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THE ROLE OF MAGNETIC STATOCONIA IN DOGFISH (*SQUALUS ACANTHIAS*)

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Summary

Mineralogical and magnetic properties of the otolithic mass in the sacculus of dogfish, *Squalus acanthias*, were investigated. The endogenous statoconia were found to be either rhombohedral crystals of calcite or spherical particles of other calcium carbonate polymorphs. From 20 to 60 % of the total otolithic mass consisted of exogenous material, sea sand, which had a high content of heavy mineral particles, some of which were magnetic. The concentration of the heavy particles was greater than that typically found in marine sand, and it is proposed that this could result from a separation process in the endolymphatic duct.

A calculation of the acceleration of the otolithic mass in the sacculus caused by the geomagnetic field showed that the maximum linear acceleration due to magnetic forces would be one or two orders of magnitude smaller than the minimum sensitivity to acceleration in the auditory frequency range. This makes it unlikely that the magnetic particles are involved in detection of the geomagnetic field.

The exogenous material raises the mass and density of the otolithic mass in the sacculus, thus increasing the sensitivity of this otolith organ.

Introduction

The endolymphatic system of elasmobranch fish is in many cases open to the external environment, which allows exogenous material to be incorporated into the otolithic masses of the inner ear (e.g. Stewart, 1903–1906; Carlström, 1963; Fänge, 1982). In the guitarfish *(Rhinobatos* sp.), a fraction of this exogenous material has been found to be magnetic and to be associated with hair cell structures in the sacculus; and it has been suggested that this could form the basis for geomagnetic orientation (O'Leary *et al.* 1981; Vilches-Troja *et al.* 1984). In connection with our studies on magnetic material in other fish species (Hanson *et al.* 1984*a,b*; Hanson and Westerberg, 1986, 1987; Hanson and Walker, 1987), we have also investigated an elasmobranch fish; the spiny dogfish *Squalus acanthias* (M. Hanson, H. Westerberg and M. Öblad, in preparation). In the otolithic mass

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of the dogfish we have found black particles similar to those seen in the guitarfish. In this paper, we investigated the mineralogical and magnetic properties of the otolith in the dogfish with particular regard to a possible magnetic function.

Materials and methods

The minute particles, both exogenous and endogenous, in the otolithic mass are termed statoconia, following Carlström (1963).

Sample preparation

Adult dogfish *(Squalus acanthias)*, 0.6–1.2 m in length, were caught by trawl at 50–100 m depth in the Skagerrack. In five sharks, the inner ear on one side was exposed and the otolithic mass from the sacculus was extracted for individual mineralogical analysis. The dissection of one individual was made with non-magnetic tools of beryllium–copper or zirconium oxide. This sample was freeze-dried and used for magnetic measurements and elemental analysis. About 15 additional individuals were dissected to study the anatomy of the endolymphatic duct and to sample the statoconia for particle size analysis.

Samples of statoconia were also taken from five shark embryos (0.15 m) and from two juveniles (0.3 m). The juveniles were kept in a glass-bottomed aquarium without sand for 4 months from birth until dissection.

Magnetic measurements

The magnetic susceptibility was measured with a Faraday balance in magnetic fields ranging from 70 $kA\,m^{-1}$ to 700 $kA\,m^{-1}$. Further details of the apparatus may be found in the paper by Hanson *et al.* (1984*a*) and references therein.

Elemental analysis by energy dispersive X-ray fluorescence

The sample for magnetic measurements was further analysed with a secondary target energy dispersive X-ray fluorescence (EDXRF) spectrometer (Standzenieks and Selin, 1979; Öblad *et al.* 1982), as used previously (Hanson *et al.* 1984*b*). The procedure for the quantitative EDXRF analysis is described in detail elsewhere (Rindby, 1983). Small amounts, of the order of 1 ng, of elements with atomic number down to 13 (aluminium) can be detected in our spectrometer. However, in thick samples the quantitative analysis is more uncertain for light elements (generally with atomic number less than 20), since their radiation is more strongly absorbed in the sample. The detection limit has to be specified for each sample because of their varying absorption and spectral background. This explains why the amount of silicon is below the detection limit in the sample of statoconia (see Fig. 1A), but well above the corresponding limit in the fractionated parts of the same sample (Fig. 1B).

Particle analysis and separation

The shapes and sizes of the individual granula in the otolithic masses of the dogfish were observed and photographed in an optical microscope. We also examined the distribution and localization of different kinds of particles within the otolithic mass. The granula in each sample were then separated with respect to their density. To get rid of the organic jelly in which the statoconia are embedded, the aggregate was placed in a beaker with distilled water and treated in an ultrasonic bath. The slurry was filtered, washed with distilled water and rinsed with alcohol. After drying, the particles were immersed in bromoform, $CHBr_3$, in a separating funnel. The sediment was run out from the separating funnel, filtered, rinsed in benzene and dried. The floating material was treated similarly. In this way the statoconia were separated into two fractions; a light fraction with densities below and a heavy fraction with densities above that of bromoform ($2.89\,g\,cm^{-3}$). All samples were weighed after washing and drying. The light fraction of each sample was further treated in dilute hydrochloric acid and the residue was weighed after rinsing and drying.

