The blind Indus dolphin, *Platanista indi*

Georg Pilleri

The Indus dolphin is an endemic, relict species, well adapted to the turbid water of the river. It is a constant swimmer with extremely short sleep phases, besides being a continuous emitter of sound. Loss of sight is compensated by an efficient sonar system. Alone among cetaceans, the Indus dolphin swims on its side, feeling its way along the bottom with the right or left flipper. These are secondary adaptations in a species whose Miocene ancestors inhabited clear coastal waters.

In all, there are some 70 different species of toothed whales, some of which are pelagic—inhabiting the open sea; others neritic—preferring coastal waters; and others again living in the brackish water close to the mouths of rivers. Lastly there are a few species of dolphins which are found exclusively in rivers and seldom venture into the tidal zone of the deltas. These are the river dolphins in the strict sense of the word, belonging to the Platanistoidea group. One species, *Lipotes vexillifer*, occurs in China, in the Yangtze River; two species are found in the Indian subcontinent: *Platanista indi* in the Indus and *P. gangetica* in the Ganges and Brahmaputra. Another two live in tropical South America: *Inia geoffrensis* in the Orinoco–Amazon river system and *Inia boliviensis* in the rivers of the Beni. The La Plata dolphin, *Pontoporia blainvillei*, also belongs to the Platanistoidea group but occurs not in rivers but along the Atlantic Coast of Uruguay (figure 1).

Relatively little is known about the evolution of the Platanistoidea. However, a few well-preserved Miocene fossils show that the river dolphins were originally a cosmopolitan family inhabiting Tethys, the tropical sea which once covered a large part of Europe. They shared the biotope along the sea coast with Squalodontidea and numerous species of shark. Casts of the cranial cavity of the Miocene species provide valuable information on the size and shape of the brain and the structure of the sense organs. We now know that the European dolphins had the smallest brain volume, an indication that the Platanistoidea group originated in Europe and that, unlike the marine species, the size of their brain has changed relatively little in the course of evolution. The recent Platanistoidea have the lowest relative brain weight of all toothed whales (figure 2). The Miocene species possessed olfactory bulbs and nerves, structures which have completely regressed in modern dolphins. They also had a well-developed auditory nerve and a functional optic nerve. The Indus dolphin, on the other hand, is almost entirely blind.

Interesting enough in themselves, these facts would have provided little new information had we not been able to examine the living animal. It was during the winter of 1969–70 that I decided to bring back two Indus dolphins from Pakistan to the laboratory in Berne. The animals survived the difficult journey and we were able to study them for seven years in the clear water of the aquarium.

The first thing we noticed was that the Indus dolphin never stopped swimming. Incredibly, it seemed to be endowed with a kind of perpetual motion. Another surprise revealed by the aquarium was that, unlike other cetaceans, which swim on their bellies, *Platanista* swam on its side (figures 3, 4) [1]. Once we had set up an oscilloscope to study the sounds made by the dolphin, we discovered that not only did it never stop swimming, but it was never silent either. In the end we recorded the sonar signals day and night on a level recorder. Careful examination of the curves showed an occasional falling off in level towards zero, which corresponded with pauses in sound emission (figure 5). The total length of all pauses over a 24-hour period was seven hours, a figure which agreed well with the normal sleep requirement of mammals [1, 4].

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The brief pauses, lasting only seconds, were therefore sleep phases in a highly differentiated polyphasic type of sleep. Why should the Indus dolphin, unlike other dolphins, sleep for such short periods of time, the shortest ever recorded in mammals? The reason is to be sought in its environment. *Platanista* lives in running water. During the monsoons the Indus becomes a mighty flood; current speed in the Brahmaputra may exceed 15 miles per hour; and great banyan trees are swept along as if no heavier than straws. Clearly, in such conditions a dolphin with longer sleep periods would be carried away by the current and soon dashed to death.

Vision in the Indus dolphin

As the Indus dolphin had always been thought to be blind, even before it was first scientifically described, we decided to make a histological examination of the eye. The results were instructive. The dolphin has an eye which can distinguish only between light and darkness. Functionally, the eye may be compared with the pinhole eye of a number of invertebrates [1, 7]. All the structures responsible for accommodation of the lens have regressed in *Platanista*. There are neither eye muscles nor corresponding nerves. The optic nerve remains but is as thin as a thread. The eye consists of an iris with a mobile pupil and a well-layered retina. Several of the eyes we examined showed the remnants of a lens behind the iris in the form of capsule fragments (figure 6). This fact leaves no doubt that the loss of vision is a case of regressive evolution, a secondary atrophy brought about by the turbid water of the Indus. Although atrophy of the lens and the accommodation apparatus means that the dolphin can no longer perceive objects and shapes, it is still able to distinguish light and the direction from whieh the light originates. To return for a moment to the dolphins' habitat, we know that beneath the muddy water of the Indus there is total darkness. I have often dived there and opened my eyes underwater. It is completely dark, whether one looks down towards the bottom or straight ahead. If, however, one peers up towards the surface, it is just possible to perceive the purple-gold shimmer of the sun. It can only be this faint light which reaches *Platanista*'s retina. Since there are no eye muscles, and the eye which is situated on the side of the head is almost immobile, if the dolphin wants to detect the gleam of light from the surface it is obliged to turn through an angle of 90°, or in other words swim on its side.

Observations in the aquarium revealed that when the dolphin was swimming on its side near the bottom it would brush the floor of the tank with one of its flippers (figure 7). Like a blind man groping with his hands, *Platanista* feels its way along the bottom of the river or the bank with its flipper. Clearly, in addition to their role as stabilisers, the flippers have developed a sense of touch to assist the eye in providing the dolphin with information about its position in the river.

Echolocation

But how does the dolphin find its way forwards, when swimming along in total darkness? Here *Platanista*, like the marine species, makes use of echolocation. It sends out pulsed signals with a frequency of up to 200 kHz [4, 5]. The dolphin uses these clicks to explore its surroundings by receiving the echoes sent back by objects. Although the clicks themselves are always the same, the repetition rate, or number of signals per unit time, can be varied almost indefinitely (figure 8).

