Side-Swimming, Vision and Sense of Touch in *Platanista indi* (Cetacea, Platanistidae)[1]

During my second expedition to the Indian subcontinent in the winter of 1969–1970, two live river dolphins belonging to the species *Platanista indi* were captured in the lower Indus and transported to Berne. Due to the care and precautions taken during the long journey, the animals adapted themselves rapidly to their new surroundings and spontaneously chased the live fish fed to them. This was the first successful attempt at keeping *Platanista* in captivity for a prolonged period, and it gave us the opportunity to study the behaviour of this extremely interesting cetacean species in the laboratory. Two other expeditions were undertaken to the same region (Lloyd and Guddu Barrages) in 1971 and 1973, and the dolphinarium of our Institute now has 4 animals (2 young ♀♀, 1 subadult ♂ and 1 ♀), kept in 2 separate tanks. These are the only live captive *Platanista* in the world (Pilleri[2–5]).

As is known, the rivers of the Indian subcontinent are so murky that visual observations are restricted to rapid glimpses of part of the animal's head and back when it is blowing. The clear water of the tank permitted us to confirm the very first day that the Indus dolphin is a side-swimmer (Figure 1). It swims on either its right or its left side, along a curved or straight course, clockwise or anticlockwise (Pilleri[2]). It is only when blowing that the dolphin turns over and its blowhole is directed upwards towards the surface of the water (Figure 2). This swimming behaviour that appeared mysterious at first was found during the course of our observations to be a significant ecological adaptation ascribable to the modification of the sense organs peculiar to this cetacean species.

Sense of vision. In the 4 representatives of the Family Platanistidae, *Pontoporia blainvillei*, *Inia geoffrensis*, *Platanista gangetica* and *Platanista indi*, a progressive reduction of the visual organ has been observed and is extremely advanced in the two *Platanista* species. Whereas *Inia* and *Platanista* inhabit tropical rivers, far from tidal limits, *Pontoporia* occurs off the Atlantic coast of Uruguay and Argentina and in the Mar de Plata and may, therefore, be considered a predominantly marine species. The Chinese species, *Lipotes vexillifer,* which is endemic to the Tung Ting Lake, has not yet been investigated. The visual organs of the above-mentioned species are shown in Figures 3–5. In *Pontoporia,* the eye is relatively large and has a well developed lens (Figure 3), the accommodation apparatus is also well developed, the retina contains a large number of cells and the optic nerve is relatively thick. Eye movements are ensured by 2 eye muscle nerves; the trochlear nerve is missing. *Inia* has a smaller lens and a still intact accomodation apparatus with a thick ciliary muscle (Figure 4), the sclera is thicker, the retina has fewer cells

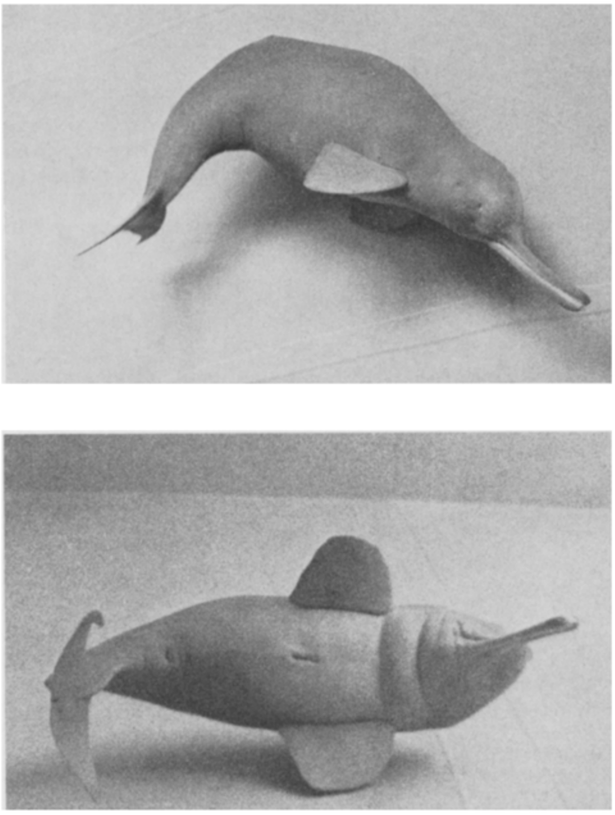

Fig. 1. *Platanista indi* swimming on its side. The lower photograph was taken through the porthole of the tank. Photograph G. Pilleri.

