On the Sensory Tubercles of Lips and of Oral Cavity in the Sei and the Fin Whale

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Knowledges upon the sensory capacity of the cetacea are not only important for the biological science, but must have also some practical meaning for the whalers. Recently a few works pertaining to this field have been published from our laboratory, viz. upon the sinus-hair of the Sei whale (Nakai and Shida), the auditory organ of the Fin whale (Yamada), and the intracerebral acoustic system of the whales (Ogawa and Arifuku); the paper last mentioned contains the authors' summarized observations upon the serially sectioned brain-stems of *Lagenorhynchus*, *Tursio*, *Cogia*, *Physeter*, and *Balaenoptera*.

In the study upon the sinus-hair of the Sei whale, Nakai and Shida were induced to believe that the scanty but very regularly arranged hairs serve not merely as a tactile organ in searching for food, but more probably as the organ to feel the stream of water. They came to this assumption chiefly from findings on the inclination of the hair-shaft and the excentric position of the hair-root within the venous sinus. Huber (1934) seemed also to have considered that the sinus-hair of the baleen whales may afford a mechanism for the appreciation of slight changes in water pressure.

While studying the sinus-hair, one of us, Shida, directed his attention to a large assembly of small granular tubercles on the inner surface of the upper and lower lip in the Sei whale, *Balaenoptera borealis*. The same structure was seen, though less remarkably, not only on the palatal surface sandwiched in between the right and left areas of baleens, but also on the tongue and on the floor of the oral cavity. Microscopically examined, they certainly represent highly sensitive tactile organs, performing no doubt a function of much importance in the sensuous life of this whale. A little later, we ascertaind in the Fin whale, *Balaenoptera physalus*, the existence of structures approximate to those of the Sei whale. Though we have not yet compared other sorts of baleen whales regarding this problem, it seems

plausible that this sensory apparatus will be found also in other whales, at least in all members of the genus *Balaenoptera*.

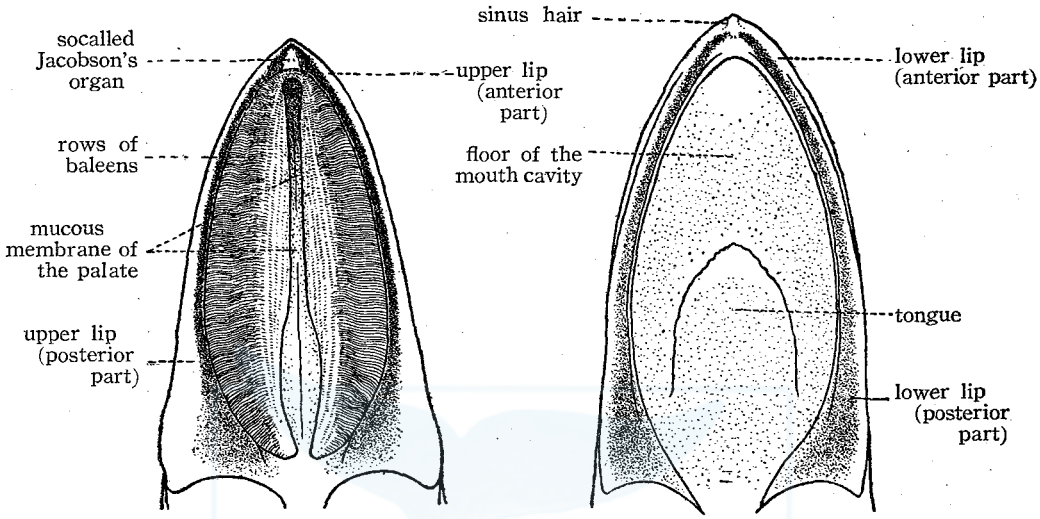
1. Distribution of the granular tubercles on the lips and in the mouth cavity.