Different theories are current concerning the transmitting and receiving apparatus of dolphins in general. Some American authors believe that the clicks are produced not in the larynx but

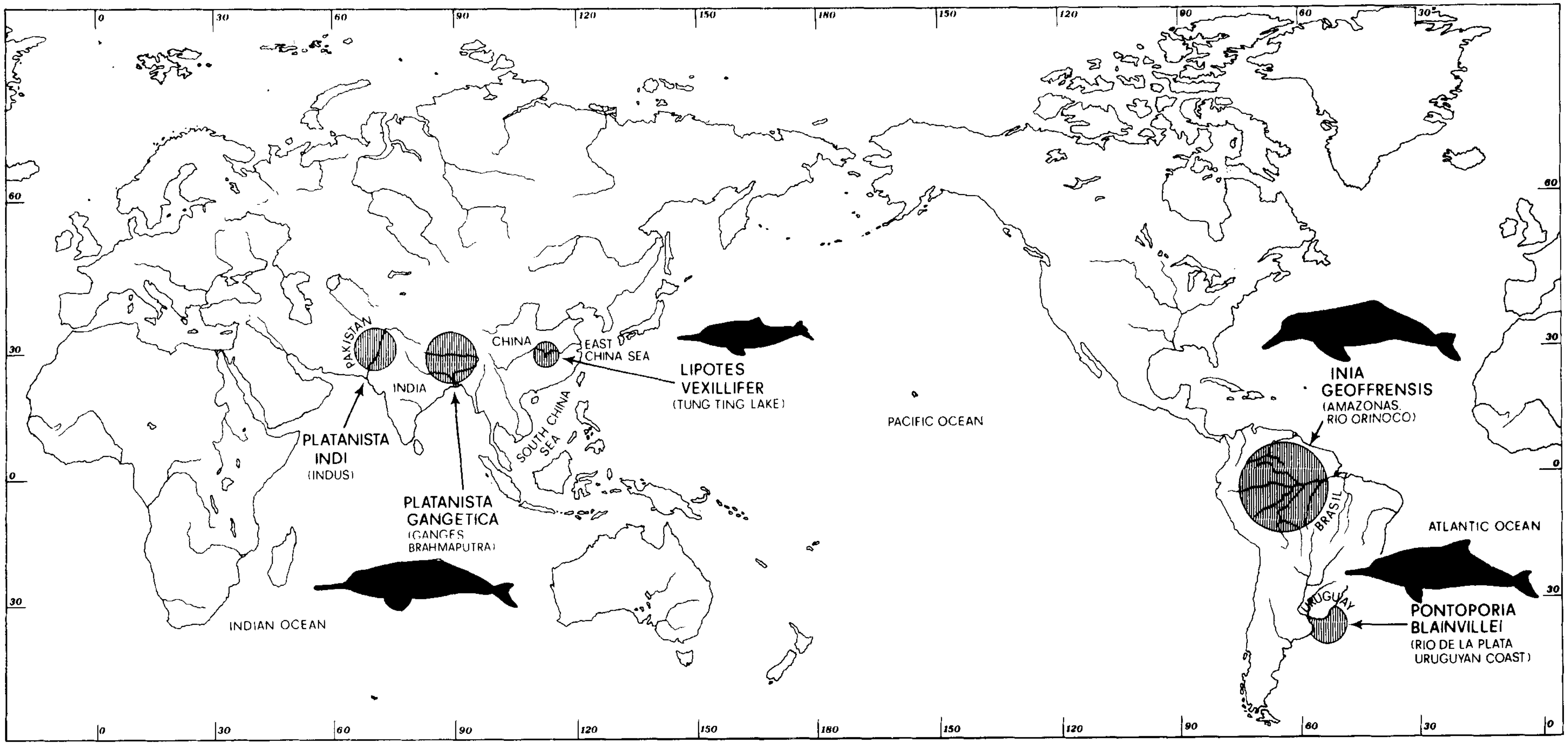


Figure 1 Geographical distribution of the Platanistoidea.

in the accessory sacs of the second pair of air sacs of the upper nares. If this were universally true, *Platanista* would not be able to make any sounds at all, as it does not possess any such accessory sacs. I myself am convinced that the clicks are formed exclusively in the larynx [5, 6]. During phonation the larynx is deeply retracted inside the posterior nares where it is encircled by the palatopharyngeal sphincter muscle. The vibrations produced by the larynx are transmitted by this muscle to the vomer and reach the outside world via the bony and soft parts of the skull. One fact points clearly to a laryngeal origin for the clicks. During swallowing the larynx must be lowered from the phonation in order to free the entrance to the oesophagus. If we follow the whole process acoustically, we find that the sounds always stop when a fish is being swallowed. Clearly, *Platanista* and other dolphins are not capable of speaking with their mouths full. Lastly, complete acoustic insulation between larynx as transmitter and ear as receiver is achieved in all dolphins by a system of air cavities which would be superfluous if the larynx in fact had a purely respiratory function.

The theory that echoes are received via transmission through the bones also seems highly questionable in view of the enormous development of the tympanic membrane and middle ear. Here no suggestion of atrophy is to be found in any cetacean species [7].

The sonar pulses produced in the larynx form an emission field which spreads out from the beak and shows pronounced directionality. We were studying the problem of directionality when one day our young female dolphin began to play with the transducer. She approached the hydrophone emitting a continuous series of signals, touched it lightly with the tip of the beak and let the instrument glide along the side of the melon (the convexity of the head between the rostrum and the nostrils) until it reached her flipper. While listening to the clicks through a loud speaker and carefully checking the position of the transducer in relation to the dolphin, I noticed that at a particular point on the melon the hitherto loud and frequent signals suddenly stopped altogether (figure 9). Later I established with the help of a specimen skull that the point at which the clicks fell silent exactly corresponded with the front edge of the maxillary crest (figure 10).