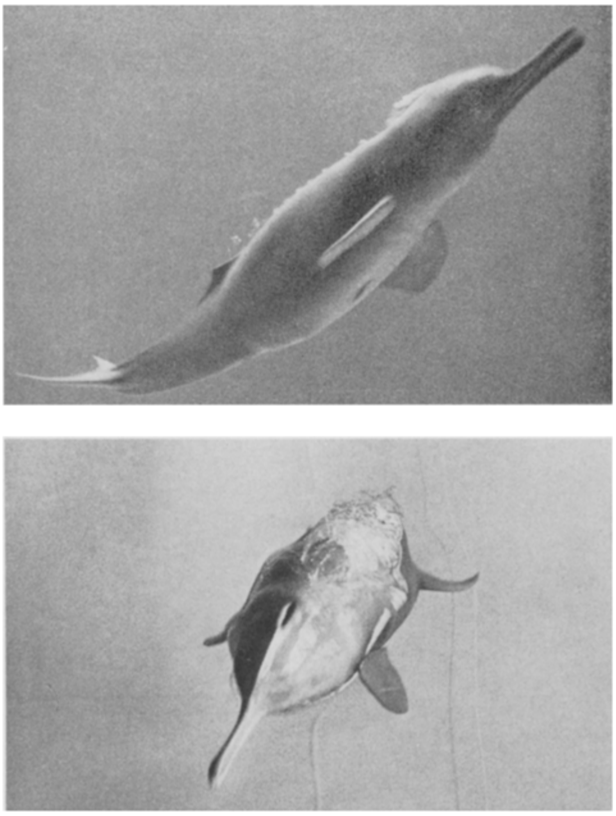

Fig. 2. *Platanista indi* blowing. The upper photograph was taken through the porthole of the tank. In the lower photograph the animal is surfacing. Photographs G. Pilleri.

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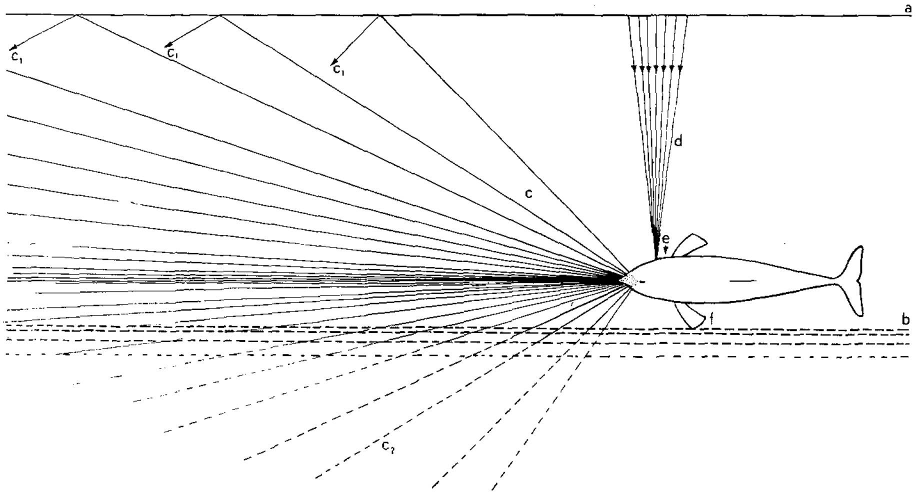
[1] The work was sponsored by the Swiss National Fund for the Promotion of Scientific Research.

