XIX.—ON THE DEVELOPMENT OF THE CETACEA, TOGETHER WITH A CONSIDERATION OF THE PROBABLE HOMOLOGIES OF THE FLUKES OF CETACEANS AND SIRENIANS.*

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INTRODUCTORY.

The acquisition of materials for the prosecution of the study of Cetacean development is attended with difficulties, and the student who is fortunate enough to have access to a rare series of even pretty well advanced embryos, measuring from 1 inch up to 5½ inches long, may well consider how precious and important such materials are at this time, when the study of the development of living forms has taken such a high place as a part of the proper scientific method to be applied by the naturalist to the resolution of questions of affinity and the genesis of extreme structural modifications.

The following notes, interspersed as they will be with reflections

*A very brief and imperfect sketch of the contents of this paper has appeared under the following title: "On the probable origin, homologies, and development of the flukes of Cetaceans and Sirenians." (Am. Naturalist, May, 1885, pp. 515–519.) The development of the mammary glands has also been more fully discussed by me elsewhere, viz, in a paper entitled, "On the development of the mammary glands and genitalia of the Cetacea." (Bull. United States Fish Commission, Vol. V, 1885.)

upon the significance of this or that peculiarity of the external or internal conformation of the different parts of these creatures, as compared with similar or homologous parts in normal mammalia, and in the aquatic *Sirenia* and amphibious *Pinnipedia*, it is hoped may help us to better understand the question of the affinities of these organisms, and perhaps afford us a slightly clearer insight into the method of phylogeny, as its obscure lines converging backwards in time, are here and there brought out a little more distinctly, by some of the conclusions which may be drawn from anatomical and ontogenetic investigations. If the view here advocated, that the flukes are probably the degenerate homologues of hind feet (not the homologues of the whole hind limb, as was held by Gray and even earlier authors) at first seems improbable, such a view may, I venture to think, impress the fair-minded student as being a little nearer the truth than the comparatively modern assumption universally sustained up to the present year by the most eminent of living morphologists, amongst whom must be named Huxley, Flower, Claus, Owen, and Parker, that the hind limbs of *Cetacea* have been totally suppressed or atrophied outwardly, thus leading to the avowed or tacitly admitted conclusion that *the flukes, like the dorsal fin, are appendages which have been secondarily acquired or added to the morphological combination presented by the Cetacean organization*, and are not to be considered as representing, as seems to me far more probable, the last degenerate vestiges of the distal portions of primordially functional hind limbs.

What has led me to the preceding conclusions are the general laws which seem to preside over limb development within the limits of the *Vertebrata*, together with the results of a consideration of the effects of certain degenerative tendencies accompanied by functional changes and adaptations manifested in definite directions, as seen in all Cetaceans, Sirenians, and *Pinnipedia*.

These views have been reached quite independently of any which have been previously expressed to the same or similar effect by other authors, and it was not until I had fully thought over the problem, with such evidence as was then in my possession, that I ventured to express my conclusions to my friend, Professor Gill, who at once agreed with me in the main, and who then stated that he had actually published an opinion upon the subject in a lecture* delivered in the winter of 1882. Professor Gill has also been kind enough to write down for me the following statement of his views: "These characteristic structures are in my opinion derived from greatly hypertrophied integuments of hind limbs analogous to such as are developed, for instance, to the hind limbs of the eared seals, while the osseous elements have been inversely atrophied, pulled forward, and reduced to supports for muscles connected with the organs of generation."

* Scientific and Popular Views of Nature Contrasted, a lecture delivered in the National Museum, March 11, 1882, pp. 10–11. Washington, 1882, Judd & Detweiler.

It now remains for me to present the data and the conclusions to be drawn therefrom in support of the hypothesis stated at the outset, and in order to render the evidence as conclusive as possible it will be necessary to consider the subject under discussion, first, in relation to the organization of the adult whales, compared with that of the Pinnipedia; secondly, in relation to the modes of development of the marine and land mammals, entering into the discussion of special sets of structures and their bearings upon the questions involved.

I.—The contrasts between the marine, amphibious, and terrestrial mammalia.

(1) *External form.*—As remarked by Huxley, in the *Cetacea* "the form of the body is still more fish-like than in the Sirenia." This is a trait especially well marked in the existing genera *Physalus* and *Leucorhamphus*, in which the caudal peduncle is vertically expanded as in fishes, with high carina on the dorsal and ventral aspects. This fish-like physiognomy is intensified by the development of the median dorsal integument into a rigid fin-like integumentary fold, filled up with tough non-contractile connective tissue, and with adipose cells filling in the meshes between the fibers. There is a superficial layer of very tough fibers just under the integument, which runs parallel with the anterior sloping border of the fin. The medullary fibers are for the most part disposed horizontally and constitute the bulk of its middle or central substance. Blood-vessels, and probably nerves, enter the base of the fin, and transverse its medulla in the plane of the vertical median line of the body, not being evident superficially.

Beyond their outward resemblance they have no morphological likeness to the mobile dorsal fins of fishes, which are actuated by paired muscles derived from the embryonic metameres.

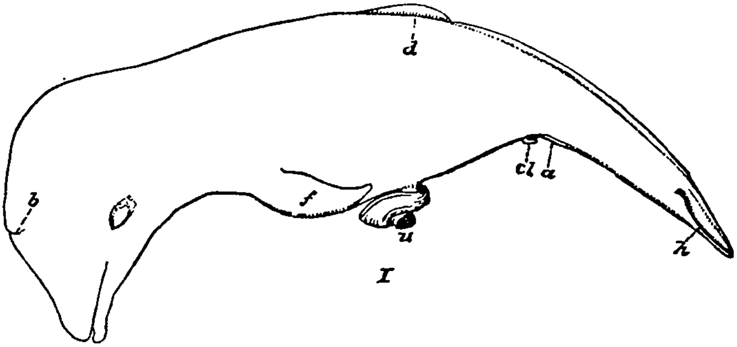
This fin is also of less morphological importance in the organization of the *Cetacea* than the flukes, for, while the latter are never wanting in any known form, the dorsal fin is absent in *Balæna*, *Rhachianeotes*, *Agaphelus*, *Neomeris*, *Beluga* and in all Sirenians; rudimentary, or only present as a ridge or as a hump, as in *Megaptera*, *Physeter*, *Inia*, *Leucorhamphus*, *Platanista;* and moderately developed in *Berardius*, *Orcella*, *Kogia*, *Physalus*, and *Sibbaldius*. These facts indicate that the dorsal fin is physiologically of subordinate importance in comparison with the flukes.

It also begins to develop in the embryo only after the flukes are considerably advanced, thus showing that it is an organ which has been acquired after the latter. In some forms there is a carina extending forwards in the embryo as far as the front of the permanent dorsal fin. It is probably by hypertrophy of the anterior part of this carina, which is really a mere integumentary fold, that the dorsal fin of adult cetaceans has been developed.

The fusiform, head, body, and tail combined, is obviously the result of extensive modifications of the original type from which the existing cetaceans have descended. It will be observed that the central axis of the head, trunk, and tail in adult cetaceans, as in fishes, are continuations of each other, that is, the head is not bent downward on the neck, and the latter thrown upwards at an angle to the trunk, and the tail bent downward as in other Mammalia; that this was not the original form of the cetacean body seems to be supported by considerable embryological evidence.

(2) *Affinities of Cetaceans.*—Huxley, with his usual insight into the probable relationship existing between living forms, holds to the opinion that the *Phocodontia* (*Zeuglodon*, &c.), constitute the connecting link between the existing *Cetacea* and the aquatic *Carnivora*, their cervical vertebræ being free and unanchlylosed. The nasal bones, though abbreviated, are longer than those of any other Cetacean; consequently the external nareal opening was more nearly terminal and normal in position than in existing forms. "The scapula appears to have had a spine and acromion like that of manatee." "The humerus is compressed from the side, and has true articular faces upon its distal end, although they are of small size." It is, consequently, to be inferred that there was greater freedom of motion of the antebrachium upon the brachium, and that the flexor and extensor muscles of the forearm were better developed than in the existing species. Others are inclined to doubt the fact that the elbow-joint of *Phocodontia* possessed greater mobility than that of the existing whales. The molar teeth of the *Zeuglodontia* or *Phocodontia* also resemble those of certain Pinnipeds more than they do the posterior portion of the series in any existing Cetaceans.

The embryological evidence is quite as conclusive as the paleontological in favor of the idea that the extremely specialized existing whales and porpoises have descended from at least amphibious, if not terrestrial four-footed carnivorous mammals. As in the embryo of the walrus, nearly 3 inches long, Fig. III, the young porpoise, Figs. I and II, its



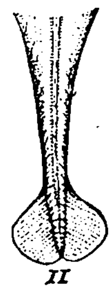


FIG. I.—Female fœtus of some Delphinoid form, from the side, natural size. (N. M. coll. 68-73. Locality not known.

FIG. II.—Tail of the same seen from above.

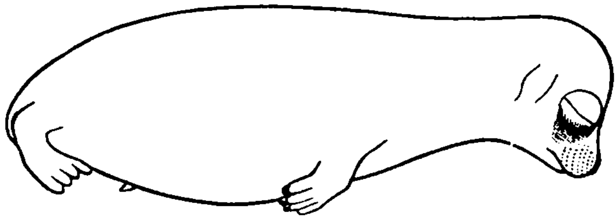


FIG. III.—Fœtal walrus from the side, natural size. After Allen, Proc. Acad. Nat. Sci., Phila., 1880, p. 38. From a specimen obtained by Dr. I. I. Hayes.

head bent downward at an angle with the trunk, and there is a perceptible neck or cervical constriction, indicating, as it seems to me, the affiliation of the two types with each other by descent from a common stem-form in which the head was differentiated from the body by a neck. This conclusion is still further supported by the pronounced fusiform shape of the neck, trunk, and tail combined, as seen in both types of embryos.

The external genitalia are far in advance of the insertion of the hind limb in the embryo walrus when compared with other embryo mammals, as, for example, with the cat, Fig. 14, Plate I, where the external genitalia are visible between the hind limbs instead of in front of them on the median line. It would thus appear that the acquisition of the fusiform or fish-like body so characteristic of *Cetacea* and *Pinnipedia* has entailed a number of changes or alterations in the morphological relations of contiguous parts.

This is shown very forcibly in the development of the tail, which has actually been hypertrophied in the *Cetacea* if the hypothesis that they have had a four-footed ancestry is correct. The tail of some of the existing Cetaceans contains about the same number of vertebræ as that of the sea-otter, *Enhydris*, but the extent to which its vertebræ and muscles have been hypertrophied in the former is nowhere approached within the limits of the *Mammalia*. None of the seals appear to have as many caudal vertebræ as the otters or *Cetacea*, and in the living *Pinnipedia* there is some evidence of caudal degeneracy which has been accompanied by another process, namely, the inclusion of more than half of the caudal segments of the spinal column by the adjacent parts and the integument, so that only the very short extremital portion of the tail is apparent externally.

In *Histriophoca* there are 18 caudals, in the fur seal 7. In many cetaceans they may somewhat exceed 25, including the sacrals, and may even number 35 when the latter are included in the estimate. In *Castor* there are 23, but in this case the segments are depressed and the transverse processes are greatly developed. *Enhydris* has 20 caudals, 24 with sacrals, with only feeble transverse processes as compared with those in the tail of *Castor*, where they are probably dependent upon the special function of the tail for their pronounced development. In the

Cetacea, the transverse and vertical processes (neural and hæmal arches) reach a more nearly equal development respectively, but they are well marked to nearer the end of the caudal series of segments than in other mammals, obviously in correlation with the subdivided tendons and penniform muscular slips into which the vast caudal musculature is broken up in these animals.

(3) *Translocation and inclusion of the hind limbs, and their degeneracy.*—Upon comparing the relation of the hind limbs to the tail in *Fissipedia, Pinnipedia*, and *Cetacea*, certain very striking facts are brought to light, the most important being that the limbs grow out and are progressively pushed backwards distally, in the series included by two of the above-mentioned groups, so that while the proximal parts, such as the pelvis and femur, retain their normal position in relation to the sacral region of the spinal column, the bones of the crus and foot are carried backwards, the proximal parts being involved by the contiguous soft parts and lost to sight externally.

This view it will be seen receives support upon comparing the position of the hind limbs of an embryo cat (fig. 14, pl. I) with that of the walrus (Fig. III). While it must be borne in mind that the tail of the walrus has undergone considerable degeneration, the cat has retained the primordial extension of the caudal appendage, but the tail even in this last instance has suffered degeneracy in volume or rather in diameter, and represents a condition which is far more rudimentary than even in the *Reptilia*, caudal degeneracy having apparently begun in the latter and *Amphibia*, unless we except the extremely specialized gephyrocercal fishes, such as *Mola*. The tail of vertebrates in reality represents a part of the body from which the body cavity and digestive canal has retreated forwards, for in all forms, the chorda, medulla spinalis, and mesenteron are at some stage practically conterminous posteriorly.

But even when we leave out of consideration the fact of caudal degeneracy, there is a residuum of other facts indicating that the limbs of pinnipeds have had their proximal parts included and that even in the embryo there is no joint of the leg visible outwardly except the ankle. This has carried the point where the embryonic hinder limb-fold first appears, farther back in relation to the pectoral limb than in the embryos of normally-developing *Carnivora*, of which the cat is the type. While the femur is directed forwards in the Pinnipeds, the crus and the foot are extended backwards, so that the legs become tied backwards, so to speak, by the integument and flesh in front of them. In the cat's embryo the joints of the limbs externally apparent, in an even less advanced one than that of the walrus here figured, are the ankle and knee joints of the hind limb, and there is nothing of that backward inclination of the proximal part of the limb as in the walrus and other Pinnipeds.

It is this backward inclination and inclusion of the proximal parts of the hind-limbs of pinnipeds which gives them an apparently longer trunk, a relatively wider interval between the fore and hind pairs of limbs. The backward inclination of the proximal ends of the hind limbs and their inclusion, together with the anterior part of the tail within or below the integumentary organs, also favors the development of the fish-like or fusiform aspect of the backwardly tapering thorax and abdomen, which will be intensified just in proportion as this process is carried to an extreme, as it seemingly has been in the *Cetacea*.

To generalize from what the foregoing data tend to show, it may be said that, in normal *Carnivora* there has been no tendency to include the femoral and crural parts of the hind limbs together with the tail, whereas there has been such a tendency in the Pinnipeds, leaving only the tarsal and pedal parts of their hind limbs exserted, so that the primary horizontal limb-folds have in consequence grown out farther back than in the embryos of terrestrial mammalia. In other words, the exserted terminal part of the hind limb of the pinnipeds has been translocated backwards in consequence of the process just described; which involves the inclusion of the proximal parts of the limb; this is the reverse of the process involved in effecting the translocation of the pelvic limbs of physoclist fish embryos, in which the shifting is sudden and occurs in another way, as may be gathered from my notice* calling attention to this singular phenomenon. The type which presents the morphological differentiation, and which would constitute it a connecting link bridging the condition between the existing position of the representatives of the hind feet, viz, the flukes in whales and the pedes of pinnipeds, has been entirely lost, yet there are existing data which support the conclusion that the flukes represent integumentary limb-folds, which have, by the method of development now known to be operative in the case of pinnipeds, been led to grow out ontogenetically far remote from and posterior to their archaic position on the sides of the tail instead of on the sides of the body. The flukes of whales, which I chose to regard as the representatives of hind-feet, according to hypothesis, have been translocated backwards over a wide interval, but no more extensively than have the pelvic limbs of certain extreme forms of physoclist fishes when that pair in the latter is compared in respect to position with its archaic place in the normal and unspecialized Physostomes.

(4) *Flower on the affinities of the Cetaceans.*—While Flower has not committed himself so far as to specify precisely the form from which the *Cetaceans* have been evolved, it seems to the writer that the difficulty of deriving their type of tail from that of a seal-like form which seems to him so insuperable is not so much so as he thinks, but I will let him speak for himself:

* On the translocation forwards of the rudiments of the pelvic fins in the embryos of physoclist fishes. (Am. Naturalist, XIX, 1885, pp. 315–317.)

"The steps by which a land mammal may have been modified into a purely aquatic one are clearly indicated by the stages which still survive among the *Carnivora*, in the *Otariæ* and in the true seals. A further change in the same direction would produce an animal somewhat resembling a dolphin, and it has been thought that this may have been the route by which the cetacean form has been developed. There are, however, great difficulties in the way of this view. If the hind limbs had ever been developed into the very efficient aquatic propelling organs they present in the seals, it is not easy to imagine how they could have become completely atrophied and their function transferred to the tail. It is more likely that the whales were derived from animals with long tails, which were used in swimming, eventually with such effect that the hind limbs became no longer necessary. The powerful tail, with its lateral cutaneous flanges, of an American species of otter (*Pteronura Sandbachii*) may give an idea of this member in the primitive Cetaceans."*

Professor Flower has since reiterated the preceding views with more emphasis, as follows:

"One of the methods by which a land mammal may have been changed into an aquatic one is clearly shown in the stages which still survive among the Carnivora. The seals are obviously modifications of the land Carnivora, the Otariæ or sea lions and sea bears, being curiously intermediate. Many naturalists have been tempted to think that the whales represent a still further stage of the same kind of modification. So firmly has this idea taken root that in most popular works on zoology, in which an attempt is made to trace the pedigree of existing mammals, the Cetacea are definitely placed as offshoots of the Pinnipedia, which in their turn are derived from the Carnivora. But there is to my mind a fatal objection to this view. The seal, of course, has much in common with the whale, inasmuch as it is a mammal adapted for an aquatic life, but it has been converted to its general fish-like form by the peculiar development of its hind limbs into instruments of propulsion through the water; for though the thighs and legs are small, the feet are large, and are the special organs of locomotion in the water, the tail being quite rudimentary. The two feet applied together form an organ very like the tail of a fish or whale, and functionally representing it, but only functionally, for the time has, I trust, quite gone by when the Cetacea were defined as animals with the 'hinder limbs united, forming a forked horizontal tail.' In the whales, as we have seen, the hind limbs are aborted, and the tail developed into a powerful swimming organ. Now it is difficult to suppose that, when the hind limbs had once become so well adapted to a function so essential to the welfare of the animal as that of swimming, they could ever have become reduced and their action transferred to the tail. The animal must have been in a too helpless con-

*W. H. Flower, Article Mammalia, Encycl. Brittan., 9th ed., 4to, vol. xv, p. 394. Edinburgh: Black, 1883.

dition to maintain its existence during the transference if it took place, as we must suppose, gradually. It is far more reasonable to suppose that whales were derived from animals with large tails, which were used in swimming, eventually, with such effect that the hind limbs became no longer necessary, and so gradually disappeared. The powerful tail, with lateral cutaneous flanges, of an American species of otter (*Pteronura Sandbachii*), or the still more familiar tail of the beaver, may give some idea of this member in the primitive Cetacea. I think that this consideration disposes of the principal argument that the whales are related to the seals, as most of the other resemblances, such as those in the characters of their teeth, are evidently analogous resemblances related to similarity of habit."*

(5) *Another view of the phylogeny of cetaceans.*—I do not assert that the hinder limbs are united to form a forked horizontal tail; what I do assert is that, in consequence of the rotation and extension backwards of the hind limbs of a type in which the hind limbs were thus thrown back parallel with the tail and included by the integument of the body, these limbs were rendered more or less immobile, as a result of which the limb skeleton, its muscles and the pelvis have atrophied, leaving, however, the integuments of the feet in a posterior position on either side of the end of the tail as the rudiments of flukes. This, I submit, is to me a far more reasonable hypothesis than any which derives the flukes from an entirely different source, viz, the cutaneous flanges of the tail of the sea-otter.

