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Morphology and Development of Blue Whale Baleen: An Annotated Translation of Tycho Tullberg's Classic 1883 Paper

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Abstract

Herein we present an annotated translation of the classic paper by Tycho Tullberg on the structure and development of baleen in blue whales. The three blue whale fetuses on which this study was based were obtained from a whaling station in Norway during a time when blue whales were still abundant enough to support a whaling industry. The value of this text for the modern reader is that it provides a glimpse into the mechanisms of development of baleen in the largest rorqual whale, which is something that modern biologists are unlikely to be able to replicate for a long time. Tullberg's careful morphology, histology, and developmental thinking provide a coherent account of how the elaborate baleen racks develop from simple epidermal and dermal origins. The figures, which we have reproduced here, are superb and provide a rare window into the morphology of blue whale baleen at three fetal stages. The histology is excellent for its time and provides insights into the various keratin tissue phases that make up the baleen plates and bristles as well as the enigmatic *Zwischensubstanz* that acts as a spacer and possible shock-absorber between plates.

Key Words: blue whale, *Balaenoptera musculus,* baleen, development, Tullberg, translation

Introduction

Here, we present an annotated translation of Tycho Tullberg's paper "Bau und Entwicklung der Barten bei *Balaenoptera sibbaldii*" ("The structure and development of blue whale baleen"), which was published in 1883 in *Nova Acta Regiae Societatis Scientiarum Upsaliensis*. Readers might be curious why we have chosen to translate and republish a paper that is 125 years old. The answer is that Tullberg's paper is not only the best we have on this subject, it could be the best we will ever have on this topic. With 31 pages of text and seven plates of superb figures, Tullberg's monograph is still the authoritative text on baleen structure and development. It covers not only gross morphology, but it presents an impressive amount of detail at the tissue and cellular levels as well. As a treatment on baleen in general, this work is invaluable, but the fact that it was done on blue whales and blue whale fetuses makes it even more special, and unlikely to be replicated with modern techniques for a very long time.

Tycho Tullberg was a prominent 19th-century Swedish zoologist and a great grandson of Carl Linnaeus. He was born in 1842 in Uppsala, and he remained there for both his graduate training and as a professor. As was common in his era, Tullberg worked on a wide variety of organisms, including springtails, rodents, lobsters, molluscs, and, of course, whales. In 1877, he took advantage of a research expedition that was being conducted by two of his colleagues to a whaling station in Vadsø, Norway. While the heyday of commercial whaling supported by large populations of sperm and right whales was certainly over at this time, a new era of modern whaling had recently begun because of the inventions of a Norwegian entrepreneur named Svend Foyn.

Foyn was responsible for several innovations that allowed rorqual species such as blue and finback whales to be hunted for the first time. In traditional whaling, sperm and balaenid whales were harpooned from rowboats deployed from large sailing vessel mother ships. Harpooned whales were then dragged back to the ship for processing. Rorquals, such as blue whales, were simply too fast and powerful to be captured by men in rowboats, and their negative buoyancy after death meant that even if they were captured, it was impossible to drag them back to the ship. Foyn overcame both of these challenges by inventing a system whereby rorquals were harpooned and killed using an exploding harpoon fired directly from a large, fast, steam-powered ship. These innovations ushered in a new era of modern whaling that led to a drastic decline in blue whale numbers that persists to this day.

As unfortunate as these inventions were for rorquals, Tullberg took full advantage of the opportunity to examine fetal development in a species that was available for rigorous study for the first time in history. Tullberg lived and worked during a golden age of comparative anatomy in Europe, and being a direct descendant of Carl Linnaeus meant that he was plugged into this community from an early age. Well before the publication of *On the Origin of Species* in 1859, biologists in Europe were carrying out anatomical studies of stunning insight and detail, and many of these persist today as the best descriptions and figures we have of many structures and species. Tullberg was also fortunate in that Svend Foyn was one of the first whalers to rely on a land-based processing station (in the Norwegian port of Vadsø), which meant that blue whale specimens were far more accessible for study than they would have been from a sea-based operation.

At the time that Tullberg undertook this study, there was a lot of interest in animal development in general, as well as interest in mammalian keratin structures such as horns and hooves. While others, including the prominent Danish zoologist D. F. Eschricht, had published on the structure of baleen and even on baleen development before Tullberg, none had done so on blue whale baleen, and none had used microscopy to examine these structures at the cellular level. Tullberg requested preserved samples from his colleagues that would help him answer two main questions: (1) How does the baleen develop in fetuses, and (2) What is the microscopic structure of both fetal and adult baleen?

The first major contribution of Tullberg's monograph is a detailed description with copious figures of the gross anatomy and histology of baleen from an adult specimen. This work could of course be done today with more modern microscopy using material from strandings or museums, but even these kinds of specimens are difficult to come by, especially ones in which the underlying dermal tissue is not completely rotted away. Far more valuable, however, are Tullberg's descriptions of baleen development that he deduced from three fetal specimens. The first specimen was "only" 1.2 m long and completely lacked any trace of baleen development. The second was 3 m long and had significant development of the oral mucosa into pre-baleen structures, but still nothing recognizable as baleen. The third was 4.55 m long and had elaborate structures that resembled small versions of baleen plates and bristles, especially in the middle and largest part of the rack. From these two specimens of intermediate baleen development, Tullberg provides a detailed and plausible account of baleen development in blue whales that is also likely to be representative of the process in all rorquals. Tullberg was limited by the two fetal baleen samples he had for study, but he managed to fill in the developmental gaps between them by taking advantage of the gradient that occurs along a baleen series, with plates at the anterior and posterior ends lagging significantly behind plates in the middle.

For our own research on baleen structure and biomechanics, we were generally interested in how the baleen develops from the epithelium of the palate and, more specifically, in how the individual plates end up with their characteristic triangular shape and lingual edge. Do the transverse plates grow *de novo* from the palate epithelium, or do bristles appear first and then merge to form the individual baleen plates? Recent work by Demere et al. (2008) suggests that the evolutionary transition from toothed to toothless mysticetes included an intermediate form that possessed both teeth and keratinous bristles, so it would not be unusual if the ontogeny of baleen plate formation started with only bristles. We also wondered whether the transverse plates emerge as a square lamina first and eventually get worn into a triangle with a fringed lingual edge by the abrading action of the tongue, or does the plate emerge early on as a triangular form before any wear occurs?

Tullberg's words and figures provide answers to all of these questions, and for those of you who are looking for a concise summary, look no further (although we, of course, recommend you read the entire annotated text!). Baleen development starts as a simple cornified papillary epidermis, with the oral epithelium differentiating into a thick stratified layer on top of a sculpted dermal layer (Figures 12 through 16). At this stage, the dermis is organized into multiple rows of cones that are each collinear with a single dermal plate that arises at the labial edge (Figures 12 & 13). The dermal plate and cones both have numerous narrow papillae emerging from their surfaces (Figure 16), and these dermal papillae are responsible for the subsequent development of the tubular structure of the baleen plates and bristles. Each plate and row of cones corresponds to a future transverse baleen plate and accessory plates, but this fate is only fulfilled after the dermal plate expands toward the lingual edge and merges one-by-one with the papillary cones. As for the triangular shape of the transverse plates, this appears to be the direct result of the developmental lag that exists between the growth of the plate at the labial and lingual edges (Figures 19 & 20), although some sculpting by lingual abrasion *in utero* cannot be ruled out by Tullberg's observations.

Through his histological examinations, Tullberg was able to describe the tissue phases that current researchers identify in papillary horn (tubular and intertubular horn), and he also identified covering horn and the enigmatic *Zwischensubstanz*, which is a rubbery stratified epithelium that acts as a spacer between adjacent transverse baleen plates. He also speculates at length about the interactions between the underlying dermis, especially the dermal papillae and the overlying epidermal layers. In addition, he points out the resemblance between the dermal papillae and elongated dermal structures seen in other tubular keratin structures such as horse hoof and rhinoceros horn, although the papillae in baleen are far longer.

Like any fruitful research project, Tullberg's study leaves us with more questions than answers (although he does provide lots of answers!). He wonders why the dermal papillae in baleen are so long, and he muses about the mechanisms that lead to the development of hollow versus filled tubules. He spends quite a bit of time wrestling with the question of whether baleen growth occurs off the steep walls of the papillae, and he eventually concludes (correctly) that it does. He understood that the basal keratinocytes are unkeratinized, alive, and even proliferative, but he most likely struggled with this question because he did not appreciate that constant linear growth of a keratin structure can be achieved from a papillary surface as long as the growth rate declines with the angle of the surface from the horizontal. It is difficult to fault Tullberg for not understanding this more deeply—researchers like ourselves struggle to this day to understand this process, and some of the more important advances in this area have come quite recently (Bragulla, 2003; Bragulla & Hirschberg, 2003).

We also came away from Tullberg's text and figures with a few new research questions of our own such as what is the nature of the *Zwischensubstanz*, and what are its mechanical properties and functions? We also became interested in how tubular structures within baleen plates ultimately break up at the lingual edge to form bristles, and why they do not break up before they are supposed to. We believe that this is likely related to the fact that most baleen is highly calcified, at least as keratins go (Pautard, 1963; St. Aubin et al., 1984). Tullberg does not mention the presence of calcium salts in fetal or adult blue whale baleen, and this is not surprising given that the histological stains that he used would not have revealed the regions of calcification that likely occur in this species.