[2] G. Pilleri, Rev. Suisse Zool. *77,* 353 (1970).

[3] G. Pilleri, in *Investigations on Cetacea* (Ed. G. Pilleri; Hirnanat. Inst., Waldau, Bern 1970), vol. 2, p. 27–60.

[4] G. Pilleri, in *Investigations on Cetacea* (Ed. G. Pilleri; Hirnanat. Inst., Waldau, Bern 1972), vol. 4, p. 44–70.

[5] P. E. Purves and G. Pilleri, in *Investigations on Cetacea* (Ed. G. Pilleri; Hirnanat. Inst., Waldau, Bern 1973), vol. 5, p. 13–58.



Schemtic representation of the sensoric functions of *Platanista*. The animal swimming on its side in the Indus; c, sound filed; c_1, sound relfections on the surface of the water (a); c_2, sound losses in the muddy river bed; d, 'field of vision'; e, position of the external auditory meatus; f, pectoral fin groping along the river bed (b).

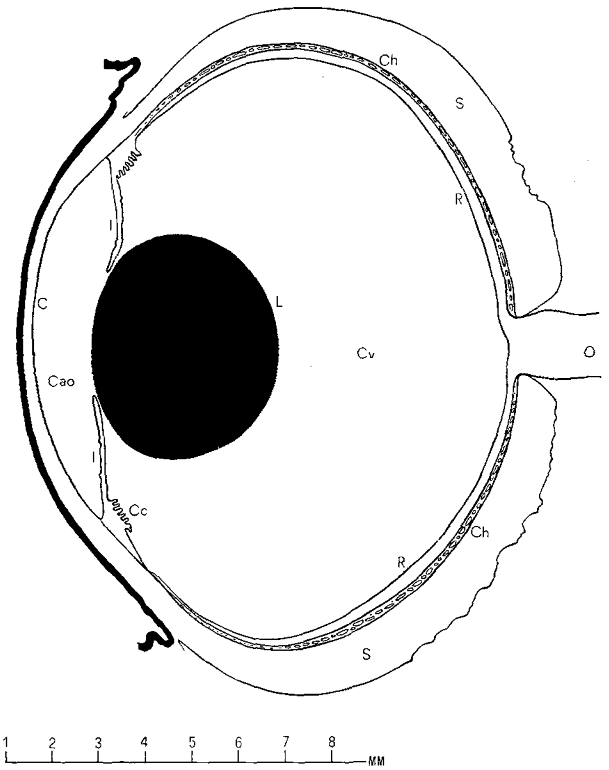


Fig. 3. Semischematic representation of the eye of *Pontoporia blainvillei* (La Plata dolphin). Horizontal section: C, cornea; Cao, camera oculi anterior; Cc, ciliary body; Ch, choroid; Cv, vitreous body; I, vis; L, lens; O, optic nerve; R, retina; S, sclera.