The argument that "the animal must have been in a too helpless condition to maintain its existence during the transference if it took place, as we must suppose, gradually," can be met by citing the seals themselves, animals which certainly are somewhat helpless on land, yet remarkably graceful and active in the water. The *Cetacea*, on the other hand, are quite helpless on land, but certainly not in the water, the medium in which this gradual transference of function must have occurred after the hind limbs became more and more useless as a means of progression on land, when such a Protocetacean form would not again venture upon the latter. It is thus rendered evident that Professor Flower's arguments are not as insuperable as they at first appear.

While the otters have the required number of caudal vertebræ which would fit them to represent in that respect the type from which the cetaceans have descended, the assumption that the lateral integumentary ridges on the tail of *Pteronura* might be exaggerated by gradual evolution into the huge flukes of a *Megaptera* or *Balæna* is, to say the least, far less satisfactory than the hypothesis that these structures are the representatives of once functional feet. Moreover, the first traces of the flukes of *Cetacea* do not at first appear ontogenetically, as they

* Whales, past and present, and their probable origin. Nature, XXVIII, 1883, p. 229. From a lecture delivered before the Royal Institution, May 25, 1883.

ought to, as longitudinal ridges or folds extending the whole length of the tail, as in *Pteronura*, *but as short, lateral, integumentary, ridge-like folds, very like limb-folds in normal types*, and very near the tip of the tail of the embryo; these folds also gradually grow out as rounded lobes, finally becoming acuminate. How little the mode of development of the cetacean flukes resembles the adult condition of the tail in the margined-tailed otter may be gathered from the following extract, descriptive of that organ in *Pteronura*, from a paper by J. E. Gray.* On *p.* 65 (*l. c. infra*) it is stated: Tail conical, tapering, rather depressed, covered with short hair and furnished with a subcylindrical prominent ridge on each side; end more depressed, two-edged, and fringed at tip.

I frankly admit, however, that the following question may be very pertinently asked by those disposed to dispute the validity of my conclusion that the flukes of *Cetacea* and Sirenians represent the feet of terrestrial mammalia; that is, "Why is it not as reasonable to suppose that the flukes may not have arisen as lateral dermal folds in the same way that the high, falcate dorsal fin of *Orca* has been unquestionably developed?" To this I have already in part replied by showing in the first place that the dorsal fin of cetaceans is not always developed, and, secondly, that when present it is always developed, so far as we know, after the flukes have been formed as lateral folds. I may therefore pertinently put the following question for objectors to my hypothesis to answer: "Why is it that the flukes are always present, and always in a lateral position, or approximately in the place of a limb laterally, and why there is not only very often a correlation in size but also of form between the fore limb and the flukes of such types as *Megaptera* and *Rhachianectes*?" And, finally, why is it that the flukes, as a rule, exceed the fore limb in size, if such fact does not indicate that the flukes have been derived from the integuments of a pes which has been developed in an ancestral form, as in the existing pinnipeds, to dimensions generally in excess of those of the manus? Another query it may also be interesting for objectors to my hypothesis to settle, viz, the variable position of the dorsal fin in respect to the paired appendages of cetaceans, showing that it grows, as I have asserted, from some part of an extended dorsal integumentary fold, as attested by the observed facts of development, as well by its extreme anterior position in *Globiocephalus* and *Orca*, and its posterior one in *Sibbaldius* and *Berardius*. Lateral carina are, on the contrary, never found in front of the base of the flukes of cetacean embryo, these organs always developing from short lateral folds at the sides of the end of the tail. Such lateral caudal carina are also absent in the adult, judging from the casts in the U. S. National Museum.

The caudal median notch posteriorly between the bases of the flukes is also developed only after the flukes are fully formed in the embryo,

* Observations on the margined-tailed Otter. (Pteronura sandbachii.) Proc. Zool. Soc., London, 1868, pp. 61–66; Plate VII.

in which the tip of the tail forms a perfectly round, sometimes slightly exserted hemispherical tip beyond the hinder end of the growing fluke folds before the latter have lost their rounded or lobate form. This notch between the flukes I regard as representing in the hind limb both the posterior axillary notches or re-entering angles behind the bases of the fore limbs in *Cetacea*. It represents the interval between the edges of the displaced and degenerate pedes, and not the perineum which has been left far in advance of the flukes, owing to the manner in which the pedal rudiments have been carried backwards in the course of the progress of the degeneration of the proximal parts of the limbs due to inclusion, and the gradual hypertrophy of other parts. The tail has therefore assumed the function of the hind limbs in the cetaceans, and although no longer available as an organ of locomotion on land, as are the hind limbs of pinnipeds: it is strange that the forces of Nature, which have obviously been tending to the same end in the latter as in the former, should have had to evolve, according to the old view, a new organ when through natural processes of degeneration in one direction, coupled with hypertrophy in another, an old one could be transformed into the structure demanded by new conditions.

The partial loss of the ungues in the pes of pinnipeds has been replaced by a condition in which they are completely absent in the flukes of the cetaceans and sirenians, the hairless pedal integuments extending in the first far beyond the nails. This hairless and nailless condition of the cetaceans is doubtless correlated with habit, and has begun to manifest itself on the limbs of pinnipeds, in fact has been almost completely attained by the nearly nude walrus, the simple teeth of which are also not to be left out of account in this comparison.

(6) *Anatomical and embryological data.*—Huxley, with his usual sagacity, has told us by implication in language of inimitable clearness, in speaking of the structural characters of the Pinnipeds, what are some of the morphological changes suffered by these animals in the course of their evolution. Although in part almost a restatement of what has been already said, I may be pardoned for quoting the observations of so eminent an authority. He says, * "The *Pinnipedia*, or seals and walruses, are those *Carnivora* which come nearest the *Cetacea*. The tail is united by a fold of skin which extends beyond its middle, with the integument covering the hind legs. These are, in most species, permanently stretched out in a line with the axis of the trunk." The English anatomist was obviously impressed by the inclusion by integument of the femoral and crural parts of the hind limbs, together with the tail, as seen in Pinnipeds.

Huxley then proceeds (*l. c.*): "The toes are completely united by strong webs, and the straight nails are sometimes reduced in number, or even altogether abortive. The inner and outer digits of the pes are very large."

* Anatomy of vertebrated animals, p. 359.

The more or less complete abortion of the interdigital emarginations in the manus and pes of pinnipeds has been quite completed in the cetaceans; the digits themselves having become in the latter much prolonged in the anterior limbs in which they have also acquired an increased number of often very short phalanges, sometimes as many as nine or even more in the second and third digits. This condition is, however, probably an adaptive structure, evolved in consequence of the acquisition of additional segments necessary when they first permanently took to the median in which they now live and through which they move. The tendency to abbreviate the mobile part of the limbs and shorten the segments is manifest in the construction of the limbs of almost all the fishes of the group *Lyrifera*, in which it has also been necessary, as in the whales and pinnipeds to shift, the insertions of the flexor and extensor muscles outward upon the more distal elements, so as to render them physiologically more effective. In most of the *Lyrifera* the muscles which move the fins have the most peripheral insertion of any to be found within the limits of the *Vertebrata*, or upon the proximal ends of the many-jointed rays shown by me to develop beneath the epidermis from coalesced rods or primitive unjointed rays, just as the limbs of the higher *Vertebrata* at first develop with an unjointed bar of cartilage extending through their central axes.

While traces of interdigital emarginations are visible in the fore limb of cetacean embryos they are much more distinctly visible in the embryos of pinnipeds where they are better developed than in the adult of the latter, the meaning of which facts will be clear to the evolutionist.* The increase in the number of phalangeal segments, however, begins abruptly in the cetaceans; in most forms the middle digits contain more than the number three, normal to the mammalian class, so that the whales and porpoises are, in this respect, very different from the pinnipeds. But it must be borne in mind that there are at least two precedents of this kind which occur within the limits of the *Reptilia* which have apparently, like the cetaceans, been modified for an exclusively marine or aquatic existence; these are the *Plesiosauria* and *Ichthyosauria*. As many as nine phalanges are found in a single digit of the pes of the first type, and twenty-six in the third digit of the manus of *Ichthyosaurus intermedius*. These forms seem indeed to have represented the existing Cetaceans in the seas of the Mesozoic ages.

This parallel is rendered still more striking when we recall the circumstance that in *Ichthyosaurus*, as in Cetaceans and Sirenians, the pelvis is not connected with the spinal column, and that it has evidently undergone considerable degeneration, but in *Ichthyosaurus* there has been no shifting of the distal part of the hind limb backwards, as in Pinnipeds and Cetaceans. The hind limb derived, in *Ichthyosaurus*, from that

* Irregular emarginations are noticeable on the hind margin of the flukes of *Megaptera*. According to Eschricht such irregular emarginations are visible along the posterior border of the flukes of an advanced fœtus of a species of this genus.

of a short-limbed reptilian type, resembling the crocodile, evidently could not be permanently extended backwards by inclusion together with the tail to such an extent as happened in the case of the cetaceans through the intermediation of a form approximating that of the *Pinnipedia*, with rather elongated hind limbs.

Ichthyosaurus may also serve to throw some light upon the genesis of the dorsal fin of Cetaceans, if it is true, as surmised by Huxley (Anat. Vertebrated Animals, p. 208), that there is some reason to suspect that it had a vertical dorsal fin-like expansion of the integument of the tail. Traces of such a structure are present in the dorsal and ventral integumentary carina of the tail of the *Crocodilia*. By local hypertrophy such a fold might, by having mesoblast proliferated from within, have its dimensions increased, but even if the process so far resembled the early stages of normal limb-formation, one could not legitimately infer for that reason that the flukes of the Cetaceans were structures of the same nature as the dorsal fin, namely, a mere integumentary fold, such as we have grounds for suspecting was evolved in *Ichthyosaurus* from an antecedent type with an extended dorsal, caudal fold, as it has been shown, on the basis of the comparison of generic types and embryos, must have been the case in Cetaceans, so that in both the reptile and mammal the dorsal fin was developed as a new structure, or was developed through reversion out of one which had been inherited from the more remote lyriferous or amphibian types, which had continuous dorsal and ventral median fin-folds, but which had no relation whatever to paired limbs.

The same immobility of the phalanges of *Ichthyosaurus* upon each other and the excessive abbreviation of the humerus, ulna, and radius, which must have involved the suppression of the finger muscles, are characters which the limbs of this reptile must have possessed in common with the fore limbs of Cetacea, but these characters obviously indicate no relationship, but rather that environing conditions of a similar nature have led to the production of very similar degrees of morphological differentiation in these two types otherwise totally unrelated.

(7) *The genesis of extra phalangeal elements in Cetacea.*—Upon making an examination of the limbs of pinnipeds it is found that in *Eumetopias* and *Callorhinus*, for example, the ungual phalanges consist of two parts, namely, a short proximal osseous part, to which the nail is attached, and a very long distal part composed of cartilage which is extended beyond the nail into the produced marginal integumentary folds of the manus and pes. A careful examination reveals the fact that the osseous portion of the ungual phalanx is actually prolonged as cartilage as above described. This cartilaginous extension of the ungual phalanges, I take it, has afforded the basis, in some ancestral seal-like form, for the development of an increased number of digits beyond the ungual phalanx, as in *Cetacea*. Let such a cartilaginous extension of the ungual phalanges become segmented, and then have ossific deposits laid

down in the center of each additional segment so formed, we would have phalanges produced in excess of the number found in the digits of normal forms. Upon comparing this hypothetical method of the evolution of the supernumerary phalanges in the digits of the manus of cetaceans with what actually happens during development in the latter, it is found that the actual development favorably countenances the hypothesis.

The terminal or distal phalanges in Cetaceans while they are indicated by segments of cartilage very early, as will be seen by the fœtal manus represented on Plate II, by fig. 17, ossify from centers which actually appear enchondrally much later than those of the proximal phalangeal joints, as minute round ossific nodules in the middle of the cartilaginous segment. These nodules or nuclei of the osseous terminal phalanges also diminish in size from within outwards. It would there fore seem that the supernumerary terminal phalanges of the cetacean manus develop last, which is in conformity with the hypothesis.

(8.) *The muscles of the limbs of seals and the vessels of the flukes of Cetaceans.*—The hind limbs of the pinnipeds and *Ichthyosauri*, however, retained their capabilities of movement through a special arrangement of muscles arising from the axial skeleton and inserted mainly into the middle third of the skeleton of the limbs. While there has been a considerble shifting peripherad of the insertions of the muscles in the former there has been a tendency for the whole hind limb to diminish in size in the latter type and no tendency towards the complete atrophy of the distal part of the appendicular skeleton and musculature of the hind limb as in Cetacea, in consequence of which in the latter the fluke or distal part of the hind limb has become a mere rigid hollow lateral diverticulum of the integument, filled with fibrous tissue and possessing no mobility distinct from that possessed by the tail as a whole. In short, the degeneracy of the hind limbs of Cetaceans is complete and presents the unexampled condition of part of a limb permanently developed in the adult to a stage which is practically comparable to a transient condition in the embryo when the limb fold is filled with undifferentiated mesoblastic cells. These folds, as the flukes, however, approximate the form of the distal half or two-thirds of the fore limbs, from which the skeleton has vanished together with the muscles, tendons, and nerves appertaining to them, the normal mammalian arrangement of the vessels and nerves being approximated by a superficial dorsal and ventral system which is not at first sight so obviously homologous with the vessels and nerves of the typical mammalian hind limb. The vessels are arranged in about ten dorsal and eleven ventral pairs just below the integument of the fluke. The fourth pair reckoning from the front is most strongly developed and extends to the tip of the fluke, giving off smaller branches on either side from its distal two-thirds. These secondary branches carry the blood supply to the tips of the flukes. The other ten pairs of vessels sent into the base of the fluke, three in front of the main vessel and seven behind it, are short and only pass out to about as far as the basal third of the fluke. In all there are 42 vessels supplying the flukes, 21 to each side, and they correspond only partially with the number of vertebral segments, of which as many as fifteen may be included between the bases of the flukes of opposite sides. This is the arrangement in *Phocæna*, and it is doubtless similar in other forms. The superficial and not axial position of the vessels is a striking peculiarity and is very different from the arrangement of the blood supply of the dorsal fin, as elsewhere described.

The arrangement of the vascular supply of the flukes thus affords a strong argument in favor of the view which I have defended, viz, that the flukes are the homologues of feet and not special lateral integumentary outgrowths. On the hypothesis that the flukes are mainly homologous with a pes, or perhaps the digital part of a pes, there *ought* to be about ten vessels present on the dorsal and as many on the ventral side of the flukes representing the paired interdigital arteries, of which there are two pairs to each digit in the manus, as well as pes of normal mammals. In the foot of the latter these arise from the dorsalis pedis on the dorsal side and from the external and internal plantar artery on the ventral side. This close correspondence between the normal number of dorsal and ventral interdigital arteries in normal forms and those found in the flukes of *Cetacea* is, to say the least, suggestive, though it must be admitted that it cannot be proved that they arise in the *Cetacea* from the femoral and popliteal continuations of the external iliac, but have acquired a new origin from the caudal continuation of the aorta and its dorsal branches serially homologous with intercostal arteries anteriorly.

The arrangement of the principal and deeper vessels of the manus of *Phocæna* I have not investigated, but it has struck me as being very remarkable that the distal third of the manus should be supplied by longitudinal vascular trunks lying between the second and third digits, these trunks giving off lateral twigs on either side to supply the whole of the terminal third of the flipper or manus, just as the distal two-thirds of the flukes are supplied by the long fourth dorsal and ventral arterial trunks, which, like the distal trunks in the former, give off lateral twigs, which run to the anterior and posterior borders of the flukes. This arrangement of vessels in both seems to me to indicate more than a mere analogical resemblance; that, in fact, the two principal trunks of the fluke are the interdigital vessels which were most strongly developed alongside of the longest, probably the second digit of the pes, before the phalanges of the others began to atrophy.

Murie* figures the principal superficial ventral vessel of the flukes of *Globiocephalus*, but does not show the accessory shorter ones running parallel with it in front and behind its proximal end. Here, as in *Pho-*

* On the organization of the Caaing whale, *Globiocephalus melas*. Trans. Zool. Soc. London, VIII, 1874, pp, 235–301 (fig. 58, pl. 36).

cœna, these arteries are probably accompanied by veins, which run parallel with the arteries of the flukes. In *Globiocephalus*, according to Murie's figure, this principal vessel gives off lateral branches nearer its origin than in *Phocæna*, and its proximal end is turned forward as though connected laterally or at the side of the vertebræ of the tail with branches given off by the median inferior caudal continuation of the aorta.

In the memoir cited above (p. 269) Murie also disputes the conclusion of Hunter and others that the abdominal aorta does not send off any external iliac branches. The arrangement which he described in the female *Globiocephalus* seems to be similar to that found in *Phocæna*. The common iliac after giving off the hypogastric divided into what he regarded as external and internal iliac arteries. The external, immediately beyond its origin, split and sent rami to the parietes of the abdomen and genital parts. Its other main branch passed beneath the os innominatum and interpelvic facia or ligaments and there broke up into several diminutive channels; some of these were distributed to the pubo and ilio-coccygeus muscle; others with a nerve pierced the interpelvic fascia at the notch, just behind the anterior capitulum of the bone. Beyond this, in consequence of the complete atrophy of the functional parts of the limb, viz: femur, tibia, bones of the pes and the muscles which actuate them, one would not expect to trace these vessels so that the flukes would seem to get their blood supply from another source through secondary adaptation, as has in fact been already stated.

(9) *The digits of pinnipeds and cetaceans.*—As in the seals the digits of the manus of Cetaceans diminish in length from within outward, that is, from the second to the fifth, the first digit or that corresponding to the thumb being anterior and exterior, so that the fore limb is permanently prone and is rotated backwards, as are the hind limbs of the former. There is, however, an even more interesting correspondence between the form and structure of the fore limb and the flukes, as seen in *Phocæna*, in which the layer of blubber extends out under the skin investing the manus for something more than one-half of its length from the base outwards. In the flukes, on the other hand, no blubber is found; in fact, the layer of fatty tissue bearing that name does not extend even as far as their anterior borders, ceasing beneath the integument covering the caudal peduncle, considerably in advance of the flukes.

The subdermal coating of blubber which invests the fore limb is interposed between the degenerate tendons of the finger muscles and the skin, whereas in the hind feet or flukes the superficial stratum of longitudinal tendon-like bundles of fibers lie immediately under the integument. These superficial tendinous bundles in the flukes I have elsewhere spoken of as possibly representing the degenerate system of the flexor and extensor tendons of the pes, though I am aware that a similar arrangement is found in the dorsal fin when it is developed, in which there is, however, no connection or close relation with the tendinous insertions of any muscles whatsoever, such as is the case in the flukes. The muscular connection of the flukes is indirect; that is to say, the tendons of the supra- and infra-caudal muscles send only a small portion of their fibers into the flukes, yet even this is a condition which contrasts very sharply with the relations of the superficial tendinous fibers of the dorsal fin, which have absolutely no connection with any muscles either directly or indirectly.

(10) *The nervous supply of the flukes of Cetaceans.*—The sensory nervous supply of the flukes has a distribution slightly deeper but similar to the vessels, and is derived from the four great lumbo-caudal cords,* which represent the lumbar plexus of normal *Mammalia* extended backwards into the tail. In my own dissections I have found it difficult to make out more than two or three pairs entering the anterior basal part of the flukes, and these arise from the dorsal pair of cords dorsally, and from the ventral pair ventrally. There are, doubtless, other smaller pairs behind those found by me, but the excessive toughness of the fibrous tissues in their vicinity has rendered the determination of their number a difficult undertaking. The nervous supply is obviously not derived from the continuation of a homologue of the great sciatic as in normal *Mammalia*, unless, as seems probable, it would be possible to trace the terminal fibers of the great caudal plexus as the homologue of those of the terminal part of the great sciatic trunk of normal forms. This aspect of the question under consideration must, however, be viewed in another connection, but it may not be amiss to now point out the fact that the four cords found to enter into the lumbo-caudal plexus of Cetaceans are represented by structures which, even in so highly a differentiated organism as man, may be homologized with what is found in the *Cetacea*. The dorsal cord in the latter is represented in man by the posterior branches of the lumbar and sacral nerves, the ventral cord by the anterior lumbar and sacral. While the ventral system is mainly developed in man in correspondence with the massive and essentially ventral musculature of the pelvic limbs, on the contrary, the dorsal and ventral systems are about equally developed in the cetaceans, in consequence of the fact that functional hind limbs have been aborted in the latter, while the dorsal and ventral caudal muscles have been more posteriorly developed, and have acquired about equal volumes, a condition which has called for an equally-developed nerve supply for both the upper and lower set of hypertrophied caudal muscles.