Results

Magnetic measurements and elemental analysis

The amount of ferromagnetic and/or ferrimagnetic material in the sample for magnetic analysis was assessed from the field dependence of the magnetic susceptibility (Hanson *et al.* 1984*a*). The elemental contents in this sample (except for a small amount that was lost during the transfer from the sample holder) were then determined by EDXRF, analysis being carried out for the whole sample and for the heavy and light fractions (Table 1). Spectra of the whole sample and the

Table 1. *Elemental content of a mixed sample of statoconia from the ear of an adult dogfish analysed by energy dispersive X-ray fluorescence*

	Elemental mass (μg)		
Element	Whole sample (47 mg)	Light fraction (13.9 mg)	Heavy fraction (3.9 mg)
Si	<2200	2200	53
K	340	79	3.4
Ca	12 000	41	87
Ti	42	5.0	9.2
Mn	5.0	0.30	1.7
Fe	180	19	67
Cu	0.58	0.40	0.34
Zn	1.5	0.062	0.15
Ga	<0.07	0.064	<0.032
Sr	38	1.3	0.71
Y	0.21	0.028	0.21

The otolithic mass of the sacculus was separated into a light fraction, density $\rho<2.89\,g\,cm^{-3}$, treated with dilute hydrocholoric acid, and a heavy fraction, density $\rho>2.89\,g\,cm^{-3}$.
The total mass of each sample is given in the heading.

light, insoluble fraction are shown in Fig. 1. If we assume that the total magnetic contribution in the sample stems from magnetite, with saturation magnetization $M_s=4.8\times10^5\,A\,m^{-1}$, this yields $32\,\mu g$ of magnetite in a total mass of 62 mg. To obtain the same amount of magnetization from some of the magnetically weaker iron oxides would require correspondingly larger masses. For hematite, with $M_s=2\times10^3\,A\,m^{-1}$, it would be 7 mg. This is far above the analysed iron content

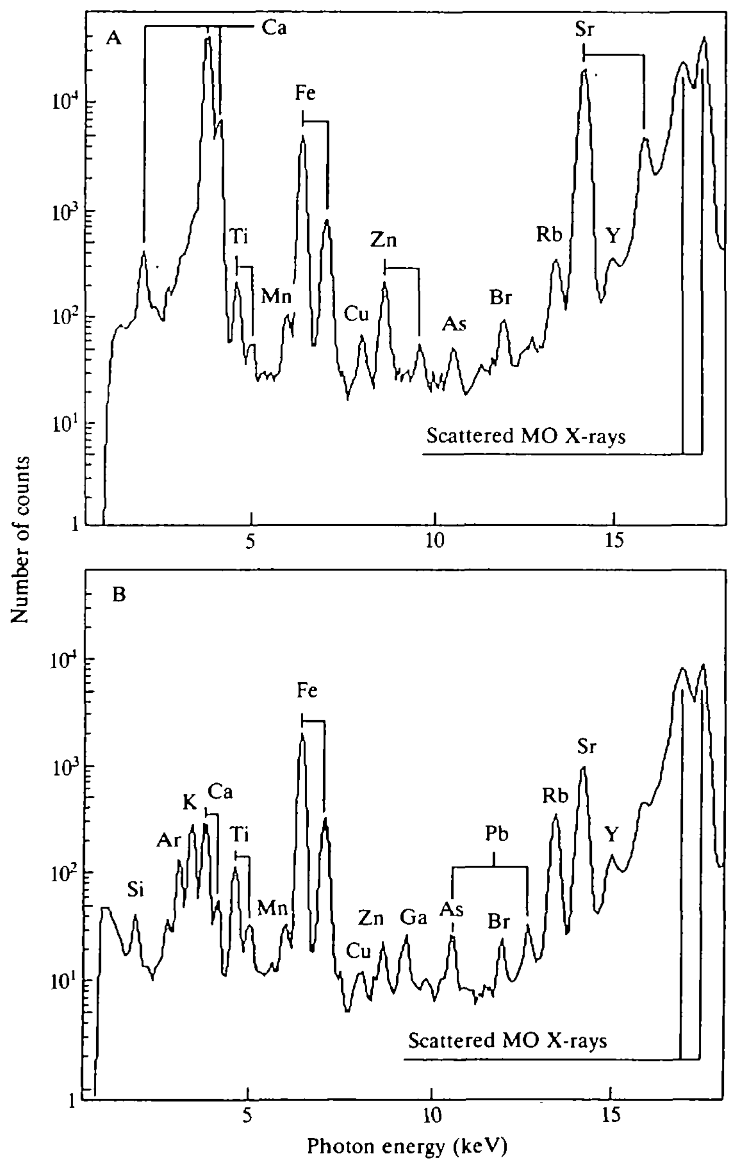

Fig. 1. X-ray fluorescence spectra of (A) a sample of statoconia from the ear of an adult dogfish and; (B) the light fraction, density $\rho<2.89\,g\,cm^{-3}$, of the same sample after treatment with dilute hydrochloric acid.