The insight and breadth of zoological knowledge that Tullberg brings to this article makes it far more valuable than it would be if it were *just* a collection of excellent figures of fetal development from the largest animal ever to live on planet Earth. In reading Tullberg's words and following his lines of thought, we are transported into the scientific milieu of his age, and we get to hear firsthand about the kinds of questions that he and his colleagues strived to answer. We also come away with the feeling that Tullberg studied biology for the same reason we do—because he was insatiably curious about and infatuated with the marvels and the minutiae of the natural world.

Acknowledgments

This project emerged from the diligence of my graduate student Lawrence Szewciw, who undertook at the start of his program one of the most ambitious literature searches I have ever witnessed. Lawrence was initially interested in baleen structure and biomechanics, which eventually led to all sorts of interesting questions about baleen development. The more he dug, the more he realized that all signs pointed to Tullberg. Our faithful librarian, Jocelyn Phillips, managed to find a copy for us, and together, we set to translating the captions to the marvelous figures that we knew would answer many of our questions. Translating the figure captions only whetted our appetites, however, and we eventually brought in Astrid Schwalb to help translate the entire text. Astrid is a native German speaker and was far more qualified to undertake this kind of task than I was with my rudimentary German learned in high school and university. Astrid did a wonderful job translating the text into English, and then Lawrence and I worked to resolve the interpretation of problematic words and make the use of scientific terms consistent with modern usage. We also spent a lot of time editing the language to give it a more modern tone and rhythm and remove as much residue of the original German word order as possible, which we knew to English readers very distracting could be. We also added several footnotes to clarify obscure allusions and connect Tullberg's findings to the modern literature and understanding. We have also included a few photographs from our own work that we hope will supplement the original figures and highlight their excellent quality.

Lastly, we would like to acknowledge the work of several other researchers whose papers helped us navigate Tullberg's text with their own careful study of baleen and other keratins. Pivorunas (1976, 1979), Werth (2000, 2001), Ruud (1940), and Williamson (1973) helped us understand baleen anatomy, and Homberger (2001), Budras et al. (1998), Kasapi & Gosline (1997, 1998), Bragulla (2003), and Bragulla & Hirschberg (2003) were essential for understanding cornified papillary epidermis. We would also like to thank Dave Hilchie for his fine histological work and Wayne Brodland and Jim Veldhuis for helping us think through the development and growth of a cornified papillary epidermis. Lastly, we are grateful to Tonya Wimmer and Donald McAlpine for collecting baleen samples for this work.

"Structure and Development of the Baleen of the Blue Whale, *Balaenoptera musculus*"

Tullberg, T. (1883). Bau und Entwicklung der Barten bei Balaenoptera sibbaldii [Structure and Development of the Baleen of the Blue Whale, *Balaenoptera musculus*]. In *Nova Acta Regiae Societatis Scientiarum Upsaliensis*, *Series III*, Volume 11, part 3, pp. 1-36, with seven plates of figures.

When studying the structure and development of keratins, the baleen of mysticete whales deserves special attention due to several characteristics that distinguish it from all other keratin structures in extant animals. It is surprising that so few authors have tackled this subject, but this may be due in part to the fact that it is very difficult to obtain suitable material for research. Of the authors who have studied the structure of baleen in more detail, the following authors deserve special recognition: Hunter, Rosenthal, Ravin, Rapp, Hesse and most of all Eschricht and Reinhardt. Hunter[1,2] describes the baleen in *Balaena mysticetus*[3] and *Balaenoptera acutorostrata*. Rosenthal[4] and Ravin[5] also report on the baleen in *B. acutorostrata*. Rapp[6] briefly mentions the form and structure of baleen in whales. Hesse[7] compares the development of baleen (in *B. acutorostrata* and *Megaptera*) with the hooves of horses and the teeth of *Ornithorhynchus*. In his excellent work on the Nordic baleen whales, Eschricht[8] offers some remarks on the structure of baleen in *Balaena*, *Megaptera*, and *B. actutorostrata* and focuses on the development of baleen in the latter. He was able to obtain a 2-m-long embryo from this species, whose baleen plates were so underdeveloped that the largest ones were only 23 mm long.

An even more detailed report on the structure of baleen is given by Eschricht and Reinhardt[9] in their work, *Om Nordhvalen*, in which they describe the baleen of an almost fully developed fetus and a newborn animal of this species.[10] These articles are, as far as I know, the only ones in which the development of baleen is mentioned. Since the majority of the above articles were written at a time when the development of keratin structures were not discussed as much as they are now, and since the work of Eschricht and Reinhardt hardly considers the microscopic structure, a new study of baleen in whales would not be without interest, especially if more information could be obtained on the early developmental stages. Thus, in the summer of 1877, when Mr. Chr. Aurivillius and Mr. C. Forsstrand[11] from Uppsala were about to start their journey to northern Norway to study the anatomy of baleen at the whaling station established by Sven Foyn,[12] I proposed that they should keep the baleen from embryos of different developmental stages, as well as parts from full-grown baleen for microscopic examination. Excellent collections were brought back to Uppsala by these gentlemen and were later appropriated by the zoological institutions of the university. The quality of these specimens is owed to the enthusiasm and skill of the gentlemen mentioned above, and the utmost friendly cooperation of Captain S. Foyn and his second-in-command Captain Bull. These

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[1] Footnotes that provide only literature citations are Tullberg's original footnotes. All others have been added by the translators to clarify the text or provide additional information.

[2] Hunter, Observations on the Structure and Oeconomy of Whales. *Philos. Transact.* Vol LXXVII. 1787, p. 371.

[3] All species names have been replaced in this translation with modern scientific names.

[4] Rosenthal, Ueber die Barten des Schnabel-Walfisches *(*Balaena rostrata*). Abhandl. der Kon. Akad. der Wissensch. zu Berlin*, 1829 (1832), pp. 127-132, p II. i-v.

[5] Ravin, Observations anatomiques sur les Fanons, sur les mode d'insertion entre eux et avec la membrane palatine. *Ann des. Sci. Nat.*, Ser. II. T. V. Zool. 1836, pp. 266-278.

[6] Rapp, *Die Cetacean*. Stuttgart and Tübingen 1837.

[7] Hesse, De ungularum barbae balaenae, dentium ornithorhynchi corneorum penitiori structura. Diss. Berlin 1939. –Fror., Neue Notizen. Bd XV, No 1. 1840, p. 1.

[8] Eschricht, *Untersuchungen über d. Nordischen Wallthiere*. B.I. Leipzig 1849.

[9] Eschricht and Reinhardt, *Om Nordhvalen (*Balaena mysticetus *L.)*. Kjöbenhavn, 1861.

[10] The species he is referring to is the bowhead whale, *Balaena mysticetus*.

[11] We can find no evidence that Aurivillius and Forsstrand published anything on the anatomy of baleen. They did, however, publish a report on a commensal harpacticoid copepod that they discovered on blue whale baleen.

[12] Svend Foyn was a Norwegian whaling captain and entrepreneur who ushered in the era of modern whaling by inventing the first successful exploding grenade harpoon, which he patented in 1870. Prior to this time, the whaling industry was on the decline, primarily due to the depletion of stocks of right, bowhead, and sperm whales, and the increasing availability of petroleum. Foyn's invention allowed whalers to hunt rorquals such as blue and finback whales, which were previously too fast and powerful to catch and subdue. The whaling station he's referring to was likely in the port of Vadsø.

collections contained not only jaws of embryos in which the development of baleen had not yet started, but also jaws of embryos with baleen in two developmental stages, of which at least one was considerably younger than the ones described by Eschricht and Reinhardt. There were also preserved pieces of fully grown baleen in alcohol.[13] This collection constitutes the basis of the present discourse, and it is my pleasure to give thanks to Mr. Aurivillius and Mr. Forsstrand for their kindness in having placed the collection at my disposal.

The Fully Grown Baleen

Before I move on to the histological observations that I have made on the fully grown baleen, I will provide a short report on the structure and arrangement of baleen in general.

Baleen consists of transversely oriented keratin plates that are attached to the lateral parts of the upper jaw, leaving open a portion of the palate along its midline. Thus, baleen forms two masses hanging from the upper jaw in the form of a comb, one on each side of the oral cavity. In finback whales, these two racks of baleen converge at the anterior end according to Eschricht and Reinhardt, but they remain separated in *Balaena mysticetus*. The plates that are closest to the labial edge of the upper jaw are the largest and are called *main baleen plates* after Eschricht; beside each of these main plates are a number of plates decreasing in size towards the interior. Eschricht called these *accessory plates*. The accessory plates associated with each main plate together form a transversely orientated row. Each of these rows (Figure 1) forms a mostly triangular form that is attached by the shortest leg of the triangle. The outer or lingual side of this triangle, which is only formed by the main plates (Figure 1a), is smooth, whereas the part that is oriented towards the oral cavity and consists of both main plates and accessory plates (Figure 1b through f) has a number of hair-like bristles (Figure 1l). Those bristles that belong to the smallest accessory plates originate from a relatively small plate (Figure 1f), and beside the smallest accessory plates, bristles occur that are not associated with a plate at all (Figure 1n). Baleen plates are largest in the middle part of the jaw and decrease in size towards both the anterior and posterior. The baleen lamina in Figure 1, shown at half its natural size, is probably one of the smallest and certainly is from the most anterior part of the jaw. As can be seen in Figure 1, the main plate (a) is shorter than the longest bristles originating from it, a little longer than the adjacent accessory plate (b), and hardly more than three times as wide as the nearest accessory plate. A more typical baleen lamina is completely different. Here, the main plate is immeasurably larger than the accessory plates, and several times longer than the bristles coming off its lingual edge. In Figure 1, which is partly schematic, the bristles are depicted as coarser and therefore also fewer in number than in reality to make them appear more distinct.