(11) *Translocation of muscular insertions in hind limbs.*—The manner in which the limbs of pinnipeds have been bent backwards has already been considered, but the remarkable shifting backwards of the muscu-

* These were first described by D. J. Cunningham, Journ. Anat. and Physiol., XI, pp. 209 to 228, Plate VII, the title of his paper on the subject being "The spinal nervous system of the porpoise and dolphin."

lar insertions of the muscles of the hind limbs of these animals must now be considered in its bearing upon the question of the evolution of the Cetacean type.

In *Phoca vitulina*, Huxley* observes that "the fore limb is buried beyond the elbow in the common integument, but the flexible wrist allows the weight of the body to be supported by the palmar surface of the manus. The hind limbs, on the contrary, are permanently extended and turned backward parallel with the tail, which lies between them, and with which they form a sort of terminal fin. When the seal swims, in fact, the fore limbs are applied against the sides of the thorax, and, the hinder moiety of the body being very flexible, the conjoined hind limbs and tail are put to the same use as the caudal fin of a cetacean. The seal has twenty dorso-lumbar vertebræ, of which five are lumbar. There are four sacral vertebræ, but only one of these unites with the ilia. Eleven vertebræ enter into the formation of the short tail."

(*Op. cit.*, p. 362.) "The ilium is short, and the long pubis and ischium are greatly inclined backward, so that the long diameter of the *os innominatum* makes only an acute angle with the spine. The femur is much shorter than the humerus. The tibia and fibula are anchylosed, and more than twice as long as the femur. The pes is longer than the tibia. The astragulus has a peculiar, roof-shaped, tibial surface, and sends a process backward which contributes to the formation of the very short heel. The hallux is the strongest of the digits; while this and the fifth digit are the longest of those of the pes.

"The cutaneous muscle is largely developed and inserted into the humerus. The *pectoralis major* is very large, and arises from each side of the prolonged manubrium, and even in front of it, beneath the neck; the fibers of the muscles of opposite sides are continuous. The *palmaris longus* is a strong muscle, but the proper digital muscles are weak or absent, as in the case of the *abductor*, *adductor*, *flexor brevis*, and *opponeus* (p. 363) of the fifth digit. A special long abductor of this digit, however, passes from the olecranon to the distal phalanx. The *iliacus* is wanting, and there is no *psoas major*; but the muscles which represent the *psoas minor* and the subvertebral muscles of the Cetacea are very large and play an important part in effecting the locomotion of the seal. The *pectineus* is very small, and the other adductors are inserted, not into the femur but into the tibia. The *gluteus maximus* is inserted into the whole length of the femur. The *semimembranosus* and *semitendinosus* are replaced by a *caudo-tibialis*, which arises from the anterior caudal vertebræ and is inserted into the tibia, some of its tendinous fibers extending to the planter aspect of the hallux. The *poplitæus* and *gastrocnemius* are strong, but there is no *solæus*. The tendon of the *plantaris* passes over the calcaneum and ends on the

* Anatomy of vertebrated animals, 361.

plantar fascia of the perforated tendon of the fourth digit. The other perforated tendons seem to arise from the fascia attached to the calcaneum."

Professor Humphrey has also noticed the inclusion of the hind limbs of the seal in a paper* from which I quote these words: "In *Phoca* the knees are bent up beneath the abdominal muscles and the two hinder limbs are inclosed with the tail for some distance, in one fold, so as to form a flattened termination to the animal, reminding us not a little of the tail of a cetacean; the wing-like processes of which (the flukes) might seem to be represented by the laterally expanded feet of the seal."

Dr. Humphrey's account of the muscles of the hind limb of *Phoca communis* differs slightly from that given by Professor Huxley. The *iliacus internus*, according to Humphrey, was represented only by a few fibers passing from the anterior surface of the ilium (internal to the attachment of the large quadratus lumborum which occupies almost all this surface of the ilium), and joining the psoas in the thigh.

The *psoas magnus* is present, according to Humphrey, in *Phoca*, arising from the lumbar transverse processes and last rib, and is inserted into the brim of the pelvis in front of the hip-joint; some of its fibers were continued down the inner side of the thigh, and inserted into the large rough supra-condyloid ridge. These were chiefly the fibers that arise lowest down, and which had therefore a nearly horizontal course. It is remarked, however, in a foot-note, that: "It may be a question whether these fibers, arising low down and passing to the femur, appertain to the *psoas* or *iliacus*.

There is no distinct internal trochanter in the seal, and none of the fibers, either of the *psoas*, or *iliacus internus*, are inserted in that situation, translocation backwards of these insertions, as noted above, having occurred.

Psoas parvus was large, and arose from the bodies of the lumbar vertebræ and slightly from the edge of the hindmost rib, and was inserted into a projecting process of the pubes internal to the psoas magnus.

The *gracilis* in *Phoca* is very broad, and covers the symphysis pubis, being continuous with the muscle of the opposite side. The chief direction of its fibers is transverse, but they radiate as they approach the leg, the upper fibers ascending nearly to the knee, and the lower fibers descending to the inner ankle, covering the interval between the internal malleolus and os calcis, and extending as a fascial expansion over the plantar fascia and muscles. Many of its fibers are inserted at right-angles, or nearly so, into a tendon which ran along its fore-part parallel with the tibia. This tendon, passing the inner ankle, is continued on the plantar aspect of the hallux into a tendon which represented the *flexor brevis* and *adductor hallucis*, and was inserted with them into the base of

*On the myology of *Orycteropus capensis* and *Phoca communis*, Journ. Anat. and Physiology, II, 1868, pp. 290–322, plates III–VI.

the first phalanx of the hallux; some of its fibers extending to the distal end of that phalanx. In one foot of this seal the hinder margin of the gracilis tendon was also thick, and formed or contributed to form the superficial flexor tendon of the fifth digit.

In *Phoca* the muscles of the front of the abdomen overhung the knee; and when these were removed a wide, deep chasm was exposed between the long pubes, on the one side, and the thigh, knee, and leg on the other. This chasm was crossed by a large muscle passing from the side of the symphysis pubis to the front of the upper part of the leg and knee beneath the *gracilis*. It may perhaps be regarded as an *adductor magnus*.

Gluteus maximus in *Phoca* arose from the back of the crest of the ilium, the sacral spines, and the sacro-iliac ligaments, and was attached to the trochanter and the external supra-condyloid ridge of the femur, while its lower part expanded over the knee joint. Some of its fibers were continuous with those of the *vastus externus*.

This somewhat extended discussion of the muscular anatomy of the hind limbs of the *Pinnipedia* has been thought necessary in order to bring out as prominently as possible the fact that some of the insertions of the muscles of the hind limb have really traveled backward behind their usual position on the bones of the same pair of limbs of normal *Mammalia*. This is obviously a teleological modification, or one which has been needed in order to make the muscles more effective upon the distal or exserted part of the limb or the pes. The fact that the abdominal muscles overlap or extend over the knees of *Phoca* shows how real is this backward extension of the musculature of the body, which has been obviously aided by the shortening of the femur and lengthening of the crus in this type, the *Pinnipedia*. In one case even the origin of a muscular pair seems to have been pushed backward somewhat; it is that of the muscle called the *caudo-tibialis* by Huxley, and regarded by him as the homologue of the *semimembranosus* and *semitendinosus* of normal mammals.

Quoting again from Humphrey, I may illustrate the fact that the posterior girdle and muscles of the pinniped are actually undergoing degeneration in certain directions. He says: "In the seal the terminal parts of the limbs, especially of the hind limbs, are large, and spread out fan-like, the digits being thin, long, of nearly equal length, and in the same plane; and the size of the fan is increased or diminished in each foot, chiefly by the distancing or approximating of the other digits to the first, and the lateral movement of the digits therefore increases from the first to the fifth.' The dorsal and plantar surfaces of the terminal parts of the hind limb are in the same plane with those of the leg; the projecting part of the heel-bone, which is small, is drawn forward or upward, and the hinder part of the astragulus, carrying the groove for the flexor tendon of the toes, is draw up with and projects nearly as far. The lumbar and hinder five or six dorsal vertebræ are constructed so as to admit of full antero-posterior movement; whereas the iliac bones are short and directed outward, presenting flat surfaces anteriorly, and the ischiatic bones, though long, are slender, showing that the muscles which pass from the pelvis to the short thighs are small. These features have, of course, relation to the fact that the propulsion of the animal is effected not, as in ordinary mammals, by the movements of the limbs upon the pelvis, but rather, as in the fish, by the movements of the hinder part of the vertebral column upon the rest of the trunk, the limbs of the seal serving chiefly like the tail rays of the fish to give width to that part of the column."

(12) *Degeneracy of the pelvis in pinnipeds.*—The relatively small pelvis, with its thin and slender pubes and ischia in the *Phocidæ*, is remarkable, though a similar pelvic degeneracy is even more obvious in the skeleton of the fur-seal *Callorhinus.* I regard this degeneracy of the pelvis and proximal musculature, and the evident translocation of some of the muscular insertions backward, the inclusion of the knees by the hinder part of abdominal musculature, as very clearly indicative of the mode in which the pes of *Cetacea* were shifted backward, the skeleton finally aborting utterly, so as to leave only a pair of pedal folds projecting from the sides of the tail, stiffened by a peculiar arrangement of fibers, fully described by Roux,* who develops an elaborate hypothesis to account for the arrangement of these connective-tissue fibers in the flukes, but he continually speaks of the flukes as *Flossen* (fins), and seems to have no suspicion in regard to their true nature, viz, that they are the degenerate translocated distal portions of the hind limb.

Dr. Gill,† who seems to have been the first author to appreciate the importance of the inclusion of the proximal parts of the hind limbs of pinnipeds, and to avail himself of it in taxonomy, uses the important character discussed above as diagnostic of the *Pinnipedia*, contrasting the latter with *Fissipedia* as follows: Body prone, with the legs confined in the common integument beyond the elbows and knees (with the feet rotated backwards, and with toes connected together), and especially adapted for swimming. Manus and pes with first phalanges and digits enlarged and produced beyond the others."

Allen‡ contrasts the *Phocidæ* and *Otariadæ* as follows:

[1] "In the *Phocidæ* the hind limbs are extended backwards in a line parallel with the body; the legs are so inclosed within the integuments of the body that they have little or no motion, and the feet are movable only in a relatively small degree, in an obliquely lateral direction.

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* Beiträge zur Morphologie der functionellen Anpassung. 1. Structur eines hoch differenzirten bindegewebigen Organes (der Schwanzflosse des Delphin). Arch. f. Anat. u. Physiol., 1883, pp. 76–161, 1 pl.

† Synoptical tables of characters of the subdivisions of mammals, with catalogue of the genera. Smihsonian Miscel. Coll. 230, Nov., 1872. In arrangement of the families of mammals.

‡ On the eared seals (*Otariadæ*) with detailed descriptions of the North Pacific species. Bull. Mus. Comp. Zool. II, No. 1, pp. 108, pls. 3.

[2] "In consequence of this peculiar structure the only purpose which these organs can subserve is that of swimming. On land progression is mainly accomplished by a wriggling serpentine motion of the body, slightly assisted by the extremities.

[3] "In the *Phocidæ* the tarsal articulation allows but a small amount of movement of the foot, which, when naturally at rest, forms but a slight angle with the leg.

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[4] "The bones of the pelvis (of the *Phocidæ*) are all thin and slender."

[1] "In the *Otariadæ* the hind limbs are somewhat free, and when in a natural position (on land) the feet are turned forward, and serve to raise the body from the ground.

[2] "They also (imperfectly) serve the purpose of walking; these animals being able to progress when out of the water several miles an hour, and to run for a short distance with nearly the rapidity of a man.

[3] "In the *Otariadæ* the foot when similarly at rest forms with the leg an angle of at least 90°.

[4] "The bones of the pelvis are all thick and stout, especially the walls of the acetabula. The acetabula are themselves very much larger than in *Phoca*."

"The length of the ischio-pubic part [of the pelvis of *Phocidæ*] to the length of the ilia is as *three* to *one*." In the *Otariadæ* the proportions of these bones is nearly as *one* to *one*.

It is thus rendered obvious that these two families are divergent and quite distinct. The effects of degeneracy are most apparent in the pelvic girdle and hind limbs of the *Phocidæ*, as is shown by the contrasts given by Mr. Allen.

(13) *Tendency to pronation of the pes in pinnipeds.*—Professor Lucæ in an elaborate paper on the osseous skeleton of the seal and otter,* has given some account of the swimming habits of *Phoca* and its osteology which are of interest in this connection. He calls attention to some of the facts already alluded to, and in addition directs attention to the strongly marked pronation of the leg and foot, the dorsum of the latter being directed outwards and the plantar surface inwards.

This pronation of the foot was probably carried still farther in the Protocetacean type, which gave rise to the existing forms. In them the foot was probably directed backward and so greatly pronated as to bring the hallux or longest digit to the outer or external margin of the extremity of the limb. The plantar surface would then be brought into its original ventral position, while the dorsal side would be superior, the reverse of which would have been the case had the limb been simply swung backwards parallel with the tail without pronation or semi-rotation upon its own axis. But the hallux, which was probably

* Die Robbe und die Otter in ihrem Knochen und Muskel-skelet, eine anatomisch-zoologische Studie. Abh. I. Senckenbergischen naturforschenden Gesellschaft, VIII, 1872, pp. 277-378, pl. 14.

the longest digit for a time, would become the fifth instead of the first, when counted from within outwards. The hallux then probably grew gradually shorter when the second and third digits became the principal ones in the pes as well as in the manus, after which they atrophied entirely, leaving only the vessels to serve as traces of their former presence.

The extremely short neck of the cetaceans, due to the abbreviation of the cervical vertebræ, has brought the origins of the fore limbs nearer the head and to some extent obscured the inclusion by the soft parts of the arm and fore-arm which has taken place in these forms. Such an inclusion of the proximal joints of the fore limbs has also occurred in the pinnipeds, but in them, as in *Eumetopias*, for example, the normal length of cervical vertebræ has been retained, so that when the living animal is observed the neck seems longer than it actually is, because of the inclusion of the upper parts of the fore limb so as to leave little more than the manus free, a condition which gives rise to the illusive appearance of a long neck; in fact, the neck of the sea-lion as beheld and understood by one knowing nothing of the internal anatomy of the animal, would include some of the anterior dorsal or trunk vertebræ, together with the true cervicals. In the whales, however, so great has been the actual shortening of the neck that the effect of the inclusion of the proximal parts of the fore limb on the apparent length of the neck is lost, but if the neck vertebræ of a cetacean are imagined to be of their usual proportional length in a skeleton, and if the extension so gained be added with a pair of dividers to a figure of the latter the effects of the inclusion of the upper parts of the fore limb at once become apparent. In fœtal cetaceans the neck is proportionally somewhat longer than in the adults.

(14) *The auditory bullæ of Phocidæ and rudimentary pinnæ in Cetacea.*—It is worthy of notice that the *bulla* tympani in the *Phocidæ* are very large and thick walled and not so intimately joined to the adjacent bones of the skull as in the typical land Carnivora, thus approximating the *Cetacea* somewhat. The eared seals have a distinct though rudimentary pinna or external ear developed, which is wanting in the *Phocidæ*. That even the ancestry of the *Cetacea* were possessed of well developed pinnæ or external ears seems to be countenanced by the fact that Howes* has found a minute cylindrical appendage close to and just behind the external auditory meatus of the embryo of *Phocæna*. Such rudiments of pinnæ seem to be unusual in embryo Cetaceans, as the writer has not found them present in any of the fœtuses of the species examined by him.

II.—DEVELOPMENT.

In all the figures of cetacean embryos which have been published and to which I have had access, the same law which presides over the

*Journ. Anat. and Physiol., XIV.

order of the outgrowth of the limbs is shown to hold as for all other vertebrates, provided the fluke folds be regarded as representative of the hinder limb folds; otherwise the cetaceans must be regarded as anomalous or exceptional in this respect and permanently without any traces of externally developed posterior appendicular organs, even in the embryonic condition. Granting, however, that the discussion of the morphology of the adult has justified the acceptance of the doctrine of the translocation of the limb backwards by the progressive inclusion of more and more of the proximal parts of the hind limbs of some decidedly ambulatory ancestral form by the gradual advance from before of the integuments of the body in common over the hind limbs and tail until nothing but the feet have remained exserted, a process which we see has already begun and reached a very marked development in the existing pinnipeds, the reader may be led to admit that my hypothesis when applied to the interpretation of the order of appearance of certain parts in the embryo is not so unreasonable as might at first be supposed. He must at any rate admit that the process which has begun to modify the limbs and pelvic girdle of pinnipeds if carried still farther must actually lead toward what now exists in the cetaceans; and that as a result of the process of inclusion of the limbs their skeleton must necessarily first become immobile and then atrophy, and that not only the muscles but the nerves and vessels must also atrophy or be so modified as to leave scarcely any recognizable representatives of their homologues as found in the hind limbs of normal mammals. We are thus, I venture to fully believe, put upon the clew which will lead us along the course which the evolution of the cetacean tail has taken; and, while asserting that the pinnipeds very distinctly give us the intimation of *how* this structure was developed, it does not necessarily follow that the pinnipeds are tending to become whales or that a typical pinnipedian ancestry for the *Cetacea* is assumed. In other words, I do not mean to imply that the latter have been evolved from seals, but I do insist that the ancestor of the *Cetacea* must have been more or less seal-like in the organization of the hind-body and hind-limbs; yet I am not at all certain after considering the many resemblances existing between the seals and whales that they are not genetically allied. In that event their common ancestry must be referred to a remote period in the history of the development of the higher organic types. That the *Cetacea* are allied through descent to the *Ungulata* is, it seems to me, founded on far less convincing evidence than the assumption that they are affiliated through descent with the terrestrial and amphibious *Carnivora*, especially the latter.

The *Sirenia* have possibly descended from a quite different ancestral type, and while they have been modified in an analogous manner, so far as the hind limbs are concerned, they present every evidence in other respects of having arisen from an herbivorous progenitor.

The mode in which the shifting of the hind limb has been accomplished being understood, we find, as already urged, that the laws of limb development support my hypothesis, as may be seen upon considering the following general principles:

1. The hindmost pair of limbs is always the last to grow out in the embryos of *Vertebrata*, the fore limb at an early stage being larger and longer as a limb fold than the rudiment of the hinder limb fold. The fluke-folds of cetacean embryos grow out after the pectoral limb has its cartilaginous skeleton well developed. The inference to be drawn from this is that the former probably represent what remains of the hind limbs to be externally developed through functional adaptation or loss of function, and its assumption by the caudal musculature actuating the whole caudal series of vertebræ, with the degenerate distal remnants of the hind limbs shoved back, as described, and more or less rigidly affixed to the sides of the tail, so that the feet or flukes have become secondarily functional, so to speak, and part of an apparatus evolved *pari passu* with the almost complete atrophy and inclusion of the pelvis and rudiments of limbs within the integuments investing the hinder part of the body and tail.