The tubercles in question are easily seen with naked eyes (fig. 8 a) on the inner surface of the lips as well as on the mucous membrane of the mouth. The size of each tubercle and their number per unit area are not equal according to the locality. On the upper lip, where their presence is the most prominent, they are seen in a long and broad zone, which extends from the anterior extremity of the lip backwards to the angle of mouth (fig. 1 a). The zone is of a breadth 3—4 cm at the anterior end, 6—7 cm at the middle part of the lip and becomes remarkably wider towards the oral angle. There remains a narrow space of mucous membrane of a breadth about 1 cm, where the tubercles are wanting, between the lateral margin of the bases of baleens and this zone (fig. 2). At the anterior end of the upper lip the tubercles are relatively large, each of them measuring about 1 mm in diameter, in the hinder parts they are smaller but more crowded, where it is difficult to determine their accurate number. The density is ca. 200 per square centimeter at the anterior end (fig. 3), about 550 at the middle part of the upper lip, and nearly equal or a little less at the posterior end.

On the lower lip (fig. 1 b), where in general the presence of the tubercles is not so prominent as in the upper lip, they are the best seen in the posterior area near the oral angle, here about so clearly as in the hinder part of the upper lip. Forewards they become within the lower lip more indistinct, and at the most anterior portion the surface is everywhere smooth, devoid of any remarkable tubercle, but instead of this, many gray spots are visible on the surface, denoting the existence of well developed papillae of the connective tissue underneath.

On the narrow palatal mucous membrane between the right and left areas of baleens, relatively large granular prominences are present only in the anterior part, about 1/5 of the entire length of the palate (fig. 1 a), while in the hinder part the surface looks quite smooth, though here also we can recognize easily through the epithelium tops of many papillae of the connective tissue.

Fig. 1. Jaws of Balaenoptera borealis; the granular tubercles are dotted.