The maxillary crest

From Georges Cuvier onwards, anatomists and cetologists have puzzled over this curious bony helmet on the skull of the Indus dolphin, but without finding any plausible explanation for it. The crest lies directly beneath the skin of the melon and is not possessed by any other living species of dolphin. With the help of

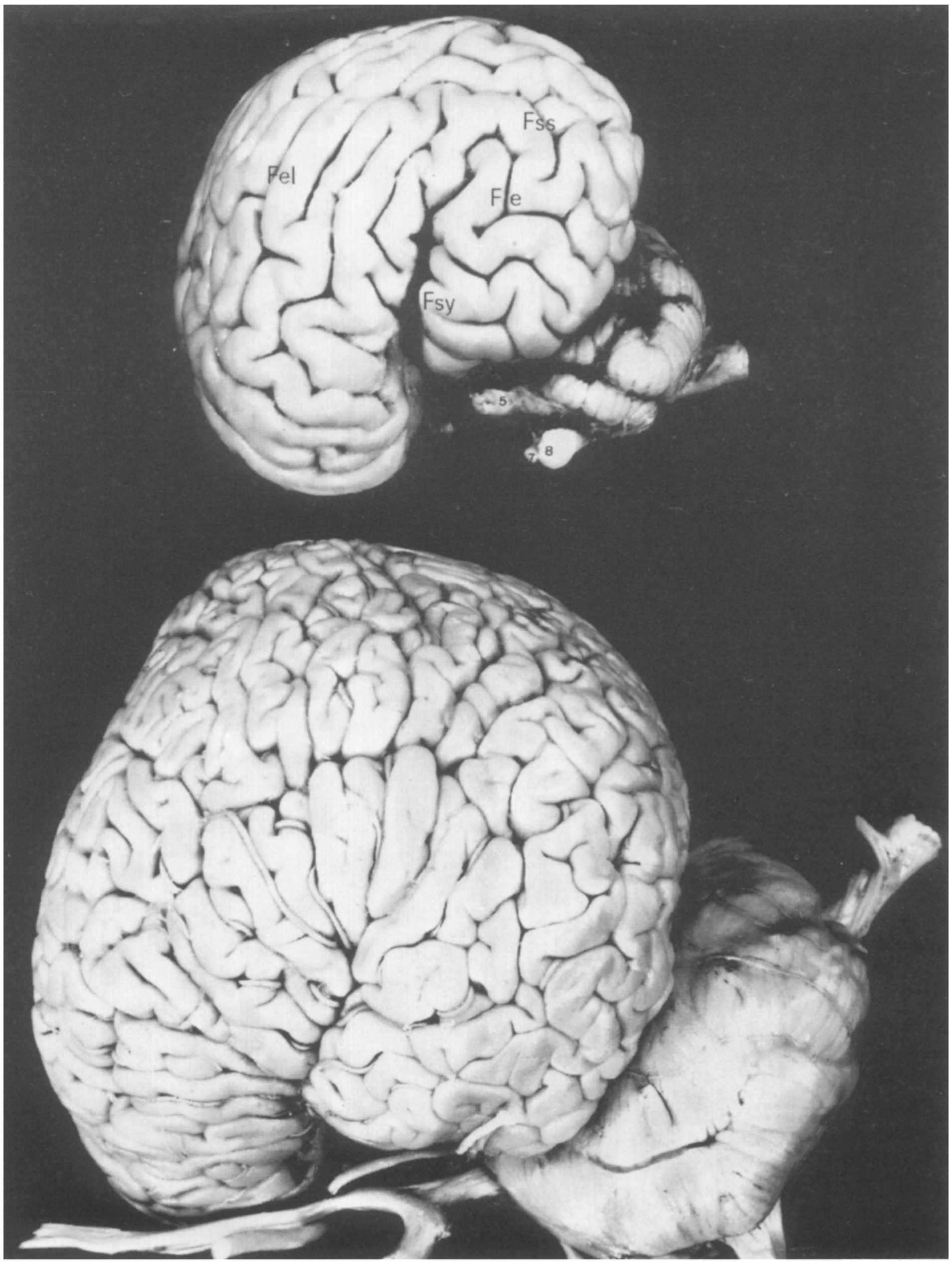
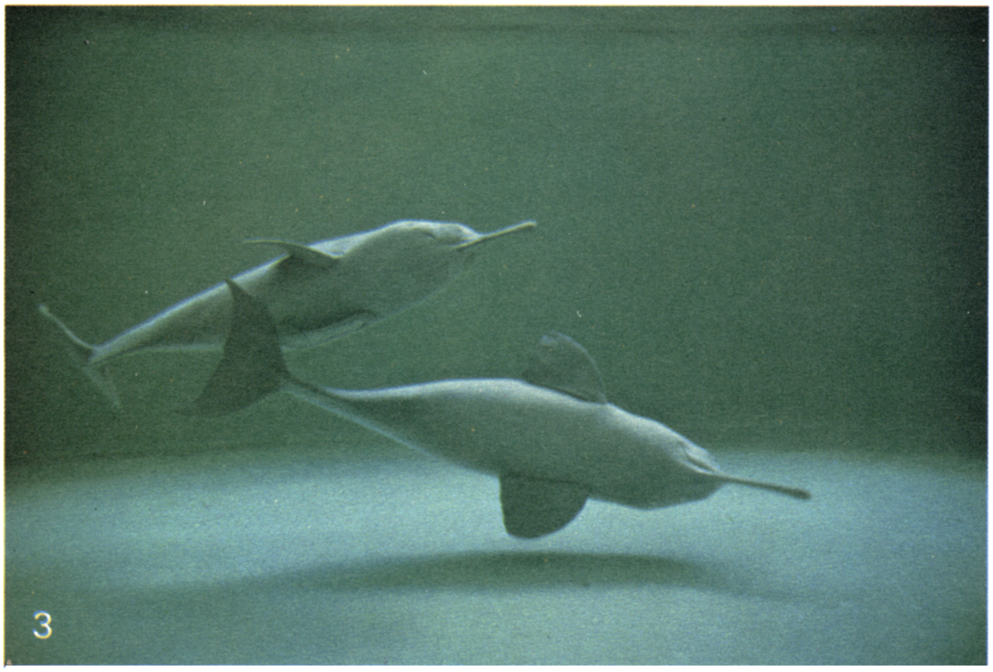
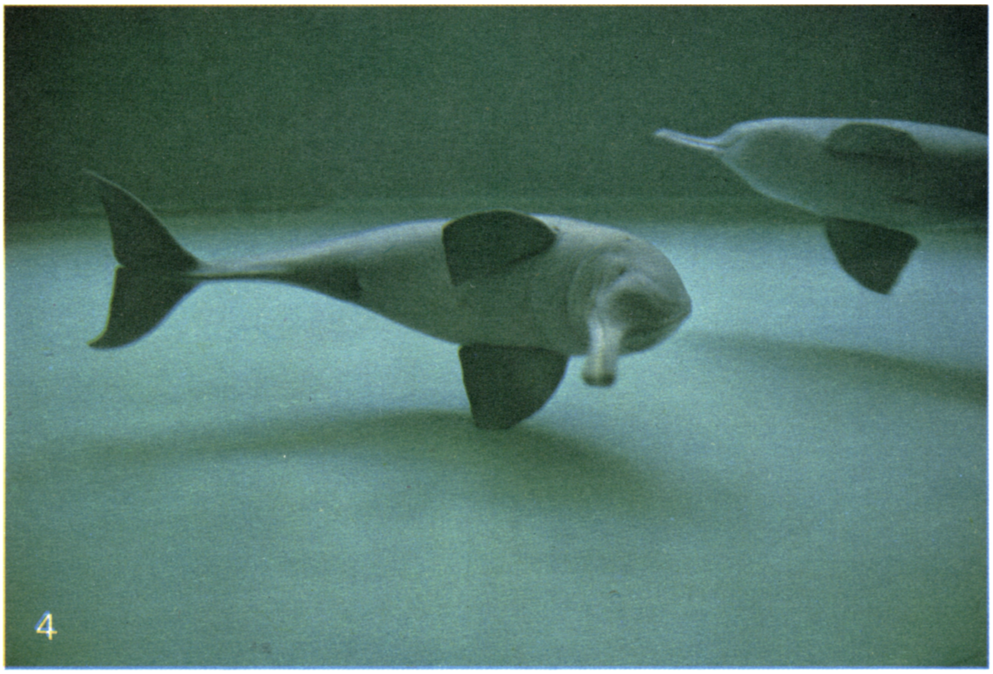