The degenerate or skeletonless state of the pelvic limb folds is so strongly influenced in this group by heredity directly that I am aware of few or no parallels. Its posterior origin is paralleled by the attypical or abnormal anterior origin of the pelvic limb folds of *Physoclisti*, as in *Lophius*, for example, in which translocation forwards of the pelvic limbs has occurred, instead of a backward translocation, as in the cetacean. But these two types again differ in that in *Lophius* it is the whole of the hind limb, together with the girdle, which is so translocated while in the *Cetacea* it is obviously only the exaggerated integumentary investments of the pes which are carried backwards at the end of the hind limb. In *Lophius* the original site where the pelvic limb fold first appears in the embryo is nearly as far in advance of its archaic site in the embryos of the most undifferentiated Physostomes as the pedal folds in cetacean embryos are behind their archaic site or position of origin in normal mammalian fœtuses.

My own observations on *Globiocephalus*, as well as those of Eschricht on *Delphinapterus* or the white whale (fig. 13 *a*, Plate II), show that the first traces of the flukes or hind feet appear in the embryo cetacean as a lateral terminal pair of very low short folds, with a gently curved margin, as seen from the dorsal side, giving the end of the tail of the embryo when thus viewed the appearance of a lance head.

Sections at this stage show no traces of a skeleton, nothing but a medullary mass of indifferent mesoblastic cells filling up these folds of epidermis, which represent the rudiments of the pedes. Coincidently with this early stage the cartilages of all the bones of the pectoral limb are fully developed; all the carpal and phalangeal cartilages are also fully formed, as shown in the enlarged figure of the manus of *Globiocephalus* (Fig. 17). No traces of interosseous muscles or of flexors and extensors of the digits were discoverable in longitudinal sections of the manus of an embryo 2 inches long. Intercossei muscles, on the contrary, are developed in a relatively earlier stage of the embryo cat, or in a normal form.

It thus appears that the displacement and degeneration of embryonic representatives of the distal portions of the hind limbs of Cetacea has greatly retarded or influenced their development as compared with the fore limb, and that the mesoblast instead of being transformed into cartilage, and finally built into bone axially, and muscle superficially, has been mostly converted into a tough kind of fibrous tissue running in two directions at right angles to each other, and in the main parallel with the dorsal and plantar surfaces of the flukes. This tissue has the appearance and consistency of tendon; in fact the longitudinal superficial fibers are in part continuous, according to the observations of Murie, Roux, and myself, with the terminal fibers of the great tendons of the flexor and extensor muscles of the tail; that is, with the tendons of the posterior extensions of the lateral *intertransversarii*, the dorsal *erector* and *multifidus spinæ* and the ventral or subcaudal system, partially homologous with psoas muscles.

This last fact shows how persistently the psoas muscles share in flexing the hind limbs of mammals; in the cetaceans some of their tendinous fibers being actually sent backwards to be inserted into the flukes and last vertebræ instead of, as usual, into the lesser trochanter of the femur, a bone which is quite aborted in most of these forms. It seems to me that there is good reason to believe that both the *psoas magnus* and the *psoas parvus* are represented by the powerful subcaudal muscles of cetaceans, and that probably both send some tendinous fibers into the flukes. This is in keeping with the hypothesis of cetacean limb development here defended; for we found that certain muscular insertions were migrating backwards on the femur and tibia *pari passu* with the demands of functional adaptation in the *Phocidæ;* this translocation backwards of the muscular insertions has reached its extremest expression in the cetaceans where the continued psoas, as infracaudal and sacrococcygeus, actually sends tendinous fibers to the flukes instead of the femur, which has long since atrophied or become functionless.

2. The development of the paired vertebrate limb begins primarily as a lateral outpushing of the embryonic skin, or as a hollow, flat, lobate, horizontal diverticulum of the epiblast, into which mesoblast proliferates and from which the appendicular skeleton and musculature are differentiated.

The cetaceans follow this rule of development but soon diverge from the normal mammalian type in two respects, viz, that the embryonic limb rudiment does not become so markedly clavate or club-shaped as in embryos of mammals with ambulatory limbs modified for terrestrial progression, but remains more distinctly flat and pinniform as in fishes. The intermediate condition in this respect between that found in normal mammals and cetaceans is seen in pinniped embryos. Finally, the posterior limb-folds also fail to develop a skeleton in their medullary substance.

Eschricht (*Untersuch. über die nordischen Wallthiere*, 1849, p. 78) remarks of the development of the flukes, "Bei ihrem ersten Auftreten erscheinen die Schwanzflügel der Cetaceen als zwei sehr zarte Hautfalten ganz am äussersten Ende des Schwanzes. Auf dieser Entwickelungsstufe hat der Schwanz die Form einer kleinen Lanze." He then describes the mode in which the folds rapidly elongate or widen laterally, becoming more and more acumniate and longer and somewhat falcate. Different stages of the lobate condition may be noted in the embryos figured in the plates accompanying this paper, as shown digrammatically in fig. 15, pl. II.

Dr. Jeffries Wyman (in Proc. Bost. Soc. Nat. Hist., III, 1848–'51, p. 355), on the 6th of November, 1850, made the following remarks on the development of the flukes of *Balæna mysticetus*, basing his observations on a fœtus of that species, 6 inches in length: "Instead of the long flukes and central depression (caudal notch) seen in the tail of the adult, the tail of the embryo was rounded as in the tail of the manatee; there was also a vertical crest above and below the tail."

Some of the older authors regarded the flukes of cetaceans as representing the hinder pair of limbs in normal mammals, such expressions as "*cum pedes in caudam coadunati*"* occurring in their writings, by which it is implied that the feet have been fused, together with the tail, into a conjoined organ. They were nearer right than they knew, but were without scientific reasons for their statements, yet, as late as 1849, D. F. Eschricht (*op. cit.*, p. 78) criticises this old view as follows and considers it to be quite untenable, urging, indeed, that when the question is viewed in the light of embryology, those data which are not at least unfavorable to such an interpretation are quite insufficient to sustain it. But I will here reproduce his remarks and then criticise them further:

"Die Schwanzflügel der Wallthiere werden sehr allgemein für rudimentäre Bauchglieder angesehen, wofür in der That ihr ausschliessliches Vorkommen bei ihnen und den Sireniformien, also grade nur bei den Säugethieren, denen wirkliche Bauchglieder abgehen, sehr viel sprechen kann. Es zeigt sich aber diese Analogie, wenn man die Entwickelungsgeschichte, diesen Probirstein der anatomischen Analogien, zu Hülfe zieht, wo nicht unhaltbar, doch wenigstens sehr unvollständig.

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* This quotation is from the *Systema Naturæ* of Linnæus, 12th ed., *Tom.* I, *pars* I, p. 105, Holmiæ, 1767. It occurs in a foot note, and entire reads as follows: "*Cetis quibusdam pinna dorsalis, omnibus pinna caudæ et pectorales; nullis p. ani, aut ventrales cum pedes in caudam coadunati.* Drs. Gill and Baur have called my attention to this interesting observation by Linnæus, who, however, does not assign any reasons for his opinion as expressed above. Gmelin, in the later editions of the *Systema*, expunged the above-cited foot-note.

Die erste Erscheinung der Schwanzflügel ist nämlich in der Form von zarten Hautlappen, ganz dicht an der Spitze des Schwanzes, in einer bedeutenden Entfernung vom After und Becken. Dagegen zeigen die Schwanzflügel sich in ihrer Entwickelung ganz analog mit der Rückenflosse, welche selbst eine in der Säugethierklasse ganz neue, nur den Wallthieren zukommende Form der Hautfaltung ist."

As I have already disposed of the last objection raised in the preceding quotation as to the dorsal fin which this author, together with later ones, so persistently compares with the flukes, I would now simply call attention to the very singular dorsal hump filled with adipose tissue so remarkably developed in certain races of the zebu or *Bos indicus*. In this terrestrial animal the dorsal hump has as much right to be called a fin as in some cetaceans. And it is but a step from the dorsal hump of the zebu to the one or two dorsal humps found in the existing species of *Camelus*. In fact, the dorsal fin of cetaceans is largely filled with adipose matter, as in these terrestrial forms, though of course it would be pushing the *reductio ad absurdum* argument to an extreme if I were to deny that the dorsal fin of Cetacea is not different in function from the adipose humps of terrestrial Herbivora. What is meant here is that the similarity or likeness existing between the flukes and the dorsal fin of whales and porpoises, is delusive and is merely analogical, and that the argument that the flukes are also mere integumentary folds, with no phyletic relation to hind limbs, is, if based upon nothing more, not a very formidable one, especially since I have demonstrated beyond any possible doubt that a limb rudiment may be and is translocated together with its girdle from its archaic position in other forms. It was the lack of a knowledge of this last fact that might well induce an anatomist to hesitate to enunciate the doctrine here developed.

The difficulty in regard to the distance (*Entfernung*) or hiatus between the point of origin of the flukes and the anus and pelvis, which Eschricht very properly considers important, I venture to think has been quite overcome by the theory of inclusion, which we may say now really assumes the dignity of a theory rather than that of a hypothesis, after the analysis and explication of the facts relating to the structure of the hind limbs, tail, and posterior part of the body of the *Phocidæ*, as developed in the foregoing pages.

3. The mammalian fœtus nearly always has the head, body, and tail flexed more or less, so that the head and tail are approximated on the ventral side.

In illustration of this, see Figs. 12 and 14, the first representing the fœtus of the cat and the latter that of *Delphinapterus*. This trait seems to be in part inherited, as a similar flexure of the embryo occurs in large yolked *Sauropsida*, but is obviously in part also due to confinement of the growing fœtus within the hollow vesicular chorion, the curvature being hence more or less mechanically adaptive in conformity with the curvature of the walls of such vesicle. That such a view is in the main true is shown by the manner in which the early embryonic axis of certain *Rodentia* is bent in the opposite direction; that is, the dorsal profile is concave and the ventral convex, or just the reverse of Figs. 12 and 14. This condition in *Rodentia* is, however, transitory, and is due to the invagination of the embryonic area or one side of the blastodermic vesicle into the opposite half, on account of which it was for a long time supposed that the primary layers were inverted in some of these animals. Later the embryo of the latter assumes the flexure normally seen in other forms and apparently for the same reason. Flexure of the embryo, to a greater or less extent, is, therefore, of little or no importance in taxonomy.

The flexure of the tail of the fœtal cat, Fig. 14, and of a fœtal porpoise, Fig. 8, forward under the body is no greater in the first case than in the latter, because the tail of the fœtal cat shown in the figure has been raised and drawn backward somewhat from between the hind limbs in order to show its length.

The hind limb of the fœtal cat is extended not quite fully so that the ends of the toes are not brought as near the tip of the tail as they might be in the figure. It is easy to see, however, that if the tail and hind limbs of this fœtus were fused together or invested by a common integumentary envelope that the volume of the tail would be thus increased threefold, and would be proportionally almost of the same bulk as the tails of the fœtuses of the cetaceans shown on the same plate. The effect of such a fusion would be to carry the pes of the cat's fœtus back to the end of the tail, leaving a little more of the latter exserted behind the pedes than is found in the fœtus of the manatee, figs. 20 and 21, Plate III.

The articulation of the teeth of many of the *Delphinoidea* with the jaw is not a fully developed gomphosis, but there are more or less well marked dental grooves filled superficially with a tough tissue, which is as essential in fixing the teeth to the jaw as the shallow, often imperfect, sockets, which are excavated in the mandibular and maxillary bones. This superficial supporting tissue around the bases of the teeth is more or less elastic, and allows more or less free motion of the tips of the teeth, which actually for this reason give one the impression of being loose.

This mode of dental implantation is primitive or embryonic or degenerate, because no such high grade of differentiation of the dental system has been attained in the *Cetacea* as in the higher land mammals which use their teeth specifically for grinding the food, whereas the *Delphinoidea* use their teeth mainly for prehension.

Eschricht's researches on the dentition of the fœtus of the Balænoid *Megaptera longimana*, shows that the number of evanescent tooth germs in the upper jaw of one side is 28 and in the lower 42. Those in the lower have a regular distribution, while those of the upper display more or less irregularity of arrangement in the dentary groove. Three germs in the upper jaw in one case are double; that is, are formed of two primary simple cusps of the haplodont form fused together. The spaces between these double or bicuspid germs is greater in two instances than between the simple haplodont germs. This raises an interesting question as to the genesis of bicuspid and two-rooted teeth. Whether, indeed, teeth of the bicuspid type have not arisen in some cases by the fusion or concrescence of two primitively distinct haplodont or unicuspid germs. Such a mode of origin of certain types of teeth from a more numerous unicuspid series of germs is, at least, worthy of serious consideration.

In the fœtus of *Globiocephalus* (Fig. 9, Plate I) the tooth germs were not yet distinguishable in sections as more than pronounced thickenings of the oral epidermis at the point where the dental furrow would appear later. No traces of the enamel organ or of the dentinal elements of the teeth could be made out.

At a similar stage the mammary glands appear as simple thickenings of the epidermis on either side of the genital opening of the female fœtus of *Globiocephalus*. There are as yet only the faintest traces of the mammary fossæ shown in the sections. The rudiment of the gland is a solid pyriform mass of cells which is thrust inwards from the epidermis into the mesoblast.

The brain is quite smooth in the fœtus represented in Fig. 9, Plate I, as in the embryos of other mammals of the same relative stage of advancement. There is a very pronounced cranial flexure, nearly or quite as great as in a human fœtus of the same stage of advancement. This flexure also involves the brain. I find no evidence of the existence of olfactory lobes such as are so well developed in the brains of fœtal Rodents. The cerebral vesicles are quite thin-walled and smooth, so that the lateral ventricles are spacious. The cerebral vesicles are also depressed, and reflected back over the mid-brain to some extent.

III.—The hypertrophy and differentiation of the caudal vertebræ of cetaceans into two series.

One of the most remarkable traits of the cetaceans is the differentiation which their caudal vertebræ have undergone. One may divide these into two groups, viz, (1) those caudal vertebræ intervening between the last of the lumbars and the first one in front of the flukes, and (2) those terminating the vertebral column and lying between the bases of the flukes. The first group is characterized by the remarkably uniform vertical diameter and length of their centra and well-developed chevron bones; the second, on the other hand, have lost all but the merest traces of processes, and rapidly diminish in size so that the last centrum may be present only as a diminutive osseous or cartilaginous nodule.

The uniform dimensions of the centra of the first or anterior group indicates that the posterior ones of that series at least have been hypertrophied, obviously in correlation with the vast supra and infra caudal musculature, while the second group shows unmistakable signs of gradual degeneracy increasing from the first to the last. The change from the type of the first series to that of the posterior or second one is remarkably abrupt in some forms, the latter exhibiting degeneracy in the most striking way by the loss of the cylindrical form characteristic of the centra of the first part of the caudal series and the assumption of a depressed, rounded, or in some cases almost globular form.

This uniformity in the length of the centra of the first subdivision of the caudal bones is probably an adaptive character, and one which has been evolved *pari passu* with the differentiation of the great caudal muscles, the caudal skeleton and musculature actually assuming the function of the hind limbs. The hypertrophy, however, which we have noticed must, since it would have tended to increase the length of each one of the first series of centra, also have tended to lengthen, as well as strengthen, the tail, and thus aid in carrying the flukes farther back from their original position in the ancestral cetacean type, with the thighs and legs of its hind limbs bound together with the tail by integument, and when the tail must still have been extended between the pedes, this supposed ancestral form doubtless being the possessor of a greater number of caudal vertebræ than are found in the existing seals.

We at any rate find nothing like such a remarkable differentiation of the caudal vertebræ in any other mammals except cetaceans, and the inference is that such a differentiation into regions is intimately bound up with the acquirement of an important new function in connection with the outward vestiges of the feet now borne upon its sides, and which, by the process of hypertrophy of the anterior series of osseous caudal segments, it aided in still farther translocating backward after the skeleton and muscles of the hind limb had atrophied in the ancestral type. In other mammals the centra of the caudal vertebræ at once gradually diminish in vertical diameter from the sacrum backwards to the end of the tail, the posterior ones often tending to become depressed, a tendency which is also exhibited by the posterior or second caudal series of whales. This character places the cetaceans in contrast with all other mammals except, probably, *Halitherium*, *Rhytina*, and *Halicore*.

"Muscles which represent the *psoas minor* and the subvertebral muscles of the *Cetacea* are very large and play an important part in effecting the locomotion of the seal," says Huxley, so that we actually find that a beginning has been made in the development of an axial muscular apparatus in the seal which in the *Cetacea* has been extended both forward and backward and has attained tremendous proportions. The movements of pinnipeds and cetaceans in the water are somewhat similar. Both can in fact move rapidly along an undulating course by flexing the hinder part of the body up and down. Such a similarity in the habits of movement of the two animals it is hard to believe are not related to each other as to origin through a remote common ancestry. It is nevertheless difficult to understand the way in which the caudal musculature of the *Cetacea* has been developed with the concomitant differentiation of the caudal vertebræ into an anterior and posterior series, unless it be supposed that, as the flukes become more or less rigid the posterior vertebræ included between their bases would tend to degenerate, whereas the anterior series of vertebræ would tend to develop in proportion to their functional importance as a substitute for the skeleton of the hind limbs. This still leaves the question as to the origin of the degenerate caudal vertebræ of the pinnipeds unanswered and brings us face to face with an aspect of the question which does seem to throw some light upon this phase of the subject. I hardly think any naturalist will dispute the conclusion that a mammalian type could have originated anywhere else than on land in order to successfully develop its air-breathing and characteristic modifications of structure. Such a conclusion carries with it the implication that the whales have been derived from land forms, as seems indeed to be conclusively proved by the adult anatomy and especially the presence of certain structures which are on the way to complete atrophy. In land mammals, however, the tail is in reality always degenerate and often quite as much so as in the seals, for no matter how long the tail may be, if the diameter of its base is far less than that through the pelvic region immediately in front of its base, we may be certain that degeneracy from the primordial type, as seen in fishes, amphibians, and some reptiles, has occurred. In the last-mentioned types there is no such abrupt distinction between the trunk and tail as in land mammals. The inference, therefore, is that the tail of cetaceans, though probably derived from one in which there were more vertebral segments than are found in the tail of any existing pinniped, has been developed from that of a land mammal in which the tail was already degenerate and of comparatively little functional importance, just as we have seen is the case in the seals.

The difficulty which seemed to present itself in regard to the degeneracy of the pinniped tail, therefore also disappears, and a new question arises, viz: How was the gradual muscular degeneracy of the hind limbs of our ideal protocetacean form related to the increasing functional importance of the tail with a gradual new development of muscle over a region where it had been once before lost, in the course of the evolution of the mammalian type? The answer to this, it seems to me, has been already given, but it may be well to discuss it anew in another form.

As the fish-like form of the hind part of the pinniped's body became more pronounced as a result of advancing inclusion, we saw that the hyposkeletal flexors of the back part of the trunk became more developed. With increasing enfeeblement of the hind limbs the caudal skeleton and musculature would become stronger, indeed the one would *gradually exchange functions* with the other, so that no violent or sudden transfer of function is contemplated or even necessary. In fact, the exchange in all probability occurred in the water, in which medium it would be alone possible to develop a tail like that found in cetaceans, in which it indeed attains the maximum of importance as an organ of locomotion. While an old organ was vanishing and itself no longer capable of dissipating vital energy in the execution of its office as a part subservient to locomotion, a part of this old organ combined with another coexisting degenerate organ, the tail was hypertrophied and assumed the office of the posterior pair of limbs.

IV.—Degeneracy of the Pelvic Girdle and Hind Limbs in Cetacea.

One of the most striking features in the structure of the pelvis of *Pinnipedia* and *Cetacea* is the absence of a well-defined *symphysis pubis*, the pubes forming no extensive amphiarthrodial union as in most *Mammalia*. A well-developed symphysis pubis is absent in all of the species of the first-named group, with the exception, perhaps, of the walrus, which seems to be less modified generally in the structure of the pelvis and hind limbs. The other types in which there is a loose or distant connection of the pubes by means of a transverse interpubic ligament are the Sloths amongst the *Edentata*. The separation of the pelvic elements in the median line is carried to an extreme degree in the existing *Cetacea*, and in consequence of the fact that the pubic bones are probably absent in these forms, Struthers has named the ligamentous bond which joins the pelvic rudiments together across the median line the interpelvic ligament. To this are attached the crura of the penis in the *Cetacea*.

