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LOCOMOTION AND LOCOMOTORY ORGANS IN WHALES
AND DOLPHINS (CETACEA)

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This paper is a review of the present status of our knowledge of the locomotion and the locomotory organs in whales and dolphins. Experiments on the dorso-ventral flexibility of the body of the Common Porpoise have shown that the thorax and the lumbar region are very rigid, but that there are regions of very great mobility at the base of the tail (anal region) and at the junction of the peduncle of the tail and the tail-fin (flukes). Films of swimming Bottle-nosed Dolphins and a Pigmy Sperm Whale show the same centres of mobility during locomotion under water. The movements of the tail are exclusively up and down, the tail-fin makes an angle with the peduncle of the tail in such way that it can exert a forward driving force on the water. The peduncle of the tail meets but little resistance.

Cruising speed and maximum speed appear to be almost the same in the small dolphins and in the big whales. This phenomenon can be explained by assuming that the flow of the water along the body of the dolphin is wholly laminar, but that in the big whales it is partly laminar and partly turbulent. The difference may be connected with the absolute size of the animals or with their shape, but it is also possible that the efficiency of the spinal muscles plays an important part in determining the speed of the animals.

The efficiency of the spinal muscles probably depends to some extent on the position of the mammillary processes in the posterior lumbar and the anterior caudal region. In the big whalebone whales the position of these processes is close to the vertebral bodies, but in porpoises and dolphins they are shifted upward. Consequently the force exerted by the muscle fibres and tendons of the longissimus and transversospinalis muscles, inserted into the mammillary processes in the regions mentioned, is increased because it is transmitted to the vertebral bodies by a very long lever arm.

The structure of the vertebral column and the spinal musculature is described. In the three divisions of the epaxial musculature as well as in the hypaxial musculature the components of the different regions are fused into single muscular masses ranging from the occiput to the tip of the tail, although the different components still may be distinguished by their innervation. The presence of long muscle fibres enables the tail to make large excursions. The development of the muscles and the insertion of the tendons is adapted to the mobility of the body-axis and especially to the centres of mobility in the anal region and at the base of the flukes. This is especially apparent in dolphins.

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GENERAL REMARKS—MOBILITY

Whales and dolphins are exclusively aquatic mammals with a streamlined, torpedo-shaped body. From species to species this shape may show a certain

variation. Some are very slender (dolphins, ziphiids, rorquals), some are rather clumsy (Right whales, Sperm whale). The species may differ moreover with regard to the relative length of the tail and the position of the flippers (pectoral fins) (Fig. 1) or with regard to the presence or absence of a dorsal fin.

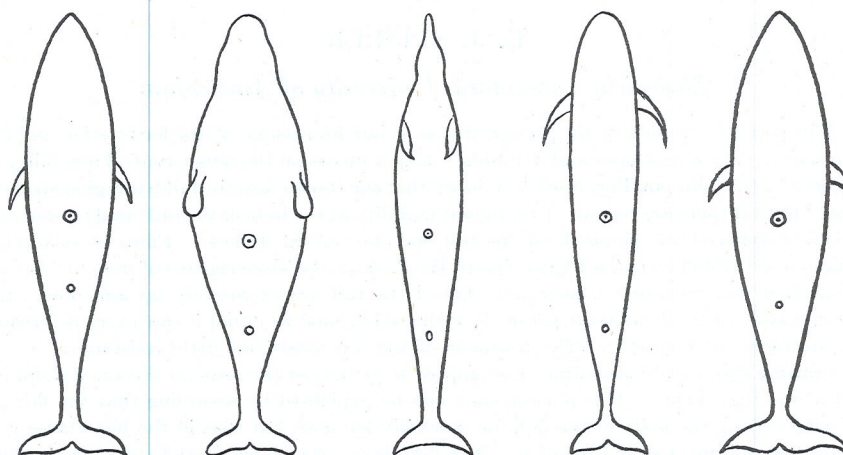


Fig. 1.—Body-shape of five different whales and dolphins. The umbilicus and the anal aperture are indicated. From left to right : Sei Whale (*Balaenoptera borealis* (Lesson)), Sperm Whale (*Physeter macrocephalus* L.), Sowerby's Whale (*Mesoplodon bidens* (Sowerby)), Pilot Whale (*Globicephala melaena* (Traill)), Common Porpoise (*Phocaena phocaena* (L.)). All animals are reduced to the same length. From Slijper, 1958.

Generally, fast swimmers like rorquals and dolphins have a slender body with a dorsal fin. In slow swimmers the shape of the body is usually clumsier and the dorsal fin may be absent. All species lack external hind limbs; the internal parts are only represented by a rod-like, rudimentary pelvic bone, that is not attached to the vertebral column.

The part of the body behind the anal aperture is called the tail. It narrows gradually towards its posterior end where it broadens abruptly into the horizontally expanded tail-fin. In the central part of this fin the vertebral column is represented by a series of small dorso-ventrally compressed caudal vertebrae, but the lateral parts of the fin (the flukes) consist only of a very tough subepidermal connective tissue. The fibres of this tissue are connected with those tendons of the spinal musculature that are attached to the vertebrae of the tail-fin (Roux 1883). The flukes are expanded in the horizontal plane because whales and dolphins are mammals. Contrary to fishes and reptiles, whose principal body movements are in the horizontal plane (laterally), the principal body movements of the mammals are in the vertical plane as may be seen in a galloping dog or cat. Consequently the body-axis of the Cetacea is also moved mainly in the vertical plane (up and down), and the flukes must be horizontal instead of vertical as in fishes and reptiles.

In terrestrial mammals the centre of motion of the body-axis is situated in the region of the so-called diaphragmatic or anticlinal vertebra, that is

usually found in the posterior thoracic region.* It is mostly represented by one of the last thoracic vertebrae (see Slijper 1946). In ungulates the centre of motion lies in the lumbo-sacral joint. Experiments on the dorso-ventral flexibility of the body of the Common Porpoise (*Phocaena phocaena* (L.))