Figure 2 Lateral view of the brain of *Platanista* (above) with a brain weight of 250g, and *Tursiops* (below) with a brain weight of 2300g. Furrowing (sulcation) is much more pronounced in the porpoise brain.

FSY= Fissura Sylvii
Fe = Fissura ectosylvia
Fss= Fissura suprasylvia
Fel = Fissura ectolateralis
5 = Trigeminal nerve
7 = Nervus facialis
8 = Nervus acusticus





Figures 3 & 4 Captive Indus dolphins in the aquarium.

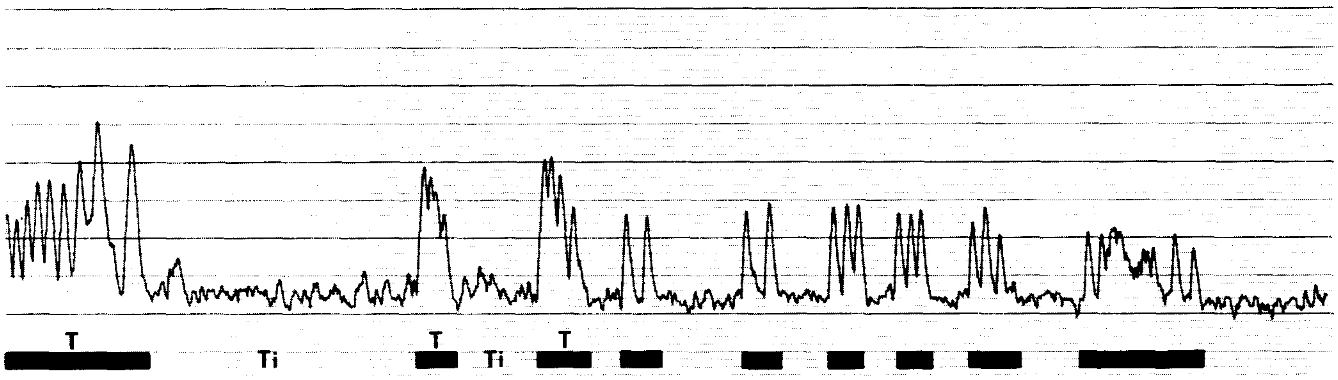


Figure 5 Transmission (T) and transmission interruptions (Ti) when the dolphin was swimming towards the hydrophone. Transmission interruptions of a captive animal alone in a tank varied from 4 to 60 sec and those of two animals together in a tank, from less than 1 sec to approximately 8 sec.

my friend Dr Peter Purves, then curator at the British Museum (Natural History) and one of the best anatomists of whales, I decided to dissect an intact head. On the visceral surface of the crest we found an extensive air sinus which communicated not with the nasal cavity but with the periotic sinus and hence with the tympanic cavity. Injection of radiopaque liquid into the periotic cavity immediately filled the entire sinus on the internal surface of the maxillary crest [7]. Obviously it was this air cushion (figure 11) in the melon which was responsible for the sudden cessation of clicks as the dolphin played with the transducer.

After establishing the directionality of the emission field and the fact that it is limited by the maxillary sinus, we went on to determine the exact shape of the sonar field. The results were very different from those obtained with other dolphins. In *Platanista* the sonar field is divided into two parts, one dorsal and one ventral. Measurements of loudness directly in front of the rostrum tip revealed a sharp decline in level almost down to zero. Here, therefore, was an acoustic 'scotoma', a kind of blind spot between the dorsal and ventral part of the sonar field [5]. At first we wondered what could be responsible for the curious shape of the emission field, but study of the dolphin's behaviour and anatomy soon provided the answer.