Struthers regards the pelvic bones of the latter as consisting of the ischium alone, since it developes from a single center of ossification, which I can fully confirm on the basis of the evidence presented by the structure of its cartilaginous rudiment in sections of an embryo of *Globiocephalus melas*, 2 inches long. In this embryo it seems to be proportionally of greater dimensions, however, than in the adult, which is simply evidence in favor of the view that it is really degenerate in the adult and has been reduced from a pelvis which in some ancestral form was still more developed.

The ilium has been atrophied, and in this way it happens that the pelvis of *Cetacea* and *Sirenia* has been separated from the vertebral column by a very considerable interval, and has been brought to assume only a subsidiary function, as shown by the researches of Struthers, viz, that of giving support and attachment to the organs of generation, and not that of giving attachment to functionally or strongly developed limb muscles as in normal mammals.

The atrophy of the pubes has left only an imperfectly developed ischium, and, perhaps, if anything of ilium, only the abaxial or distal part. The nodules of cartilage observed at the ends of the pelvic element in some forms do not necessarily indicate rudiments of the ilium and pubes, but possibly epiphyses only.

The displacement of the pelvis of cetaceans downwards, it seems not unlikely, has been helped by the great development of the bellies of the psoas or hyposkeletal group of muscles above it, as the massive flexors of the tail.

Rudiments of the femur and tibia were discovered by Reinhardt in 1843 in *Balæna mysticetus*. Since then the most valuable contributions to this subject have been made by Dr. John Struthers in papers* dealing with the anatomy of this region.

In a number of specimens Dr. Struthers obtained the following measurements: Length of pelvis of males, $8\frac{1}{4}$ to 20 inches; in females, $10\frac{3}{8}$ to $18\frac{7}{8}$ inches; length of femur in males, $5\frac{1}{2}$ to $8\frac{1}{4}$ inches; in females, $3\frac{5}{8}$ to $8\frac{1}{2}$ inches; the length of the rudimentary tibia ranged from $2\frac{3}{8}$ to $4\frac{1}{4}$ inches. It is thus rendered obvious that there is a great range of variation in the development of these elements, in fact in one instance it was found that in a female the head of the femur of one side was anchylosed to the pelvic bone of the same side.

The femora were found to be flattened laterally, the head and neck partaking of this character. A posterior proximal tubercle was observed which was regarded as a *trochanter major*. "If the ordinary mammalian femur, much shortened, be flexed, adducted, and rotated outwards, it will be brought into the position of the femur of *mysticetus*; more exactly, if the pelvis and femur of a seal be taken in the hands and so manipulated, the correspondence becomes evident, and it is seen then that this tubercle is the *trochanter major*." (*Op. cit.*, p. 155.)

Cartilage was markedly developed on the upper and condylar extremities, and the head was received into an imperfectly developed acetabulum in some cases. The tibia was represented by what is evidently only its proximal end, and was wholly cartilaginous and pyriform in shape.

Struthers† states that in *Megaptera longimana* "he found the thigh bone to be entirely composed of cartilage, of a conical shape, the length being $5\frac{1}{2}$ inches on the right side and 4 on the left. It was encased in a mass of fibrous tissue. This fibrous case was connected internally to its fellow of the opposite side; superficially and on the outside to the posterior pelvic muscular mass, and anteriorly passing from the thigh bone itself, was a special band appearing like a fibrous prolongation of the bone. The thigh rested loosely on the pelvic bone without articular surface, but was bound loosely to the latter by a strong posterior ligament, and by a weaker ligament in the position of the hip joint in the

* The bones, articulation, and muscles of the rudimentary hind limbs of the Greenland right whale (*Balæna mysticetus*). Journ. Anat. and Physiol. XV, 1880-'81, pp. 141-176 and 301-321, with Plates XIV-XVII.

† On the rudimentary hind limb of *Megaptera longimana*. (Am. Naturalist, XIX, 1885, p. 125.)

right whale. A muscle about the size and shape of a forefinger, within a ligamentous tube, connected the thigh bone backwards to the great interpelvic ligament. This was the only muscular structure directly connected with the thigh bone. It would retract the bone. The fibrous connections of the bone were mainly adapted to resist outward and forward traction." This quotation, I think, indicates quite clearly that the most recent functional relations of the muscles of the rudimentary thigh in the series to which *Megaptera* belongs were posterior to it, as in fact all the other available evidence has tended to show.

In every specimen of these parts from *Balæna* figured by Struthers the femur had its lower end swung forward, as it seems the femur of the seals usually is, and as it is found in the living eared fissipeds when standing on all-fours. The tibial rudiment, on the other hand, lies with its axis in a horizontal position or nearly, such as is assumed by that bone in the pinnipeds, the distal apex being directed backward toward the flukes.

This arrangement of the limb bones of *Balæna* not only justifies to a great extent the views here assumed as to the nature of the flukes, but also that of Struthers, who, on the basis of his observations on the rudimentary finger-muscles of *Megaptera longimana*,* concludes that the *Cetacea* have descended from a form in which limbs were much better or functionally developed; an opinion also entertained by Flower. Such a conclusion is also justified by the existence of synovial bursæ between the head of the femur and the pelvic bone and between the femur and tibia of *Balæna*, according to the former author's observations.

I think, indeed, we may go a step farther and declare with perfect safety that inasmuch as only the proximal end of the tibia is developed in *Balæna* as a degenerate element, which is not even ossified, and which has its distal end pointing backwards, the tibia, if fully developed and extended posteriorly to its normal length as found in other mammals, or as in the seals with the tarsus superimposed upon its distal extremity, it must be evident to every reasonable morphologist that the limb or pes would not be extended outward laterally from the body in a transverse vertical plane with the acetabulum, as is the case in terrestrial mammals, but would be extended back horizontally from the lower end of the femur as in the seals, and the limb not become outwardly apparent until some distance behind the vertical line drawn through the hip-joint. It thus becomes obvious that translocation of the distal part of the pelvic limbs of cetaceans has positively taken place, or, in other words, that the crural, tarsal, and phalangeal parts of these limbs have been rotated backward, and included from before backward by the integuments as in the seals. This inclusion, however, has probably been even more complete in cetaceans than in pinnipeds as a consequence of disuse of the still exserted feet as ambulatory organs and their utiliza-

* See American Naturalist, Feb., 1885, XIX, pp. 126, 127.

tion as swimming paddles or oars in the water exclusively, thus affording an explanation of the atrophy of the bones and muscles of the crus and pes. That the inclusion of the hind limbs has been more extensive than in the seals is shown by the fact that the end of the caudal series of vertebræ is included between the bases of the flukes or pedes of cetaceans, and that no trace of the end of the tail as found in the former is externally visible, unless the rounded tip of the early embryo cetacean's tail is comparable to that part of the seal's which is still exserted.

"In the small *Balænoptera rostrata* a few thin fragments of cartilage, embedded in fibrous tissue, attached to the side of the pelvic bone, constitute the most rudimentary possible condition of a hind limb, and could not be recognized as such but for their analogy with other allied cases. In the large Rorqual, *Balænoptera musculus*, 67 feet long, previously spoken of, I was fortunate enough in 1865 to find attached by fibrous tissue to the side of the pelvic bone (which was 16 inches in length), a distinct femur, consisting of a nodule of cartilage of a slightly compressed irregularly oval form, and not quite 1½ inches in length. Other specimens of the same animal dissected by Van Beneden and Professor Struthers have shown the same; in one case partial ossification had taken place."*

It is singular that no traces of rudiments of these proximal limb-bones are to be seen as cartilaginous nodules in the region of the pelvis of very young *Delphinoidea*, but I find no evidence of the existence of any such structures in sections of the pelvic region of a very young fœtus of *Globiocephalus*.

In the cases of the adult specimens of *Balæna* dissected by Struthers there was an interval of several inches between the pelvic bones, which was bridged by an interpelvic ligament. On comparing the pelvis of a pinniped (*Otaria* or *Phoca*) with that of a Cetacean, a very great difference is apparent. While in the former there is no well-developed symphysis pubis, the pubic bones are not widely separated in the middle line as in the latter. In the former also the pelvis is posteriorly prolonged and the pubic bones together form an acute angle with each other, the opposed bones forming a sort of pubic carina, with the ischia as well as pubes drawn together posteriorly.

The pelvis is quite well developed in the walrus, but in *Phoca* and *Callorhinus* there is obviously a tendency on the part of the whole *os innominatum*, to degenerate and become weak. This fact becomes very obvious when the thin slender ischia and pubes of some pinnipeds are brought to mind, and becomes still more apparent upon comparing the pelvic girdle with the well-developed scapula of the same skeleton, though in order to thoroughly realize the fact that the pelvis of the pinnipeds is degenerating one must compare a skeleton of the latter with the skeleton of a Fissiped of about the same size. The very great

* On Whales, past and present, and their probable origin. Nature, XXVIII, 1883, p. 228. A lecture by W. H. Flower, before the Royal Institution, May 25, 1883.

disparity in the size and strength of the scapula and pelvic bones of *Callorhinus* is obviously indicative of the commencing atrophy of the latter elements.

The fact of the proximal parts of the limbs and pelvis becoming included in the pinniped, as already described, explains how this tendency toward degeneration of the pelvic girdle has been brought about. If we now imagine such a process of inclusion to be carried still farther so that even the tarsus becomes tied down to the side of the tail, the pes will become immobile even though there were an exertion of power manifested by the muscles of the limb. This would carry the condition of inclusion of the hind limb a step farther than that found in any seal and represent a condition intermediate between the latter and the whales, and, as a result of the increased immobility of the hind limbs following upon the supposed condition, not only the muscles but also the bones of the leg and pes would atrophy. In consequence of this atrophy of muscles and bones two other systems of organs would become involved, viz, the blood-vessels and nerves, especially all the distal branches or continuations of the external iliac and femoral arteries, and the efferent veins would suffer modification and gradual diminution, because they had now become more or less useless as conveyers of nutriment and waste to and from muscles which were becoming useless. The motor and sensory nerves in like manner which pass to the hind limb would for similar reasons atrophy, inducing profound changes in the structure of the lumbar plexus, involving the suppression or abortion of the great sciatic, crural, and obturator nerves, and concomitantly with the atrophy of the nerve supply ordinarily passing to the skeletal, muscular, and dermal parts of the functional limb, there would follow a hypertrophy of the nerves of the tail, commensurate with its functional importance, ending in the formation of a lumbo-caudal plexus extending from the lumbar region to its termination.

The atrophy of the parts of the skeleton of the limb ought to occur on my hypothesis, in an order which, passing from without inwards, would be just the reverse of that of its development. Upon comparing the mode in which the pelvic girdle and the limbs develop, with the different degrees of atrophy as displayed in a number of cetacean forms, we find that the preceding statement is verified.

It is found in fact that the pelvis at an early stage of development is separate from the vertebral column and that the girdle and limb bones are formed as segments in a serial order from within outwards, the pelvis and femur being first developed, then the tibia and fibula, then the tarsus, and finally the phalanges. In this same order they also become differentiated as distinct pieces, or from within outwards.* The reverse of this is obviously the order in which the skeleton of

*See a paper entitled: On the development of the pelvic girdle and skeleton of the hind limb in the chick, by Alice Johnson. Studies from the Morph. Laboratory of the University of Cambridge. II, pp. 3-25, pls. IV-V.

the limb in the cetaceans has atrophied, that is, the phalanges first, then the tarsus, then the fibula and tibia, and finally the femur, affecting also more or less the degeneration of the pelvic girdle.

But it will be inquired, why do the limb-folds, or pedal folds, which represent the former in cetaceans, grow out at all after such extensive atrophy of the limb skeleton? To this it may be replied that the distal parts of limb-folds generally do not at first have the skeleton developed within them at all, and that, as I have pointed out, the limb bones develop from within outwards; the terminal part of the limb-fold, or epidermal pocket representing it, contains at first nothing but undifferentiated mesoblast. It thus seems to me that in the skeletonless flukes we have this inverse method of development illustrated, and that the flukes represent the earliest condition of a pes and therefore the last to vanish, unless indeed the flukes represent the produced integuments distad of the last phalanges of pinnipeds, which I think hardly probable, for the reason that their blood-supply, as already described, simulates that of the normal mammalian pes.

Struthers' figures indicate that the femora are adducted distally in *Balæna mysticetus* to a remarkable extent, in fact to such a degree that if the limb were fully developed with the crus extended in a line with the shaft of the femur, the limbs of opposite sides would cross each other. This adduction of the femora by which their distal moieties approximate each other, is probably due to the after effects of the process of inclusion which must have begun with a seal-like ancestral form, and which has reached its extremest expression in existing cetaceans, where the growth of the subcaudal muscles has influenced their final position.

The inclusion and degeneracy of the pelvis of cetaceans being so complete, there is however not so great a posterior extension of the abdominal muscles backward as one might be led to expect, but certain muscles are nevertheless provided with remarkably posterior insertions.

V.—THE CAUDAL MUSCLES OF CETACEA.

These are dorsally continuations of the deep *multifidus spinæ* and the superficial *erector spinæ*, posteriorly; anteriorly as continuations of the above, as found in the human subject, the *sacrolumbalis*, *longissimus dorsi*, *spinalis dorsi*, and possibly the *semispinalis* of man are represented in the vast dorsal and supracaudal musculature of whales. Murie* states that in the black-fish "the longissimus dorsi and spinalis dorsi are most intimately bound up together in the dorsal region, forming a long, but enormous fleshy mass, interwoven spinally and costally with tendinous fascia. That which may be considered equivalent to a transversalis cervicis commences by a short, strong tendon at the paramastoid. Immediately becoming fleshy and thick, it ascends posteriorly

* On the organization of the Caaing Whale (*Globiocephalus melas*), Trans. Zool. Soc. London, VIII, 1872-'74, pp. 235-301, pls. 30-38.

on the side of the neck to the anterior dorsal region, and is lost in the combined longissimus and spinalis dorsi. Where the body begins to taper behind a division of the two latter is perceptible. Hereabouts a superficial tendon passes obliquely upwards and backwards from the outer longissimus to the inner spinalis. A little way behind, another bridge of two oblique tendons similarly crosses, and immediately posterior to this five more, which together unite into a strong cord, wrapped one within the other. Meanwhile from each muscle there is continued posteriorly, quite to the end of the spinal column, a single, thick, massive tendon. Besides the foregoing, both longissimus and spinalis dorsi possess a deep series of long, narrow tendons, one to each vertebra, but mingled together by interstitial fleshy fibers. It results that these dorsal muscles act upon every vertebra independently, whilst at the same time the motor power of the fibro-cartilaginous tail is derived from the lengthened and more powerful cords, for from these there extends backwards a firm, glistening fascia, spread over and incorporated with the deep tail substance.

"Supra caudal. The single muscle (or compound muscle, if so regarded) to which I give this appellation lies external to the last, along the narrow portion of the caudal vertebræ and on the upper side of the transverse process, narrow in front, where fleshy, it widens somewhat and forms a tolerably thick fusiform belly, which again flattens and becomes tendinous. In its course it is attached partly to the vertebral bodies and partly to the transverse processes, sending off a special tendon to each of the latter. Posteriorly the flattened tendon lies against the sides of the bodies of the terminal vertebræ, and ultimately is lost in the general expansion of the upper surface of the tail flukes.

"Coming under the denomination of multifidus spinæ and rotatores spinæ, because of their position, origins, and insertions, are a great number of musculo-tendinous bundles, very apparent and well marked, but difficult individually to separate and define. These are still more numerous and closely packed together in *Lagenorhynchus* than in *Globiocephalus*, in consequence of the number and approximation of the vertebræ in the former. Stannius recognizes such a deep set of muscles in the porpoise; and I can corroborate his observation in that genus. Their general arrangement is by tendons from the dorsal metapophyses, and trending forwards and inwards are attached muscularly to the sides of the roots of the spinous process in advance of their origin. The most anterior one is fixed to the atlas.

"But there are besides a deeper layer of fascicles springing tendinously from the spines and dorsal arches, and these becoming fleshy are inserted into the transverse processes of the same vertebræ, doubtless semispinales ,as Stannius* names them in *Phocœna*. He alludes, moreover, to another set of fasciculi, close to the last, and connected with the vertebral processes, but he has not named them.

* "Muskeln des Tümmlers," Muller's Archiv, 1849, p. 30.

"In the four-limbed mammals generally there are three, or at most four, muscles described as occupying the iliac region, viz: the psoas major, psoas minor, iliacus and quadratus lumborum. But in cetaceans, as most writers state, there is only one enormously large inferior lumbo-caudal muscle, which, at first sight, might be supposed either to represent the psoas magnus alone, or the psoas minor, iliacus, and quadratus lumborum incorporated with it. Whatever relation exists, division at least is inappreciable in *G. melas*. This enormously developed sacro-coccygeus muscle is long and fusiform. On each side it occupies the lateral and inferior surfaces of the vertebræ and their transverse processes from the ninth dorsal vertebræ backwards; and as the transverse processes of the caudal elements are lost, it still continues upon them in the shape of a bundle of tendons continued on to the very end of the spinal column. The volume of its solid fleshy fiber may best be comprehended in the fact that it ranges in our specimen of *Globiocephalus* from one foot to six inches in transverse diameter, and with a corresponding thickness or depth. Further to particularize attachments and relations, it passes beneath the diaphragm, has the kidneys, &c., lying upon it, and narrowing behind the rectum sends off, downwards and backwards, superficially, a series of flat tendons. These are so connected together as to constitute a very strong tendino-aponeurotic sheath, spreads out and is continued on to the inferior surface of the broad fibrous tail. The main body of the fleshy mass meanwhile terminates in a single strong tendon, which passes direct along the spine and is fixed to the very last vertebra. Moreover, there is an appreciable flat layer of fleshy fibers, which come from the sides of the vertebræ and spread over part of the aforesaid tendinous sheath. This muscular layer appears to be a kind of reduplication of the body of the muscle itself.

"A muscle, the exact counterpart of the supracaudal, lies on the under side of the transverse processes of the caudal vertebræ, and it bears the same relation to the sacro coccygeus' that the supracaudal does to the longissimus dorsi, save the fact of inversion of position. I distinguish it as the infracaudal.

"The long spinal muscles of Cetacea have received different names and significations from successive anatomists, though the descriptions, save that of Stannius, tally. Meckel * demonstrates the parts in the narwal (*Monodon communis*) and the dolphin (*Phocœna communis ?*). His text appears to me to imply that he considers present and more or less differentiated: 1. An equivalent of the spinalis dorsi, biventer cervicis, and complexus, a longissimus dorsi, trachelo mastoid, and splenius capitis; 2. A sacro-lumbalis with cervicalis ascendens anteriorly ('trachelo-mastoïdien, ou l'intertransversaire du cou' of his translators); 3. Flexor caudæ lateralis; 4. Depressor caudæ, quadratus lumbarum, psoas and iliacus; 5. An inferior depressor caudæ. Frederick Cuvier † speaks of

* Anat. Comp. Vol. VI., p. 128 *et seq.*

† Art. Cetacea. Cyclop. Anat. and Physiol. I, p. 569.

a levator caudæ, evidently No. 3 above. Rapp* and Stannius† coincide that there obtains: A splenius capitus longissimus and spinalis dorsi, sacro-lumbalis and transversarius superior and inferior. The former thinks the great lower loin-muscle a psoas major; to the latter it implies more. Stannius, moreover, describes a caudalis superior, a caudalis inferior, a longissimus inferior, a sacro-lumbalis inferior, and a set of caudal muscles unnamed by him. He also traces the short, deep spinal muscles, of which more hereafter. Carte and Macalister, in the piked whale,‡ have noticed a trachelo-mastoid, a longissimus dorsi, a sacro-lumbalis, with a slip supposed to be the homologue of splenius capitis, a levator caudæ, a depressor caudæ major, and depressor caudæ minor.