(a) Upper jaw seen from below (b) Lower jaw seen from above

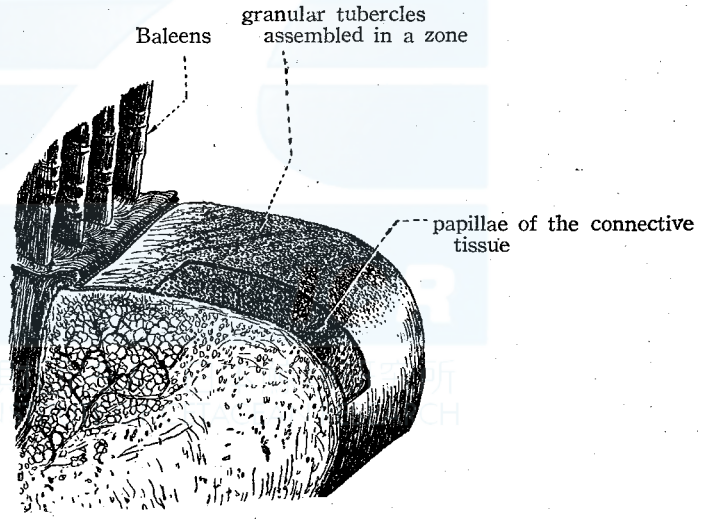


Fig. 2. A part of the upper lip of Balaenoptera borealis

Fig. 3. Anterior end of the upper lips of Balaenoptera borealis

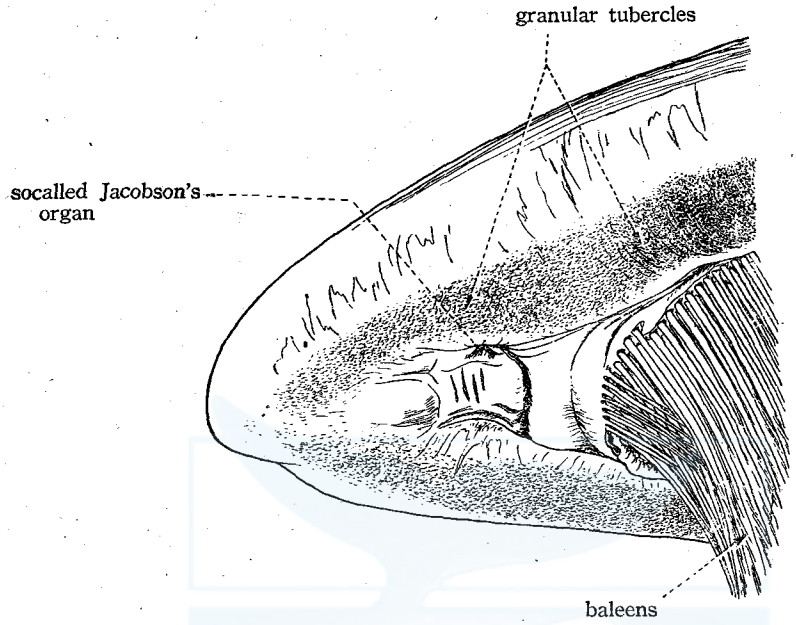
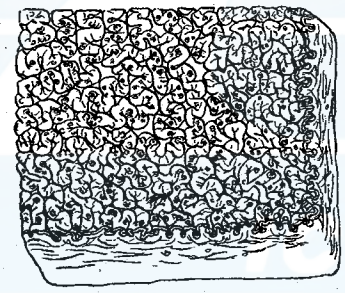
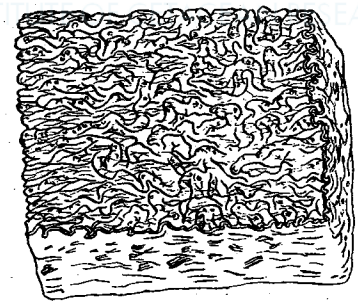


Fig. 4. Balaenoptera borealis

a) An excised part of the lingual surface





b) Excised mucous membrane from the floor of the oral cavity

In addition, the dorsal surface of the tongue and the floor of the oral cavity have also the granular tubercles nearly all over the surface, except the most anterior parts (fig. 1 b), and backwards on the tongue they become sparse, disappearing completely at the fauces. The tubercles disseminated in the posterior part of the oral floor do not show any clear boundary against those in the hindermost portion of the lower lip. On the dorsal surface of the tongue, where the mucous membrane forms a great number of soft and gyrate folds, the tubercles are seen only on the summits, but not in the valleys between the folds (fig. 4 a). The same circumstance applies also to the floor of the oral cavity (fig. 4 b). In these localities the density is about 70 per square centimeter in the normally contracted mucous membrane. So when the membrane is distended, their number per unit area will be much decreased.

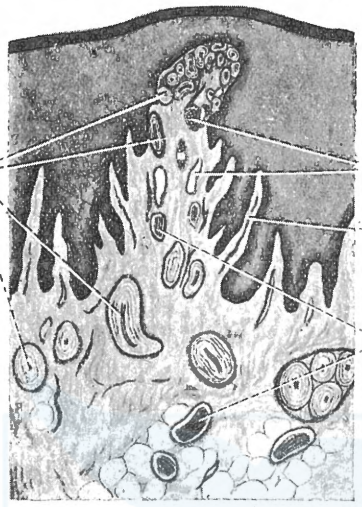
In the Fin whale, compared with the Sei whale, we saw a difference of little significance, only in regard to the upper lip, for the tubercles are within this lip the most easily recognized in the hindermost portion, and forewards they become relatively less distinct, being much smaller at the anterior end than those at the corresponding part of the Sei whale. But as to the tubercles of the lower lip, the palate, the tongue, and other parts of the oral cavity there is no remarkable difference between the two kinds of *Balaenoptera*.

2. Papillae of the connective tissue.

Microscopical examination reveals, that just under the tubercles papillae of the connective tissue are very well developed, protruding deep in the layer of epithelium, and approaching very near the epithelial surface. The form of these papillae is not always equal according to the locality, but usually they are more or less swollen near the summit and show secondary branchings. Especially at the anterior end of the upper lip of the Sei whale the papillae are thick and high, providing with 3—5 elongated branches (fig. 5 a), while at the posterior part of the upper as well as of the lower lip they are in form somewhat like mushrooms, having less branches (fig. 5 b). At the palate and at the anterior part of the lower lip they are more cylidrical (fig. 5 c), and on the tongue as well as on the floor of the oral cavity their form is irregular, though thick and short in most cases (fig. 5 d).