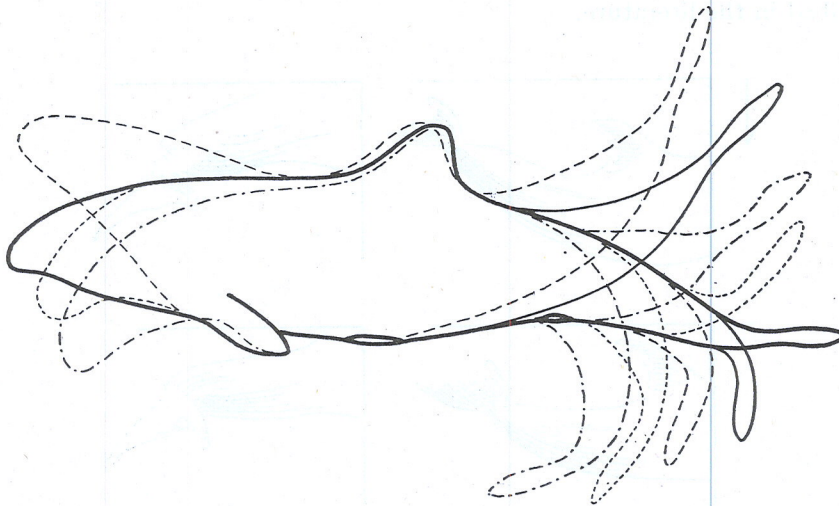


Fig. 2—Flexibility of the body of a Common Porpoise (*Phocaena phocaena* (L.)) in the vertical plane. From Slijper, 1936.

(Fig. 2) show that in this respect the Cetacea differ markedly from their terrestrial relatives (Slijper 1936, 1946). The short cervical region has a certain degree of mobility, but the thorax and the anterior part of the lumbar region are rigid and show only a very small degree of mobility. The posterior lumbar region is a little more mobile and a point of extreme mobility is situated in the anal region, i.e. at the base of the tail. The tail itself is fairly mobile. At the junction of the tail and the tail-fin (the flukes) there is a second centre of extreme mobility. The flukes themselves are fairly rigid.

LOCOMOTION

Underwater films have been made of the swimming movements of dolphins and sperm whales. Those made in the Marineland Aquarium (Florida) show particularly well that the swimming movements of the Bottle-nosed Dolphin (*Tursiops truncatus* (Mont.)) and the Pigmy Sperm Whale (*Kogia breviceps* (Blainv.)) fully correspond with the mobility of the body and tail of the Common Porpoise. The anterior part of the body shows almost no movements required for ordinary locomotion, although from time to time the animals

* The diaphragmatic vertebra is the vertebra in which the position of the articular surfaces of the zygapophyses (articular processes) changes from the horizontal into the vertical position. The anticlinal vertebra is the vertebra in which the neural spine changes its direction. In the pre-anticlinal vertebrae it is inclined caudally, in the post-anticlinal vertebrae it is inclined cranially. In many species the diaphragmatic vertebra is the same as the anticlinal vertebra. In the other animals they are near each other (Slijper, 1946).

make movements of the head, that may be necessary for orientation or for catching prey. A special centre of extreme mobility is situated at the base of the tail (anal region) and another one at the junction of the peduncle of the tail and the flukes. The movements of the tail are exclusively up and down. There are no indications of a sculling movement as has sometimes been described in the literature.

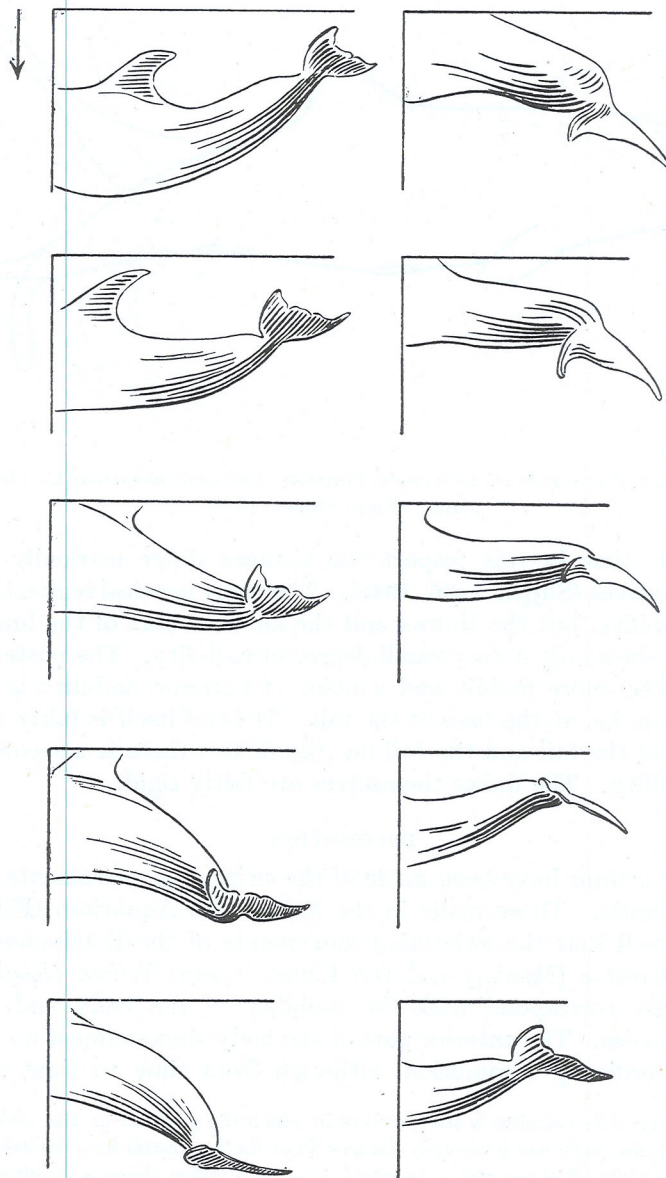


Fig. 3—Ten stages of the motion of the tail and flukes taken from a film of a swimming Bottlenosed Dolphin (*Tursiops truncatus* (Mont.)) in the Aquarium Marineland, Florida. Modified after Parry, 1949, from Slijper, 1958.

Parry (1949) has made an analysis of these movements. It shows that in the upstroke as well as in the downstroke the flukes make an angle with the peduncle of the tail (Fig. 3). It gives the impression that during the up and down movements the flukes remain a little bit behind, which means that during the downstroke they exert on the water a force in a ventro-caudal direction, whereas during the upstroke they exert a force in a dorso-caudal direction. The dorsal and ventral components of these forces neutralize each other and the resultant force in the caudal direction drives the animal forward through the water (Fig. 4). It is very difficult to determine whether the