"Notwithstanding the amplitude of nomenclature and recognition of two or more *en masse* or separate, the anterior divisions of the various observers present a certain harmony; but there is less concord of opinion regarding the posterior tendinous parts and infero-lumbar region. Rapp and Stannius differentiate as transversarius superior the compound tendinous enwrapping sheath of the longissimus and spinalis as described by me. But the latter, moreover, unites it with the anterior fleshy belly of my supracaudal, and traces it forwards to the ribs, thorax, and neck, *i. e.*, includes part of what more strictly is sacro-lumbalis and cervicalis ascendens. Carte and Macalister's levator caudæ agrees partially with Rapp's transversarius, and partially with Stannius's caudalis superior. The latter muscle, again, is equivalent to Meckel's flexor caudæ lateralis and F. Cuvier's levator caudæ, one and the same with my supracaudal. None suggest the superior superficial terminal tendons, or aggregate fibrous investing-sheaths of the longissimus and spinalis dorsi, as the homologues of the levatores caudæ externus and internus of other mammals. Yet in every sense they are undoubtedly such, continuity with the dorsal fleshy masses being the only special deviation from their usual condition. The cetacean supracaudal, again, offers homology in its posterior short slips with the intertransversarii caudæ of the quadrupeds; it is longer bellied and more fleshy, anterior moiety being occasionally in mammals almost separate from the intertransversarii caudæ, though not specially recognized as a distinct muscle. In *Manatus*, however, it is uncommonly well developed, and has been named by me lumbo-caudalis. The inferior depressor caudæ of Meckel, depressor caudæ minor of Carte and Macalister, caudalis inferior of Stannius, and his unnamed musculo-tendinous caudal bundles, correspond with the present infracaudal.

"As regards the depressor caudæ of Cuvier and Meckel, the depressor caudæ major of Carte and Macalister, this undoubtedly is Rapp's psoas major, &c. Stannius viewed it as composed of three divisions,

* *Die Cetaceen*, zool-anat. dargestellt, 1837, p. 92.

† Muller's Archiv, 1849, pp. 22–32.

‡ On the anatomy of *Balænoptera rostrata*, Philos. Trans., 1868, p. 225.

equivalent to the dorsal muscles, and named by him respectively longissimus inferior, sacro-lumbalis inferior, and transversarius inferior. So far I agree with the latter, and therefore differ from Rapp, that the great sublumbo-caudal cetacean muscle is not purely an ilio-psoas. This latter, I believe, as in *Manatus*, is all but aborted, certainly not recognizable. The homologue of the cetacean sublumbar muscle, then with its tendons and investing sheath, seems to me to be the sacro-coccygeus, whatever its significance as to the dorsal series. My infracaudal may represent partly inferior intertransversarii caudæ or perhaps include infracoccygeus.

"In default of being able to determine with accuracy spinal insertions in *Globiceps* I was more fortunate in *Lagenorhynchus*. In this genus the rectus abdominis tapers to a point at the fortieth vertebra, behind this intermingling with the caudal fascia. The pubo-coccygeus goes to the chevron bones as far as the sixtieth sacro-coccygeus, muscular to forty-fifth, tendons to sixtieth; between these points the secondary tendons which form the sheath emerge. Supracaudal from fortieth to sixty-sixth vertebra; the infracaudal is from two to three vertebræ shorter. Longissimus dorsi, &c., narrows at sixtieth; two oblique tendons given off at thirty-seventh; the others behind, ere producing aponeurotic sheath the spinalis dorsi, &c., its final tendons inserted from the sixty-fourth to the seventieth vertebral diapophyses.

"A series of levatores costarum, of moderate strength, and passing from the transverse processes to the ribs, exists in all the species of whales I have dissected.*

"In the lumbar region of *G. melas* the intertransversales† are powerful, they diminish in strength forwards, and can barely be detected in the most anterior dorsals and cervicals. In *L. albirostris*, whilst fleshy, they are shorter, owing to the close approximation of the very numerous and long divergent transverse processes. In *P. communis* caudally they are tendinous; in the lumbar region, semitendinous and fleshy, a superior and inferior division is noticeable.

"According to the development of the neural spines, cervical, dorsal, lumbar, and caudal, so are the interspinales‡ strong or weak. But as a series of muscular bundles they are, I believe, present in every cetacean. They have been met with by me in five genera.

"Both Rapp§ and Stannius|| have described in the porpoise a set of muscles linking together the chevron bones. They name these M. interspinales inferiores. They are distinctly marked in *Globiceps*, *Grampus*, and the white-beaked Bottle-nose and Rorqual. They undoubtedly resemble the interspinales superiores of these authors, but pass from one chevron hæmo-spinal element to the adjoining. I prefer to designate

* Described also by the oft-quoted German authorities.

† The intertransversarii of the foregoing.

‡ The m. interspinales superiores of the preceding writers.

§ *Op. cit.*, p. 83. || *Op. cit.*, p. 40.

them as interhæmo-spinales, this term being more in accordance with morphological anatomy. Stannius likewise differentiates and names as m. interaccessorii a number of tendino-fleshy fascicles which intervene between the one and the other accessory spinous processes of the lumbar and dorsal vertebræ, in a longitudinal direction. These have not been observed by me, but I am inclined to regard them as intermetapophysiales."

As already urged there can be no doubt of the fact that the great infracaudal or hyposkeletal muscles of the tail of cetaceans are in part homologous with the psoas major and minor of quadrupeds. In fact, the infracaudal and sacro-coccygeus of Murie are but a system of psoas muscles prolonged rearwards together with caudal muscles, and developed to an extent not encountered in other types. The quadratus lumborum may also be represented. Whatever is the truth as to the exact homologies of these muscles, a fact which will not have escaped the critical reader's attention, is Murie's mention of the final direct and indirect insertion of the tendons of the caudal musculature into the flukes. The psoas being represented in the hyposkeletal musculature is thus found to have had its insertion greatly shifted in a posterior direction so as to act upon the flukes—degenerate pedes of *Cetacea*—instead of upon the lesser trochanter of the femur as in normal forms. We thus find that the backward translocation of the muscular insertions of the limb muscles which began in a seal-like type has reached its extremest expression in the whales, in which we can with certainty, however, assume this much of what is in reality part only of the psoas of land forms, in which it is usually inserted into the femur.

This tendency towards a backward extension of its insertion is also obvious, for instance, in the rectus abdominis. Murie* remarks of it: "The rectus abdominis, which I have already described, partly mingles with the generative muscles, inasmuch as its posterior narrowed extremity and terminal tendon enclasp the deeper fleshy structures of the vulva and winds round each innominate bone, finally being inserted into the neighborhood of the chevron bones."

VI.—The Lumbo-caudal Plexus of Nerves in Cetaceans.

The only published account of the posterior part of the spinal nervous system of cetaceans which I have been able to find and which is at all complete, is that given by D. J. Cunningham, based on dissections of the porpoise and dolphin.† In the porpoise, Cunningham found that the spinal cord extends from the foramen magnum to the interval between the sixth and seventh lumbo-caudal vertebræ, and ends opposite the foramina giving exit to the twenty-seventh pair of spinal nerves.

* *Op. cit.*, p. 288.

† The spinal nervous system of the porpoise and dolphin. Journ. Anat. and Physiol., XI, pp. 209–228, Plate VII.

The *filum terminale* passes back into the vertebral canal for a short distance and is lost. The origins of the spinal nerves are crowded together in the cervical region in correspondence with the shortening of the vertebræ of this portion of the column. In the dorsal region the origins of the pairs are farther apart, but from the lumbar enlargement backward they are much crowded together. The seventh, eighth, ninth, tenth, and eleventh pairs of the lumbo-caudal nerves unite to form the genital or internal pudic, but as there is no functionally mobile hind limb, the branches corresponding to the genito-crural, obturator, external cutaneous, anterior crural and sciatic are absent. The internal pudic is well represented. Small twigs only from the seventh and eleventh lumbo-caudal pairs enter into the formation of this nerve. It pierces the great inferior lumbo-caudal muscular mass, and passing obliquely backward through it divides inferiorly into several branches which innervate the reproductive organs.

From the eleventh lumbo-caudal pair all the inferior divisions join to form the inferior longitudinal cord or plexus, the last pair entering the lower cord opposite the twenty-sixth lumbo-caudal vertebra. The inferior lumbo-caudal cord supplies the psoas or infracaudal muscles in *Cetacea* the same as do the ilio-hypogastric and ilio-inguinal nerves in man.

The hinder pairs which go to form the great inferior and superior lateral cords, the first above the latter below the transverse processes, pass backwards for a long distance, the hinder ones for about the extent of nineteen vertebræ as a strongly developed bundle or cauda equina, twigs from which pass out on either side, a dorsal one to the dorsal cord, and a ventral one to the ventral cord, through the intervals between the neural arches of the lumbo-caudal vertebræ. The ventral twigs pass down between the transverse processes.

The four great lumbo-caudal cords, two above the transverse processes and two below them in the porpoise, judging from the muscles which they innervate in the latter, are respectively the homologues of the "posterior" and "anterior" branches of the lumbar nerves in man. Unlike the latter, however, in consequence of the great bulk of the dorsal extensors of the tail, *longissimus dorsi*, *erectores spinæ*, and *multifidus spinæ*, there has also been a dorsal plexus differentiated which leads to the formation of the dorsal lumbo-caudal cord. Inferiorly the plexus has not the limited extent posteriorly as found in man where it is partially represented by the lumbo-sacral cord, but is extended backwards quite to the flukes, as the inferior lumbo-caudal cord.

Comparing the nervous system of the fish and cetacean, Cunningham remarks: "From the spinal cord passing so far back in the vertebral canal (in the former) it follows that the nerves which supply the caudal apparatus have a very short course to run from their points of origin to their distribution. Very different is the arrangement of the corresponding nerves in the *Cetacea*, which spring from the lumbar enlargement at a point far in front of their areas of distribution. In the first, therefore, there is no need for the longitudinal cords for the purpose of conveying the nerves to the caudal apparatus—the spinal cord is their substitute." He also points out that the vagus trunks running back to the tail in fishes are not homologous with the lateral caudal trunks of *Cetacea*.

While the adult anatomy of the caudal nervous systems of Cetaceans and most fishes are dissimilar (for it must be borne in mind that some Teleosts have a cauda equina developed, *Mola* for example), in the early embryonic condition the medulla spinalis of the mammalian embryo is without a cauda equina. This is so in the human fœtus (*vide* Kölliker, *Entwick. des Menschen*) and is also the case in the Cetacean fœtus according to my own researches on the fœtus of *Globiocephalus melas*, represented in Fig. 9, Plate I, where, as in the former, the medulla spinalis extends to the end of the tail, and, as shown by its microtomy, contains a central canal when examined in consecutive longisections. It is thus rendered obvious that the mammalian embryo recapitulates the ichthyopsidan mode of development of the nervous system, but subsequently reverts to the more recently evolved mammalian type as respects its posterior extension. Its rearward extension in the mammal is shortened in consequence of caudal degeneration and the development of tendons as the terminal or caudal extensions of muscles developed from a succession of muscular somites or myotomes, from between which intermyocommal septa on fasciæ have disappeared. The principal muscles which may be considered to have arisen directly from single myotomes are the intercostals and intertransversarii. The *rectus* is known, according to researches on fishes, to arise from the lower portion of a series of successive myotomes, from between which intermyocommal fasciæ have partially or wholly disappeared. Other muscles, such as the *trapezius* of man, arise proximally according to embryological theory from 17 myotomes; the *latissimus dorsi* from 20; the *rhomboideus major* and *minor* from 5. The manner in which the shifting of the course of the fibers from the direction which they originally pursued in the indifferentiated myotomes and the acquisition of restricted insertions is still one of the greatest problems of embryology, for which we may hopefully look forward to a solution, only through extensive studies on the development of the muscular system from the amphibians upward.

The rearrangement, differentiation, and great specialization of the muscular system of higher forms through the suppression of the myotomes, as seen in fish-like forms, has affected the development of the nervous system and led to the differentiation not only of ganglionic centers along the course of the medulla spinalis, such as the cervical and lumbar enlargements, from which arise the nerves which innervate the fore and hind limbs, but also conditioned the evolution of the limb-plexuses and caudæ equina. *Mola*, a fish which presents a remarkable differentiation of the lateral musculature, accompanied with extensive abortion of the myotomes, illustrates this principle. In this case, the tail being aborted for the most part, the muscles of the sides of the thorax, which is much elevated, are prolonged backwards and end in tendinous cords which actuate the rudder-like caudal as well as the dorsal and anal fins. The consequent advance of the origins of these muscles forward admits of their nerve supply being sent to them farther forward. We have apparently, as a consequence of this advance forward, the restriction backward of the medulla spinalis.

The inconsiderable development of the musculature of the paired fins of most fishes, and the segmental arrangement of that of the vertical fins, would obviously tend to maintain the uniform backwardly tapering form of the medulla spinalis, as seen in its simplest form in *Branchiostoma*, in which we also behold the most unmodified and archaic type of the myotome or muscular segment.

A consideration of these facts therefore leads me to state the following as a general principle, viz, that *pari passu* with the gradual suppression of myotomes in the course of the progressive evolution of forms and the differentiation of the musculature of the appendicular skeleton was the medulla spinalis differentiated into regions and its rearward extension curtailed in consequence of the degeneration into tendon of the musculature of the urosome.

While the muscles of the base of the tail of cetaceans are prodigiously developed, as rearward extensions dorsally of the *erectores* and *multifidus spinæ* and ventrally as extensions of the system represented by the *psoas* of terrestrial types, they nevertheless, in the region of the caudal peduncle end as tendons, these animals therefore so far resembling other land forms with degenerate tails, so that it is altogether doubtful if motor nerve fibers enter into this portion at all, the presence of sensory and vaso-motor fibers alone being indicated.

The *Cetacea*, according to Cunningham, have the medulla spinalis swollen in the same way as other mammal in the cervical and lumbar regions, whence the limb plexuses originate. A similar differentiation is foreshadowed in the anterior part of the medulla spinalis of the skate, *Raia batis*, according to Owen, in which there is "a slight (brachial or pectoral) enlargement of the myelon, where the numerous large nerves are sent off to the great pectoral fins; a feebler brachial enlargement may be noticed in the sharks. I have not recognized it in osseous fishes, not even in those with enormous pectorals adapted for flight, *e. g.*, *Exocœtus* and *Dactylopterus*; in the latter the smaller ganglionic risings upon the dorsal columns of the cervical region of the myelon receive nerves of sensation from the free soft rays of the pectorals and the homologous ganglions are more marked in other gurnards (*Triglæ*), which have from three to five, and sometimes six, pairs, e. g. in *Trigla Adriatica*. Similar myelonal cervical ganglions are present, also, in *Polynemus*. In the heterocercal sturgeon there is a feeble expansion of the myelon at the beginning of the caudal region, whence it is continued, gradually diminishing to a point along the neural canal in the upper lobe of the tail. In some bony fishes (trout, Blenny) the caudal ganglion is not quite terminal, and is less marked than in the cod and bream, in which it is of a hard texture, but receives the last pair of spinal nerves.*

A little further on the same author states that in *Mola* the myelon "has shrunk into a short, conical, and, according to Arsaki,† gangliated appendage to the encephalon. A like singular modification, but without the ganglionic structure, obtains in *Tetrodon* and *Diodon*, in a species of which latter genus I found the myelon only four lines long in a fish of 7 inches in length and measuring 3 inches across the head. The neural canal in these plectognathic fishes is chiefly occupied by a long 'cauda equina.' But, insignificant as the myelon here seems, it is something more than merely unresolved nerve fibers; transverse white striæ are discernible in it, with gray matter, showing it to be a center of nervous force, not a mere conductor. In the *Lophius* a long cauda equina partly conceals a short myelon, which terminates in a point about the twelfth vertebra. In other fishes the myelon is very nearly or quite co-extensive with the neural canal, and there is no cauda equina or bundle of nerve roots in the canal; a tendinous thread sometimes ties the terminal ganglion to the end of the canal." (Owen, Anat. Vertebrates, I, 272.)

In *Gastrostomus Bairdii*, a fish with an attenuated flagelliform tail, the medulla spinalis at its extreme posterior end becomes very greatly depressed so as to assume in sections the form of a flattened band in which it is almost impossible to discern the existence of a central canal. In very young eels the hinder end of the medulla appears to be connected with a globular enlargement which is quite terminal and possibly external to the neural canal.

Amongst the reptiles, says Owen, "With the exception of the anurous Batrachia, the myelon (spinal chord) is continued into the tail, gradually decreasing to a point, and is not resolved into a 'cauda equina.' Such, indeed, is its condition in the tadpole state of the frogs and toads; but, with the acquisition of the mature form, the myelon shrinks in length and terminates midway between the fore and hind limbs, being resolved in the frog into the three pairs of nerves which form the sciatic, and into a few filaments passing on to the sacrum." (Anat. Vertebrates, I, 295–6.)

The development of the *Anura* therefore confirms the rule, which was laid down above, as to the genesis of a cauda equina. In them the whole of the caudal musculature aborts, together with the caudal end of the myelon, while the hind limbs attain an extraordinary development and specialization of the muscular system, calling for an extraordinary motor nerve supply such as is rarely encountered amongst fishes,

* Owen, Anat. Vertebrates, I, 271.

† De Piscium Cerebro et Medullâ Spinali, 4to, 1813.

and in the latter only when specialization of the lateral musculature has proceeded in another direction, as in the cases of *Mola*, *Tetrodon*, and *Diodon*. The case of *Lophius* is more difficult to understand, though it is a fact that several of the last caudal vertebræ are co-ossified in this genus into a rigid piece, a fact which very possibly indicates a corresponding modification of the musculature of the end of the urosome. In respect to the other modifications, that in *Gastrostomus*, for example, is correlated with the development of a flagelliform tail; that of the eel is not so easy to understand.

The manner in which the lumbo-caudal plexus of cetaceans is developed is not wholly without partial parallels, for the lumbar nerves as they are continued beyond the end of the medulla spinalis subdivide and give off branches to the dorsal and ventral cords external to the neural canal. It results in this way, that two series of commissures are formed, a dorsal and a ventral one; but the latter is in reality formed of fasciculi which are sent down from the dorsally-placed cauda equina, between the transverse processes; the continuous accession of such fasciculi by the ventral trunk, as well as by the dorsal, from each lateral interspinous opening, leads to the formation of what have been called "cords," but they really represent a continued plexus, the segmentally arranged fasciculi of which are easily separated, as I find in *Phocæna*, and traced to their sources. Such a splitting or subdivision at each vertebral segment is apparent in the last pair of lumbar nerves, forming part of the short and rudimentary cauda equina of *Rana*. The formation of the so-called lumbo-caudal cords in *Cetacea* has obviously occurred through adaptation in response to the requirements of the caudal musculature. The suppression of the crural, obturator, and sciatic pairs, on account of the abortion of functional hind limbs, has left over the nerve pairs ordinarily entering into the formation of those trunks, so that their homologues are sent back into the tail, and they therefore potentially, if not actually, enter into the lumbo-caudal plexus, and thus ultimately send filaments at least to the caudal muscalature, and not improbably sensory fibers to the flukes.