(Table 1). Hence the sample could contain a mixture of magnetite with some of the magnetically weaker iron oxides.

Particle characterization

A pattern of darker (yellowish) and lighter (white or clear) bands is visible on the surface of the otolithic mass in the sacculus of an adult dogfish (Fig. 2). This gives the impression that there are different kinds of mineral particles ordered in a layered structure. The innermost part is not coloured. In the darker bands one can also see scattered black particles. After closer examination it becomes obvious that the otolithic mass contains statoconia with a variety of shapes and colours (Fig. 3). To discuss the origin and possible function of the mineral particles we have divided them into four main groups that we characterize as follows. (1) Transparent, uncoloured, rhombohedral crystals with plane surfaces. These exhibit optical activity, their density is less than 2.89 $g\,cm^{-3}$ and they dissolve with effervescence in dilute hydrochloric acid. (2) Colourless, semitransparent, spherical particles containing a radial striation. These particles are recovered in the light fraction and they are soluble in dilute hydrochloric acid. (3) Irregular particles of different shapes and colours. They are insoluble in dilute acid. Some belong to the heavy fraction and exhibit a variety of colours; green, blue and red like emerald,

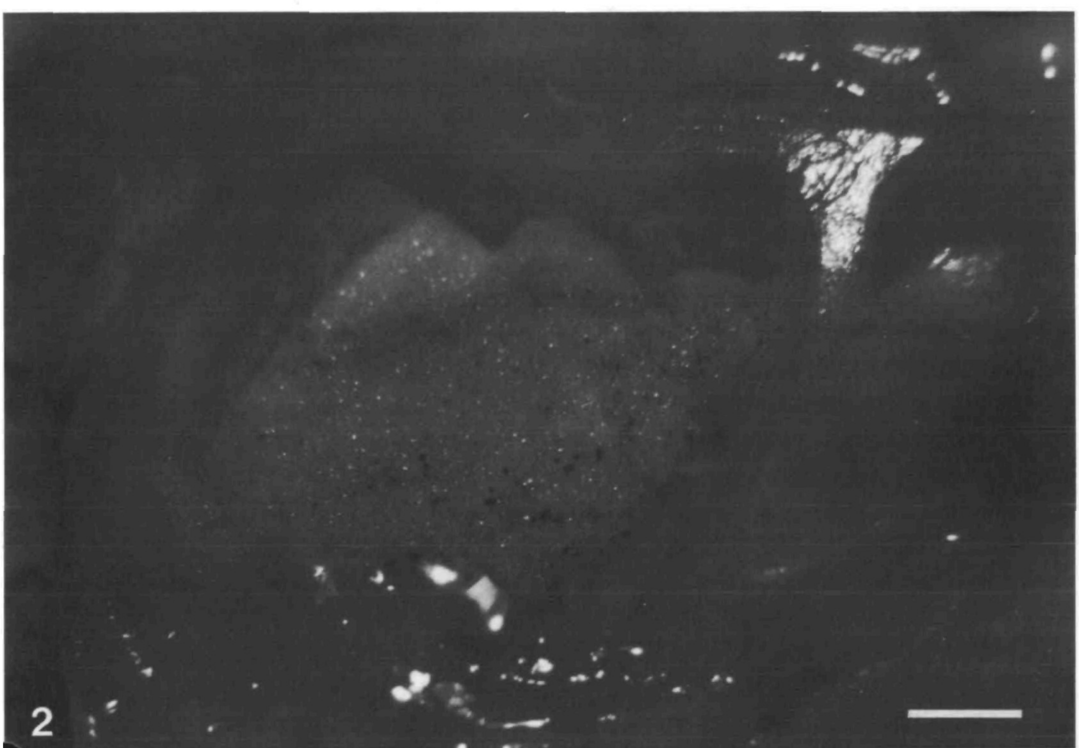

Fig. 2. Dorsolateral view of the otolithic mass of an adult dogfish. Scale bar, 2 mm.