The baleen plates are enclosed by a grey-white substance at their base, which we call *Bartenzwischensubstanz*[14] since it also fills the space between the base of each neighboring plate. According to Eschricht, the baleen is attached to the part of the mucosa of the oral cavity that is delineated by two elevated wrinkles. The outer wrinkle is significantly higher, and both wrinkles together form the so-called "wreath-ligament."[15] The baleen plates consist of two substances, which have been referred to as cortex and medulla, but I will call them the outer layer or covering substance and the inner layer of tubules to avoid confusion with the cortex of hairs and with medullae in other keratins. The layer of tubules (Figures 1i & 5b) consists, as the name implies, of tubules (Figures 1k & 5c) embedded in "intertubular material" consisting of keratinized cells (Figure 5i) that correspond completely to the cells that connect the tubules in more commonly described tubular keratin structures.[16] Typically, the free ends (Figure 1l) of these tubules form the bristles at the inner edge of the baleen plate. This layer of tubules, except for the edge from which the bristles protrude, is completely enclosed by the covering substance, which forms a compact horn layer around the tubules that helps to hold them together. Since this layer penetrates further into the *Zwischensubstanz* (Figure 1h) than the layer of tubules, the baleen plate becomes hollow at this point, and an extension of the underlying connective tissue penetrates into this cavity. On the side oriented towards the

[13] The original German here is *Sprit*, which translates literally to "spirits," which could mean one of many things such as alcohol or mineral spirits, but is most likely the former.

[14] Literally, *Bartenzwischensubstanz* means "Baleen-in-between-substance." Tullberg refers to this tissue hereafter as simply *Zwischensubstanz*, and we have chosen to do the same.

[15] The word *ligament* is generally reserved for connective tissue structures that link bones, and by this definition, the structure to which Tullberg refers is not a true ligament.

[16] Tullberg is referring to keratinous structures such as horse hoof and rhinoceros horn, both of which possess a similar tubular structure to that of baleen plates.

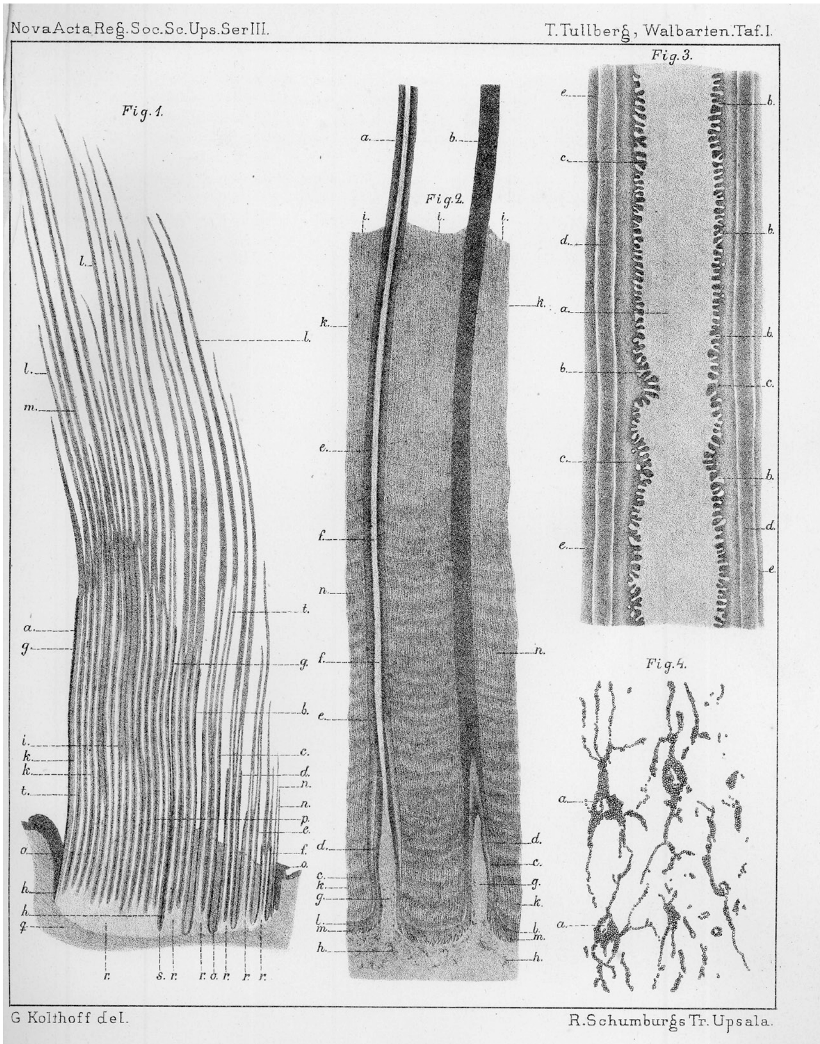

Plate I. Fully grown baleen

Figure 1. Schematic cut through a transversely oriented baleen plate, likely from the front part of the oral cavity, presented at half size; for the sake of clarity, bristles are presented as thicker and fewer in number than in reality: a: main plate; b, c, d, e, and f: accessory plates, the largest of which is about to merge with the main plate; g: covering layer of the main plate; h: the part of the covering layer that is deeper than the connective tissue plate; i: the layer of tubules of the main plate; k: tubule; l: the free ends of the tubules (i.e., the bristles); m: the medulla of a tubule; n: free-standing bristles on the inner edge of the baleen lamina; o: *Zwischensubstanz*; p: its borderline; q: connective tissue; r: penetrating connective tissue plates in the base of the baleen from which the main plate and the closest accessory plate begin to merge with each other at s; and t: tubule papillae. ***Figure 2.*** Vertical section through the base of two baleen plates: a and b: the two baleen plates; c: beginning of the outer layer of the covering layer; d: the inner soft layer of the covering layer, which more distally becomes the inner layer e of the tubules; f: tubule papilla; g: connective tissue plate; h: pigment in connective tissue; i: *Zwischensubstanz*; k: the outer layer of the *Zwischensubstanz* (i.e., *stratum subcorneum*); l: the inner layer of the *Zwischensubstanz*, merging on the base of the connective tissue plates with the inner layer of the covering layer; m: papillae that penetrate the *stratum mucosum*; and n: the vertical stripes in the *Zwischensubstanz* caused by the medullae that emerge from the tips of the papillae of the *stratum mucosum*. ***Figure 3.*** Horizontal section through a piece of the distal portion of a connective tissue plate with surrounding structures: a: the connective tissue plate; b: cross-sectioned borders of the same; c: the inner soft layer of the covering layer; d: the horny layer of the covering layer; and e: the *Zwischensubstanz*. ***Figure 4.*** Branching pigment cells on the border of the papillae that penetrate the *Zwischensubstanz*: a: nuclei.

baleen plate, these plate-like extensions (Figure 1r), which we call "connective tissue plates," break up into many thread-like papillae (Figure 1t), each enclosed in a tubule. Eschricht and Reinhardt were not able to indicate how far these reach in *Balaena*, but they have found that the same structures in *Megaptera* extend approximately halfway into a baleen plate.

I will now focus on more specific observations that I have made on parts of fully grown baleen plates of *Balaenoptera musculus* that were placed at my disposal and stored in alcohol. If we look in more detail at the layer of tubules in baleen plates, we find, as mentioned above, that it consists of closely packed tubules that are united through a thin intertubular material that is also formed out of keratinized cells. While most of these tubules reach the edge of the baleen plate, where they form bristles, some tubules within larger baleen plates terminate before reaching the edge. A cross section through a baleen plate (Figure 5) always shows tubules of very different diameters, and normally the ones with the largest diameters are also the longest ones. These tubules are like the cuticle of ordinary hairs in their structure and similarly consist of flat keratinized cells without distinct nuclei oriented concentrically. These cells contain many small brownish pigment granules which, based on their position, appear to have been grouped around the nuclei before the cells became keratinized. A medulla (Figures 1m & 5h) extends through the distal part of these tubules, which like the cortex of hair, consists of irregularly oriented cells with spaces among them. Such a formation of tubules with medullae is found in most of the largest keratin structures in mammals, but in general, it is not as pronounced as it is in baleen, which is one reason why the tubules can be separated into bristles at the edges. With respect to its formation of tubules, a baleen plate is best compared with the chewing plate of the Steller sea cow (*Hydrodamalis gigas*) as far as I could gather from Brandt's excellent study.[17] Distinct and regular tubules are found in rhinoceros horn; however, they differ from the structure in baleen in that they cannot be torn apart into threads. This is, of course, primarily based on the fact that rhinoceros horn and the chewing plate in *Hydrodamalis* do not form thin plates but a compact material. The pronounced tubules in whale baleen are undoubtedly based on the extremely long papillae. The other two aforementioned keratin structures also have enlarged papillae, but they do not compare with the baleen in whales. As mentioned above, Eschricht assumes that the papillae in the baleen plates of *Megaptera* extend at least into the middle of a baleen plate, and I have found in my study that the papillae extend even further in the larger baleen plates of *B. musculus*. These larger baleen plates were dried out and therefore were not useful for histological examination. However, some of the smallest plates were available and preserved in alcohol. These undamaged plates were probably from the anterior part of the oral cavity and still had parts of the mucosa attached. One of these is shown schematically in Figure 1 at half its natural size, as mentioned above. The *Zwischensubstanz* between these smaller baleen plates reaches a height of approximately 5 cm,[18] the free part of these baleen plates is approximately 12 cm long, and the longest bristles reach up to 19 cm above the top of the plate. The distance from the inner boundary of the *Zwischensubstanz* to the top of the longest bristles is thus approximately 36 cm. The connective tissue plate that penetrates into each baleen plate is about 1.5 cm high. Therefore, the length of the longest bristles, if calculated from the boundary of the connective tissue plate to the top of the bristles, is approximately 34.5 cm. The accessory plates here are very small, and all contain a few bristles, but several of these reach a length that is only a few cm shorter than the longest bristles of the main plates. The difference in length between the largest bristles from the inner parts of the main plate and the largest ones from the top of the main plate is also insignificant. Alongside these longer bristles, however, there are a lot of smaller ones of variable length in both the main plate and the accessory plates. Between the baleen laminae, where bristles (Figure 1n) grow directly out of the *Zwischensubstanz*, the longest ones are hardly more than 10 cm in length, calculated from the base within the *Zwischensubstanz*. The longest papilla that I have encountered in these smaller baleen plates belonged to a bristle on the inner boundary of the main plate and reached a length of approximately 16 cm, calculated from the boundary of the connective tissue plate and ending approximately 15 cm from the top of the bristle. Otherwise, the length of the papillae in the longest bristles varied between 14