If it is admitted that inclusion and abortion of the function of the hind limbs has occurred in the way that I have urged, a transfer of the crural and sciatic fasciculi from the limbs to the tail must have occurred. The anatomical facts show that such a transfer has taken place. I therefore see no reason to doubt the sufficiency of my hypothesis, because I find no evidence of the presence of the nerves which ordinarily pass to the hind limb, as such; on the contrary they ought to be found incorporated into the caudal plexus according to the requirements of the hypothesis. One set of muscles have been almost wholly, or, in some cases, entirely suppressed, and their offices assumed by another set, either of which the same set of nerves can alone supply with motor impulses. Then comes in the suppression of myotomes in the extensor and flexor muscles of the tail, in *Cetacea*, for instance, where the myotomes over 12 to 14 vertebræ are obliterated and converted into tendon posteriorly, so as to call for a new mode of distribution of the nerves different from that which obtains in fishes in which the paired nerves and muscular segments correspond almost exactly in number with the vertebral segments.

VII.—Translocation of the distal ends of the hind limbs in the sirenians.

The fœtus of *Halicore dugong*, figured by Harting,* about 11 inches long, Fig. 22, Plate III, shows the flukes well developed and of much the same form as in cetaceans. Judging from the permanent adult form of the tail of *Manatus* (outer outline, Fig. 20, Plate III), which has the most rudimentary type of fluke, found either amongst cetaceans or sirenians, it is probable that the flukes, in those types having them well developed, viz, *Halicore* and *Rhytina*, grew out as in the former as low lateral horizontal folds. It seems that in Manatee the flukes have been arrested in development so that they simulate somewhat the early stages of the outgrowth of the cetacean flukes, as shown in the accompanying figures of embryos of the latter.

In those fossil forms which are less degenerate than the existing species, *Halitherium Schinzi*, for example, had the rudimentary femur directed backwards towards the flukes just as in the tibia in the existing cetaceans and pinnipeds, according to the interpretations of Lepsius,† who has given excellent figures of the skeleton of this type. This direction of the femur, as already urged in the case of analogously modified forms, is very significant, and goes a great way in helping to substantiate the view that the flukes are also modified hind limbs in the sirenians.

In *Halitherium* there is a well-developed acetabular fossa developed on the pelvic bones for the reception of the head of the femur. Neither femur nor acetabulum is developed in the living genera *Halicore* and *Manatee*. Rhytina probably had the pelvic bones as well developed as in *Halicore*, in which they are present as two pieces, an anterior probably corresponding to the ilium and ischium of normal mammals. The pelvis in *Manatee* seems to be composed of a single almost quadrate element, as seen from the side, and is so reduced that it represents the extremest condition of atrophy of the pelvic elements yet known, unless, as Mr. F. W. True thinks, after an unsuccessful search for this element, it is altogether absent in *Kogia*, the pygmy sperm whale.

This condition of degeneracy of the pelvis of sirenians is manifested

* Description de l'œuf et du placenta de Halicore dugong, suivie de considerations sur le valeur taxonomique et phylogénique des caractères différenticls, fournis par le placenta des mammifères. Tijdschrift der Nederlandsche Dierk. Vereen, Dl. IV, 1879, pp. 1–29, pls. I–II.

† Halitherium Schinzi, die fossile Sirene des Mainzer Beckens. Abhand., des Mittelrheinischen geolog. Vereins, I, Lieferungen 1 and 2, 4to, Darmstadt, 1881 and 1882.

in three well-marked stages, starting with *Halitherium* and ending with *Manatee*. The extreme degeneracy of the pelvis of the latter it would seem is in keeping with the undeveloped flukes of this type, which are mere rounded expansions of the tail, which seems to be simply flattened and widened posteriorly into a sort of spatulate form, as in Fig. 20, Plate III, showing in the outer outline the form of the adult and in the inner outline that of the tail of the embryo, both being quite unlike the tail of *Halicore*, Plate III, Fig. 22, and *Rhytina* with their pointed flukes.

That *Halitherium* ever possessed external limbs appears to me to be exceedingly doubtful inasmuch as its femur is more rudimentary than in *Balæna mysticetus*, and no tibial rudiment seems to be developed.

There is no dorsal fin developed in any one of the three genera of sirenians which have fallen under the observation of naturalists.

As to the affinities of the sirenians, I think it very doubtful if they are to be regarded as having descended from the same mammalian type as the cetaceans, for, with the exception of the degenerate pelvis and distal remnants of hind limbs, they diverge from the normal type far less than do the cetaceans; in fact, relatively but little more in other respects than do the Pinnipedia. That it is possible that they were differentiated by a process similar to that which has brought about the modification of the cetaceans, but from a quite distinct form, I think quite conceivable. Indeed it is quite easy to understand that a perfectly similar change might be induced in two types originally very greatly dissimilar through the long-continued action of similar influences affecting the functional adaptation of the hind limbs, as already suggested in the case of *Ichthyosaurus*.

The length of the free parts of the pectoral limbs of the fœtal Dugong described by Harting was almost exactly half of the total width across both flukes, the length of the former being 5 centimeters, and the transverse width of the latter 10.3 centimeters. This is a very suggestive correspondence, but need not be insisted upon as indicating anything like so near a likeness between the manus and pes as in *Cetacea*, because the fore limb in Sirenians has the arm bones better developed than in the former and extended outward farther beyond the level of the common integumentary covering of the animal. The nails are also more or less well developed on the manus in the manatee.

The smallest fœtal sirenian of which I have been able to find figures and a description is by Prof. B. G. Wilder.* This specimen, of which I reproduce Wilder's original figures, measured 2.3 inches from the vertex to root of tail, 3.7 inches if fully extended. Greatest width of tail 11 millimeters or nearly one-half inch. A view of the hinder part of this embryo, Fig. 20, Plate III, from below shows that the trunk is much more abruptly swollen at the point in front of where the tail begins

* On a fœtal manatee and cetacean, with remarks upon the affinities and ancestry of the Sirenia, Amer. Journ. Sci. and Arts, 3d ser. X, 1875, pp. 105–114, plate VIII.

than the adult, as shown in the outer outline, Fig. 20. The flat lobes of the tail are relatively not as wide transversely as in the adult, and are more gently rounded laterally so as not to have that squarish posterior outline from above as in the adult. It is thus very evident that the tail of the manatee in all probability at first grows out as in the *Cetacea*, as a low longitudinal fold on the side of the tail.

Wilder, however, describes and figures a feature in this embryo which is probably one of the most important which we have had to discuss in this paper. I refer to what he calls a median papilla. He says: "The tail forms nearly a right angle with the trunk. *Upon its ventral border near the tip is a minute median papilla*, which does not appear to have been observed in larger specimens, but there is no trace of the notch or depression described by Dr. Murie in both of his specimens." (P. 106, *l. c.*) I have italicized part of one of his sentences.

This "minute median papilla" is obviously nothing more than the last remaining vestige of the end of a tail exserted beyond the lateral flanges or flukes in this type, and which, as development proceeds, is covered in by the tail folds from before backward; that is to say, as the flukes or pedal folds during development grow still more in length they include this papilla, and finally leave the median notch figured by Murie. The above is nearly the same as what happens in the embryos of Cetacea, as the flukes become falcate, when the tip of the tail proper is found to lie in a more or less well-marked notch, Fig. 15, Plate II, between the flukes of opposite sides, whereas in the very early stages the tip of the tail proper, and not the fluke, is the most posterior point of the creature's backward extension.

But Professor Wilder expressly states (*op. c.*) that "it may at first seem strange that there are no traces of hinder limbs in this fœtus, and that the front limbs are not more like the legs of its supposed quadrupedal ancestors."

"It is by no means *impossible* that an embryo just forming would present rudimentary hind limbs in accordance with the usual vertebrate type." When farther along, Professor Wilder states in his summary that "this, while contrary to the usually accepted rule, may be really an exemplification of a more comprehensive law, namely, *that the young of animals resemble their ancestors*," he has stated a generalization which is to a larger extent true than generally supposed, as I have sought to show in previous papers.

The question here, however, is, have all external traces of hind limbs vanished? The median caudal papilla we have regarded as the end of the tail proper in the fœtal manatee; the great lateral expansions of the tail therefore become comparable to lateral limb folds or to the last vestiges of external limbs, heredity having attempted after complete atrophy of the hinder limb skeleton to repeat the story of their development. So it has happened that their present condition as lateral folds filled with comparatively undifferentiated mesoblast coincides with the first stages of the development of the vertebrate limb. In other words, the general law that the first stage of limb-growth to be evolved by the class is the last to disappear is here most emphatically confirmed by the development of the backwardly translocated distal vestiges of the limbs of sirenians.

The argument from *Pteronura* here also utterly fails to be satisfactory because the terminal exserted end of the tail of the fœtus of the Manatee shows that the limb folds are truly to be considered lateral as in other vertebrates, and are not evolved from a continuous marginal caudal ridge or fold extending along the whole length of the tail, but from short folds representing limb rudiments which have been derived from functional limbs.

A consideration of the muscular system is important in its bearings upon my hypothesis, so it will be desirable to cite Murie's * observations on the muscles of this region of the Manatee. We will first note the dorsal muscles of the tail, or those lying above the vertebral column.

"What corresponds to the combined or continuous *spinalis dorsi* and *levator caudæ internus* is a long, narrow, but in the back vertically, deep muscle, which runs from the neck backwards as far as the end of the tail. Anteriorly, where laterally compressed but fleshy, it fills vertically the hollow between the cervical spines and transverse processes. Posteriorly it becomes tendinous and aponeurotic, and is fastened to the caudal vertebræ superiorly.

"There is a massive and in great part fleshy *longissimus dorsi*, which extends outside the last from the first rib backwards to the very end of the caudal vertebræ, thus including what constitutes the levator caudæ externus of most other mammals. Like the preceding, the tail-tendons are interwoven into an aponeurosis, partially fixed to the transverse and to the spinous processes." (*Op. cit.*, p. 144.)

The ventral or hyposkeletal, lumbo-caudal system is not prolonged so far forwards, and has a posterior insertion different from the dorsal set.

"The first and notable muscle is that which in the profile and underview appears as a great and only mass filling the interval between the last rib and the caudal extremity and the space between the chevron bones and the tips of the lumbo-caudal transverse processes. This aspect is in some respects deceptive, as the muscle, when manipulated by the scalpel, is found to be only one of two thick and long layers occupying the area in question. The superficial stratum or musculo-tendinous lamella arises from the outer half and inferior surface of the last rib, being here partially overlain by the external oblique and panniculus; thence, with inwardly oblique fibers, it is inserted mesially from the third chevron bone backwards to the termination of the spinal col-

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* On the form and structure of the manatee, by Dr. James Murie, Trans. Zool. Soc. London, VIII, 1874, pp. 127–202, pls. 17–26.

umn, and outwardly is fixed to the tips of the transverse processes. Anteriorly, the muscle is strong, thick, and very fleshy; but half-way along the tail, and nearly throughout the middle line, it becomes tendinous, by degrees thinner, and towards the end is little else than a glistening aponeurotic fascia with coarse, tough fibers. These fibers, when unraveled with care, separate into broadish tendons, one to each vertebræ, which posteriorly commingle with the great flat-tail aponeurosis.

"The second or deeper muscular lamella, also taper-shaped, is, as a whole, much thicker and fleshy, but not quite so broad as the last. Besides a very small slip anteriorly derived from the last rib, it has firm attachments along the under surfaces of the two lumbar and all the caudal vertebræ, filling the interspace betwixt the vertebral bodies, the sides of the chevron bones, and the distal extremities of the transverse osseous elements. This sheet, like the former superficial one, is fleshy anteriorly and tendinous inwardly and behind. Its terminal fasciæ or tendons are more cord-like, and with less difficulty resolvable into separate elements." (*Op. cit.*, pp. 145, 146.)

Dr. Murie then continues and describes a lateral subcaudal muscle, which is of considerable interest, in that it sends its tendinous insertion backward to the vicinity where the margin of the great lateral tail folds end anteriorly. His account of it is as follows: "Lastly, if considered amongst the subcaudal muscles, and not what it to some extent simulates, a continuation of the sacro-lumbalis, we have the lateral or superficial outlying fusiform muscle intermediate between the dorsal and ventral surfaces of the tail. This numerically fifth infracaudal muscle, narrow, roundish, and tapering, has origin close to the termination of the sacro-lumbalis, from the cartilaginous tip of the transverse process of the sacral or first true caudal vertebra, and lies horizontally along the next eight processes. It terminates in a long but strong tendon upon the surface of the subcaudal muscle, mingling with its fascia." (*Op. cit*, p. 146.)

Dr. Murie also speaks of an anterior subcaudal pair, which are marked *quadratus lumborum* in his plates.

While the writer would not wish to appear hypercritical, he cannot agree with Murie and Stannius in regard to the homologies of the hyposkeletal muscles of the tail. It is of course obvious from the preceding description that the whole of the infracaudal muscular mass in the Manatee cannot be homologized with the psoas muscles of human anatomy, but it is evidently impossible to homologize the anterior muscular bundles of the deeper of these muscles, arising from the under face of the two lumbar vertebræ, with anything else than the psoas magnus of man. Obviously, if we bear in mind the importance of serial homologies, the muscular slips arising from and behind the sacrum cannot be psoas, and *infracoccygeus* and *sacrococcygeus* may therefore be good names for those hinder portions. The inner pair of muscles alluded to above as quadratus lumborum, have a far better right to be considered psoas parvus than to bear the former name, because it must be remembered that the vertebræ from which they arise, though dorsal in Manatee, are lumbar in man.

It is thus made evident, it seems to me, that tendinous terminations of a muscle in the Manatee perfectly homologous with the psoas usually inserted into the trochanter minor of the femur of normal forms, actually find their way to the tendinous aponeurosis of the great flat tail which represents the feet of normal forms. This would seem to follow from the consideration of the arguments adduced in favor of the doctrine that the insertions of certain limb muscles are translocated backwards in the pinnipeds.

The fibers in the great lateral tail folds have a generally backward and outward direction from the spinal column, according to Murie's figures, and the great medullary plate of "aponeurotic fibers" along its inner border or attachment to the side of the caudal chain of vertebræ lies below the level of the transverse processes, its anterior portion showing a very strongly marked inclination to assume a ventro-lateral position, which, if continued forward, would strike the pelvis lying some distance below the axial column.

It is probably along this line extending from the pelvis to the flukes that the atrophy of the limbs of the sirenians has occurred.

VIII.—On what appear to be tactile hairs or vibrissæ in cetaceans and sirenians.

A few scattered hairs are found about the lips of the adults of some of the right whales, and it may be interesting to call attention to an embryonic trait of *Rhachianectes*. In an embryo of *Rhachianectes*, Fig. 1, Plate I, there are present minute dermal pits having a very singular distribution between the external openings and the tip of the muzzle. A smaller number of them are found just below the edge of the lower lip, as seen in the side view of this embryo. The distribution of these rostral hair follicles is shown from above, in Fig. 2. There is some evidence that these structures, as in those from which the vibrissæ of the upper lip of *Carnivora* grow, are arranged in rows, but not so regularly as those shown in the embryo walrus, as seen from the side. In the embryo kitten about an inch long, as in the walrus, they are confined to the upper lip on the sides of the muzzle, and are limited to a small circumscribed area somewhat elevated from the adjacent integument. In none of the other cetacean embryos studied by me were these pits for the vibrissæ so numerous as in *Rhachianectes*, and in an embryo of *Phocœna communis*, Fig. 7, there is a single row of seven of them on either side of the muzzle lying in a shallow groove one-eighth of an inch above the edge of the upper lip; none present on the sides of the lower lip. In the younger ones and in *Globiocephalus* they were not present or at least distinguishable with the aid of a pocket lens.

In an advanced fœtus of *Phocæna communis*, in the museum collections, there are present on either side of the snout two strongly developed vibrissæ in the situation corresponding to the position of the vibrissal pits or follicles noticed in a much younger specimen, in which these are, however, much more numerous. This advanced stage was kindly brought to my notice by Mr. True. Eschricht, however, calls attention in his *Untersuch. über nordischen Wallthiere* to a number of the earlier allusions to the occurrence of such hairs on young cetaceans, figuring the distribution of the follicles which give rise to them, especially those seen on the snout of the fœtus of *Megaptera longimana*, Fig. 16, Plate II, between the blowholes and the end of the muzzle, where a considerable number of dermal follicles are shown as elevations of the integument, though they do not show much greater regularity of arrangement in rows than do those of *Rhachianectes*. Eschricht also figures their follicles in a fœtus of *Balænoptera rostrata*, Figs. 18 and 19, Plate III, where three are shown above the margin of the upper lip, and four on the lower, the upper series being arranged more like the seven shown on the upper lip in Fig. 5, Plate I, or in a single row, yet it appears in this last case, after comparison of this stage with later ones of the same species, that only two of the follicles develop outwardly apparent bristles, five of them subsequently aborting when the young animal is about a foot in length. Between this last-mentioned stage and the adult condition the two remaining vibrissæ seem to disappear so that in the adult *Phocæna* no vibrissæ are distinguishable.

Inia, with its feebly developed dorsal fin we have already had occasion to notice as less specialized in that respect than other forms, has the beak provided over both its mandibular and maxillary halves with short bristles, apparently indicating that in this form there has been a less marked loss of what were once, in part at least, vibrissæ, such as are found over the upper lip of fissipeds and pinnipeds, and below the mouth and above it in *Dicotyles*.

The strong short vibrissæ of the walrus on the sides of the muzzle and the vibrissæ found within the inflected margins of the lips of the Manatee are somewhat similar, but it is very possible that the protractile and retractile lips of the latter animal enables it to use these stiff bristles as prehensile organs, and in part as substitutes for incisors in grasping and tearing off the soft aquatic or marine vegetation upon which it feeds.

The distribution of the vibrissæ on the snout in carnivorous types seems to be mainly over the sides of the muzzle above the mouth, but in the Ungulates, especially the suilline group, vibrissæ are found both above and below the mouth. Inasmuch as the whales and porpoises exhibit both of these distributions of their vibrissæ, it is impossible to draw any conclusions from their mode of arrangement which will be of any value in determining their taxonomic relations. The most that can be said is that the Balænoid cetaceans seem to approximate the suilline Ungulates in the distribution of the vibrissæ in the fœtal condition. The Delphinoid forms, on the other hand, show three types of distribution of the same organs, namely, that seen in *Inia*, which approaches that of the pigs, that of *Phocœna*, which approximates slightly that of the *Carnivora*, and a third which approaches neither, all indications of vibrissæ being absent even in the fœtal condition. That the distribution of tactile hairs cannot be of much importance in taxonomy is shown by the fact that a cluster of tactile hairs is found above the eyes in the pig, dog, and seal, and another at the lower border of the cheek near the angle of the lower jaw in *Dicotylés* and *Canis*.

It may occur to the reader to ask why the dermal follicles found about the muzzle of cetacean embryos should be considered to give rise to vibrissæ and not simply to hairs. The reasons why I chose to consider them in the former light is this: They resemble singly very strikingly in the cetacean fœtus the appearance of the single follicles forming the cluster found in the same vicinity, but above the mouth only, in the fœtus of the cat and seal. A tactile hair or vibrissa is only a hair developed to an unusual size, and in *Cetacea* as well as in *Carnivora* these organs seem to have their follicular rudiments formed in the latter at least before the follicles which give rise to the general hairy covering of the body are apparent. Their situation close to the mouth is another reason. The remarkably regular arrangement of the vibrissæ of the muzzle of *Carnivora* in rows, which may be traced in two directions at an acute angle with each other, is not apparent in any cetacean.

In none of the early fœtuses have I found vibrissæ actually developed so as to be outwardly visible; the follicles which give rise to the latter alone seem so far to have been formed in the fœtuses. This is the case so far as I have been able to make out in both the early fœtuses of *Carnivora* and *Cetacea*.

IX.—Summary.

The results of the preceding studies may be briefly embodied in the following paragraphs:

1. The structure of the pinnipeds indicates that the process by which their hind limbs were directed backward and partially included together with the tail in a common integumentary investment, would, if exaggerated, lead to the translocation and fusion of the feet with the end of the sides of the tail as in the cetaceans, in which the now degenerate, backwardly-displaced feet are represented by the flukes.