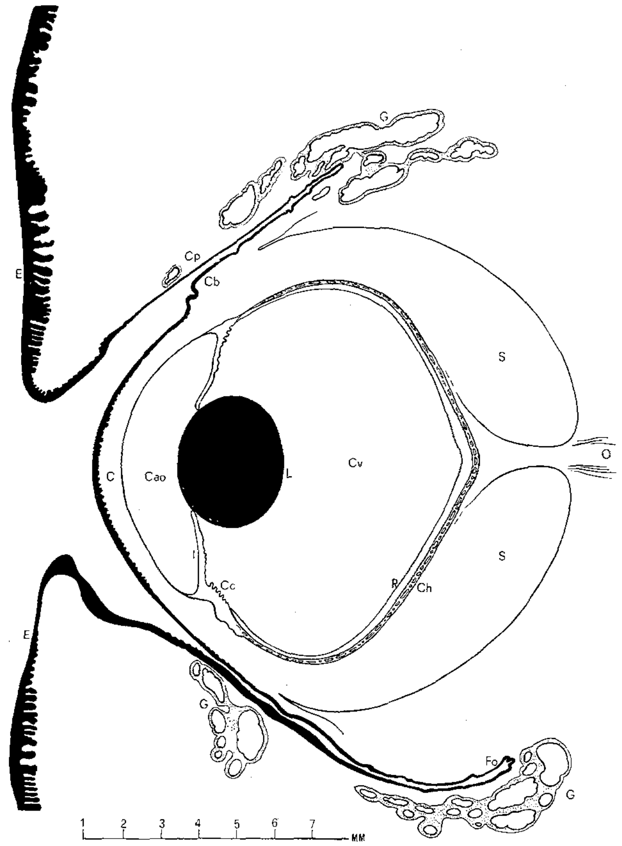


Fig. 4. Semischematic representation of the eye of *Inia geoffrensis* (Amazon dolphin). Horizontal section: Cp, conjunctiva palpebrarum; Cb, conjunctiva bulbi; E, shin epithelium; G, glands. For other letters, see Figure 3.

and the optic nerve is relatively thinner than in *Pontoporia*. The trochlear and abducens nerves are lacking (PILLERI and GIHR[6]; Table).

Platanista exhibits the most advanced degree of microphthalmia (Figure 5). It has no lens, the anterior chamber is broader than in the other species, the ciliary body is atrophic but the iris is well developed and has a dilator and sphincter muscle. The retina is thick but its cell content is lower than that of *Inia* and the optic nerve is a mere filament. The eye muscle nerves are lacking entirely (PILLERI[4]). The bulb is further from the surface, and the eyelid opening is only a few millimeters in diameter.

Functionally, the microphthalmic, lensless eye of *Platanista* may be compared to the copula eye (pinhole camera) of many invertebrates. With such an eye it is virtually impossible to reproduce an image; at the most, the direction of the light can be determined and a distinction made between light and dark. This has been confirmed by experiments carried out in our laboratory.

Sense of touch. The loss of such an important sense is compensated by the activation of two other functions, the sense of touch and hearing. When observed through the porthole of the tank, *Platanista* is generally seen swimming on its side keeping the right or left pectoral fin in constant contact with the floor of the tank (Figure 1). If the latter is covered with a layer of algae, the fins leave traces, and after some time the floor of the tank resembles a skating rink. Just as a blind person feels his way with his hands, *Platanista* seeks the bottom with its fins. To do this the animal is forced to swim on either its right or left side. Unlike in marine species, the position of the pectoral fin is distinctly lateral. The animal often presses a fin down on the bottom, curving it slightly.

The sense of touch in the fins may, therefore, account for side-swimming. This position also permits the perception of light which, due to the distance of the eye from the surface, the narrow eye slit and the thick, rigid lids, must penetrate axially. In the biotope, all light occurs on the surface of the water and can only be perceived if the eye of the animal is directed towards the surface. Here again, this is only possible when the animal swims on its side.

Acoustic orientation. Next to the greatly reduced visual apparatus and the well developed sense of touch, the acoustic system of *Platanista* is the most important sense organ and it plays a predominant role in orientation. We were able to establish that *Platanista*, like marine cetaceans, emits supersonic exploratory sounds, echoes of which are picked up by the highly sensitive organ of hearing (PILLERI, KRAUS and GIHR[6-8]). The sound is formed in the larynx. Other authors postulate that the air sacs contained in the melon (diverticula of the nasopharyngeal space) are the only sources of the above-mentioned exploratory sounds (NORRIS[9]; NORRIS et al.[10,11]). If this were the case, *Platanista* would be unable to produce sounds as it does not possess these air sacs (PURVES and PILLERI[5]). We are also able to refute the theory subscribed to by many other researchers according to whom acoustic stimuli are transmitted via the bones, this being the only possibility of sound transmission in cetaceans. Both the meatus acusticus externus and the structures of the middle ear are fully developed and in no way atrophied. In addition to the supersonic sounds of more than 160 kHz, *Platanista* also emits low frequency sounds far down the human range of hearing. Two pneumatized maxillary crests cause the whole of the sound field formed by the larynx to converge forwards (PURVES and PILLERI[5]). Although the exact shape of this sound cone is not yet known, we have been able to determine 2 diameters by placing the hydrophones in appropriate positions in the tank.