[17] The Steller sea cow is an extinct marine mammal that was first described in the scientific literature by the German naturalist Georg Steller in 1751 and was hunted to extinction by Europeans by 1768.

[18] Judging from the fact that it is not nearly as stiff as the baleen plates, *Zwischensubstanz* may be considered a form of soft α-keratin and, as such, it is quite extraordinary. Typical soft α-keratins like the outer layer of skin in mammals (*stratum corneum*) usually consists of only 15 to 20 cell layers. However, at a thickness of 5 cm, *Zwischensubstanz* likely consists of about 10,000 cell layers.

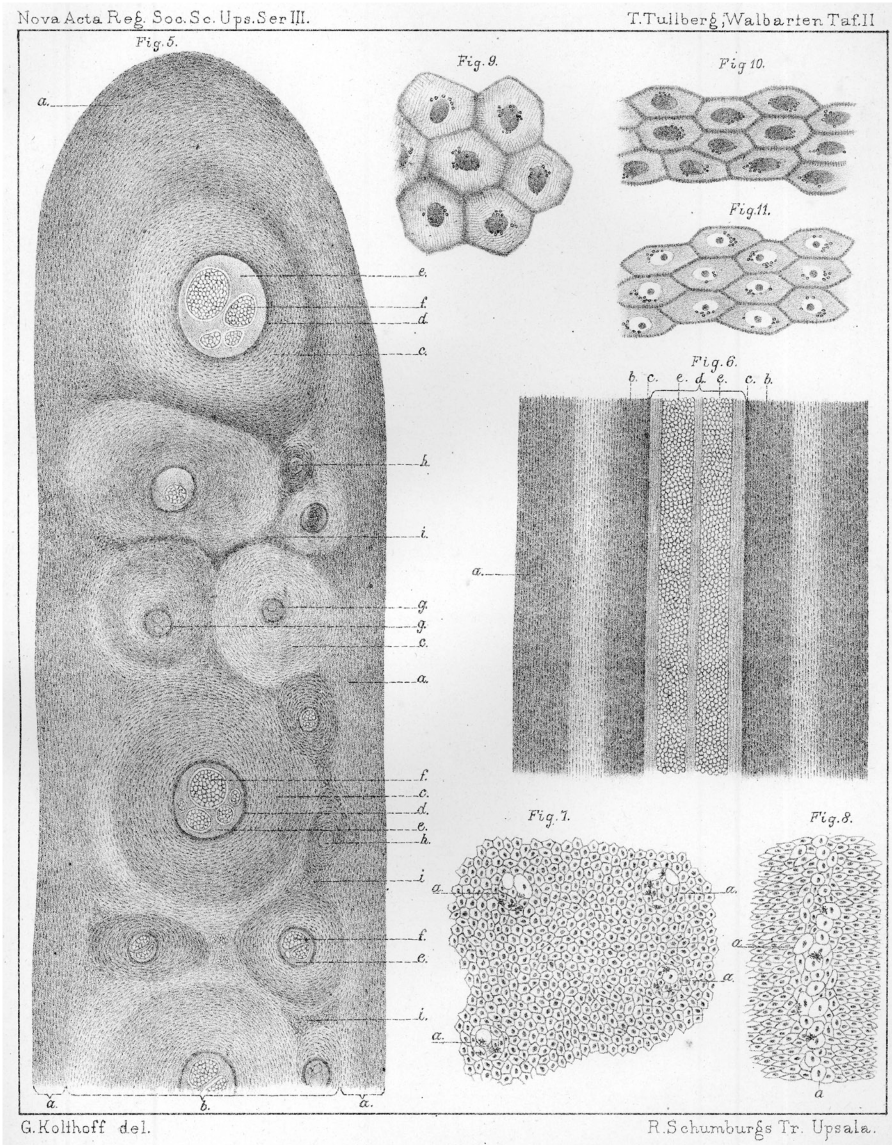

Plate II. Fully grown baleen

Figure 5. Cross section through a piece of baleen plate: a: covering layer; b: tubule layer; c: tubules; d: the inner layer of the tubules; e; papillae; f: blood vessels of the papillae; g: destroyed papillae ends; h: medullae; and i: intertubular material. ***Figure 6.*** Longitudinal section through a piece of baleen plate, at a right angle to the plate: a: covering layer; b: outer layer of the tubule; c: the inner layer of the tubule; d: papilla; and e: blood vessels. ***Figure 7.*** Horizontal section through the *stratum subcorneum* of the *Zwischensubstanz*: a: medulla. ***Figure 8.*** Vertical section through the *stratum subcorneum* of the *Zwischensubstanz*: a: medulla. ***Figure 9.*** Horizontal section through the *stratum mucosum* of the *Zwischensubstanz*, greatly enlarged. ***Figure 10.*** Vertical section through the *stratum mucosum* of the *Zwischensubstanz*, greatly enlarged. ***Figure 11.*** Vertical section through the *stratum subcorneum* of the *Zwischensubstanz*, greatly enlarged.

and 15 cm. These papillae, which are normally formed by the connective tissue, thin out gradually from the base, and the proximal part seems to have small, distinct ridges oriented lengthwise, similar to those under the nails of humans. As mentioned above, the papillae originate from the connective tissue plate that penetrates into the base of the baleen plate. It should be noted, however, that the papillae merge at the base, with no space between them. They also do not arise from the same height; instead, the connective tissue plate gets divided into extensions, which further split into papillae. Several relatively large and straight blood vessels (Figures 5f & 6e) extend more or less centrally through the entire length of the papilla (Figures 5e & 6d), and the ones I studied were always filled with blood cells. In the periphery of the papillae, however, there is a network of finer vessels. It seems that as soon as these papillae have reached a certain length, they are generally destroyed at their tip. That is, at the boundary between the fresh papillae formed out of distinct connective tissue and the medullae of the tubules, you can always find a yellow or reddish substance formed by destroyed blood. Such a substance can also occur scattered in the medulla itself, which can be best compared with the reddish welts on the hooves of horses, which are called "stone-galls." The yellowish substance that occurs at the tip of the papilla could also have been formed by blood that is exuded from the tip. The notion that other regions of the papilla have been destroyed can be inferred with certainty from the fact that one can usually follow this substance (Figure 5g) clearly into the contours of the central blood vessels. Now and then I have also found a similar yellow substance at the base of the papillae, but only within the vessels, which were filled with it over a variable distance. In the tubules of the smaller baleen plates mentioned above, this substance only occurs over a few mm, but it occurs over a longer distance in the larger, dried baleen plates that I examined. However, it is difficult to decide where this substance ends and where the fresh papilla starts since the samples were essentially destroyed by drying. Since this problem could be solved with greater ease with fresh baleen plates, I did not want to spend much time on the solution and I leave it proposed until further study is possible. Based on my examinations, for now, it has to be assumed that the undamaged papilla in the baleen plates of about 1 m length, including the bristles and the part that is sunk into the *Zwischensubstanz*, reaches a length of ~60 cm. The idea that this yellow substance is formed during the lifetime of the animal and not during the drying of the baleen is supported by the fact that it is found in the finer tubules in the inner part of the baleen plate, while the larger tubules at the same height have distinct connective tissue papillae. If the yellow substance at the end of the papillae were formed by the drying of the baleen, before it was put in alcohol, no fresh papillae could be found in the closely located tubules. Nor could such a substance be found in the vessels at the bases of the papillae, which lack this substance entirely a small distance upwards. I can only assume that this yellow substance has been formed out of blood, and the same substance looks completely like the substance that occurs in the Haversian canals of fully grown horns in cervicornia,[19] which is formed undoubtedly during the dying off of blood vessels.