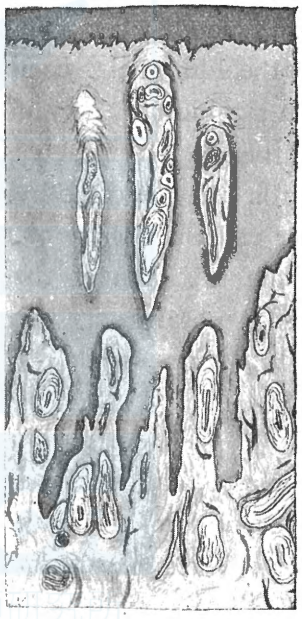
Fig. 5. Balaenoptera borealis; sections showing the sensory papillae

a) from the anterior end of the upper lip



b) from a middle portion of the upper lip

c) from the anterior end of the lower lip



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d) from the dorsal surface of the tongue

In the Fin whale we see very slender papillae well developed, reaching near the surface of the epithelium, at the anterior end of the upper lip, where as mentioned above the granular prominences are indistinct. As to other places, no remarkable difference was ascertained between the two kinds of *Balaenoptera*, concerning the development of the papillae in question.

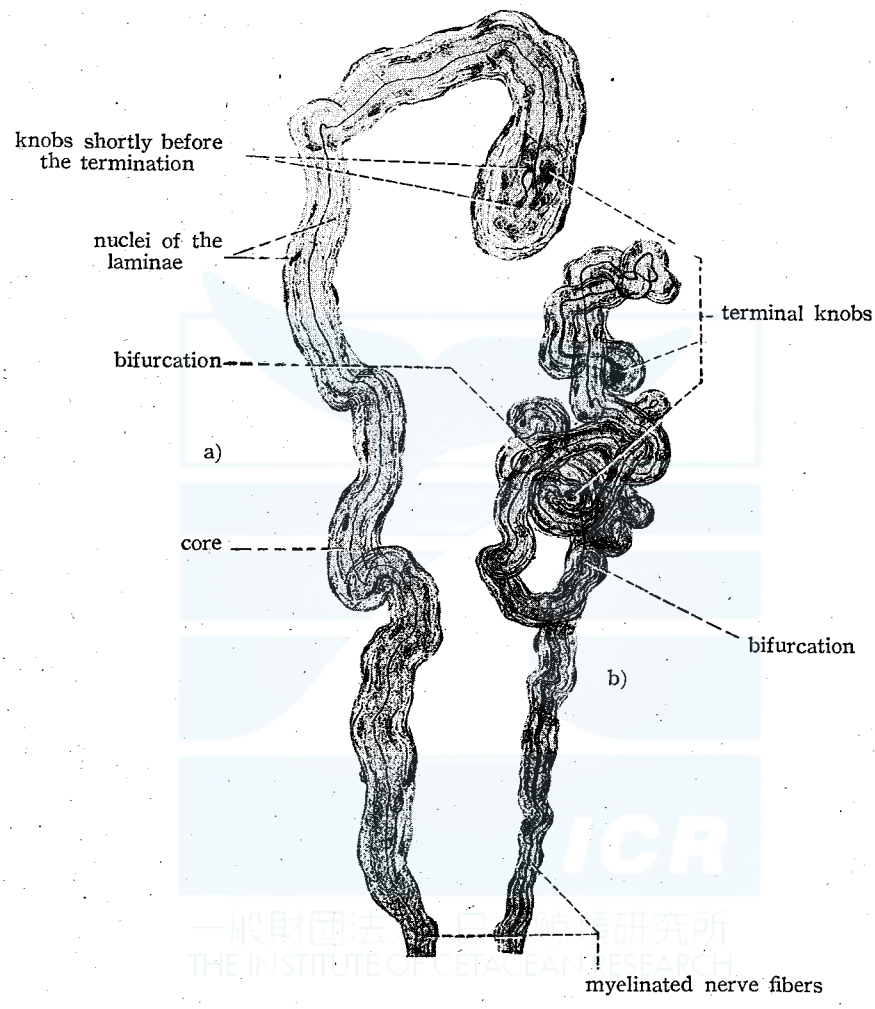
3. Nerve endings in and near the papillae under the tubercles.