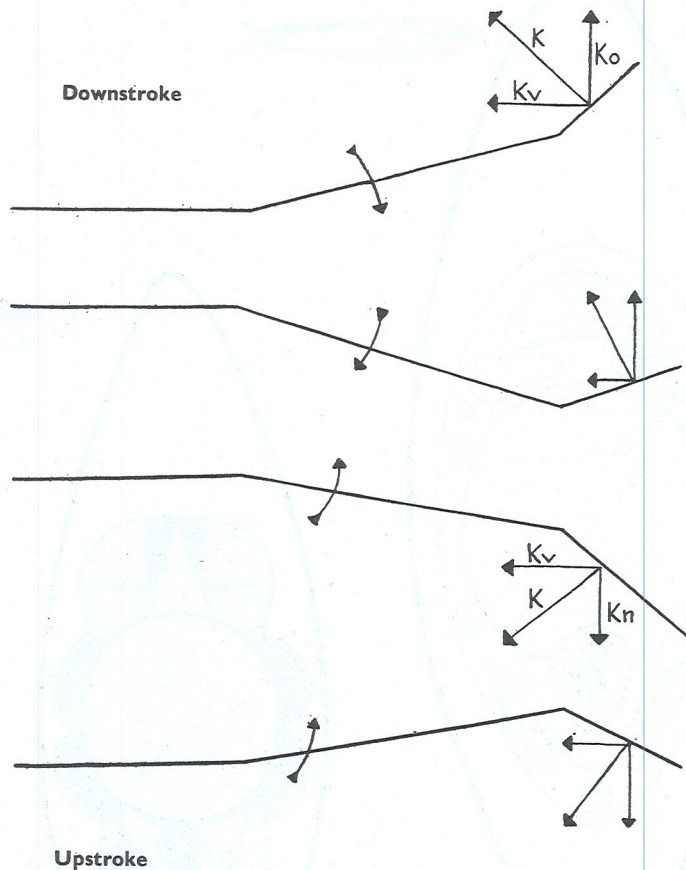


Fig. 4—Forces exerted on the water during the upstroke and downstroke of the tail of a swimming dolphin. From Slijper, 1958.

movements of the flukes against the peduncle of the tail are passively caused by the resistance of the water or whether they are actively effected by contractions of the muscles of the tail. The fact, however, that a special bundle of tendons of the tail muscles runs to the vertebrae of the tail-fin, may serve as an indication that the position of the flukes in relation to the peduncle of the tail is caused, or at least controlled, by contractions of this special part of the musculature.

In its up- and downward movements, the peduncle of the tail meets only very little resistance in the water. One might say this part of the tail cuts the water like a knife because it is laterally compressed and tapers off rather sharply at the upper and lower side. A cross section through the tail shows that this particular shape is caused by high crests of subcutaneous blubber at both the upper and lower side of the tail (Fig. 5).

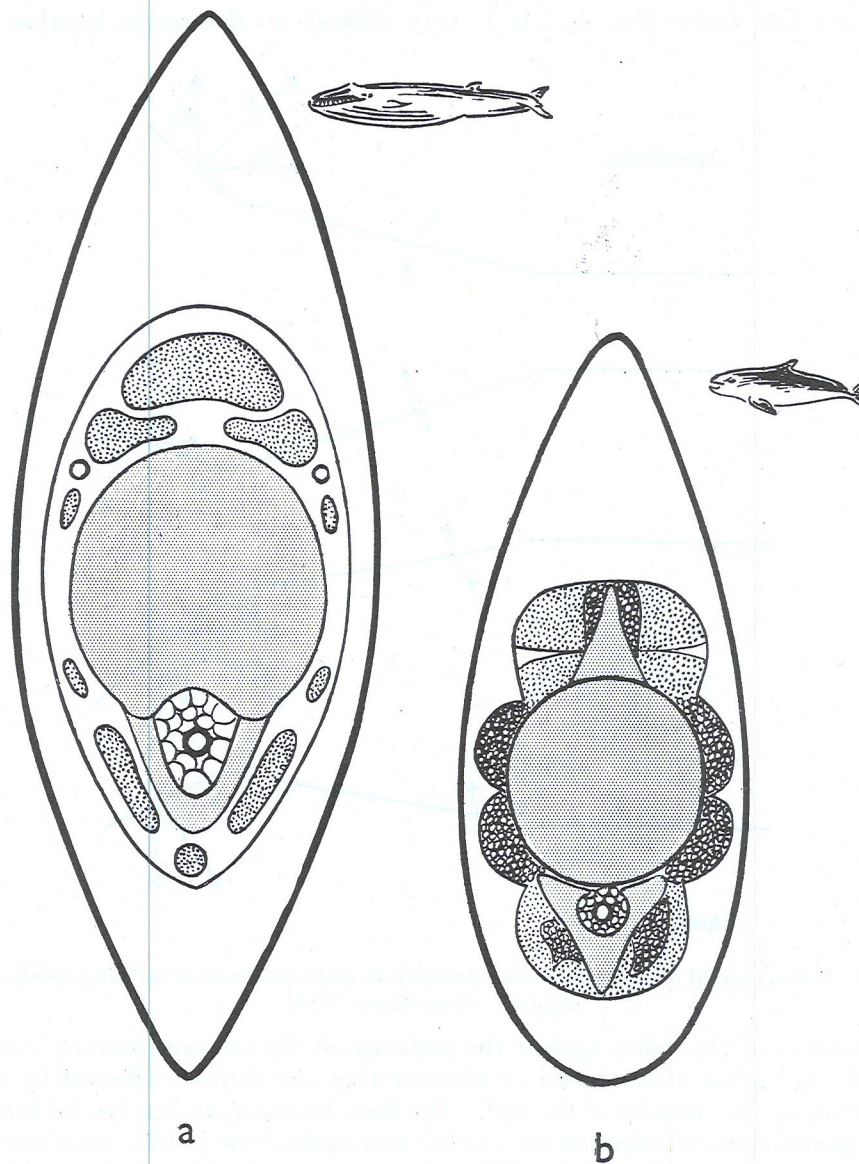


Fig. 5—Cross section through the peduncle of the tail of a Blue Whale (*Balaenoptera musculus* (L.)) (left) and a Common Porpoise (*Phocaena phocaena* (L.)) (right).

The movements described above are seen when the animals swim in a straight line. When they make a turn, lateral movements of the head and tail as well as different movements of the flippers and flukes may be observed. Experiments have shown that the body of the Common Porpoise shows the same mobility and rigidity with regard to the mobility in the horizontal plane (lateral movements) as have been described with regard to the movements in the vertical plane, with this exception, however, that at the base of the flukes there is no special centre of great lateral mobility (Slijper, 1936).

Woodcock (1948) observed that in dolphins swimming at a speed of 20 m.p.h. the tail moved with a frequency of two strokes up and down per second. This is confirmed by Gunther (1949), who recorded 1-2 strokes per second in a Fin Whale (*Balaenoptera physalus* (L.)) swimming at a speed of 10-12 knots.

It is not easy to say what is the swimming speed of whales and dolphins. In the first place there are very great differences between the different species and in the second place a distinction must be made between animals swimming in a sprint at a speed they can maintain only during a few minutes, and those swimming at cruising speed, which they can maintain for hours. A third type of locomotion that is called riding on the bow wave of a ship, is often observed in dolphins. In this case the body of the animal seems to be motionless. The details of this way of swimming are not yet fully known, but it appears to be related to the so-called "surf-riding" of man. Probably the flukes are brought in such position that the animal is propelled by the up-welling water of the bow wave. It has been studied—among others—by Hayes (1953), Woodcock & McBride (1951) and by Scholander (1960).