The sound emission was followed on the oscilloscope and through the loudspeaker. As soon as it ceased, the position of the animal in relation to the hydrophone was registered with a video-monitor. It was easier to work with young animals in that they developed the habit of 'playing' with the hydrophone suspended in the water, i.e. they rubbed

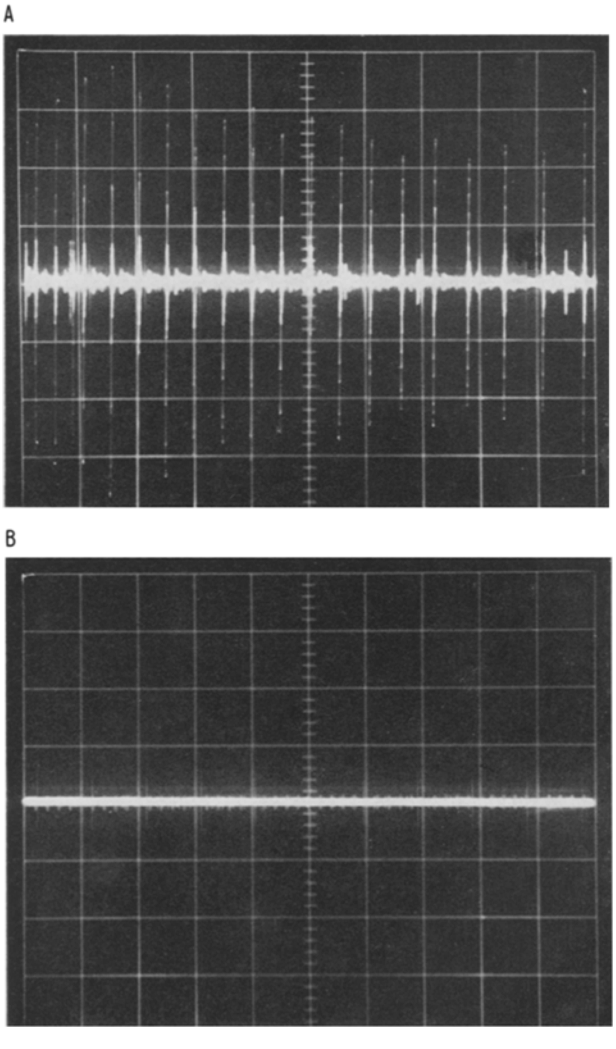


Fig. 7. Oscilloscopic polaroid recording of the sonar sounds: A) Hydrophone at the tip of the rostrum (position c of Figure 6); B) Hydrophone immediately behind the anterior edge of the maxillary crest (position e of Figure 6). Impulse recordings have ceased (Photographs: K. ZBINDEN).

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[6] G. PILLERI and M. GIHR, Experientia *24*, 932 (1968).

[7] G. PILLERI, M. GIHR and C. KRAUS, in *Investigations on Cetacea* (Ed. G. PILLERI; Hirnanat. Inst., Waldau, Bern 1971), vol. 3, p. 22–30.

[8] G. PILLERI, M. GIHR and C. KRAUS, in *Investigations on Cetacea* (Ed. G. PILLERI; Hirnanat. Inst., Waldau, Bern 1971, vol.) 3, p. 34–44.

[9] K. S. NORRIS, in *Marine Bioacoustics* (Ed. E. N. TAVOLGA; Pregamon Press, Oxford 1964), vol. 1, p. 317–336.