Within the papillae, especially near the summit of them we see many terminal bodies of very characteristic form, to which sensory nerve fibers are continuous. The intrapapillary terminal bodies are aggregated especially in a large number at the anterior end of the upper lip of the Sei whale. But the apparatuses denoting the nerve ending are also found outside of the papillae near the bases of them in the subepithelial layer. These extrapapillary terminal bodies are the most frequently seen at the anterior end of both the upper and the lower jaws, less in other parts of the lips as well as in the anterior portion of the palate. In these places we see here and there within the depth of 0.4 mm from the base of the epithelium a small group of 2—6 terminal bodies, sectioned in various directions and accompanied by a nerve bundle.

The general form of the terminal bodies within or near the papillae is known easily by examining the serial sections, stained simply with haematoxylin-eosin. But we further tried block-staining by the Bielschowsky's method, and prepared the serial sections and stained them with van Gieson's picrofuchsin, in order to study the finer structures, especially of the axons.

In the basal part of the papilla the terminal bodies are comparatively large in size, but less in number, while near the top of the papilla they are relatively small but more numerous (fig. 5). Calculated at the base, each papilla seems to receive from one to several nerve bundles, each of which contains a number of nerve fibers. Sometimes we see a very small bundle, consisting of only a single nerve fiber. A terminal body near the top of the papilla measures 15—48 μ in breadth, while its length can not be easily determined, as its very long body is wound in a complicated manner, not unlike the secretory part of a sweat gland. The terminal body has in the interior a relatively thick, eosinophile core and the core

Fig. 6. Terminal bodies, not branched (a) and branched into three (b), both of which are much convoluted near the summit of a papilla (×500). Reconstructed from sections.



is covered externally by several thin sheets of collagenic nature. This apparatus belongs certainly to the category of the lamellar corpuscles of Vater and Pacini, but the number of lamellae is in this case very few. So they seem to be the nearest to the Golgi-Mazzoni's corpuscles, as described by Dogiel and van de Velde especially in the tactile balls of the cat. But compared with these corpuscles already known, they are surpri-

singly long and much convoluted (fig. 6). Because of the convolution a single terminal body appears on the cut surface several times, which may lead to an estimation of them too much in number. But in reality, even at the anterior end of the upper lip, where the terminal bodies are the best developed, their number is in one papilla a little more than ten.

Each terminal body seems to receive only a single nerve fiber. But we encountered bifurcations of the terminal body, the axon with core and lamellae being divided into two or three equally thick branches, which are proximally united together, but have their ends separately (fig. 6 b). Such a remarkable branching of the terminal body was observed especially at the anterior end of the upper lip of the Sei whale. In the Fin whale bifurcation of the axon occurs within the core very rarely.

The axon forms at the termination a small rounded or more irregularly formed knob, which is not always the same in size (fig. 7). In the knob we see a network or a glomerule-like group of fine fibrils, with which neurofibrils of the axon are directly continuous (fig. 7).