Right Whales (*Balaenidae*), Grey Whales (*Eschrichtius gibbosus* (Erxleb.)) and Humpbacks (*Megaptera nodosa* (Bonnat.)) appear to be slow swimmers, their cruising speed being about three knots and their top speed about seven knots. Sperm Whales (*Physeter macrocephalus* L.) may show short sprints of 16-20 m.p.h., but their normal speed in most cases does not exceed six miles an hour. Recent observations of Fin Whales (*Balaenoptera physalus* (L.)), that were frightened by the Asdic apparatus of whale catchers, have shown that they could leave the range of this apparatus within a few seconds, demonstrating thereby that they can reach a speed of 30-40 m.p.h. This speed was already known for the Sei Whale (*Balaenoptera borealis* Lesson)) (see Andrews 1914) and it may be supposed that the Blue Whale (*Balaenoptera musculus* (L.)) may also attain this speed. The normal cruising speed of these rorquals as well as of the Minke Whale (*Balaenoptera acutorostrata* (Lacép.)) is 10-15 miles.

Almost the same speed has been observed in dolphins. Several observers (among others Captain Mörzer Bruins; see also Lane 1953 and Gunter 1943) have stated that Common Dolphins (*Delphinus delphis* L.), Bottle-nosed Dolphins (*Tursiops truncatus* (Mont.)), Red Sea Bottle-nosed Dolphins (*Tursiops aduncus* Ehrenberg), False Killers (*Pseudorca crassidens* (Owen)) and some species belonging to the genera *Prodelphinus* and *Steno* can maintain a speed of 15-20 m.p.h. during a fairly long time, even when they do not swim on the bow wave of a ship. According to Backhouse (1960) a sprint of 25 knots has been observed in the Common Dolphin. Freshwater dolphins appear to

be slower. Layne (1958) observed a cruising speed of two miles and a top speed of ten miles in the Boto (*Inia geoffrensis* Blainv.), whereas six miles has been observed in a dolphin of the Indian coastal waters (*Sotalia plumbea* Cuv.).

All these data clearly show that in any case whales and dolphins are able to attain an underwater speed that is much higher than that of an ordinary submarine (six to eight miles). Another very remarkable phenomenon is the fact that on the average the speed of the small dolphins is the same as that of the big whales whose weight is about 1000 times that of their small relatives. In ships of the same type the speed generally increases with the size of the ship. The explanation of the phenomenon was discussed at length at the annual meeting of the British Association for the Advancement of Science in 1949. Especially by the work of Gray (1936; see also Gray & Parry 1948), Kermack (1948) and Hill (1950) it has been shown that the phenomenon might be explained by assuming that the flow of the water along the body of the dolphins is entirely laminar, but that along the body of the big whales it is partly laminar and partly turbulent. It may be supposed, for example, that along the anterior two thirds of the body it is laminar, whereas it is turbulent among the posterior one third. A turbulent flow causes a much higher resistance and consequently a much lower speed than a laminar flow.

It cannot yet be proved that along the body of a dolphin there is indeed an entirely laminar flow of the water, because it has not yet been possible to make experiments with a model that shows the same active motions as the body of a swimming animal. It may be assumed, however, that along such a body the flow differs from that along a rigid or along an only passively movable model. Probably it is entirely laminar. Observations made by Steven (1950) of dolphins swimming in a phosphorescing sea, give a strong indication that an entirely laminar flow indeed occurs. If this is true, it may be further assumed that the difference between the dolphins and the whales is in the first place connected with the length of the body because the longer the body is, the sooner a turbulent flow will arise. In the second place it may also be connected with the shape of the body. The further the greatest girth of the body lies to the anterior, the greater is the possibility that the flow will be turbulent. The greatest girth of the body is found more to the anterior in whales than in dolphins. In the United States of America some people engaged in technical research hold the opinion that the laminar flow may be connected with the way in which the epidermis of Cetacea is attached to the underlying layer of blubber, viz. : by means of very long papillae. With the aid of a silica-gel some models have been constructed, but definite results are not yet available.

LOCOMOTORY ORGANS

The principal locomotory organ of whales and dolphins is the body-axis, i.e. the vertebral column and the spinal muscles of the back and tail. The flippers (pectoral fins) are only used in very slow motion and in steering, but the abdominal musculature and the *levator ani* muscle may assist the muscles on the ventral side of the vertebral column (hypaxial muscles) to a certain degree. The neck is very short (Fig. 6) and has always seven cervical vertebrae. These are highly compressed in the longitudinal direction, and in Right whales,