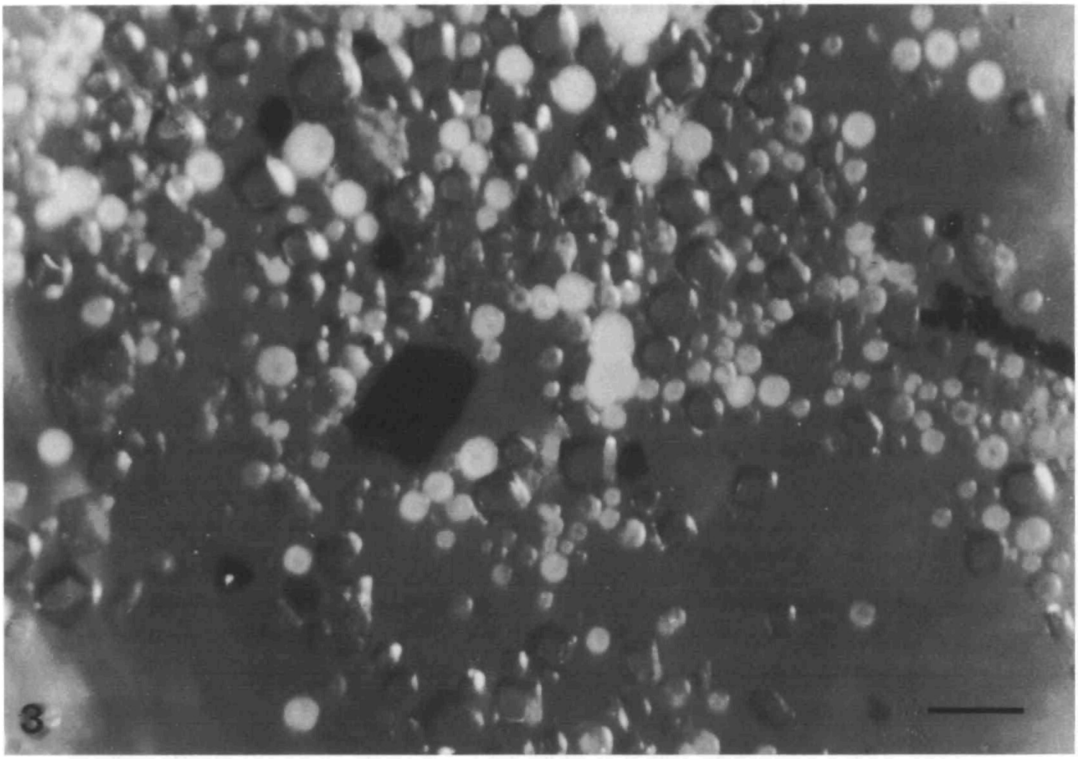

Fig. 3. A mixed sample of statoconia from the ear of an adult dogfish. Scale bar, 0.2 mm.

sapphire, ruby, garnet and other gems. The majority of the irregular particles belongs to the low-density fraction. (4) There are a few very dark particles among those in the heavy fraction. Some of these are strongly magnetic; for example, those that have formed a chain (Fig. 3). The particles in the chain are black and could possibly be of magnetite, Fe_3O_4. There are also less magnetic particles (we did not observe any movement when a permanent magnet was held close to them) with a metallic appearance, which resemble hematite, the α-phase of Fe_2O_3.

We found particles of the categories described above in all the adult dogfish investigated. In the embryos and juveniles, however, only type 1 statoconia were found. Such statoconia have been shown by X-ray diffraction (Carlström, 1963) to consist of single crystals of calcite. Although we did not analyse the structure, it is evident that these particles were calcite crystals. This conclusion is supported by the observation that the calcium content of statoconia of the adult dogfish was reduced by treatment with acid (Table 1).

Since the type 2 statoconia were very regular, exhibited internal radial striation and were soluble in dilute acid we conclude that they are of endogenous origin. Similar statoconia containing aragonite, another polymorph of calcium carbonate, have been described in other species (Carlström, 1963). Pure aragonite has a density of 2.93 $g\,cm^{-3}$ and hence would not be found in the light fraction. However, the density could easily be lowered sufficiently; for example, if the particles were composed of agglomerates of crystallites or contained a mixture of calcium carbonate polymorphs.

The type 3 and 4 particles are most likely to be exogenous; probably grains of sea sand that enter through the endolymphatic ducts. Their elemental composition, except for aluminium, which cannot be detected in our spectrometer, agrees well with that of sedimentary rocks (Table 1).

The major part of the light fraction of statoconia was insoluble in dilute hydrochloric acid. From this and the elemental analysis, which shows that silicon was a major component left in the light fraction after treatment with acid, we conclude that the grains are of quartz. Our suggestion that the heavy fraction contains particles of magnetite and of hematite is consistent with the amount of iron in this fraction as well as with the magnetic data discussed above.