Before we leave the tubules and their papillae, I have to mention a remarkable fact. The innermost parts of the tubule (Figures 5d & 6c) (i.e., those that lie closest to the papillae) are stained by carmine and hematoxylin (i.e., the nuclei are stained and as such appear distinct). This is in contrast to the main substance (Figures 5c & 6b) of the tubule. According to this result, cells in the vicinity of the papilla are not entirely keratinized.[20] We will call the layer that is closest to the papilla "the inner layer of the tubule," as opposed to the entirely keratinized part of it, which we will call "the outer layer of the tubule." The boundary between both layers is clearly evident when stained with carmine and hematoxylin, and it is easy to differentiate both layers in a cut through the baleen plate. As far as I could observe, the inner layer extends to the distal end of the tubule as far as the papilla extends and merges at its tip into the medulla, which is stained clearly by carmine and hematoxylin, and in whose cells I could see indication of nuclei. The inner layer extends farther toward the proximal end of the tubule than the outer one, that is, to the bases of the papillae, where the different inner layers of the tubules meet each other. Here, the inner layer

[19] Tullberg is referring to an outdated classification system for the ruminants. Cervicornia included species such as deer and elk in which males shed their antlers, and Cavicornia included species such as cattle, goats, and antelope, whose horns are not shed and consist of bony skull projections covered in hard α-keratin. The "dying off" of the blood vessels to which he refers occurs after the breeding season in deer and elk and before the antlers are shed.

[20] The significance of this observation is that a germinitive layer of basal keratinocytes overlies the dermal papilla, and it is these living cells that ultimately give rise to keratinized cells of the tubules. This is not qualitatively different from α-keratins that arise from other dermal papillary structures. Although Tullberg struggles with this idea here, he eventually arrives at this possibility in the "Summary."

is largest, and its cells are less flat and have large, distinct nuclei. However, the more peripheral cells are flatter, and the outer keratinized layer starts only a few mm away from the connective tissue plate. At first it is very thin, but it rapidly becomes thicker at the same rate that the inner one becomes thinner. The inner layer becomes thinner to the same degree that its cells become flatter, and long before the baleen plate emerges from the *Zwischensubstanz*, this layer looks like the more distal portion of the baleen plate (i.e., the cells are very flat and its cells stain less distinctly than other parts, including the layer that surrounds the base of the papilla). Where the baleen plate leaves the *Zwischensubstanz*, the inner layer is very thin and gradually becomes thinner.

When we move to the outer layer of the baleen or the covering layer, we find that it is formed by the same flat, pigment-bearing keratinized cells as the inner layer of tubules. These cells occur together in a layer (Figure 1g) that surrounds all of the tubules in the same way that keratinized cells in a single tubule surround the papillae. The covering layer, however, as mentioned above, penetrates further into the *Zwischensubstanz* than the layer of tubules and encloses (Figures 1h & 2c) the connective tissue plate (Figures 1r & 2g). Starting where the layer of tubules ends, the keratinized part of the covering layer gradually thins until it disappears entirely at the base of the connective tissue plate. Between this keratinized part and the connective tissue plate is an inner layer (Figure 2d) of the same structure as the inner layer of tubules that encloses the bases of the papillae, although it is considerably larger. In the same way as this part of the inner layer of tubules is the source of their growth, the source of the covering layer also lies in its inner layer. This layer is largest at its base and gradually thins to the same degree as the outer layer thickens; it ultimately merges into the inner layer of the tubules (Figure 2e) without a distinct boundary. In the same way that the bases of the papillae bear small ridges, the upper parts of the connective tissue plate do as well. At the base, on the other hand, and a short distance along its sides, it is covered with small papillae that have the same outline as those that penetrate into the inner layer of the *Zwischensubstanz*. Here, the inner layer of the covering layer merges with the inner layer of the *Zwischensubstanz* without any hint of a boundary.

The *Zwischensubstanz* consists of a huge cell mass that is penetrated in its most inner part by the papillae from the connective tissue plate. In the anterior baleen plates that I had for examination, these papillae (Figure 2m) are relatively small and only reach a length of approximately 1 mm, but they should be longer in the middle part of the baleen series where the *Zwischensubstanz* is much thicker. Although there is no actual *stratum corneum* on the *Zwischensubstanz*, it is possible to differentiate between an inner mucous layer (Figure 2l) and an outer, more keratinized one (Figure 2k). Both are stained by hematoxylin and carmine, but the first one is more pronounced, and the boundary between them is quite distinct. The inner layer extends over 1 mm between the small, anterior baleen plates, but it becomes thinner towards the baleen plates and merges at their bases into the inner layer (Figure 2d) of the covering layer. The nuclei of the cells (Figures 9 & 10) that form this layer are large and distinct and stain conspicuously with hematoxylin and carmine. On the other hand, in the outer layer, which covers the entire remaining part of the *Zwischensubstanz*, the stained part of the nuclei is greatly reduced. The entire remaining part of the cell, which is occupied in the inner cells by the stained nuclei, is entirely uncolored (Figure 11). For this layer, I suggest the name *stratum subcorneum* because of its structure and appearance. The pigment granules occur mainly around the clear patches in the cells of this layer and also around the nucleus in the inner layer. These resemble pigment granules in the baleen plates, but they are less abundant in the *Zwischensubstanz*, except in those areas that are adjacent to the connective tissue. These parts are strongly pigmented in *B. musculus*, which is why I could not clearly see the structure of the inner cell layer. In one cut through the corresponding parts in *B. musculus* where pigment is sparser, however, I could clearly see that neither the innermost cells in the *Zwischensubstanz* nor the outer part of the connective tissue plates consist of cylindrical cells. I was also not able to discern whether these inner cells are so-called "spiny cells"[21] (Figures 9 through 11). From the end of these connective tissue papillae arise distinct medullae (Figures 7 & 8a), which are characterized by bubble-shaped holes that occur between their cells. At the boundary of this medulla, there is occasionally a flattened cell, but there is no actual formation of tubules in the *Zwischensubstanz*, at least not in the parts that I have examined.[22] These medullae are equivalent to the ones found in the developing baleen of embryos, which I will describe in more detail below.

I was not able to find the substance that Ranvier called *Eleidine*, which occurs in the epidermis of the skin in humans and many vertebrates. It is also thought to occur in other keratin structures, but I could find it in neither fully grown nor embryonic baleen. It is possible that the material that was

[21] Tullberg is almost certainly referring to melanoctyes, which are highly branched pigment cells.

[22] It is not clear to us what the functional significance of these holes in the *Zwischensubtanz* is or if there is any.