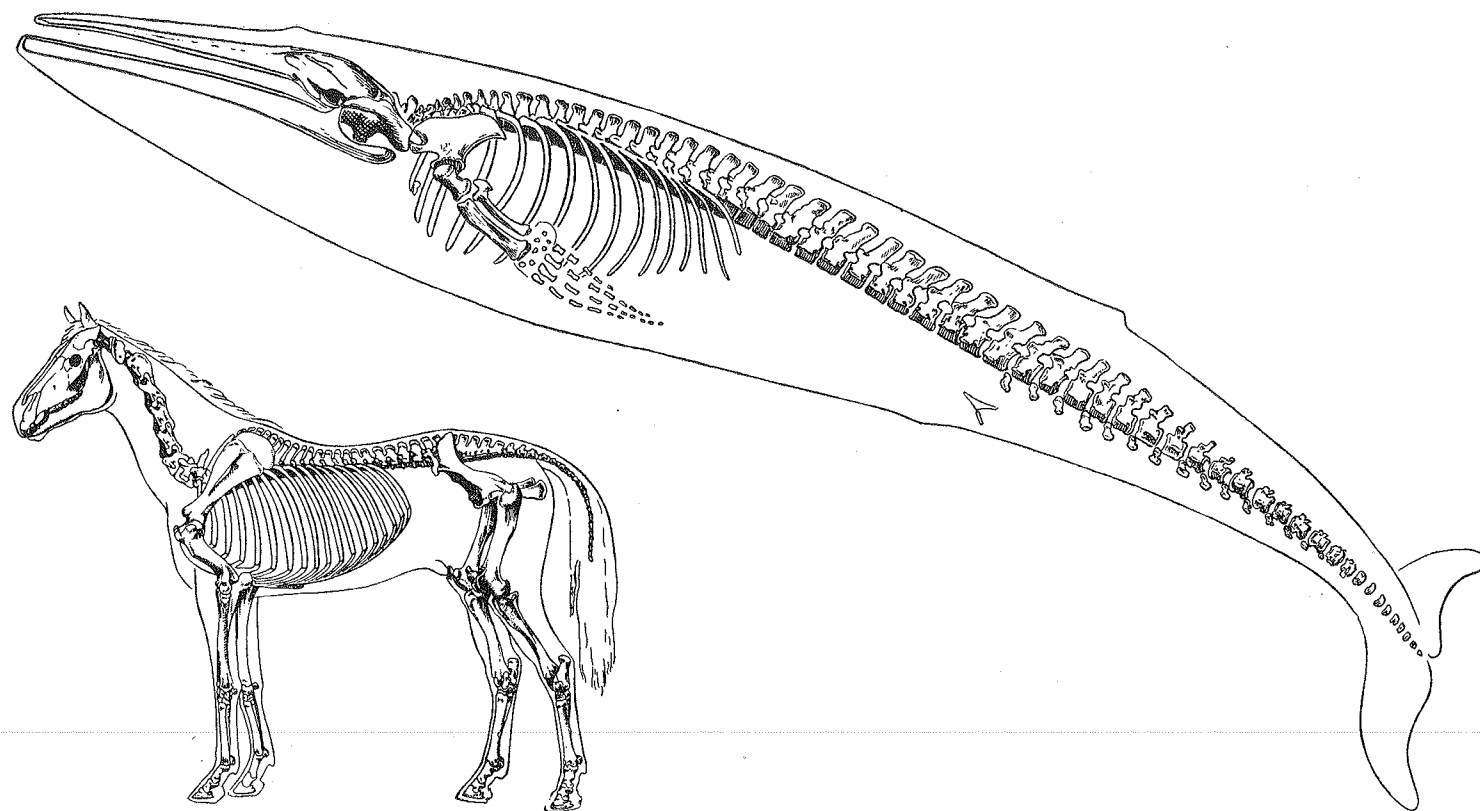


Fig. 6—Comparison of the skeleton of a Blue Whale (*Balaenoptera musculus* (L.)) and a horse. From Slijper, 1958.

dolphins and porpoises they are fully or partly coalesced. Consequently the mobility of the head mainly depends on the occipital joint, which in some dolphins is fairly mobile but which may be restricted in its motion in others, as for instance in the Pilot Whale (*Globicephala melaena* (Traill)). The shortness of the neck and its rigidity are necessary because the propulsive powers of the animal are concentrated in the posterior part of the body-axis.

The number of thoracic vertebrae is almost the same as in terrestrial mammals. They show a very small degree of mobility. The lumbar region is very much lengthened, sometimes by an increase of the number of lumbar vertebrae, sometimes by an increase in length of the vertebral bodies and sometimes by a combination of both phenomena. The same may be observed in the tail. The highest total number of vertebrae is found in the White-beaked Dolphin (*Lagenorhynchus albirostris* Gray) which has 93 vertebrae, but even a Blue Whale with 63 has more vertebrae than a dog, which has 50. A distinct tendency to increase in the number of vertebrae is also apparent when the geologically younger representatives of the different groups of Cetacea are compared with their older relatives. This increase in number of the vertebrae causes an increase in mobility and elasticity of the vertebral column because the amount of cartilage (intervertebral discs) is greatly increased, especially when the vertebral bodies are comparatively thin (short) as for example in dolphins.

There is no sacrum because the rudimentary pelvic bone is not attached to the vertebral column, but the original sacral vertebrae can still be found by determining the nervous roots that are homologous with those leaving the vertebral canal between the sacral vertebrae in terrestrial mammals (plexus pudendus). If the sacral vertebrae are determined in this way, it appears that the first caudal vertebra does not follow immediately on the last sacral. In the Common Porpoise (*Phocaena phocaena* (L.)), for example, there are six so-called postsacral vertebrae.

The first caudal vertebra lies at the level of the anal aperture. All caudal vertebrae—with the exception of those of the flukes—bear at the ventro-cranial side of their bodies a pair of chevron bones (Fig. 6). As with the very long neural spines at the dorsal side of the lumbar and caudal vertebrae and the long transverse processes at their lateral side, so these chevron bones at the ventral side give the muscles a large surface for their origin and a long lever arm for their inserting tendons. The principal task of the body-axis in whales and dolphins is not to carry the body-weight, as in terrestrial mammals, but to serve as a surface for the attachment of the locomotory muscles.

The musculature of the Cetacea is very well developed. In the big Blue Whale (*Balaenoptera musculus* (L.)) the total weight of the musculature is about 40 tons, i.e. 40 per cent of the body weight (weight of the skeleton 17 per cent), and in some other whales and dolphins it may be even about 50 per cent. The musculature is characterized by the fact that the muscles of the neck, the trunk and the tail are completely fused. Consequently each of the three big epaxial muscular systems is represented by one single functional unit ranging from the occiput to the tip of the tail. Apart from the muscles at the ventral side of the cervical vertebrae, the hypaxial muscula-

ture consists also of a practically indivisible muscular mass, ranging from the last four or five ribs to the tip of the tail. It originated from the fusion of the psoas-muscles (which are not attached to the rudimentary pelvic bone) with the musculature of the ventral side of the tail. The components may still be distinguished by their innervation, and this innervation also shows that the original border between the muscles of the trunk and those of the tail (epaxial and hypaxial) lies at the level of the anal aperture and the first chevron bone. All these muscular systems show a distinct tendency to develop long muscular and tendinous fibres, but a certain number of short fibres can still be distinguished. The presence of long muscular fibres means that, especially in the tail, large excursions can be made.

In the toothed whales the *iliocostalis* muscle expands as a broad sheet over the lateral surface of the ribs, but in whalebone whales the thoracic part is comparatively narrow. The lumbar part, continued in the tail as the *intertransversarii caudae dorsalis et ventralis*, is a comparatively narrow muscular band embracing the outer part of the transverse processes. This muscle is not very strongly developed but its effect is highly enlarged by the lever-arm of the long transverse processes. A part of the lumbo-dorsal fascia separates the *iliocostalis* from the adjacent spinal muscles, but a fascial separation between the *longissimus* and the *transverso-spinalis* is only present in the tail.

In terrestrial mammals the majority of the fibres of the *longissimus dorsi* show an arrangement around the diaphragmatic (or anticlinal) vertebrae (Fig. 7; Slijper 1946). Most of the fibres originate from the pre-diaphragmatic vertebrae and their ribs; they are inserted into the neural spines and the mammillary processes of the postdiaphragmatic vertebrae. In ungulates there are strong sacral attachments. Because of the different type of mobility of the vertebral column in Cetacea, the *longissimus* complex of these animals originates at the occiput, at the ribs and at the transverse processes and neural arches of all thoracic, lumbar and caudal vertebrae as far back as the middle of the tail. There are three systems of inserting tendons, viz. (Figs. 8 and 9): 1. Superficial tendons running to the summits of the neural spines from the first lumbar vertebra to the vertebra that lies at the junction of the peduncle of the tail and the flukes. 2. Deep tendons running to the mammillary processes from the first thoracic vertebrae to the junction of the tail fin and the peduncle of the tail. 3. A special system of long tendons inserted into the vertebrae of the flukes.