[10] K. S. NORRIS and W. E. EVANS, in *Marine Bioacoustics* (Ed. W. N. TAVOLGA; Pergamon Press, Oxford 1966), vol. 2, p. 305–316.

[11] K. S. NORRIS, K. J. DORMER, J. PEGG and G. J. LIESE, Proc. 8th Ann. Conference Biology, Sonar and Diving Mammals (Stanford University, Stanford, California 1971), p. 1–11.

it over the tip of their snout caudalwards, sliding it along the left or right side of their head to their pectoral fin (Figure 6). While observing these antics we noticed that, in the region of the anterior edge of the pneumatized maxillary crests, the sounds suddenly ceased and no more pulses appeared on the oscilloscope (Figure 7). This result enabled us to establish the direction of the sounds and to determine the limits of the sound field.

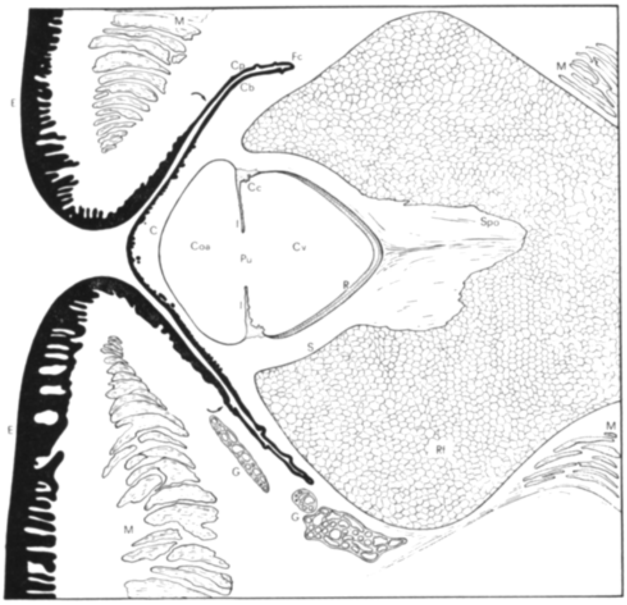

Fig. 5. Semischematic representation of the eye of *Platanista gangetica* (Indian river dolphin). Horizontal section: Cp, palpebral conjunctiva; Cb, bulbar conjunctiva; Fc, fornix conjunctivae; M, muscle, Rf; retrobulbar fat body; Spo, scleral process round the optic nerve. For other letters, see Fig. 3.

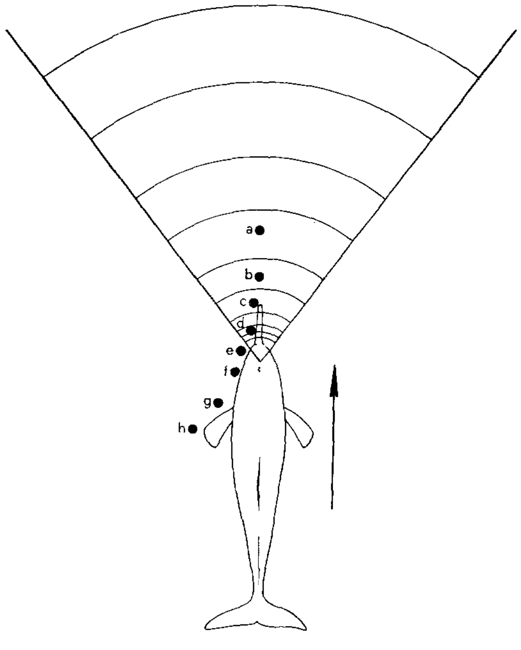

Fig. 6. Position (a–h) of the transducer while a dolphin 'plays' with the instrument. When the hydrophone has passed beyond the anterior edge of the maxillary crest, the signals suddenly cease (see Figure 7).