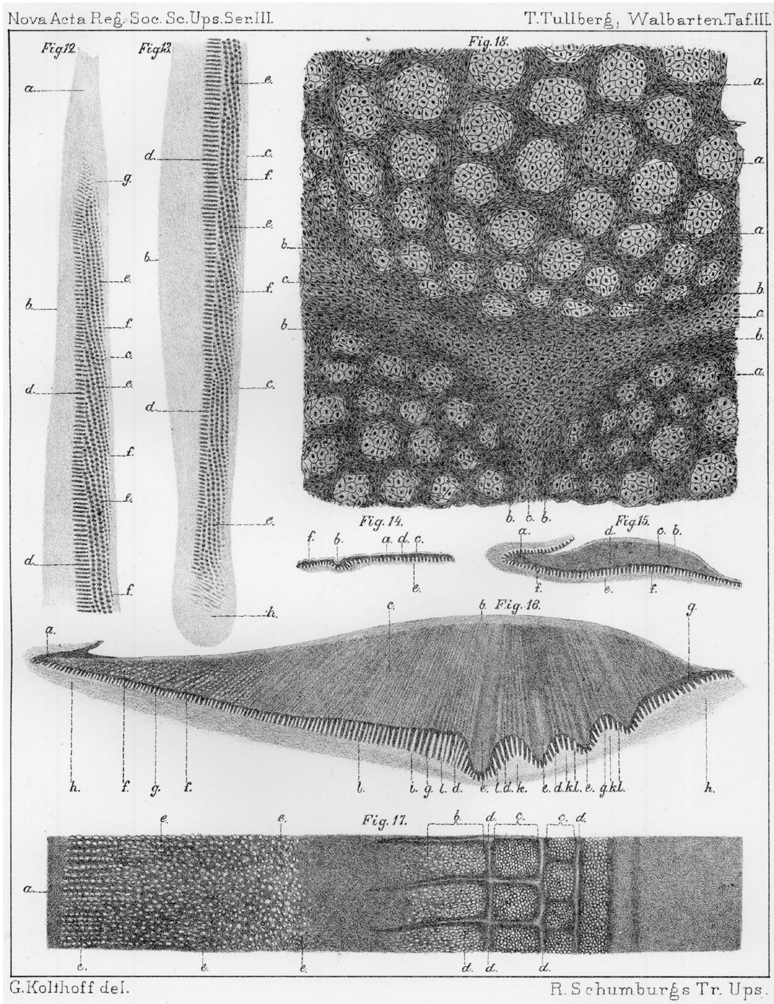

Plate III. Developing baleen of a 3-m-long embryo

Figure 12. Anterior portion of the developing baleen, shown at half its natural size, from the connective tissue side out; a: the anterior end that lacks depressions; b: the outer edge; c: the inner edge; d: transverse depressions of the transversely oriented connective tissue plates; e: rows of depressions behind the conical connective tissue extensions (cones); f: the inner end of these rows; and g: beginning of similar rows. ***Figure 13.*** The posterior portion of the developing baleen—shown at half its natural size—seen from the side facing the connective tissue; b, c, d, e, and f: as in the previous figure; h: the posterior end of the baleen, similar to the anterior end without the depressions behind the connective tissue extensions. ***Figure 14.*** Vertical cross section through the anterior end of the developing baleen and a piece from the unkeratinized mucosa: a: the developing baleen; b: its outer edge in the direction toward the mucosa; c: *stratum corneum*; d: *stratum mucosum*; e: connective tissue with papillae; and f: unkeratinized mucosa. ***Figure 15.*** Vertical cross section through the developing baleen about 5 cm from the anterior end: a: the outer edge of the developing baleen that penetrates into the connective tissue; b: *stratum corneum*; c: *stratum subcorneum*; d: *stratum mucosum*; e: connective tissue; and f: elongated connective tissue papillae. ***Figure 16.*** Vertical cross section through the most developed portion of the developing baleen: a: the outer edge of the developing baleen; b: *stratum corneum*; c: *stratum subcorneum*; d: tubules; e: embryonic *Zwischensubstanz*; f: columns of bubble-like cells; g: *stratum mucosum*; h: connective tissue; i: one of the outer, transversely oriented connective tissue plates; k: connective tissue cones; and l: elongated papillae. ***Figure 17.*** Horizontal section through the same portion of the developing baleen: a: the outer edge; b: groups of tubules that arise from the transversely oriented connective tissue plates; c: groups of tubules that arise from the connective tissue cones; d: embryonic *Zwischensubstanz*; and e: bubble-like cavities. ***Figure 18.*** Part of the previous section, greatly enlarged: a: tubules; b: the parts surrounding groups of tubules consisting of a few flattened cells of the embryonic *Zwischensubstanz*; and c: the central parts of this *Zwischensubstanz*.

available to me might have been unsuitable for such an examination.

Before we leave the fully grown baleen, we must add a few words about pigmentation. As mentioned above, small black-brown granules, which are scattered in the epithelial cells of baleen plates and in the *Zwischensubstanz*, occur both in the living cells but also in the keratinized cells. Moreover, special pigment cells occur at the boundary between the connective tissue and the epithelium of the *Zwischensubstanz* and are most distinct around the small papillae that penetrate into the *Zwischensubstanz*. In these pigment cells (Figure 4), the pigment is of the same structure as in the epithelium cells and also consists of small round black-brown granules. The cells themselves possess long extensions and a distinct nucleus, that is, as far as I could see, without a distinct membrane.[23] Around the distal furrowed parts of the connective tissue plates, I found none of these spiny pigment cells, but the inner parts of the epithelium here are extremely pigmented. This also applies to the basal parts of the tubules. Farther out, the tubules are not more strongly pigmented at the boundary of the papillae than at the more peripheral parts. Also, pigment granules occur in the medullae of the tubules and in the *Zwischensubstanz*, where they form small clumps of irregular shape.

In addition to the boundary between the connective tissue and the epithelium, there are also pigment cells scattered here and there within the connective tissue (Figure 2h). In general, these cells exhibit a very irregular structure. Here, the pigment also contains small granules that are equivalent to those that occur in the epithelium and at the boundary of these cells.

Developing Baleen in Embryos

The youngest embryo of *Balaenoptera musculus* in which I examined the mucosa of the jaw had a length of 1.2 m and showed no trace of developing baleen. In contrast, the developing baleen was very distinct in a 3-m-long embryo. It can be seen as a thicker epithelium inside the periphery of the upper jaw in which disk- or cone-shaped extensions force their way into the underlying connective tissue. In the above-mentioned collection is an almost complete epithelium structure of the left baleen series (Figures 12 & 13), which has separated from the connective tissue because of some deterioration. The extensions from the connective tissue that invade this epithelium structure have naturally left corresponding depressions in the epithelium structure after it was removed. The depressions in the middle and posterior parts are already a few mm, and they decrease gradually in size towards the anterior, disappearing completely in the most anterior parts. In this way, it is easy to observe the form and arrangement of these extensions in these preparations when they first occur.

This thicker epithelium structure, which is shown in Figures 12 and 13 on the side facing the connective tissue, has a length of 53 cm and a width of 4 cm at its widest point. The widest part, which stretches for a length of ~10 cm, occurs just posterior to the middle. From here, the epithelium structure becomes gradually smaller towards the anterior and posterior ends. While the posterior end (Figure 13h) rounds off suddenly with a width of ~3 cm, the anterior part (Figure 12a) decreases gradually to a width of 8 mm, enlarges slightly, and terminates in this specimen with a width of 1.4 cm. Unfortunately, I could not see the outer boundary of the developing baleen in this specimen because it was slightly damaged. Connective tissue extensions do not penetrate into the entire structure of the thick epithelium. The first 4 cm of the anterior end (Figure 12a) completely lacks depressions; they are also missing over 1.5 cm of the posterior end (Figure 13h) and at the part facing the outer edge of the jaw (Figures 12b & 13b). The extensions are therefore placed closer to the inner edge of the developing baleen and occupy an area 47.5 cm long and ~1.5 cm wide. The width of the part penetrated by these extensions is constant along its entire length, except at the anterior end, where it becomes slightly pointed. On the outer side, this epithelium structure forms a fold that inserts slightly into the neighboring connective tissue, which forms the boundary between the developing baleen plate and the lip.

As can be seen in the form and arrangement of depressions in Figures 12 and 13, the outer row of the connective tissue extensions consists of transversely oriented vertical connective tissue plates, which leave transverse depressions in the epithelium structure (Figures 12d & 13d). They have different lengths in different parts of the developing baleen; the longest ones are 8 mm. Beside these extensions, as can be seen in the depressions left in the epithelium structure (Figures 12e & 13e), are conical extensions. They lie in rows, which extend from the inner edge diagonally outwards and anteriorly. Each row of these conical extensions or connective tissue cones is attached to a slightly elevated border, which corresponds to a weak indication of a groove in the epithelium structure. At the anterior end, the extensions form

[23] It is very unlikely that the nuclei he described lacked nuclear membranes. It is more likely that he was unable to see them because of a limitation of his microscopy or because of inadequate tissue preservation.

quite irregular ridges, and the cones extend further forward than the transverse plates. Here, it appears that the plates have formed by the merging of these cones. The plates enlarge inwards via merging with new cones. This occurs via the elevation of the border between a plate and an adjacent cone. The transverse plates also undoubtedly enlarge outwards since, as will be shown later, they extend close to the outer edge in a subsequent developmental stage. Thus, while the front and outside ends of the rows formed by the cones merge with the transverse plates during their inward growth, the inner and posterior ends (Figures 12f & 13f) of these rows continually enlarge by extending more and more posteriorly and inwards, and, simultaneously, the ridges, which are insignificant at first, slowly increase in size. The development of new rows (Figure 12g) of cones occurs as soon as the developing baleen attains a certain degree of development, mainly in the front end of its inner boundary.

As we have seen already, the baleen plates in a fully grown animal form around the connective tissue plates, which are arranged in transverse rows. The beginning of these transverse rows of plates consists of the transverse embryonic connective tissue plates, which, as mentioned above, extend gradually inwards by merging with adjacent cones on the lingual side. At the surface of the developing baleen, there is no indication of the ridges at this point in development. However, in the sample on which I am basing this description, there were small rows of very faint, round ridges here and there, which correspond with the outer parts of the diagonal rows of cones on the connective tissue that abut the connective tissue plates. It is possible that this could also be an effect of the shrinking of the sample in alcohol.

When we look at the microscopic structure of the baleen at this developmental stage, we find that the epithelium consists of one cell mass, which is similar to the *Zwischensubstanz* in fully grown baleen, but also differs from it in several ways.

A cut through the front of the developing baleen (Figure 14a) reveals the first changes in the mucosa in its transformation into developing baleen. Here, we see that this transformation consists of a gradual thickening of the epithelium structure and an enlargement of the connective tissue papillae that correspond with this thickening. As soon as the developing baleen differentiates in this way from the mucosa, it becomes delineated outwards by a depression (Figure 14b) in the connective tissue (Figure 14e), but this soon becomes insignificant (Figure 15a). The outer part of the epithelium is already keratinized on the undifferentiated mucosa (Figure 14f) and forms a *stratum corneum*, which is not stained by carmine, and is not especially stained on the inner side either. We can distinguish such a keratinized layer on the undifferentiated mucosa from a sort of *rete mucosum*.[24] During the thickening of the epithelium in the developing baleen (Figure 14a), both layers (Figures 14c & d) become thicker, but the boundary between the layers is less distinct, and one can distinguish three layers over a distance of a few cm. Between the inner mucosa (Figure 15d), which stains strongly with carmine, and the outer keratinized layer (Figure 15b) appears a transition layer (Figure 15c), which is stained weakly by carmine. This layer, which will eventually be the thickest, is very similar to the outer layer of the *Zwischensubstanz* in terms of its appearance and the morphology of its cells and, therefore, calling it *stratum subcorneum* may be most reasonable. *Stratum corneum*, as can be seen above, is not represented in the *Zwischensubstanz*. In the inner layer of this part of the developing baleen, I have seen cavities that are reminiscent of the bubble-like cavities in the medullae of the *Zwischensubstanz* and the cavities in more highly developed baleen. However, they are completely empty in the samples I prepared, which could have been due to deterioration of the tissue. The middle layer in this part of the developing baleen is almost evenly distributed over the inner layer, and without any hint of the formation of tubules. Its cells become increasingly flatter towards the boundary with the keratinized layer, which consists only of flat cells.