In terrestrial mammals the fibres of the *transverso-spinalis* show the same arrangement around the diaphragmatic vertebra as those of the *longissimus*. The fibres of the *semispinalis* and *spinalis* originate at the neural spines of the prediaphragmatic vertebrae. They are inserted into the mammillary processes and the neural spines respectively of the postdiaphragmatic vertebrae (Fig. 7). In all Cetacea there is an undifferentiated *transverso-spinalis*, reaching from the skull or the first cervical vertebrae to the junction of the tail and the flukes. In the neck and thorax it consists almost entirely of *multifidus*- and shorter fascicles, but in the caudal part of the thorax the number of *semispinalis* fibres increases and in the lumbar and caudal region there may be even very long muscular fascicles and tendons. All tendons are inserted into the mammillary

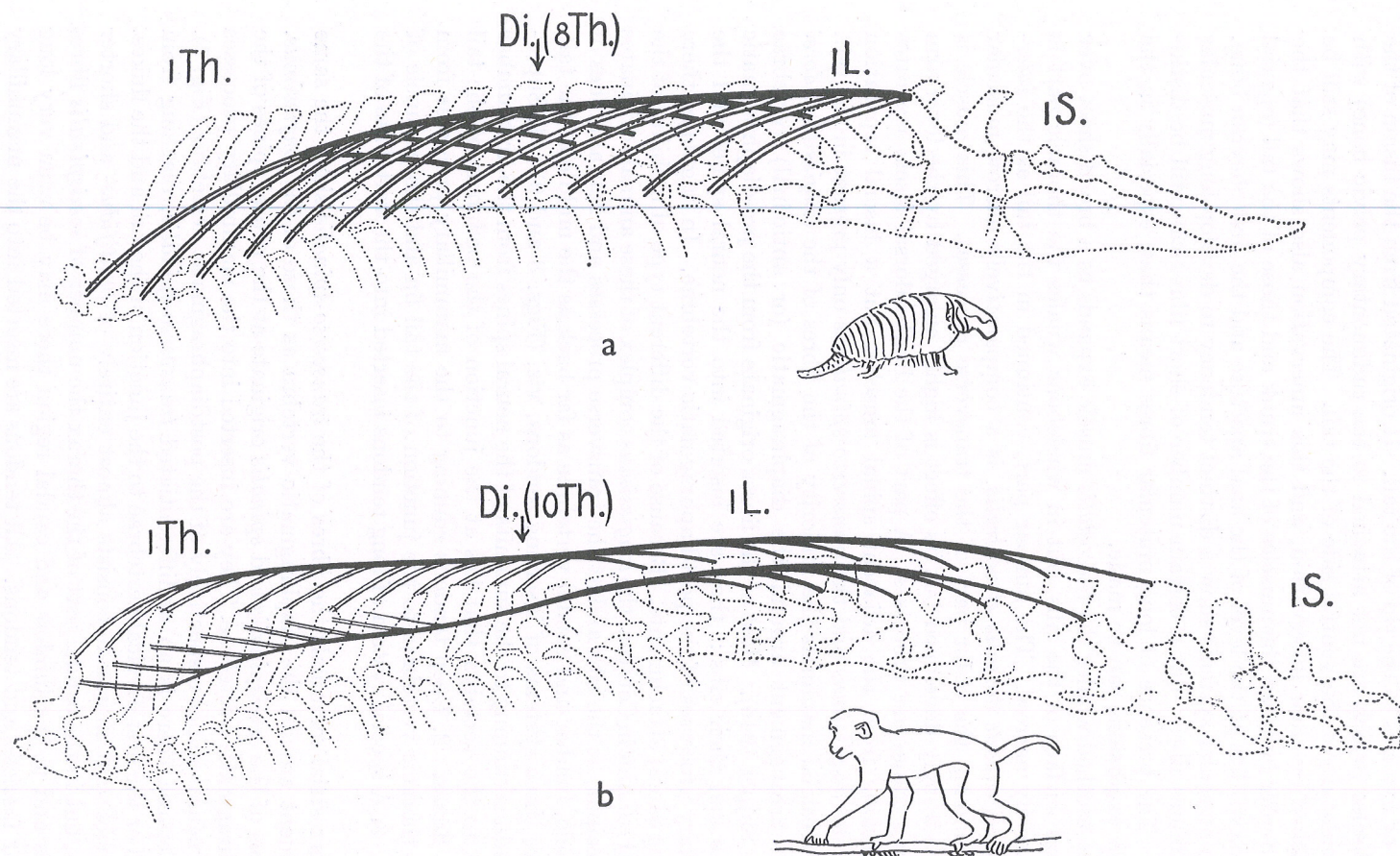


Fig. 7—Above : Schematic drawing of the structure of the *longissimus dorsi* muscle in the Peba-Armadillo (*Dasypus novemcinctus* L.). Below : Schematic drawing of the structure of the *transverso-spinalis* muscle in the Macaque (*Nemestrinus nemestrinus* (L.)). From Slijper, 1946.

