Large eyeballs in diving ichthyosaurs

The huge eyes of these extinct reptiles may have been useful deep in the ocean.

Ichthyosaurs are marine reptiles that existed about 250 million to 90 million years ago. They had fish-shaped bodies, which were exceptional among Mesozoic marine reptiles[1]. Here we report that ichthyosaurs also had huge eyeballs — larger than those of any other vertebrate. We infer that the genus *Ophthalmosaurus*, whose eyes were particularly large and sensitive, used to dive to depths of 500 metres or more.

Absolute size is an important property of eyes[2–4], because larger eyes can house more retinal photoreceptive cells and receive more light per solid angle of image space[2–4]. Eye size also usually reflects the importance of vision in animals[4]: for example, the horse has among the largest eyeballs of any land animal alive today[4], about 50 mm across, which may be important, given its fast speed[3]. But eye size also scales with body size[3] — for example, the blue whale has the largest eyes of any living vertebrate[4], about 150 mm across, although this is small for such a colossal body. These scaling effects should be considered when discussing eye size.

We used the sclerotic ring diameter to estimate the eyeball diameter of parvipelvians, an ichthyosaurian group with tuna-shaped bodies[5] (Fig. 1), and compared its scaling with other tetrapods (Fig. 2). Eyeball diameters of tetrapods of a given body size are usually restricted within a narrow range[3] (Fig. 2). Parvipelvian ichthyosaurs, and some birds with sensitive vision, did not share this constraint, having large eyes relative to body length (Fig. 2).

The largest sclerotic ring we examined, 253 mm in its external diameter, belongs to *Temnodontosaurus*, which had a body length of about 9 m. There also is a poorly known parvipelvian ichthyosaur that may have been 15 m long[6], so the largest ichthyosaurian eye was probably more than 300 mm in diameter. The giant squid *Architeuthis* is thought to have the largest eyeball of any extant animal, having been estimated as approaching 250 mm in diameter[7].

Ophthalmosaurus had the largest eyes (more than 220 mm in diameter) of any ichthyosaur for its body length (Fig. 2), and the largest sclerotic ring aperture, with a diameter of about 100 mm. We estimated the minimum *f*-number (the same measure of relative aperture as is used for camera lenses) of several ichthyosaurian eyes (see Supplementary Information). The minimum *f*-numbers for typically nocturnal and diurnal vertebrate eyes are about 0.95 and 2.1, respectively[3]. The minimum *f*-number of an *Ophthalmosaurus* eye, the lowest of any ichthyosaur, was calculated to be between 0.76 and 1.1, so the genus seems to have been capable of seeing in low-light conditions.

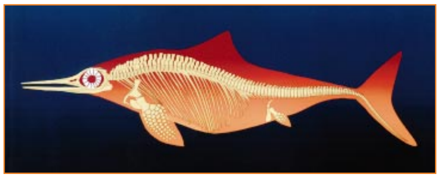

Figure 1 Artistic impression of the ichthyosaur *Ophthalmosaurus*.

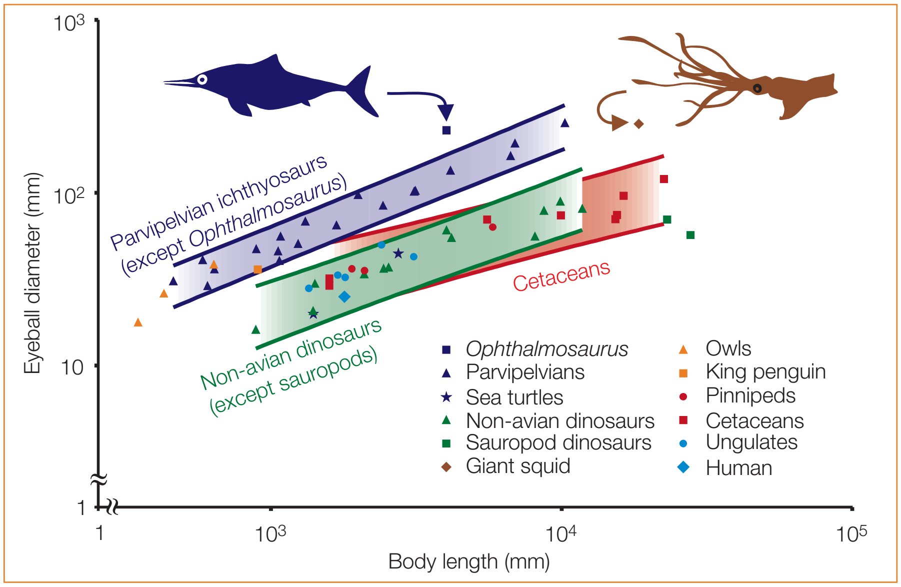

Figure 2 Logarithmic plot of eyeball diameter against body length. Bands show 95% confidence ranges for the least-square regression lines for parvipelvian ichthyosaurs except *Ophthalmosaurus* ($n=19$), non-avian dinosaurs except sauropods ($n=12$), and cetaceans ($n=8$). Eyeball diameters for dinosaurs and ichthyosaurs are based on the external diameter of the sclerotic rings (which were sometimes estimated from the height of the orbit in ichthyosaurs). Data for non-ichthyosaurs were derived from the literature.