We had already noticed that the Indus dolphin used only the ventral field when locating fish or other objects. If we now examine the path taken by the sounds through the dolphin's head, we find that the clicks are beamed from the larynx and transmitted via the palatopharyngeal muscle, vomer, and soft parts to the outside world. Here they form a cone with high frequencies on the axis and low frequencies at the periphery. This is the direct path or dorsal signal. The ventral signal, on the other hand, has no direct path. Sounds emitted from the larynx reach the sinus of the maxillary crest and are reflected ventrally and

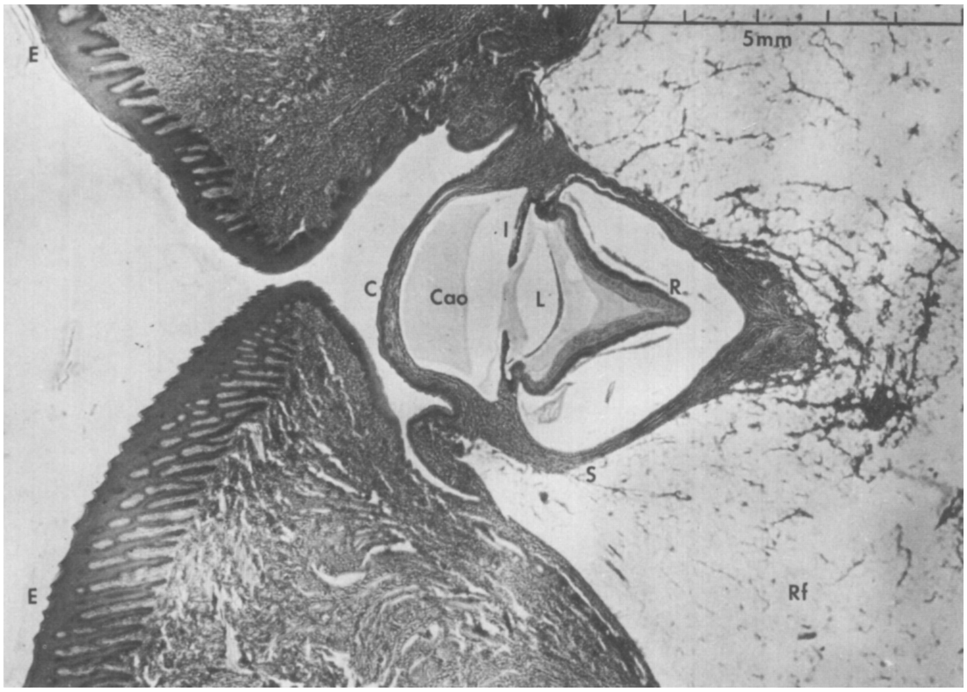


Figure 6 Histological section through the left eye (*in situ*) of *Platanista*: C = Cornea, Cao = anterior chamber, E = Epidermis, I = Iris, L = rudiment of the lens with preserved posterior capsule, R = Retina, Rf = large retrobular fatty body.

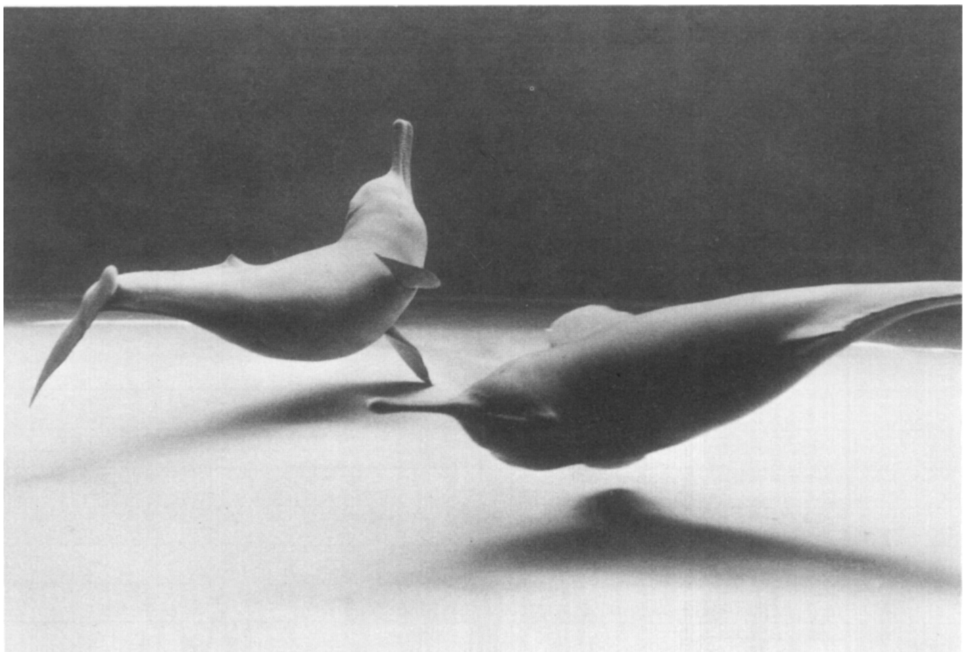


Figure 7 When swimming, *Platanista* brushes the floor with the pectoral fin.