This general thesis is supported by the following minor considerations which have been developed in the successive subdivisions of the preceding memoir as follows:

1. The inconstancy of the dorsal fin; its variability in size, from none at all to a well-developed one, and its variable position.

2. The non-connection of the dorsal fin with any muscles and its

median blood supply. Its late development in the embryo after the pectoral limbs and flukes are formed, and its evolution from a median dorsal tegumentary fold or carina.

3. The presence of a well-marked cervical constriction in early cetacean fœtuses, indicating a closer affiliation at some remote period with ambulatory amphibious or terrestrial mammals than the type now manifests.

4. The probable evolution of extra terminal phalangeal segments in the digits of *Cetacea* from cartilaginous terminal prolongations of the ungual phalanges developed in a seal-like ancestral type.

5. The presence of two sets of vessels in the flukes corresponding to a dorsal and a plantar set, and arranged somewhat after the manner of the vessels on the manus, and the probably similar position of the hallux and pollex on the outer border of the manus and pes in the *Protocetacea* as well as in the *Pinnipedia*.

6. The connection of the hyposkeletal muscles of the tail with the flukes by tendinous fibers or fascia in both *Cetacea* and *Sirenia* as a result of the translocation backwards of the insertions of the muscles corresponding partly to the ilio-psoas, which is partly inserted in terrestrial forms into the femur.

7. The tendency to shift the insertions of the muscles of the hind limbs rearward in pinnipeds, a process which was also presumably active in the protocetaceans.

8. The belated outgrowth of the rudiments of the hind feet (flukes) of cetaceans, in conformity with the general embryological law that the rudiments of fore limbs in vertebrate embryos generally appear somewhat earlier than the hinder ones. Degeneracy in the *Cetacea* has also affected their unusually belated outgrowth in this type.

9. The lateral position of the flukes, as corresponding serially with rudiments of hind limbs.

10. The mode of development of the flukes as diverticula of the epiblast filled with indifferent mesoblast the same as the primary limb rudiments of other vertebrates.

11. The hypertrophy of the caudal musculature and skeleton of the *Cetacea* and the differentiation of the tail vertebræ into two well-marked series.

12. The atrophy in cetaceans of the elements of the pelvis and limb skeleton in exactly the inverse order in which they are developed in normal forms.

13. The tendency to degeneracy of the pelvis and proximal elements of the limbs of pinnipeds, which are tending to degenerate in the same direction as have the same elements in the cetaceans.

14. By the tendency in cetaceans to prolong the lumbar plexus towards the tail to supply the cenogenetically developed caudal musculature.

15. The direction of the axis of the bones of the crus, when developed, towards and in a line with the pes in swimming, in both pinnipeds and cetaceans.

16. The direction of the axis of the rudimentary femur in *Halitherium*, and the tibia in *Balæna*, towards the flukes.

17. The presence of a supposed free rudiment of the tail in the fœtus of the manatee, which is exserted beyond the flukes.

18. The effect of the translocation of the paired limbs as observed in other types, especially as indicating that the outgrowth of the limb folds in advance of or behind their original or archaic site is influenced by heredity, which acts more powerfully through immediate than through remote ancestry, in this as in many other cases.

EXPLANATION OF PLATE I.

Reference letters: *a*, anus; *b*, blow-hole or holes; *cl*, clitoris; *d*, dorsal fin; *e*, external auditory meatus; *f*, flipper, or fore limb; *h*, lateral fluke folds or outward rudiments of pedes; *m*, mouth, in Fig. 8; *p*, penis; *u*, umbilical cord or navel-string.

Fig. 1. Female fœtus of *Rhachianectes glaucus*, or California gray whale, natural size, seen from the side, showing the distribution of the follicles for the vibrissæ on the snout above and below the cleft of the mouth (N. M. Coll.).

Fig. 2. Head of the same, seen from the front, showing the separated blow-holes and the follicles for vibrissæ between the nostrils and the tip of the snout.

Fig. 3. Sketch of the perineal region of the same, as seen from below, showing the anus, the vulva behind the clitoris, and the very minute mammary fossæ or clefts on either side of the latter.

Fig. 4. The tail of the same, as seen from below, to display the rounded or lobe-like fluke folds.

Fig. 5. Male fœtus of *Phocæna communis*, natural size (N. M. Coll. 14294, Provincetown, Mass., Freeman & Hillman), showing follicles for seven vibrissæ on the side of the snout above the mouth.

Fig. 6. View from below of the perineal region of the preceding.

Fig. 7. View from above of the tail of the same.

Fig. 8. Side view of a somewhat damaged fœtus of *Phocæna* (N. M. Coll. 11204, Eastport, Me., G. B. Goode.)

Fig. 9. Side view of a female fœtus of *Globiocephalus* the Caaing whale or blackfish, natural size (N. M. Coll. 14295, Wood's Holl, Mass., V. N. Edwards).

Fig. 10. View of the tail of the same, showing the very low horizontal fluke folds just beginning to be apparent on the sides of the end of the tail.

EXPLANATION OF PLATE II.

Fig. 11. Fœtus of the narwhal, natural size, from the side. After Eschricht.

Fig. 12. Male fœtus of the white whale, *Delphinapterus*, from the side. After Eschricht.

Fig. 13. Male fœtus of *Delphinapterus* as seen somewhat obliquely from below, natural size. After Eschricht.

Fig. 13*a*. Tail of the preceding, showing the first stages of the outgrowth of the fluke folds. After Eschricht.

Fig. 14. Fœtal kitten, twice natural size, to show the relatively early differentiation of digits and the outwardly apparent wrist, elbow, ankle, and knee joints, and the similarity in curvature of the cetacean and fissiped embryo of relatively the same age. From a specimen given me by Mr. J. L. Wortman.

Fig. 15. Diagrammatic figure illustrating six stages of the outgrowth of the flukes of cetaceans, the successive contours being compiled from various sources; the last stage being approximately that of the flukes of the adult to show the way in which the caudal notch is developed over the end of the tail.

Fig. 16. View of the top of the head of a fœtus of *Megaptera longimana*, natural size, to show the arrangement of the hair follicles or vibrissæ on the snout. After Eschricht.

Fig. 17. View of right flipper or fore limb of the fœtus of *Globiocephalus* represented in Fig. 9, Plate I; drawn after the whole limb was detached and rendered transparent with clove oil. Enlarged 16 times, *h* humerus, *r* radius, *u* ulna, *p* pisiforme, I pollex, and II, III, IV, and V, digits.

EXPLANATION OF PLATE III.

Fig. 18. Head of male fœtus of *Balænoptera rostrata*, natural size, showing the two blow-holes and three follicles on either edge of the snout for vibrissæ. After Eschricht.

Fig. 19. Side view of the same fœtus displaying four follicles for vibrissæ below the edge of the lower lip, and showing the median notch at the end of the tail. After Eschricht.

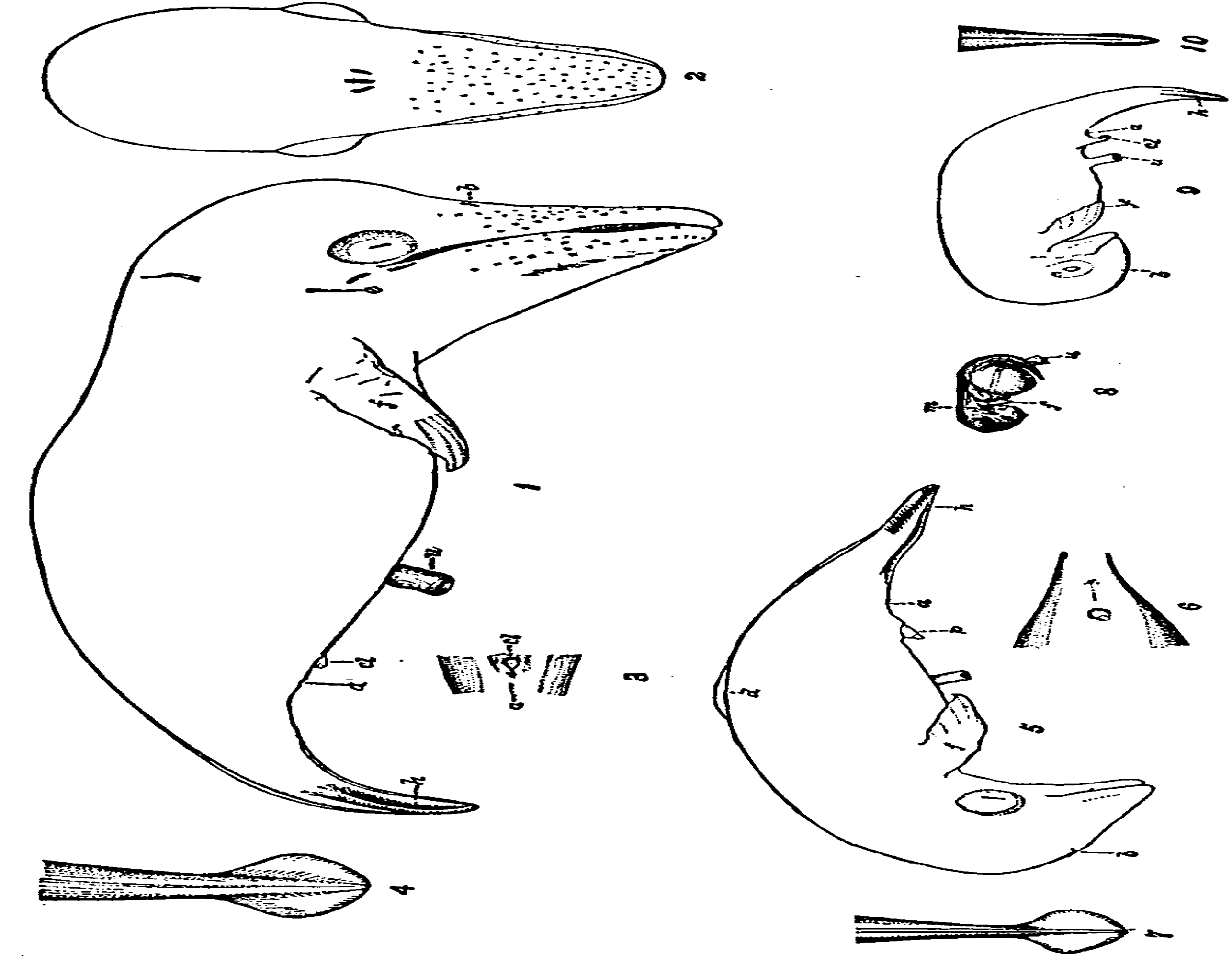
Fig. 20. The inner contour lines show the form of the tail of a fœtal manatee, natural size, from below, with a median papilla near the end and within the lower margin, *a* anus, *cl.* clitoris. After Wilder.

The outer contour shows the configuration of the tail of a young male manatee 4 feet long, as seen from above, and reduced from Murie's figure to nearly one-fifteenth natural size in order to show the changes of form undergone by the tail in passing from the fœtal to the adult condition.

Fig. 21. Female fœtus of manatee, 3.7 inches long, obtained by the late Professor Orton, and figured by Wilder. Natural size, viewed from the side, *a* point of elbow, *c* carpus, *n* nostril, *e* ear. After Wilder.

Fig. 22. Male fœtus (?) of *Halicore dugong*, one-half natural size, *n* nostril, *e* ear, *u* umbilical cord, *p* penis (?), *a* anus. After Harting.

PLATE I.



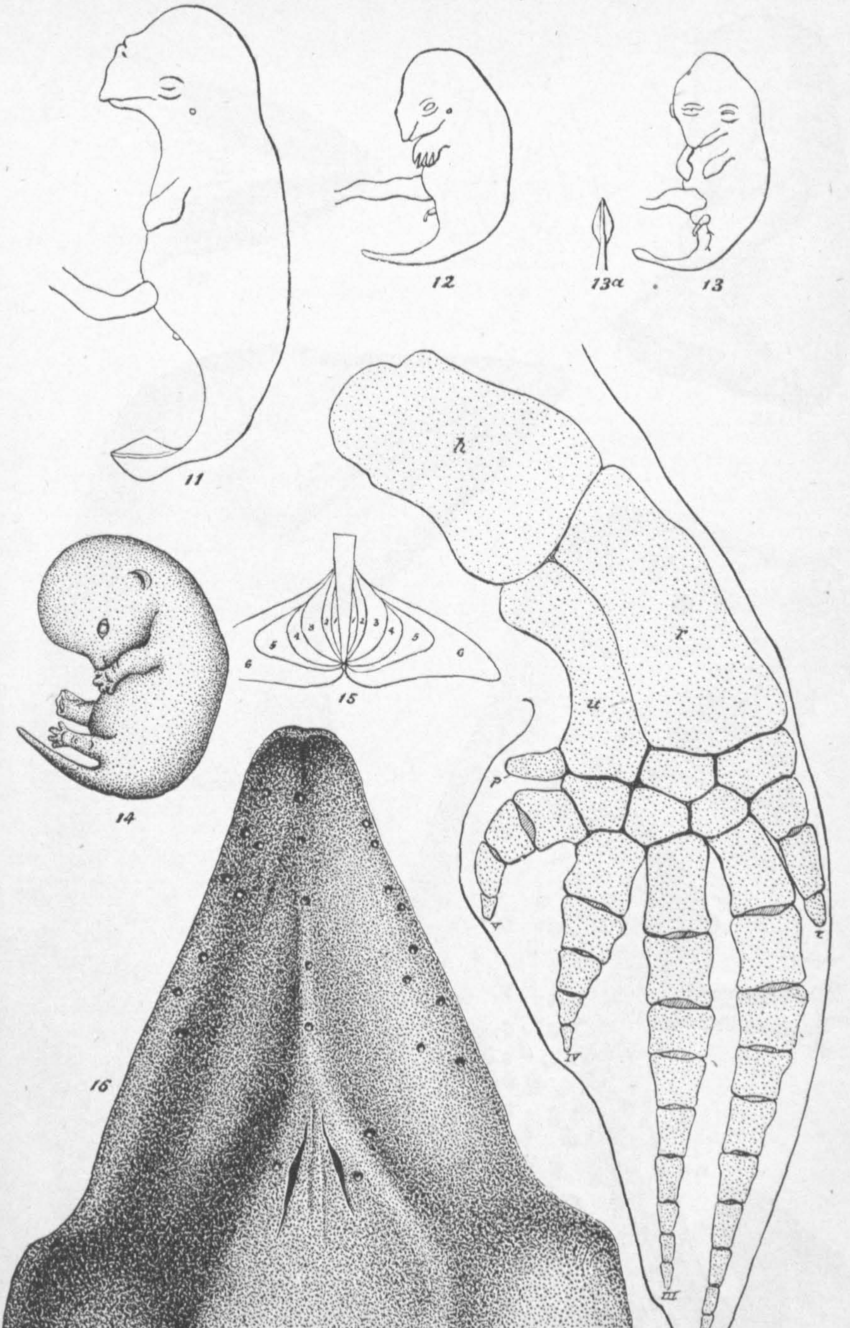

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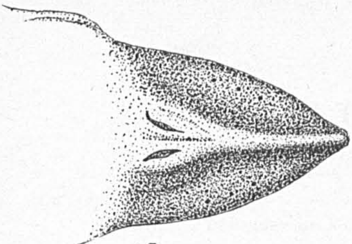
PLATE III.



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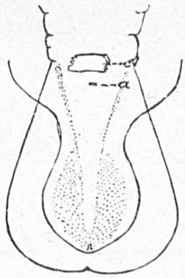

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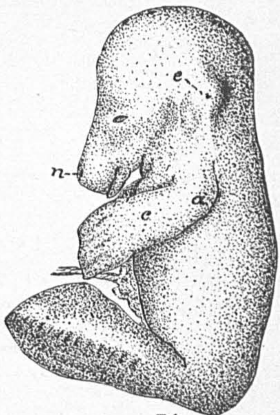

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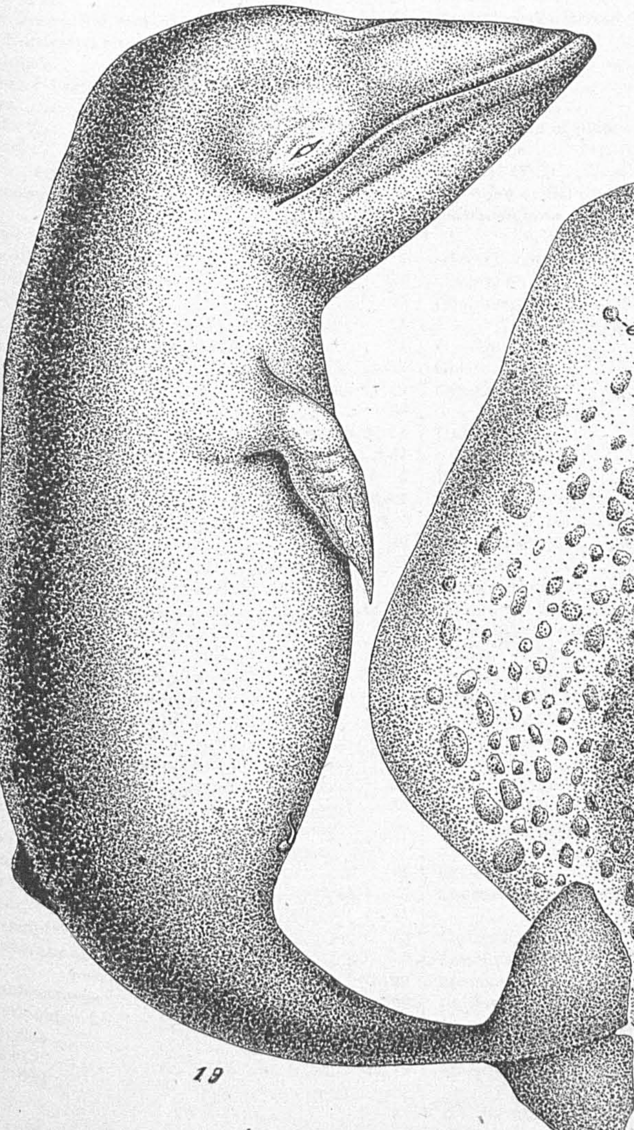

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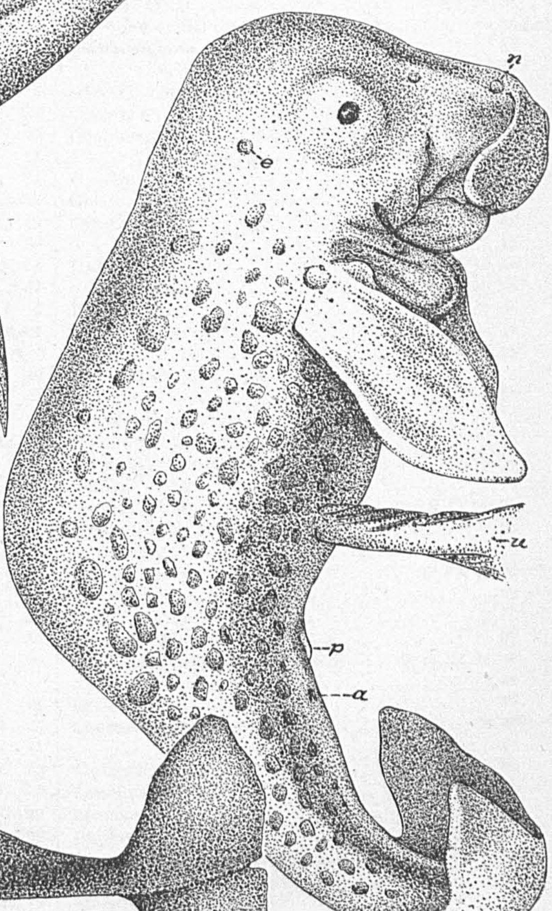

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