The angles measured by us, from the larynx, are a horizontal angle (horizontal to the sagittal plane of the body of the animal) of 90° and a vertical angle of approx. 150°. When the animal swims on its side the vertical angle is particularly advantageous as it takes in a very large space in front of the animal. This form of sound field, which is broader than it is deep when the dolphin swims on its side, is admirably suited to the biotope as the Indo-Pakistani rivers are generally shallow. Furthermore, the head is bent and streched alternatively, thereby widening the sound angle still further. This pendulum exploratory movement of the head is kept up constantly during swimming.

Tests carried out in our laboratory have shown how subtle the transmittor-receiver apparatus is. A piece of shot of 3–4 mm in diameter suspended in the tank by a nylon thread was immediately located and the young animals even began to play with it by butting against it with their head or snout. If one considers how very small the reflective surface of such a shot is, it is evident that the sonar apparatus must have evolved to an extremely high degree of perfection. The dolphins locate the fish fed to them in the dark and even make a careful selection. When fed with trout (*Salmo trutta*) and whiting (*Leuciscus leuciscus*) of the same size, they chose and went after the whiting, leaving the trout undisturbed. A similar selection was made in the case of whiting and perch (*Perca fluviatilis*); unless they were very hungry, the dolphins left the latter species untouched.

Discussion. How can side-swimming be explained from a phylogenetic standpoint? It is highly probable that the ancestors of the Platanistidae inhabited coastal waters. They came to their present distribution regions where they have formed recent endemisms during transoceanic migrations (the oldest fossils were found in North America) undertaken during the Middle Eocene and later. It is known that the temperature of the sea remained constant during this geological era and the fossile found have shown that the Platanistidae of those days were sufficiently good swimmers. These two factors render such long migrations plausible, also in the case of other species. The present distribution does not, therefore, correspond to the original distribution and the ecology has also changed. Muddy water has replaced the originally clear medium and led to a regression of the visual apparatus. The ancestral (see bats, fossil cetaceans) sonar functions has remained and ensured the survival of the species. The change in ecology led to the following situation which still prevails today. Imagine a *Platanista* swimming in the Indus just above the river bed (Figure 8). The surface of this river is often as calm as a millpond. The high frequency sonar apparatus of the animal and the low frequency sounds it emits are directed forward and travel along a clear path from which no echoes arise. Below, the muddy river bed is an excellent sound absorber, so here too no sound is reflected. Above, the smooth surface of the river reflects the signals that strike it diagonally like a mirror and the reflected sound waves are lost in the distance; it is only when there are waves on the surface that these can be located. In such a situation the only possibility the animals have of checking their position in the water is to grope with a fin – and they can only do that if they swim on their side.

Considered from this angle, sideswimming is a secondary functional adaptation of a later phylogenetic period. Another argument in favour of this theory is that sideswimming is less evident in young *Platanista* than in subadult and adult animals.

Zusammenfassung. Das Schwimmen in Seitenlage ist ein Hauptcharakteristikum von *Platanista indi*. Es handelt sich sehr wahrscheinlich um eine spätere phylogene-

tische Anpassung und ist durch die taktile Funktion der Brustflossen und die besondere Struktur und Lage der Augen bedingt. Das Auge von *Platanista* ist durch eine oekologisch bedingte regressive Evolution extrem zurückgebildet und kann praktisch nur axial eintreffende Lichtreize wahrnehmen. Der hochdifferenzierte akustische Apparat (Sonar) steht im Vordergrund der Orientierung. In Seitenlage ist das Schallfeld des Delphins breiter als hoch, was eine günstige Anpassung an die seichten Gewässer des Indus bewirkt. Durch pendelnde Bewegungen des Kopfes in der Horizontalebene während des Schwimmens und Ortens in Seitenlage kann das Tier seinen Sendewinkel noch erheblich vergrössern.