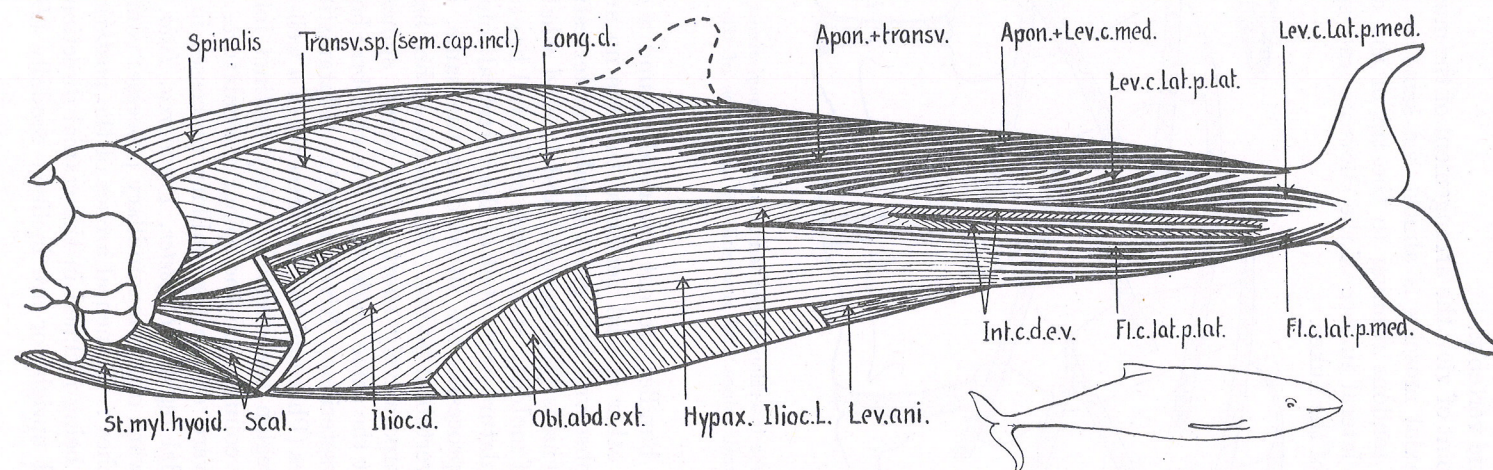


Fig. 8—Musculature of the trunk and tail of the Common Porpoise (*Phocaena phocaena* (L.)). *Apon.* = superficial tendons of *m. longissimus dorsi*. *Lev. c. lat.* = tendons of *longissimus* complex inserted into mammillary processes. *Lev. c. lat. p. med.* = tendons of *longissimus* complex inserted into the vertebrae of the flukes.

processes (Fig. 9). There are no *spinalis* fibres and there is not the slightest relation to a diaphragmatic vertebra.

From the functional point of view the arrangement of the muscular fascicles and tendons of the hypaxial muscles is almost the same as in the epaxial musculature. There are tendons running to the tip of the chevron bones, tendons inserted into the lateral surface of the chevrons and special tendons running to the vertebrae of the flukes.

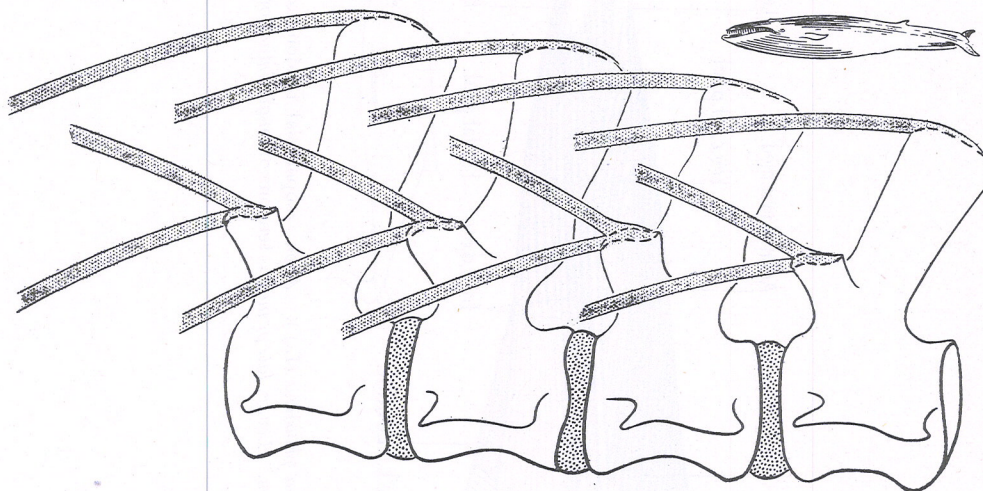


Fig. 9—Schematic drawing of the insertion of the tendons of the *longissimus* complex and the *transverso-spinalis* into the neural spines and mammillary processes of the posterior lumbar vertebrae in a baleen whale.

Because the muscular bundles are not arranged around a diaphragmatic vertebra nor around any other special vertebra, there is no anticlivity of the neural spines, as can be observed in a great number of terrestrial mammals. In *Archaeocetes*, baleen whales (*Mystacoceti*) and beaked whales (*Ziphiidae*) the presence of a centre of mobility at the base of the tail has no influence on the structure of the musculature or on that of the vertebral column. In these animals all mammillary processes are situated at the same, comparatively short, distance from the vertebral bodies. All neural arches have almost the same length and are comparatively short. All neural spines are inclined backward and make about the same angle with the vertebral bodies (Fig. 10).

In sperm whales (*Physeteridae*), River dolphins (*Platanistidae*), dolphins (*Delphinidae*) and porpoises (*Phocaenidae*) the presence of a well-marked centre of mobility in the anal region has exerted a very distinct influence on the structure of the vertebral column and the spinal musculature. Some species show only a shifting upward of the mammillary processes in the posterior lumbar and anterior caudal region (*Physeter*, *Pseudorca*, *Inia*, *Stenodelphis*), others show a shifting upward of the mammillary processes combined with an anticlivity of the neural arches: the neural arches of the posterior lumbar and anterior caudal vertebrae being inclined in the cranial direction, whereas the other neural arches stand upright or are inclined caudally (*Delphinapterus*,