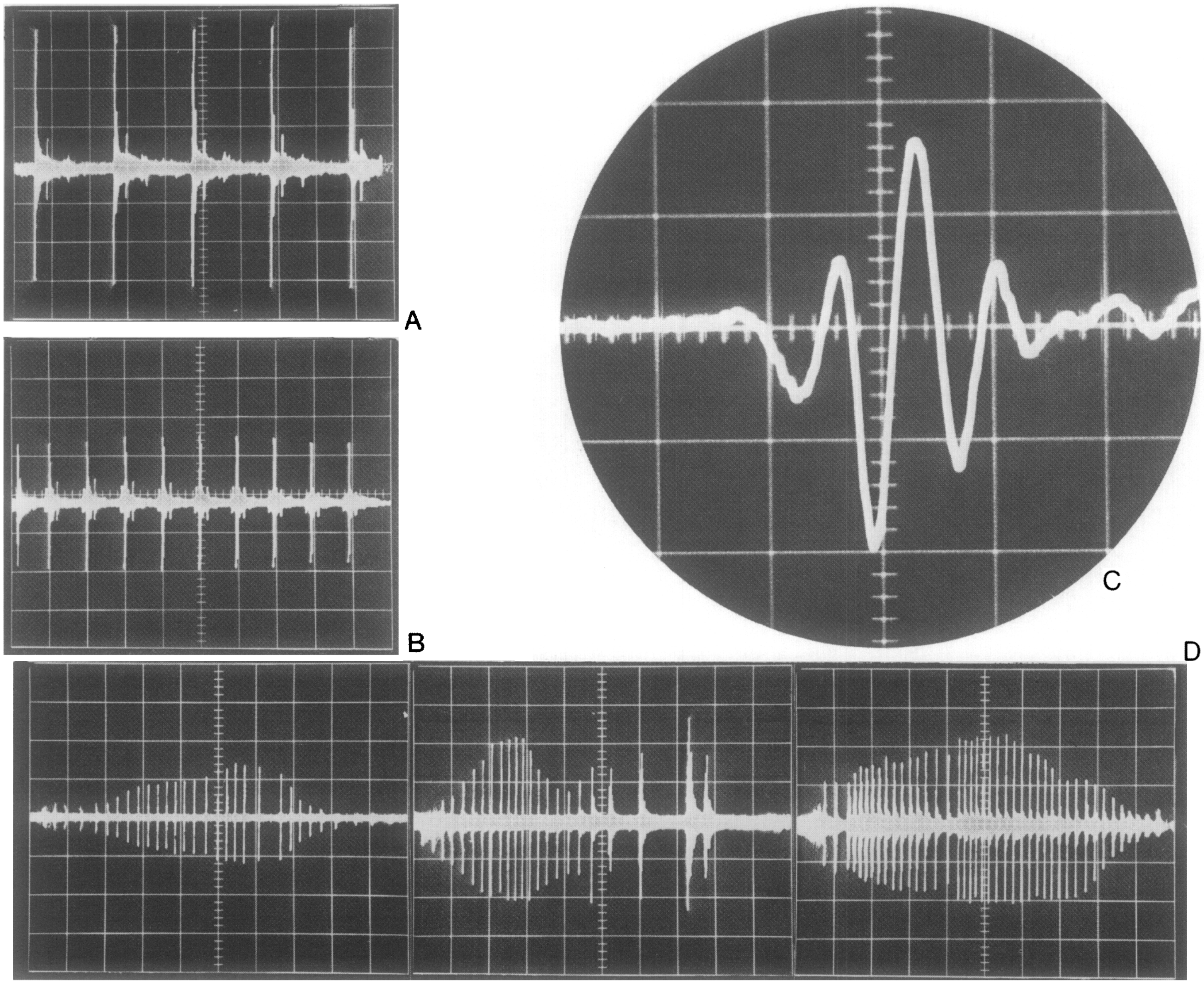


Figure 8 A Series of 5 clicks. The arrows show the echo following the click.
B Regular emission of signals, with echoes visible on some of them.
C Single click of *Platanista* on the oscilloscope screen. Horizontal scale shows loudness level, vertical scale indicates frequency (30μ sec/div).
D Chain of signals with transmission breaks and varying repetition rates.

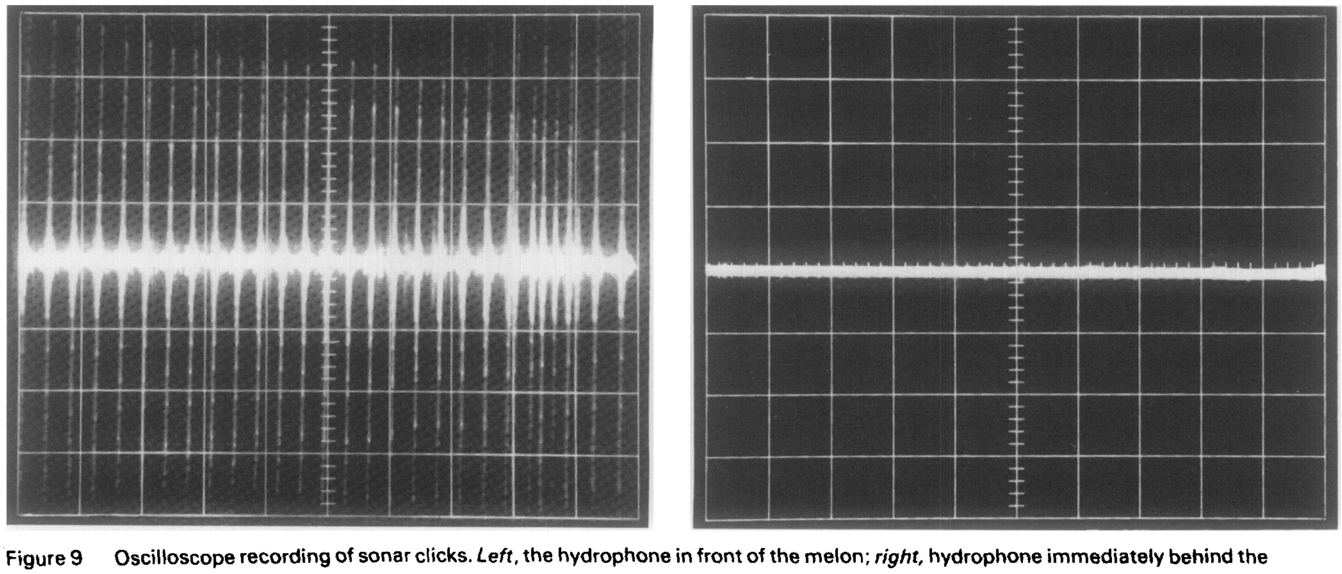


Figure 9 Oscilloscope recording of sonar clicks. *Left*, the hydrophone in front of the melon; *right*, hydrophone immediately behind the anterior edge of the maxillary crest.

forwards by the air which it contains. The ventral field is, therefore, formed exclusively by reflected larynx signals. The fact that the air-filled pterygoid sacs lie immediately in front of the larynx means that no sounds can pass through them to be emitted directly forwards. This explains the scotoma round the rostrum with its sudden decline in sound level [5].

reasoned that if it was true that two separate sonar fields existed with a common sound source, then because of the longer path from the larynx to the crest and down again, the signal from the ventral field should take longer to reach the two-channel oscilloscope. In fact the two hydrophones showed a time lag of 160μsec between the dorsal and ventral signals (figure 12) [5].