Heavy mineral content and particle size distributions

The total mass of the statoconia in each ear of a dogfish was of the order of 70 mg. The mass of the heavy and light fractions, and of the soluble part, are expressed as a proportion of total mass in the bar charts in Fig. 4. The soluble part

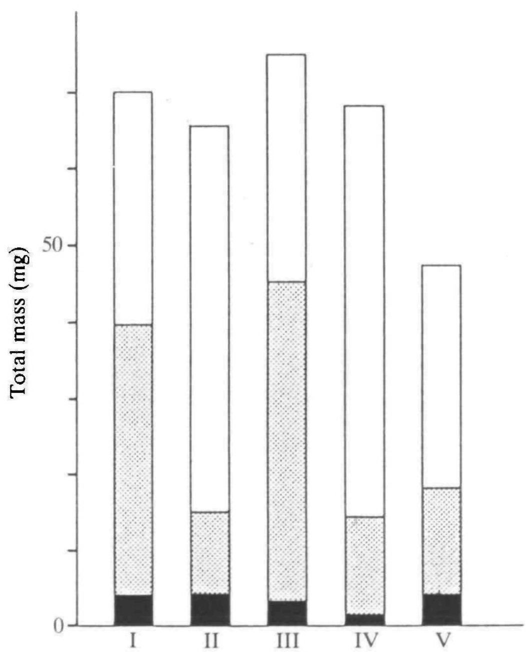

Fig. 4. The total mass of five sacculus otolithic masses separated into the following fractions: solid bar, statoconia with a density $\rho > 2.89\,g\,cm^{-3}$; shaded bar, light statoconia, $\rho < 2.89\,g\,cm^{-3}$, insoluble in 10 % hydrochloric acid; open bar, light statoconia, soluble in acid.

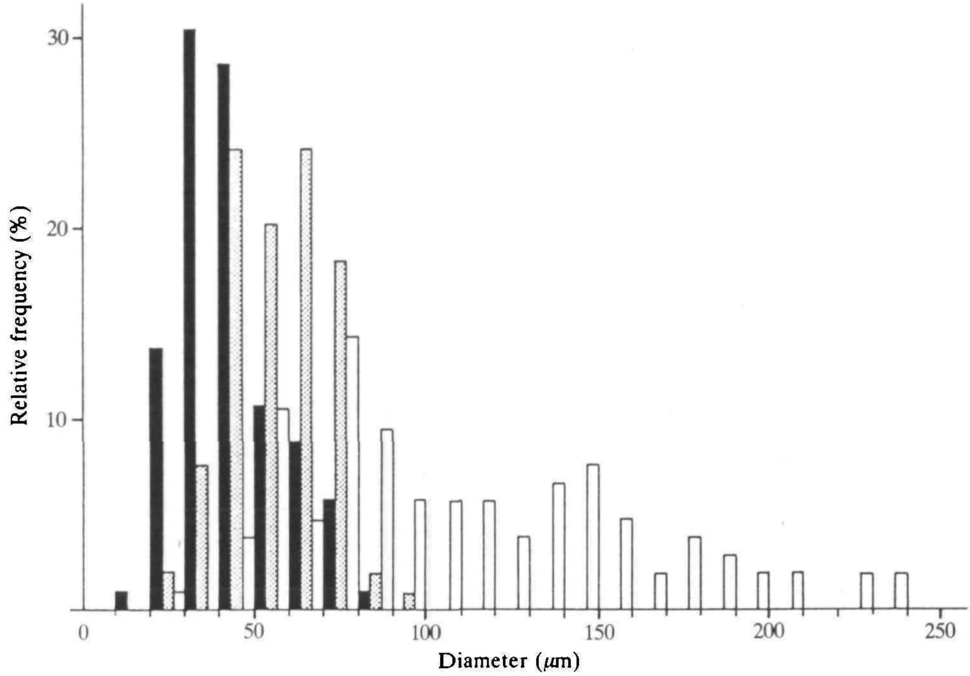

Fig. 5. Size distributions of the different kinds of statoconia in one individual sacculus otolithic mass. The class intervals are 10 μm and the sample size is 100 for each type of statoconia. Solid, black bars, spherical statoconia, probably aragonite; shaded bars, regular, rhombohedral calcite crystals; open bars, irregular sand grains, mainly quartz.

of the statoconia, which we assume to be endogenous, varied from 40 to 80 % in the investigated samples. Thus, it is evident that the total mass of statoconia is considerably increased by the uptake of sand. The ratio between the mass of the heavy fraction and the mass of the light insoluble fraction varied from 7 to 28 % in our samples.

The particle sizes, measured in a sample of statoconia from one adult dogfish, are presented in the histogram in Fig. 5. The diameters of the endogenous statoconia lay in the range 10–100 μm and the mean diameter of the spherical particles was approximately 45 μm. Samples from adult dogfish with lengths between 0.6 and 1.2 m exhibited a very small variation of particle sizes, with no evidence of dependence on body length. The calcite particles may be described by a size distribution approaching a log-normal function with a mean diameter of about 65 μm. The embryos, however, have smaller statoconia. Fig. 6 shows the size distributions of calcite statoconia from an adult and an embryo. The former sample was taken in the lateroventral part of the otolith, which has a pure white colour and contains calcite statoconia only. We consider this region to be the remains of the embryonic otolith.