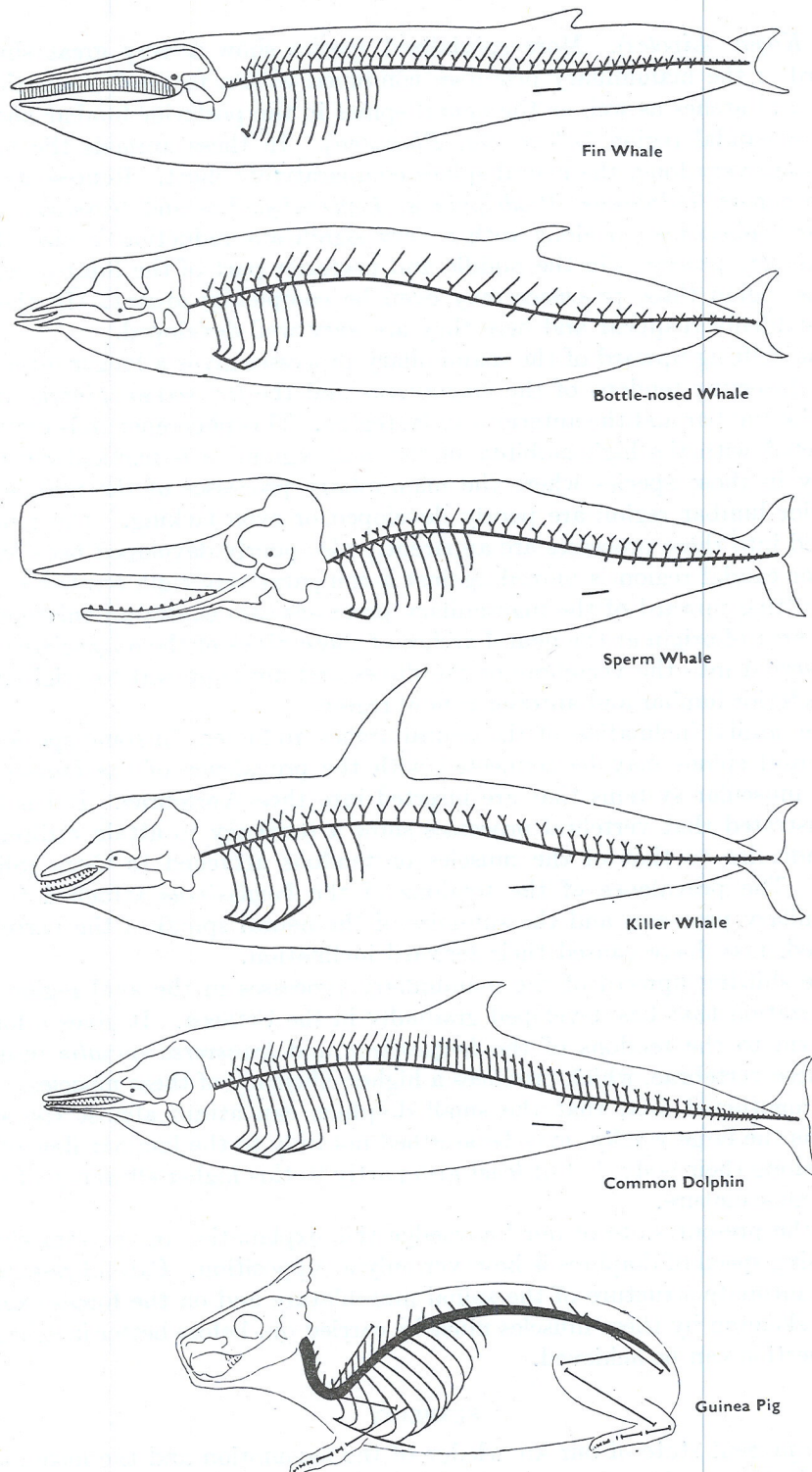


Fig. 10—Schematic drawing of the skeleton of five Cetacea, to show the different types with regard to the position of the mammillary processes and the direction of the neural arches and neural spines. Fin Whale (*Balaenoptera physalus* (L.)), Bottle-nosed Whale (*Hyperoodon ampullatus* (Forster)), Sperm Whale (*Physeter macrocephalus* L.), Killer (*Orca orca* (L.)), Common Dolphin (*Delphinus delphis* L.). Below: Guinea Pig, a typical terrestrial mammal. From Slijper, 1958.

Orca, *Kogia*, *Lipotes*). More specialized species show a very great shifting upward of the mammillary processes combined with a forward inclination of the neural arches as well as the neural spines in the posterior lumbar and the anterior caudal region (*Platanista*, *Phocaena*). In these animals the neural arches are very long, the neural spines comparatively short. Representatives of the genera *Delphinus*, *Prodelphinus*, *Lagenorhynchus* and *Grampus*, show the same phenomenon along with a very significant reduction in size of the mammillary processes in the middle and posterior part of the lumbar region. In this region these processes may even be completely absent. In the tail they suddenly reappear and here they are very well developed.

The shifting upward of the mammillary processes gives a longer lever arm to the inserting tendons of the *longissimus* and the *transverso-spinalis* in the posterior lumbar and the anterior caudal region. This phenomenon is certainly connected with the high mobility of the anal region, as is particularly noteworthy in those species where the mammillary processes of the middle and posterior lumbar region are poorly developed or even lacking. The tendons inserted into these processes are apparently also poorly developed because the anterior caudal region is moved against a comparatively rigid lumbar region. The shifting upward of the mammillary processes also causes an enlargement of the area of origin at the neural arches of those fibres of the *longissimus* that are inserted into the vertebrae of the flukes and are supposed to originate in the posterior lumbar and anterior caudal region.

The cranial inclination of the neural arches and even (in some species) of the neural spines may be connected with the prevalence of the *longissimus* in the muscular systems that are inserted into these vertebrae. It has been demonstrated that vertebral processes show a tendency to attain a direction perpendicular to that of the muscles or tendons attached to them (Slijper 1946). The prevalence of the tendons of the *longissimus* attached to the mammillary processes and the summits of the neural spines of the vertebrae involved, may have caused their forward inclination.

The shifting upward of the mammillary processes in the anal region is a specialization that has developed gradually in the Cetacea. It gives a longer lever-arm to the tendons of the *longissimus* and *transverso-spinalis* inserted into these vertebrae, which produces a higher efficiency of these muscles. The above-mentioned fact, that the small dolphins can attain almost the same speed as the large whales, may be ascribed not only to the laminar flow of the water along their body, but at least also partly to this higher efficiency of their spinal musculature.

In the present state of our knowledge this explanation of the remarkable swimming speed of dolphins is however only a supposition. Careful researches on the intimate structure of the spinal musculature and on the forces exerted on the skeleton by these muscles must be carried out before better insight into this question can be achieved.

SUMMARY

The present state of our knowledge of the locomotion and the locomotory organs in Cetacea is reviewed.

The results of experiments on the flexibility of the body of the Common Porpoise have been confirmed by films of swimming Bottle-nosed Dolphins and a Pigmy Sperm Whale.

Cruising speed and maximum speed appear to be almost the same in the small dolphins as in the big whales. This phenomenon can be explained by assuming that the flow of the water along the body of the dolphins is wholly laminar, but that it is partly turbulent in whales. Another plausible explanation is furnished by the supposition that in dolphins the development and the insertion of the spinal musculature shows a higher degree of efficiency than in whalebone whales, as may be deduced from the shifting upward of the mammillary processes of the posterior lumbar and the anterior caudal region in dolphins.

The development of the muscles and the insertion of the tendons is adapted to the presence of two centres of extreme mobility, viz. : at the anal region and at the junction of the peduncle of the tail and the flukes.

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GENERAL DISCUSSION

Chairman : Professor Sir James Gray, C.B.E., F.R.S.

A speaker asked if the function of the "melon" on the porpoise and dolphin could be to provide a lift of the head, counteracting the apparently excessive power of the upstroke in the tail.

Dr Slijper doubted the asymmetry of the power stroke, pointing out that hypaxial and epaxial musculature were almost equally developed.

Dr Manton mentioned Dr Hill's contention that inertia could be an important factor in swimming speeds. The weight ratio of whale to porpoise was 1000 to 1, and the greater inertia of the larger animal, leading to a tail beat which is about one tenth as fast in the whale, could be responsible for the relatively slower speed of this animal. In smaller animals the inertia effect is apparently negligible. The speed of running of diplopods where the movement of the limbs is not very fast, is almost proportional to their length, over a weight range of 6000 to 1. Centipedes on the other hand do not increase their speed in proportion to their length.

Dr Slijper doubted whether the frequency of beat in the large whales differed so much from that in the porpoise, and pointed out that in terrestrial mammals, the large animals were capable of much higher speeds than the small ones.