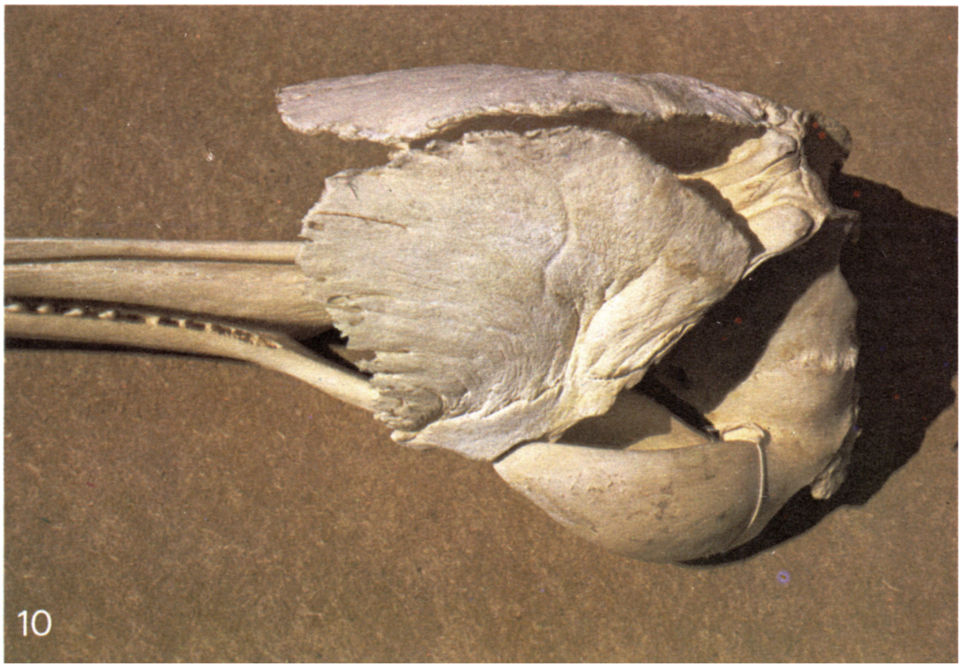


Figure 10 Lateral view of the skull of *Platanista* showing the maxillary crests.

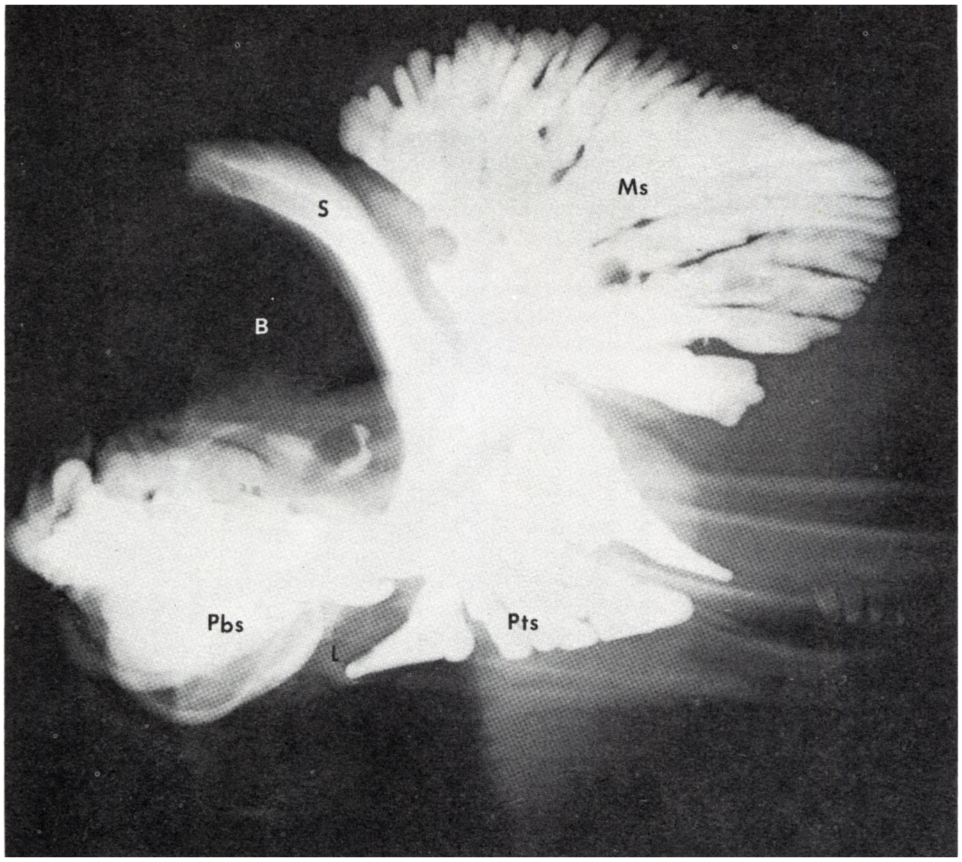


Figure 11 X-radiograph showing complete filling of tympanic cavity, ventral and rostral regions of pterygoid sinus, and complete filling of maxillary crests. The brain (B) has been removed.
Ms = Maxillary crest, Pbs = Peribullary sinus, Pts = Pterygoid sinus, S = Skull.

We had already noticed in the early days of captivity that, while swimming on its side, the dolphin would move its head backwards and forwards in the horizontal plane. It seems likely that this movement, made possible by the free cervical vertebrae of the species, is used to eliminate the acoustic blind spot. We

As already explained, *Platanista* always uses the ventral sonar field for exploring objects or locating fish. This is because the ventral field is vitally important for feeding. If the dolphin only had a dorsal field, it would not be able to eat at all. Once the fish lies between the wide open jaws, it can be reached only by the clicks reflected from the maxillary crest.