The exogenous particles have a wider range of sizes, from that of coarse silt to

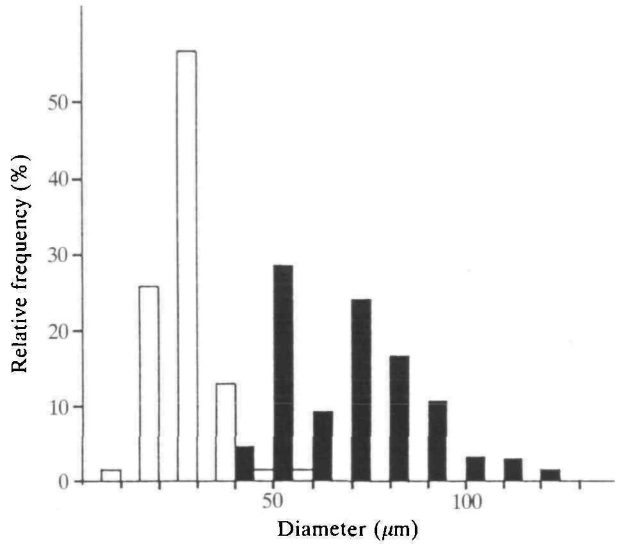

Fig. 6. Size distributions of calcite statoconia of an adult dogfish (solid bars) and an embryo (open bars). The class intervals are 10 μm and the sample sizes are 65.

that of fine sand sediment fractions. There were no significant size differences between individuals in the present material.

Discussion

Do the exogenous statoconia, in particular the magnetic ones, have any physiological function? We first discuss how exogenous particles enter the sacculus through the endolymphatic duct. Then, we discuss how magnetic forces might be sensed in the otolith organ. Finally, we estimate the strength of the magnetic forces experienced by the observed particles in the earth's magnetic field and relate these forces to what is known about the sensitivity of the otolith organ.

Uptake of exogenous material

The heavy mineral content (HMC) of the exogenous portion of the statoconia, about 10 %, was much higher than that typical of marine sand, of the order of 0.1 % (Pettijohn, 1949). Local wave action or tidal currents can concentrate heavy minerals by selective sorting. It can thus not be excluded that the high HMC reflects the composition of the sediments at the site where the dogfish pick up the statoconia. Since the high HMC is common to all the individuals examined and, furthermore, each shark seems to have collected sand several times this would require that the dogfish actively searches for places with exceptionally high values of HMC. However, a more likely explanation is that an enrichment of heavy mineral grains takes place during the uptake process. The morphology of the endolymphatic ducts suggests how the uptake as well as the increase of HMC could be brought about.

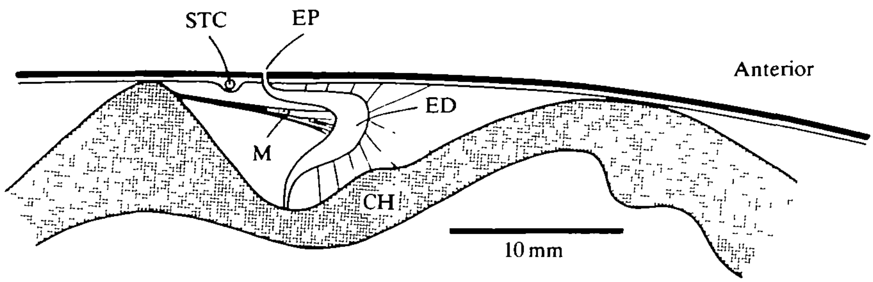

Fig. 7. Schematic longitudinal section through the parietal fossa of the dogfish. ED, endolymphatic duct; EP, endolymphatic pore; CH, chondrocranium; M, muscle; STC, supratemporal canal.

The entrances to the endolymphatic ducts are located on the dorsal surface of the head close to the median line and just posterior to the eyes. The aperture is approximately 0.5 mm in an adult dogfish. Below the skin the duct expands and makes a loop anteriorly inside the parietal fossa, which is a funnel-shaped depression in the chondrocranium (Fig. 7). The fossa is filled with a loose, jellylike substance and the endolymphatic duct is suspended in this cavity by thin elastic fibres connecting to the dermis and the chondrocranium. A thin muscle extends from each side of the fossa anteriorly to the middle portion of the ducts. The dermis connects tightly to the rim of the fossa. Any pressure increase on this part of the head will be transmitted through the skin to the jelly in the fossa and the contents of the duct will be squeezed out. This will happen if the dogfish buries itself in the sediments or turns upside down pressing the head against the bottom substratum. Another squaliform shark, *Oxynotus centria*, has a peculiar feeding behaviour during which it turns upside down and uses the dorsal spines to dig in the sediments (de Andrés *et al.* 1987). This behaviour exemplifies the situation we describe. When the external pressure is released, the skin over the fossa stretches, the duct expands and sediments and water are sucked in from the outside. Contraction of the fan-shaped muscle between the chondrocranium and the duct will also pump water in and out of the duct. If such pumping occurs in clear water, the water flow will transport the smaller and lighter sediment particles out. This will result in an enrichment of the heavy mineral content of the sand remaining in the duct.