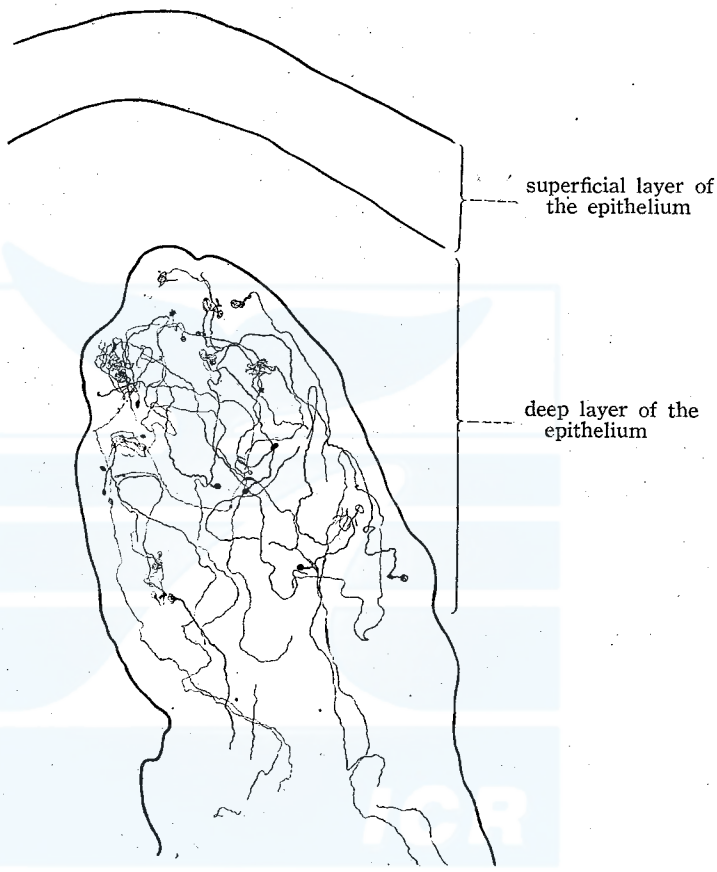
Moreover, we observed the axon in the terminal body a short distance before its real ending to be divided suddenly into several fibrils; the frayed fibrils are conglomerated, forming a knob, and then unite together into a single axon, and advance further to attain its real ending. Such a fraying occurs 1—3 times during the course of an axon. Van de Velde seems also to have seen the same relation in the Golgi-Mazzoni's corpuscles of the cat (1907, fig. 8 of his paper).

The extrapapillary terminal bodies in the subepithelial layer are elongated ovoidal or rod-shaped, provided with a core internally and with a lamellated capsule externally. The number of lamellae is as few as within the papilla. Also there they are wound, though the windings are not so numerous, compared with the intrapapillary terminal bodies. They are various in size; we measured a breadth of 38—170 μ and a length of 150—615 μ (in the relatively straight ones). The core is 7—23 μ in breadth; this is swollen at the end usually to a diameter of 30 μ. Within the core a single axis cylinder is contained, and its terminal portion is dilated into a spherical or irregularly formed knob, with a network of fine fibrils.

4. Considerations upon the functional meaning.

The papillae mentioned above, being provided with so well developed

Fig. 7. Reconstructed figure, showing various courses of nervous axons in a papilla.



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terminations of nerve fibers, are certainly an exquisite sensory organ for the oral and labial stimulations. The impulses must be conducted from them to the brain-stem by the maxillary and mandibular nerves of the trigeminus.

Concerning the problem, whether the sensation caused by these papillae has anything to do with the gustatory sense, we suppose, that it can not

belong in its nature to the sense of taste, for histologically the terminal apparatuses, showing no intraepithelial nerve endings, quite different from the well known structures of the taste-buds with the intra- and intergemmal nerve fibers. From every point of views this labial and oral apparatus does not seem to be a chemoreceptor but merely a tangoreceptor, receiving mechanical impulses, therefore very different from the taste.

On the other hand, we are at present uncertain, whether the cetacea be endowed with the gustatory sense, for we have not yet found the taste-bud in them, though Wolf (1911) is said to have seen it in toothed whales. Moreover, considering the meagre development or the complete absence of the olfactory nerves in the whales or dolphins respectively, it is quite possible in our opinion, that the oral sense treated especially in the present paper may substitute for the gustatory and olfactory senses in the cetacea. It may also compensate in a certain degree the insufficiency of the visual sense, for the comparatively small eyes of the whales, situated far behind and directed to the side, do not seem to be a very effective organ for the perception of food entering the mouth.

The sinus-hair might also be effective as a tactile organ for food, but they serve probably more for appreciation of the pressure or stream of water, having functionally much in common with the lateral line system of the fishes. Nearly eighty years ago Malm (1866) reported an interesting experience upon a Blue whale stranded alive at Göteborg, that "Der Mann, welcher den Walfisch erlegte, bemerkte ebenfalls, dass die Lippen unter den zugänglichen Teilen die empfindlichsten waren, da das Tier durch Berührung derselben in die grösste Raserei versetzt wurde." Japha (1910) quoted this story to explain for the high sensitiveness of the hair for touch, but in our opinion the granular tubercles with the richly innervated papillae are far more responsible for the sensitiveness of the lips than the hair. At present one of our eager wishes lies in a repetition of such an interesting experiment as Malm reported.