In evolutionary terms, the maxillary crest is undoubtedly a comparatively late acquisition which probably developed parallel with regression of the eye to compensate for the loss of vision. In the evolutionary history of whales and dolphins, living members of the Platanistoidea must be considered as relict species. The Indus dolphin may well owe its survival to development of the maxillary crest.

In conclusion, I should like to point out that scientific discoveries, however exciting, are often of interest only to experts and may never emerge from the specialist literature. But today it is no longer possible to think of carrying out pure research on dolphins without first taking steps to ensure their protection. According to the censuses we made in 1974, there were then only about 150 Indus dolphins remaining between the barrages of Sukkur and Guddu [1]. The decline in numbers was due to regular hunting to obtain the dolphin oil which is used in folk medicine. This alarming situation at last caused the World Wildlife Foundation to take action, and, with the help of the Pakistani authorities in Sind, we managed to make this particular stretch of the Indus into a nature reserve [3]. By 1978, the dolphin population had already risen to 241. This was not only a reward for our efforts but proof that even theoretical work can have positive practical results.

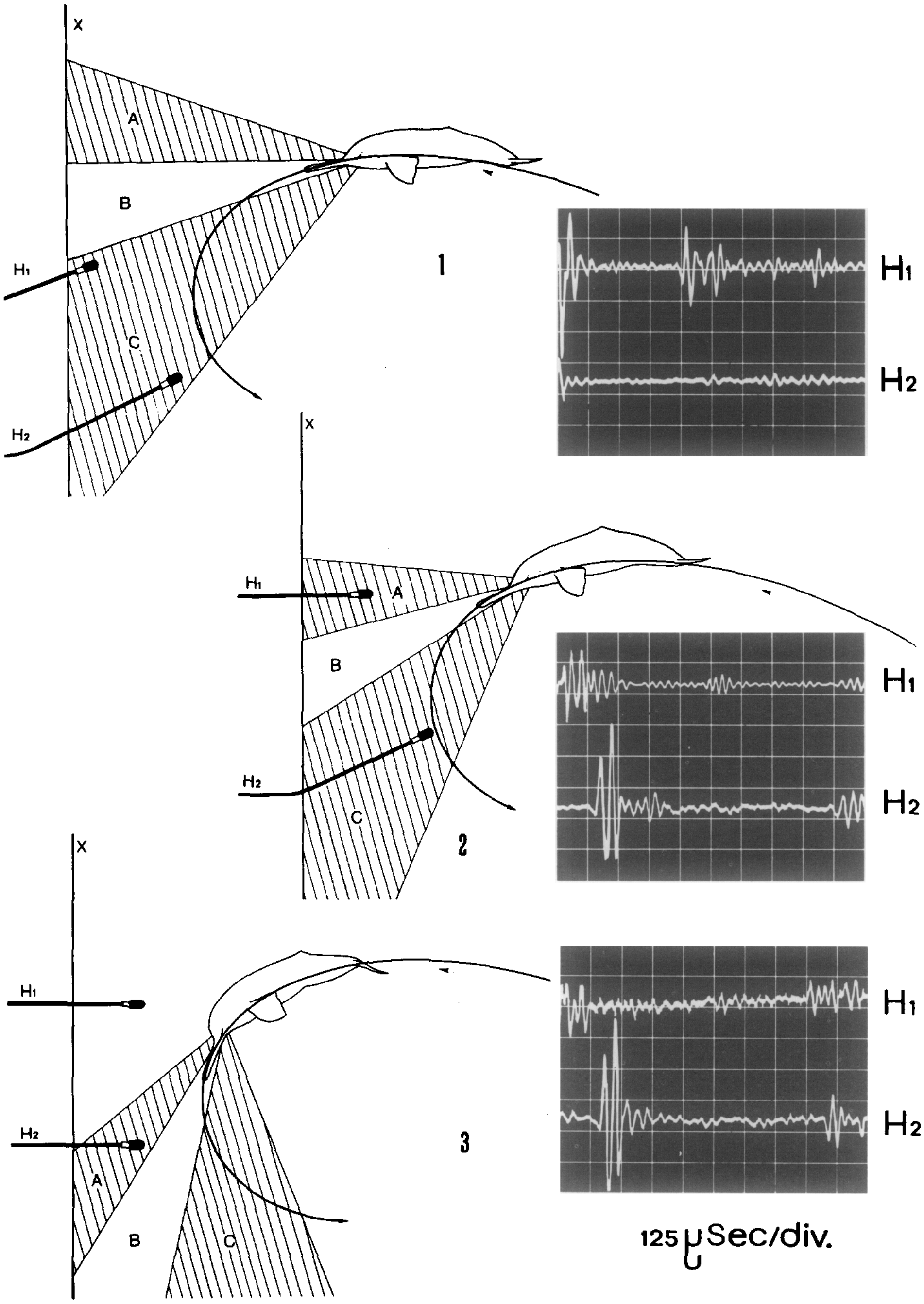


Figure 12 Test assembly to determine the time lag of signals from the dorsal (A) and ventral (C) sectors of the emission field. B = axial sector of the emission field. Top plan view of the tank and the dolphin swimming on its side towards the tank wall (X). Both hydrophones (H_1 and H_2) are hanging vertically 165 cm apart. On the right-hand side, the oscillogram from situation 1 and two oscillograms from situation 2. Signal from the tape, filtered at 30 kHz (1/3 octave).

Our research in the Berne Brain Anatomy Institute, in conjunction with several expeditions to the Indus and Brahmaputra, has enabled us to shed a little more light on the puzzling natural history of this curious dolphin—an animal which has proved to be different indeed from the primitive creature of popular belief. In carrying out studies of this kind a multidisciplinary approach seems to me essential. Acoustic research, for example, would have been meaningless without an accompanying study of the dolphin's anatomy.

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