The large sclerotic ring aperture indicates that *Ophthalmosaurus* could probably detect point light sources, such as luminance from the photophores of prey[8], a useful ability in the mesopelagic layer of the ocean (depths of 200 to 1,000 m). Cats, whose eyes have a similar minimum *f*-number, could theoretically see to a depth of 500 m in most oceans (based on data from refs 8–10; see Supplementary Information). *Ophthalmosaurus* was roughly 4 m long, with a mass of 930 kg, comparable to the size of living mesopelagic diving animals[11]. Conservative estimates of diving duration and swimming speed indicate that it could dive to a depth of 600 m (see Supplementary Information).

To test whether *Ophthalmosaurus* was a deep diver, we examined the frequency of pathology arising from Caisson disease (also known as the 'bends') in the humeri and femora of various ichthyosaurs (see Supplementary Information). Deep-diving animals do not usually suffer from bends[12], although some turtles do when an accident or escape response forces them to depart from their normal diving pattern, causing a high partial pressure of carbon dioxide in the blood[13]. We found that the two genera with the lowest minimum *f*-numbers had the highest frequencies of the bends.

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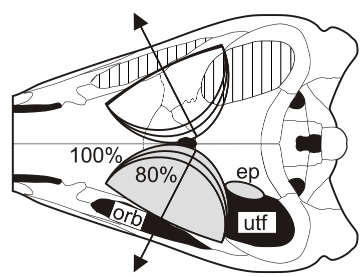
Supplementary information is available on *Nature*'s World-Wide Web site (http://www.nature.com) or as paper copy from the London editorial office of *Nature*.

MINIMUM *f*-NUMBER ESTIMATION

Hughes[3] found that the retinal magnification factor was relatively fixed for vertebrate eyes with a given axial length. This enables estimation of PND (posterior nodal distance) of a given eye based on its axial length. Hughes[3] derived the equation RMF = 0.11 L, where RMF and L stand for the retinal magnification factor and the axial length of eye. This gives PND=0.63L. The diameter of dilated pupil was estimated to be 90% of the lens diameter[3]. Corneal refraction, and hence the difference between the entrance and real pupil diameters, was ignored because ichthyosaurs lived in water. The minimum *f*-number, PND/Dp, can then be calculated as 0.7L/Dl, where Dp is the diameter of dilated pupil and Dl is the diameter of the lens. In living reptiles, the lens diameter is usually about 55 to 80 % of the diameter of the sclerotic ring aperture (Dsa; measured from refs. 14 and 15). Estimating eyeball length is more difficult. First, the maximum possible eyeball length was estimated by placing a half ellipse in the position of the eyeball in computer images of ichthyosaurian skulls, and maximizing its axial length so that the left and right ellipses touch. However, if this maximum possible length were assumed, the eyeball would interfere with the jaw adductor muscles that attach to the parietal flange; therefore the true eyeball length was probably shorter. This interference would be very small if the eyeball length were about 80% of the maximum possible value in all taxa examined, and this length was arbitrarily chosen as the estimate of the true eyeball length. These estimates gave a range of minimum *f*-number from 0.76 (if Dl/Dsa=0.80) to 1.1 (if Dl/Dsa=0.55) for *Ophthalmosaurus* (CM 878, Carnegie Museum, Pittsburgh; 0.94 to 1.4 if the eyeball was maximally long). Using the same ratios, minimum *f*-numbers were estimated for three-dimensional skulls of *Ichthyosaurus* (NHM R8177, Natural History Museum, London), *Stenopterygius* (NHM 33157 and 32681), *Cymbospondylus* (UCMP 9913, University of California Museum of Paleontology, Berkeley), and an undescribed eurhinosaurian that is probably related to *Leptonectes* or *Excalibosaurus* (NHM R3000).

Figure: Estimation of the axial lengths of ichthyosaurian eyeballs. The skull roof of *Ichthyosaurus* is depicted with overlaid half ellipses that approximate eyeball shape. The skull is based on the cranial reconstruction of *Ichthyosaurus* in ref. 16. Abbreviations: ep, general area occupied by epipterygoid; orb, orbit; utf, upper temporal fenestra.