When extensions of the connective tissue membrane below the epithelium (Figures 16i & k) appear along with an elongation of the papillae (Figure 16l) on these extensions, an important change occurs in the middle layer of the epithelium structure. At this point, the first indications of developing tubules, baleen plates, and *Zwischensubstanz* appear. The cells around the longest papillae flatten, and tubules (Figure 18a) are thereby formed, which slowly push forward over the papillae. As they push forward, they are filled with epithelium cells, which are constantly formed anew at the tips of the papillae. Since they are not exposed to pressure from the sides, they are not pushed together in the same way as the cells that form the tubules, but they instead form a sort of medulla in the tubules. However, no big,

[24] The *rete mucosum* was a hypothesized mucoid layer of the skin first proposed by the Italian anatomist Marcello Malpighi in 1667. The existence of this fluid layer and its contribution to skin color in humans was a controversial subject for almost 200 years until it was discovered that intracellular pigment granules within melanocytes were responsible for the pigmentation of skin.

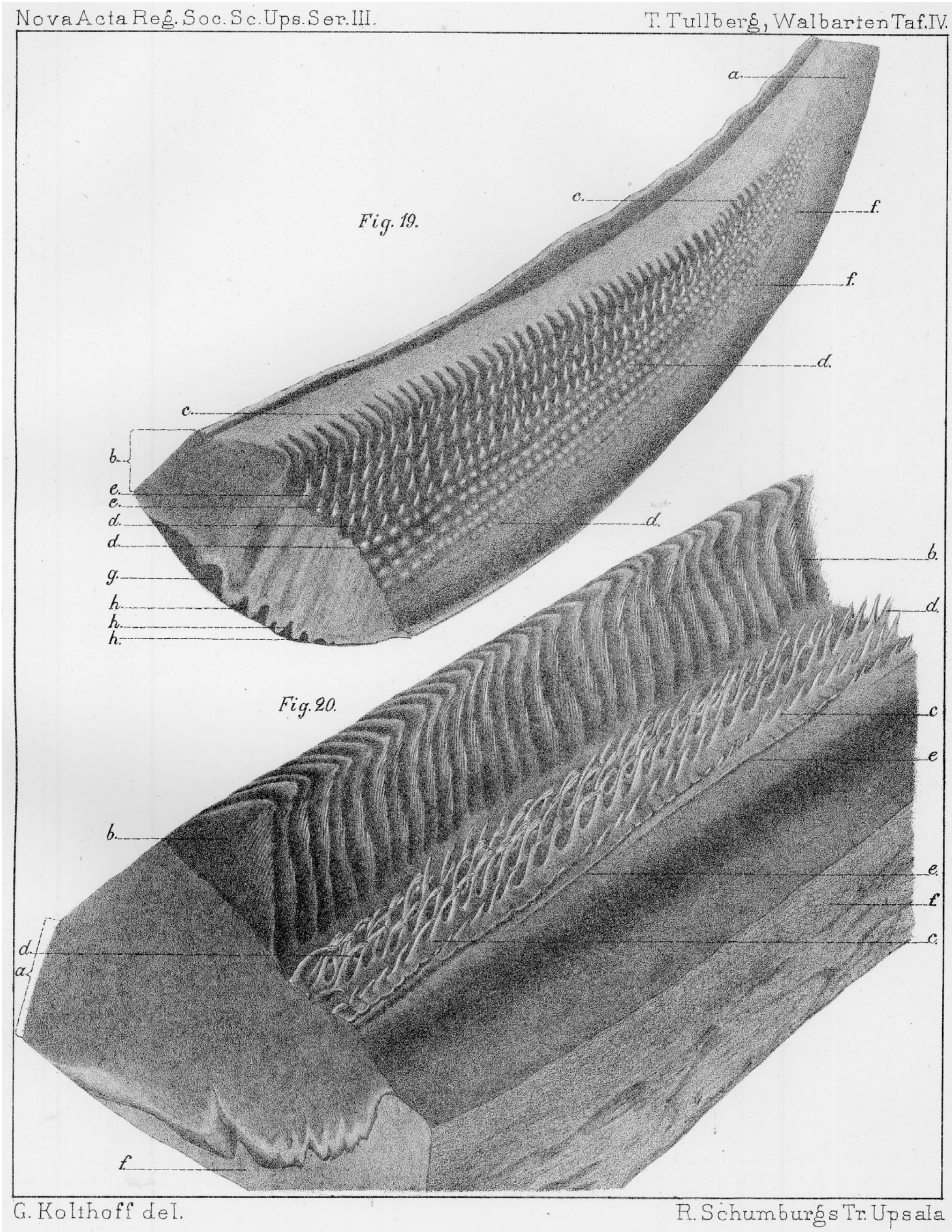

Plate IV. Developing baleen of a 4.55-m-long embryo

Figure 19. The anterior part of the baleen structure shown at twice its natural size: a: anterior end without ridges on the surface; b: the outer edge that is sunk into the connective tissue; c: transversely oriented plates on the surface, beginning of the main plate; d: borders with cones; e: cones breaking up on the tip into bristles; f: beginning of the border with ridges; g: depression behind a connective tissue plate; and h: depressions from the cone-like connective tissue extensions. **Figure 20.** A more developed part of the developing baleen shown at twice its natural size: a: the outer edge that is sunk into the connective tissue; b: embryonic main plate; c: border with the cones; d: cones broken up into bristles near the tips; e: the inner, youngest part of the borders; and f: connective tissue.

bubble-like extensions occur in these medullae. Since these tubules, as mentioned above, arise from the papillae on the edges and tips of the connective tissue extensions, they naturally tend to form groups (Figures 16d, 17b & c). These groups of tubules form the precursors of the developing baleen plates. In the same way, the epithelium structure in between (Figures 16e & 17d) is the precursor of the *Zwischensubstanz*. Among the single tubules within these groups of tubules exist a large number of undifferentiated cells, which are a sort of embryonic intertubular material. At this stage, the covering layer of the baleen plates is not present if one does not consider the part of the *Zwischensubstanz* adjacent to the groups of tubules that consist of flattened cells as such. As the cells around the elongated papillae are flattened and form the tubules, the cells next to the tubules (Figure 18b) also become more or less flattened. In contrast, the cells in the *Zwischensubstanz* that lie between the connective tissue extensions and the groups of tubules, and which are therefore not exposed to pressure (Figure 18c), for the most part do not become flattened.

An indication of column formation also appears in the parts of the epithelium structure that lie close to the edge of the jaw in front of the connective tissue extensions, and here the formation of columns also starts at the tips of the papillae. However, these columns (Figures 16f & 17e) are not surrounded by distinct tubules but contain numerous bubble-like cavities. These columns appear 15 cm from the front end of the developing baleen and in the widest part. The region containing these cavities (Figures 16f & 17e) is so wide that it extends from the outer end of the transverse connective tissue plates to the outer edge of the developing baleen.

The keratinized layer that was particularly distinct in the front part of the developing baleen also covers the more developed parts of the epithelium structure (Figure 16b). However, in these regions it is undoubtedly not the original layer. Namely, it is likely that this layer was destroyed in the oldest parts and replaced by a new one, which was gradually formed by keratinization of the outer parts of the *stratum subcorneum*.[25]

Before we leave this stage of the developing baleen, we must direct our attention towards the pigmentation. The pigment in the oral mucosa consists of little granules of exactly the same form as in the baleen plates. In addition, these granules are similarly found partly in epithelial cells and partly within specialized cells at the boundary between the epithelium and the connective tissue. Due to the strong pigmentation, it is difficult to see the form of these pigment cells clearly; they probably also possess branching extensions, but the extensions are certainly not very significant. During the transition of the mucosa to the developing baleen, these cells around the papillae become larger and more conspicuous, as well as more distinct from each other. Soon they will show up as distinct branching cells, similar to those that surround the papillae in the *Zwischensubstanz* in fully grown animals. As in the fully grown baleen plates, the pigment cells here also seem to lack an actual membrane,[26] but are provided with a nucleus, which is difficult to identify due to the strong pigmentation.

In a 4.55-m-long embryo, the developing baleen is by far more developed, and the baleen plates have started to elevate above the remaining epithelium structure. Since I have only received parts of the developing baleen of this embryo, I am able to state neither the entire length of the developing baleen nor the number of the protruding baleen plates. However, with a ~40-cm-long piece, which forms the front end of the developing baleen, I was able to observe the baleen plates during their initial protrusion from the free outer area of the developing baleen.[27] This piece is, as described for the specimen above, separated from the underlying connective tissue and clearly exhibits depressions that correspond to the connective tissue extensions as well as the young baleen plates protruding on the free side of the epithelium structure. In the front end of this piece, which is not the most anterior part of the developing baleen, it reaches a width of 1 cm and a thickness of ~1 mm. Towards the back, it increases in width and thickness and

[25] The evidence on which Tullberg bases his conclusion about the keratin layers wearing away and then reforming is never made explicit and is almost certainly erroneous based on what we now know about keratin growth.