Otolith organ and magnetic forces

The otolith organ is considered to be a sensory system that can detect gravity and linear acceleration (Lowenstein, 1971; Lindeman, 1973). The inertia of the statoconia causes a deflection of the hair cell cilia as the head of the animal shifts position with respect to gravity or when the animal accelerates. Each of the receptor cells in the macula sacculi is provided with a bundle of sensory hairs consisting of one kinocilium and numerous (50–110) stereocilia. The kinocilium, the longest of the sensory hairs, is located eccentrically at the periphery of the hair bundle. This morphological polarization of the sensory cells coincides with a functional polarization. A deflection of the sensory hairs in the direction from the stereocilia towards the kinocilium excites the sensory cell, whereas a displacement in the opposite direction has an inhibitory effect. According to Vilches-Troya *et al.* (1984) the magnetic statoconia in the otolithic mass of the guitarfish are asymmetrically distributed, forming curved bands positioned over two separated regions of the macula with opposite polarization. The authors suggested that the rotation of the magnetic particles in a magnetic field could be sensed by the hair cells in their vicinity. Thus, the otolith organ could possibly be able to sense magnetic fields in addition to gravity and linear acceleration.

The magnetic particles in the statoconia of the dogfish were distributed randomly, rather than systematically, in the otolithic mass. The bands of lighter and darker statoconia that we observed can be explained by the difference in colour between the endogenous clear, or white, calcite crystals and the exogenous mineral grains. The innermost parts were always white, suggesting that these bands appear chronologically. The variation between individuals regarding the arrangement of the magnetic particles in the dogfish implies that they have not been systematically ordered with respect to the structure of the macula. In only one case did we observe ordered magnetic particles, namely the chain shown in Fig. 3. We do not know whether this chain was present in the intact otolith. It is quite possible that it was formed during the preparation of the microscopy sample. Thus, there is no reason to expect the magnetic particles to act in cooperation.

The effects of a magnetic field on a single particle can be estimated. A magnetic dipolar moment, **m**, exposed to an external magnetic field, **B**, experiences a torque, $\boldsymbol{\tau}$, that tends to align the magnetic moment along the field direction. The numerical value of this torque is:

$$\tau = \mathrm{mB}\sin\theta \leq \mathrm{mB}\,,$$

where θ is the angle between the directions of the moment and the field (Fig. 8A). A small particle with volume V of a ferromagnetic or ferrimagnetic substance with saturation magnetization $\mathbf{M}_s$ can have a maximal magnetic moment $\mathbf{m}_s = \mathbf{M}_s V$. For real particles the moment is always smaller, since there exists a surface layer with a lower magnetization. If the particle exceeds a certain size, determined by the particle's shape and crystal structure, magnetic domains having their magnetization in different directions develop. This leads to a further decrease of the remanent moment compared to $\mathbf{m}_s$. As an example of the magnetic particles that we observed among dogfish statoconia we may take an orthorhombic particle of size $50\,\mu\mathrm{m} \times 20\,\mu\mathrm{m} \times 20\,\mu\mathrm{m}$. If we assume that it consists of magnetite with $\mathrm{M}_s = 4.8 \times 10^5\,\mathrm{A\,m^{-1}}$, its maximal moment $\mathbf{m}_s$ will have a value of $9.5 \times 10^{-9}\,\mathrm{A\,m^2}$. Magnetite particles of this size are multidomain particles which after saturation in a magnetic field will have a remanent magnetization of the order of 0.01–0.3 times the saturation value (Banerjee and Moskowitz, 1985). As an estimate of the remanent magnetic moment we may take $\mathrm{m_r} = 1 \times 10^{-9}\,\mathrm{A\,m^2}$. A single-domain hematite particle of this size would have a magnetic moment smaller than

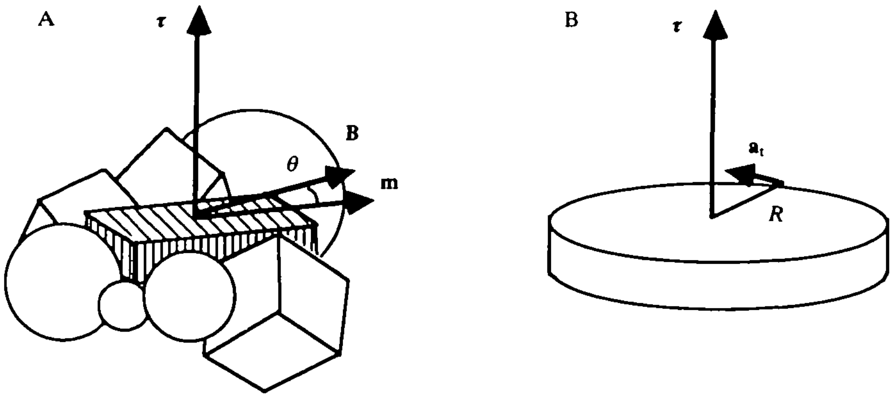

Fig. 8. (A) the torque, τ, experienced by a particle with magnetic moment **m** in a magnetic field, **B**, and (B) the linear acceleration, $\mathbf{a}_t$, caused by the torque τ at a point on the periphery of the otolithic mass in the form of a disc with radius R. θ is the angle between the directions of the moment and the field.