MARINE OPTICS

The absolute visual threshold of the domestic cat was obtained from ref. 10. *Ophthalmosaurus*, with its large eyes, probably had higher visual sensitivity than a cat, so the use of a cat leads to a conservative estimation. The irradiance transmittance ratios for lights of various wavelengths in the ocean are as in ref. 9. Optic types I, IA and IB occupy the majority of Recent oceans[9]. Estimates of depth are based on refs. 2 and 8.

BODY MASS AND DIVING DURATION

The body mass of *Ophthalmosaurus* was estimated based on a two-dimensional skeletal reconstruction based on refs. 16 and 18. First, the fins were removed from the reconstruction, and the remaining body was sliced into 584 vertical strips. Each strip was rotated parasagittally around its centre to form a disk, and then the volumes of the disks were summed (9.3e-4 m^3). Assuming approximate neutral buoyancy in water, the volume was converted into the body mass (930 kg). The maximum duration of diving was estimated by substituting this estimated body mass into the equation for all air-breathing divers in ref. 11 (table 2), which gave a value of about 20 min. This is probably an underestimate because reptiles have longer diving durations than other amniotes with equal body mass[11]. With the estimated sustained speed of 2.55 m/s (ref. 19), *Ophthalmosaurus* was probably able to swim over 3000 m in 20 min, and 1240 m even if the speed was overestimated by 2.5 times[19].

BEND FREQUENCY.

Presence/absence of pathology from decompression syndrome was judged as described in refs. 13 and 17. The number of individuals represented in the specimens observed is unknown, because many of them were isolated humeri and femora. Therefore, our analysis is based on the count of elements rather than the number of individuals.

Two-tailed Fisher exact tests were performed for the taxa with sample numbers above 10 (labelled A-E). Significant differences in bend proportions were found in the comparisons between (*Ophthalmosaurus* or *Ichthyosaurus*) and (*Stenopterygius* or *Leptonectes*), the former two having higher proportions than the latter. The former group has low *f*-numbers of the eye and the latter high *f*-numbers (Fig. 2; *Leptonectes* is closely related to NHM R3000), so there seems to be a correlation between the bend ratio and light collecting ability of the eye. See supplementary information for the lists of specimens with bend-positive elements and of collections studied.

	Genus	# Positive Elements	# Elements Examined	Bend Frequency	Fisher exact P (two-tailed)				
					A	B	C	D	E
A	*Platypterygius*	1	11	0.09	—	0.69	0.66	0.41	0.27
B	*Ophthalmosaurus*	14	82	0.17	0.69	—	0.81	0.035	0.020
C	*Ichthyosaurus*	8	41	0.20	0.66	0.81	—	0.031	0.017
D	*Leptonectes*	1	37	0.027	0.41	0.035	0.031	—	1.0
E	*Stenopterygius*	0	31	0	0.27	0.020	0.017	1.0	—
	Temnodontosaurus	1	6	0.17	1.0	1.0	1.0	0.26	0.16
	Nannopterygius	0	1	0	1.0	1.0	1.0	1.0	1.0
	Californosaurus	0	2	0	1.0	1.0	1.0	1.0	1.0
	Shonisaurus	0	1	0	1.0	1.0	1.0	1.0	1.0
	Shastasaurus	0*	5	0	1.0	0.59	0.57	1.0	1.0
	Mixosaurus	0	1	0	1.0	1.0	1.0	1.0	1.0
	Cymbospondylus	0*	1	0	1.0	1.0	1.0	1.0	1.0
	Grippia	0*	6	0	1.0	0.58	0.57	1.0	1.0

Specimens with positive elements:

Platypterygius (h) YPM 537
Ophthalmosaurus (h) NHM R10031*, R4752, R2143, R2155, R2160, 47409*, 43989; TM 52096, 50096, 0034.101, 34-25
(f) NHM R3894,
Ichthyosaurus(h) NHM R1071, R1162, R2013, R1214; ROM 324*; AMNH 27633*
Leptonectes (h) NHM R1127b
Temnodontosaurus (f) NHM R2003

* specimens with two positive elements

Collections examined:

AMNH, American Museum of Natural History, New York.
CM, Carnegie Museum, Pittsburgh, Pennsylvania.
FHSU, Fort Hayes State University, Fort Hayes, Kansas.
KU, Kansas University, Lawrence, Kansas.
NHM, Natural History Museum, London.
PMU, Paleontologiska Museet, Uppsala Universitet, Sweden.
ROM, Royal Ontario Museum, Toronto, Canada.
RTMP, Royal Tyrrell Museum of Paleontology, Drumheller, Canada.
SDSM, South Dakota School of Mines, Rapid City, South Dakota.
TM, Tate Museum, University of Wyoming, Casper, Wyoming.
UCMP, University of California Museum of Paleontology, Berkeley, California.
YPM, Yale Peabody Museum, New Haven, Connecticut.

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