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Flavonoids of *Parthenocissus* Tissue Culture

In the course of a continuing search for plant tissue cultures which are able to express their biosynthetic potential for flavonoid compounds[1–3], we found that a light-grown callus culture obtained from stem segments of the Virginia creeper, *Parthenocissus tricuspidata* Planch. (Vitaceae) produces 1 anthocyanin and 2 flavonol glucosides. STANKO and BRANDINSKAYA[4] reported the presence of cyanidin, delphinidin and malvidin glucosides in a 'chemical tumor' callus culture obtained from the same species. The investigation of the nature of these flavonoids was undertaken with the view of using this culture system to study the regulation of flavonoid formation in vitro.

Experimental. The callus tissue was cultured on HELLER'S medium[5] containing glucose (5%), α-naphthalene acetic acid (0.1 mg/l) and solidified with 0.7% agar. The cultures were maintained under continuous illumination (300 fc) and a temperature of 27 ± 1 °C. Standard chromatographic and spectroscopic methods[6,7] were used for the isolation and identification of flavonoids from 4-week old callus tissue.

Results and discussion. The spectral characteristics and Rf values of compounds A–C are given in the following Table. Compounds A and B on acid hydrolysis yielded quercetin and glucose which co-chromatographed with authentic samples. The bathochromic shifts exhibited by both compounds in the presence of NaOAC (in the short UV-range) and $AlCl_3$ (in the long UV-range) indicate that the 5- and 7-positions are free. Furthermore, the instability of their $AlCl_3$ complexes in presence of HCl is indicative of glucosylation at the 3-position[7]. On the basis of their Rf values in both organic and aqueous solvents, compounds A and B have been identified as the 3-mono- and 3-diglucosides of quercetin, respectively. Compound C was identified as cyanidin-3,5-diglucoside by comparison of its chromatographic and spectral characteristics with those of an authentic sample[6]. Its identity was confirmed by acid hydrolysis and characterization of the hydrolytic products.

Whereas these compounds constitute the major flavonoid components of the callus tissue, it is of interest to note that intact leaves of this species contain the same compounds although this has not been previously reported. These flavonoids were only formed when the tissue was cultured on Heller's medium containing 5% glucose. However, when either fructose (5%) or sucrose (2.5%) was used as the carbon source no flavonoid formation was observed[8].

Chromatographic and spectral characteristics of the major flavonoids of *Parthenocissus* callus tissue

Spectral values	*γmax* (nm)		
	A	B	C
80% MeOH	255, 267[a], 352	255, 268[a], 350	273, 525
+ NaOH	275, 300, 410	278, 310, 414	
+ NaOAc	270, 375	272, 372	
+ NaOAc + H_3BO_3	285, 375	259, 375	
+ $AlCl_3$	272, 303[a], 420	275, 300[a], 418	275, 545
+ $AlCl_3$ + HCl	270, 302[a], 405	272, 302[a], 401	
Rf values (×100)			
BAW[b]	57	48	30
15% HOAc	30	48	39

[a] shoulder (inflection); [b] *n*-Butanol-acetic acid-water (4:1:2.2, v/v)

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[1] R. K. IBRAHIM, M. L. THAKUR and B. PERMANAND, Lloydia *34*, 175 (1971).

[2] S. LIAU and R. K. IBRAHIM, Can. J. Bot. *51*, 820 (1973).

[3] G. BRUNET and R. K. IBRAHIM, Z. Pflanzenphysiol. *69*, 152 (1973).

[4] S. A. STANKO and M. S. BRADINSKAYA, Proc. Acad. Sci. USSR *146*, 1152 (1962).

[5] R. HELLER, Ann. Sci. nat. Bot. Biol. Vég. Ser. II, *1*, 1953.

[6] J. B. HARBORNE, *Comparative Biochemistry of the Flavonoids* (Academic Press, New York 1967).

[7] T. MABRY, K. R. MARKHAM and M. B. THOMAS, *The Systematic Identification of Flavonoids* (Springer-Verlag, New York 1970).

[8] E. BLEICHERT and R. K. IBRAHIM, Pl. Physiol. *51*, suppl. 23 (1973).