10.2 km hr^{-1}), a 10-s aerosol spritz of either DMS (0.02 mol per spritz) or water was delivered once every 2 min for 40 min. Aerosols were delivered from a height of 6 m above the ocean's surface using a hand-held aerosol sprayer (Preval, Inc.). At 50 min the stimulus presentation was alternated. Again, odour plumes were designed as outlined above (Fig. 2 legend), except that we presented birds with an intermittent odour gradient aerosoled downwind. As animals tend to turn in response to abrupt changes in odour concentration, we reasoned that an intermittent presentation would maximize the likelihood of seeing such behaviour. As discussed in Fig. 2 (legend), we assumed that each 0.02 M DMS spritz would disperse as a cone-shaped plume downwind of the slick, with edges 20 deg from the axis. Estimates based on relative wind velocities suggested that aerosols would be transported 1 km or more within 2 min. As a conservatively high estimate, however, we calculated an average DMS concentration based on a 300 m transport distance to be about 10 nmol m^{-3} .



species feeding aggregations that have been intensively studied near South Georgia²². In addition, all are cryptically coloured, visually inconspicuous birds, and often forage at night when olfactory cues might be especially valuable^{21,24}. Nevertheless, all the Procellariiform species tested here possess a strikingly large and complex olfactory anatomy²⁵, suggesting that, whether or not birds can detect DMS, this particular odourant may be a more compelling foraging cue for some species than for others.

How might an ability to detect DMS be advantageous to a seabird? Marine DMS is a byproduct of the metabolic decomposition of dimethyl sulphoniopropionate (DMSP) in marine phytoplankton (most notably *Phaeocystis pouchetii*), and this process is dramatically accelerated during grazing by zooplankton^{12,26}. The ability to detect and recognize DMS as a potential feeding cue could thus be advantageous in locating and exploiting zooplankton-rich areas, especially as natural DMS emissions are not strictly ephemeral, but can persist for hours

or even several days¹⁷. In addition, because DMS concentrations tend to be highest in surface seawater associated with oceanic features such as upwelling zones and shelf waters¹¹, these features, reflected in the atmosphere as elevated DMS profiles, could present a navigable olfactory landscape to seabirds²⁷. This is an intriguing idea as Procellariiforms live highly pelagic life styles, and are also known for seasonally migrating extreme distances by navigational mechanisms that are not well understood²¹. The use of odour gradient maps has been proposed for pigeon homing, but the identification of natural biogenic aromatics has proven elusive^{27–29}. Our study now adds an additional clue to understanding how natural odour landscapes aid vertebrate search behaviour, first by identifying DMS as one of the naturally occurring components of the olfactory landscape overlying the Southern oceans, and second, by experimentally demonstrating that members of at least one vertebrate group, the Procellariiform seabirds, are capable of exploiting this natural biogenic aromatic to guide their foraging behaviour. □

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