1×10^{-10} A m^2. The torque our particle experiences in the earth's magnetic field will then be $\tau\leqslant5\times10^{-14}$ Nm. The condition that this torque should cause the particle to rotate is that the magnetic moment is spatially fixed within the particle. In multidomain grains, the domain walls often move and the moment may rotate into alignment in the external field without causing the grain to rotate physically. By neglecting this possibility our estimated value yields an upper limit for the resulting torque.

What kind of movement would result from the torque exerted upon the particle? The statoconia were very densely packed in the otolithic mass, leaving practically no freedom for a granule to move individually. Even if a grain of sand or a magnetic particle that enters the sacculus were initially loosely coupled to the rest of the otolithic mass, it would soon sink through the gelatinous surface layer and adjust itself in some position fixed to the surrounding statoconia. Thus, we consider it most realistic to treat the otolithic mass as a solid body, moving, according to its inertia, relative to the underlying receptor cells. For a disordered assembly of magnetic particles, the randomly distributed torques would almost cancel. The resultant torque would be of the same order of magnitude as the torque on a single particle. The largest effect would be obtained for a particle positioned in the centre of the otolithic mass. The torque on the magnetic particle would then cause the otolithic mass to rotate with an angular acceleration $\boldsymbol{\alpha}$ around an axis through the centre of the particle. With I being the moment of inertia with respect to this axis we obtain:

$$\boldsymbol{\tau}=I\boldsymbol{\alpha}\,.$$

The linear acceleration, $\mathbf{a}_t$, experienced by a point at a distance $\boldsymbol{d}$ from the axis is:

$$\mathbf{a}_t=\boldsymbol{\alpha}\times\boldsymbol{d}\,.$$

For simplicity we assume that the otolithic mass is a circular disk of radius $R=5$ mm, mass $m=100$ mg and moment of inertia $I=mR^2/2$. The peripheral points obtain the maximal linear acceleration, $\mathbf{a}_{t,max}$, for the case when the magnetic particle is in the centre, $d=R$, and the torque perpendicular to the plane of the disk (Fig. 8B):

$$\mathbf{a}_{t,max}=2\boldsymbol{\tau}/mR\ .$$

Our estimate then yields an upper limit of $a_{t,max}=2\times10^{-7}\,m\,s^{-2}$ for the linear acceleration. This value should be compared to the detection thresholds of the otolith organ.

The sensitivity of fish to linear acceleration is difficult to study experimentally and little is known about threshold values. Harden Jones (1956) found a reaction in blind goldfish to accelerations of the order of magnitude $1\,m\,s^{-2}$. Similar results were obtained by von Baumgarten *et al.* (1971). No experiments have been reported on elasmobranchs.

Information about the sensitivity to linear acceleration may, however, also be indirectly obtained from investigations of the auditory response. The most relevant data for comparison are, of course, obtained from the studies covering the lowest frequency ranges. In the lemon shark, the displacement threshold for low-frequency sound between 20 and 1000 Hz lies between 5×10^{-10} and 4×10^{-9} m (Corwin, 1981). This yields a lower limit of $2\times10^{-6}\,m\,s^{-2}$ for the sensitivity to linear acceleration. At lower frequencies, the sensitivity decreases, but in the extreme infrasound region the sensitivity may increase again, as observed in cod (Sand and Karlsen, 1986). In the cod, the threshold values, measured as particle acceleration, show a steady decrease below 10 Hz. The value at 0.1 Hz is close to $10^{-5}\,m\,s^{-2}$, which is approximately equal to the threshold in the most sensitive auditory range (Sand and Karlsen, 1986). It is not improbable that sharks have a similar sensitivity behaviour, since the otolith organs of teleosts and elasmobranchs have the same principal function. With these assumptions, we arrive at an estimate of the minimum threshold for linear acceleration of $10^{-5}-10^{-6}\,m\,s^{-2}$, which is 10–100 times higher than the maximum acceleration signal caused by the magnetic forces on the exogenous magnetic particles in the earth's magnetic field. The conditions for detection of these forces in the otolith organ are thus not fulfilled.

From our investigation of the sacculus of *Squalus acanthias* we conclude that the magnetization of the heavy particles cannot be of any biological significance. However, the uptake of exogenous minerals and the enrichment of the high-density content of the otolith may be important: they increase the mass and mean density of the otolith, and this leads to an increase of the sensitivity to gravity and linear acceleration of the otolith organ.

We do not imply that our conclusions would also be true for *Rhinobatos*, since there may be differences in the physiological mechanisms of the ear of *Rhinobatos* and that of *Squalus*. To elucidate the problem of magnetic sensitivity, further comparative studies should be made including other species.

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