In the human anatomy it is well known, that the inner surfaces of the lips and of the cheek have in the newborn infants as well as in the advanced foetuses numerous villi, which resemble therefore in localisation the granular tubercles of the whales; they however begin to disappear in the fourth week after the birth (Ramm, Heidsieck). In other mammals, it deserves also noticing, that villi are well developed on the mucous mem-

brane of the lips and of the cheek of ruminants and of many marsupials (Owen, Immisch, Schulze, Sonntag). Though coincident in a certain degree as to the localisation, the villi in question of these animals seem to have only a mechanical meaning in food-taking or in mastication; they have probably not the meaning of highly sensitive organs as in *Balaenoptera*. Neither can we expect any important function in the labial and buccal villi of the human being, which disappear very soon after the birth.

Lastly we wish to consider briefly the interrelationship between the cetacea and other mammals. Since old time the opinion has prevailed, in the realm of comparative anatomy, that the whales are the most kindred to the ungulates. Relatively recently Anthony (1926) insisted upon the affinity between the whales and the perissodactyla, and later Ommanney (1932), studying the urogenital system of the Fin whale, agreed with Anthony on this point. On the other side, many palaeontologists have been inclined to look for the ancestor of the living cetacea in carnivora, taking chiefly the dental characteristics of *Zeuglodon* in comparison.

Of course we can ourselves say nothing definite upon this important problem, but would only refer to the fact, that the remarkable development of the palatal crests simultaneously with the high villous state of the labial and buccal mucous membrane is met with in ruminants. And the baleens of the whales have been explained since Tullberg (1883) as specially differentiated sort of the palatal crests, an opinion, which seems to have much truth. Moreover, the palatal crests of some ruminants are closely related to the baleens of whales, inasmuch as they are frayed at the margin. This combination of structures, that is, the simultaneous presence of palatal crests and of labiobuccal villi, is found in a very accentuated and specially differentiated form also in the whalebone whales. Naturally it does not mean an important thesis in determining the relationship of the baleen whales, but a comparative anatomical fact not unworthy of being borne in mind at such a discussion. Of course the toothed whales stand here out of the question, but we think there may be phylogenetically a pretty large distance between the toothed and the baleen whales.

Summary

1. On the lips as well as in most parts of the oral cavity of the Sei whale a great many sensory tubercles are found, especially well developed at the

anterior portion of the upper lip. In the Fin whale the circumstance is nearly the same, with only the difference, that in this species the elevations are at the anterior portion of the upper lip comparatively less distinct.

2. Microscopically examined, we see underneath the tubercles well developed papillae of the connective tissue, containing numerous sensory apparatuses, with which the nerve fibers are directly continuous.

3. The terminal bodies in question show the structure the most approximate to the so-called Golgi-Mazzoni's corpuscles. But they are characterized by the remarkable elongation. They have a core with the axon internally and a few sheets of collagenic lamellae externally.

4. Successive bifurcation of a terminal body into equally thick branches occurs in the Sei whale. We found also sometimes the axon before its real ending to be frayed out suddenly into a number of neurofibrils, which after forming a knob unite together into a single axon, to proceed further toward its termination.

5. Because of the presence of the granular tubercles, the lips and the mucous membrane of the oral cavity seem in *Balaenoptera* to be a highly sensitive tactile organ, which is very important for the perception of foods, while the sinus-hair are believed to have the functional meaning more for the appreciation of pressure or stream of water.

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Literature

R. Anthony: Les affinités des Cétacés. Annales de l'Institut Océanographique. Nouvelle Série. 3, 1926.

A. S. Dogiel: Der fibrilläre Bau der Nervenendapparate in der Haut des Menschen und der Säugetiere und die Neuronentheorie. Anat. Anz. 27, 1905, 97—118.

K. B. Immisch: Untersuchungen über die mechanisch-wirkenden Papillen der Mundhöhle der Haussäugetiere. Anat. Hefte. 35, 1908, 759—759.

A. Japha: Die Haare der Waltiere. Zool. Jahrb., Abt. f. Anat. 31. (Habilitationsschrift, 1910, 1—43).

E. Heidsieck: Die Rückbildung der menschlichen Lippen- und Wangenzotten. Anat. Anz. 61, 1926, 321—347.

Ernst Huber: Anatomical Notes on Pinnipedia and Cetacea. Carnegie Inst. Wash. Publ. 447, 1934, 105—136.

A. W. Malm: Einiges von den Walfischen im Allgemeinen und Balaenoptera Carolinae im Besonderen. Berlin, 1866. (Cited from Japha, 1910, p. 36—37).

J. Nakai and T. Shida: Sinus hairs of the Sei-whale. Scientific Reports of the Whales Research Institut, Tokyo. 1, 1948, 41—47.

T. Ogawa and S. Arifuku: On the Acoustic System in the Cetacean Brains. Idem. 2, 1949, 1—20.

F. D. Ommanney: The Urino-genital System of the Fin Whale. Discovery Reports. 5, 1932, 363—466.

M. Ramm: Ueber die Zotten der Mundlippen und der Wangenschleimhaut beim Neugeborenen. Anat. Hefte. 29, 1905, 55—98.

F. E. Schulze: Die Erhebungen auf Lippen- und Wangenschleimhaut der Säugetiere.
I. Ruminantia. Sitz. -ber. Akad. Berlin, math. -nat. Kl. 1912.
II. Beuteltiergattung Macropus (Shaw). Idem. 1913.

T. Tullberg: Bau und Entwicklung der Barten bei Balaenoptera Sibbaldii. Nova Acta Societatis scientiarum Upsala. (Cited from W. Leche in Bronn's Klassen und Ordnungen. 6, Abt. 5, 1887—1898, and from G. Retzius in Biol. Unters. N. F. 13, No. 15, 1906, p. 122).

Em. van de Veldé: Die fibrilläre Struktur in den Nervenendorganen der Vögel und der Säugetiere. Anat. Anz. 31, 1907, 621—634.

E. A. Wolf: Ueber die Zungenpapillen der Wale. (Dissertation) Berlin, 1911. (Cited from S. Schumacher in Möllendorff's Handb. d. mikrosk. Anat. 5, Teil 1, 1927, p. 56).

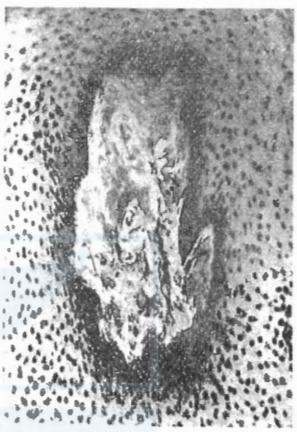
M. Yamada: Auditory Organ of the Whalebone Whales. Scientific Reports of the Whales Research Institute, Tokyo. 2, 1949, 21—30.

Fig. 8.

a) Granular tubercles at the anterior end of the upper lip; with naked eyes, Sei whale.

b) Cross-section of a papilla at the anterior end of the upper lip, containing many terminal bodies. Sei whale (×65).

c) Axons seen here and there in the papilla at the anterior end of the upper lip; a terminal knob is visible. Fin whale (×95).



d) Oblique section of a terminal body, showing core and lamellae, at the anterior end of the upper lip. Fin whale (×160).

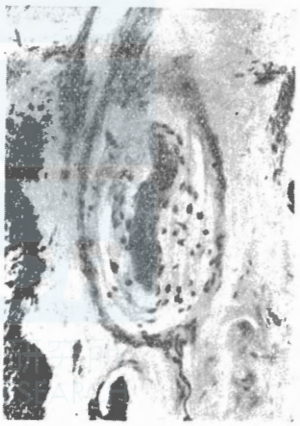


Fig. 9. Various aspects of axons in the papillae at the anterior part of the upper lip. Sei whale (×740)