[26] Tullberg's inability to see the plasma membrane in pigment cells is likely due to a lack of contrast between the membrane and the dark cytoplasm in these cells.

[27] Tullberg is pointing out that the developmental differences between the early embryo he described, which was only 3 m long, and this one, which is 4.55 m long, are significant, which could have been problematic for describing all the stages of baleen development *in utero*. However, by taking advantage of the fact that the baleen structure expands toward the anterior and posterior ends as the fetus grows, he was able to find areas in the developing baleen of the older specimen that were similar in size and development to the most highly developed baleen in the younger one. In this way, he was able to bridge the large developmental gap between the two specimens. He explains this in more detail three paragraphs down.

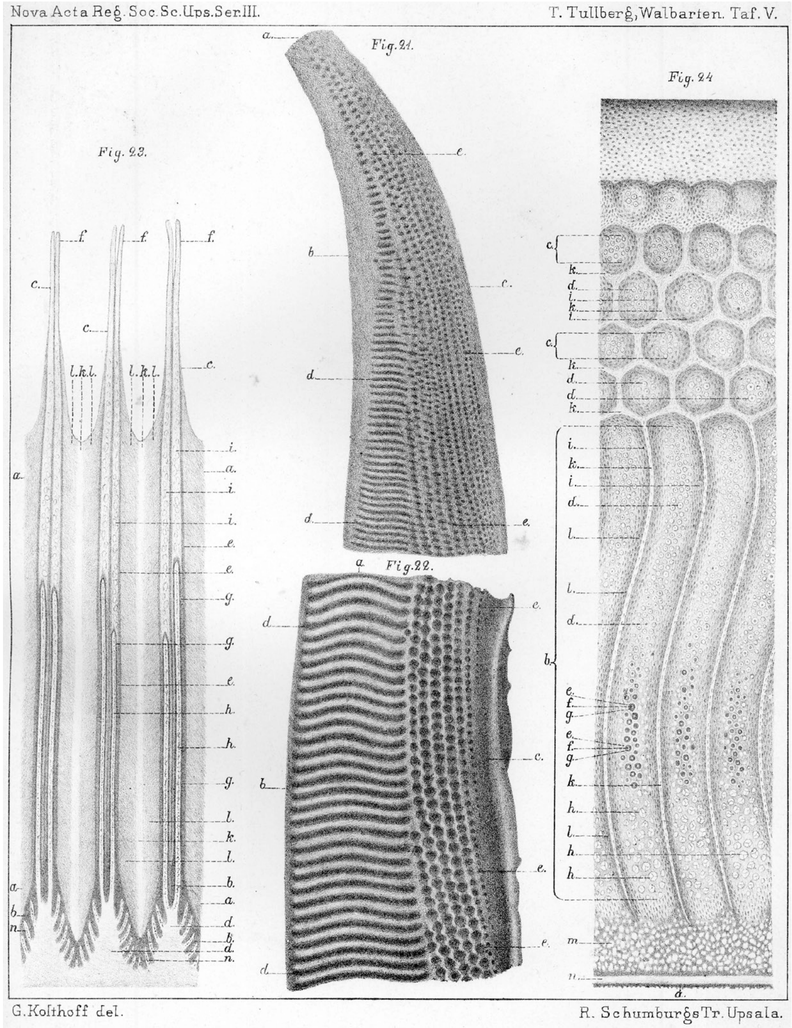

Plate V. Developing baleen of a 4.55-m-long embryo

Figure 21. A piece of the anterior portion of the developing baleen that was shown in Figure 19, shown here from the side facing the connective tissue—at its natural size: a: the anterior end of this piece; b: the outer edge; c: the inner edge; d: depressions from the connective tissue plates; and e: depressions from the connective tissue cones. **Figure 22.** A more developed part of the developing baleen that was shown in Figure 20, shown here from the side facing the connective tissue—at its natural size; letter labels as in the previous figure. **Figure 23.** Longitudinal vertical section through three developing main plates in the aforementioned part of the developing baleen; enlarged approximately four times: a: *stratum subcorneum* (the *stratum corneum* from this piece was already gone); b: *stratum mucosum*; c: developing baleen plates; d: their corresponding connective tissue plates; e: tubules, presented for the sake of clarity as thicker and fewer in number than in reality; f: their outer free portions, the first bristles; g: inner, soft layer of the tubules; h: elongated connective tissue papillae (the longest papillae are likewise as in Figure 25 drawn too long); i: medullae; k: the central part of the embryonic *Zwischensubstanz*; l: its parts formed by more compressed cells next to the groups of tubules; and n: papillae in the *stratum mucosum* layer. **Figure 24.** Horizontal section through a piece of the same structure—enlarged approximately four times: a: the outer edge; b: groups of tubules arising from the connective tissue plates; c: groups of tubules arising from the connective tissue cones; d: stiffer tubules, sectioned above the tips of the papillae; e: stiffer tubules, sectioned below the tips of the papillae; f: the papillae; g: the inner layer of these tubules; h: poorly developed, but broader tubules with very large bubble-like cavities; i: part of the embryonic *Zwischensubstanz* composed of compressed cells; k: part of the embryonic *Zwischensubstanz* not composed of compressed cells; l: medullae in the *Zwischensubstanz*; m: cross-sectioned columns from bubble-like cavities; and n: outer edge of the part of the developing baleen that borders with the connective tissue.

at the back end, it is ~5 cm wide and 4 cm thick, including the young baleen plates.

In the previous developmental stage, as we saw before, the outer edge of the developing baleen was sunk into the connective tissue, whereas the inner edge is always at the same height as the surface of the mucosa. At the thickened end of this sample, the epithelium structure at the outer edge is sunk into a 1.5-cm-deep depression in the connective tissue (Figure 20a).

The thinner front end of this sample (Figure 19a)[28] shows no hint of baleen plates on its upper surface, and only minor depressions are visible adjacent to the connective tissue extensions on the attached part of the piece (Figure 21a). A few mm to the back, however, ridges start to appear on the upper surface of the developing baleen.

As expected, the ridges on the surface (Figures 19 & 20) exhibit exactly the same form and arrangement as the extensions of the underlying connective tissue and, therefore, occur at the outer edge of the developing baleen as transversely oriented plates (Figures 19c & 20b) and on the inner side as diagonal rows of cones (Figures 19d & 20c). Here, I should mention that the cones arise from much more distinct and more pronounced borders. Naturally, I am not able to tell where the initial ridges develop on the surface of the developing baleen since I have not examined any developing baleen at that developmental stage. However, based on the fact that the ridges of the connective tissue in the earlier stage described above reached almost the same level of development over a large part of the developing baleen, the formation of the ridges on the surface of the developing baleen should start almost simultaneously over a large stretch. It then continues forward via the formation of new rows of cones (Figure 19f) at the inner edge of the front end, which are incorporated into the existing ridges. During subsequent development of the baleen, these rows, as well as those on the connective tissue, stretch continuously further back and inwards (Figure 20e), while the inner edge is shifted further inward by the growth of the developing baleen.

Since the youngest parts of these rows are naturally the lowest, and the oldest ones are the highest, it is clear that the cones from the inner edge of the developing baleen, which are completely flat with a width of approximately 5 mm, grow gradually up to the point where they border on the transversely oriented plates. These cones, which can be best identified in Figures 19 and 20, arrange themselves gradually into transverse rows corresponding with the connective tissue cones and merge one after the other with the transverse plates in exactly the same way that the connective tissue cones merge with the connective tissue plates. The superficial transverse plates, which are the beginnings of the developing main plates, rise above the cones almost from their first appearance. This rapid growth of the plates arises partly from the strong development of the entire epithelium structure in the outer part of the developing baleen, and partly from their own rapid push forward.[29] At the thicker end of the sample mentioned above, the superficial plates, including the parts that are split up into bristles, are 1.5 cm high along the inner edge and 1.2 cm high along the outer edge, while the largest cones only reach a height of 6 mm, even when the bristles are included.

The next phenomenon we must describe is the disintegration of the superficial cones and plates into bristles. It is peculiar that although the plates are larger and have already started to adopt the plate-like form of the developing baleen plate, they do not start dividing into bristles earlier than the cones, but rather later. However, only the largest cones (i.e., those located closest to the plates) are subject to such a division.

At this developmental stage, the inner part of the epithelium structure (i.e., the side facing the connective tissue) (Figures 21 & 22) is also provided with depressions that correspond with the connective tissue extensions and are arranged in the same way as the depressions on the inner side of the younger baleen sample described above. These depressions become deeper and wider, depending on the growth of the developing baleen. I would especially like to point out that the transverse connective tissue plates correspond with the superficial plates protruding from the upper side of the developing baleen, and they grow in such a way that they reach the outer edge of the developing baleen. This is why the corresponding depressions (Figure 22d) at the attached side of the epithelium structure at this stage also stretch to the outer edge. At the front, and probably also at the back end, where the connective tissue plates lack corresponding ridges on the free surface, the epithelium structure outside the transverse depressions still exhibits a relatively wide edge (Figure 21b) without furrows as can be found outside the entire row of transverse depressions on the developing baleen during the earlier stage described above.

[28] The original figure reference was for 18a, but this is clearly a labeling error.

[29] When he says that the plates "rapidly" push forward, he obviously is not basing this on observations of baleen growth over time. Instead, he is once again taking advantage of the developmental gradient that occurs in the developing baleen due to its anterior and posterior expansion.

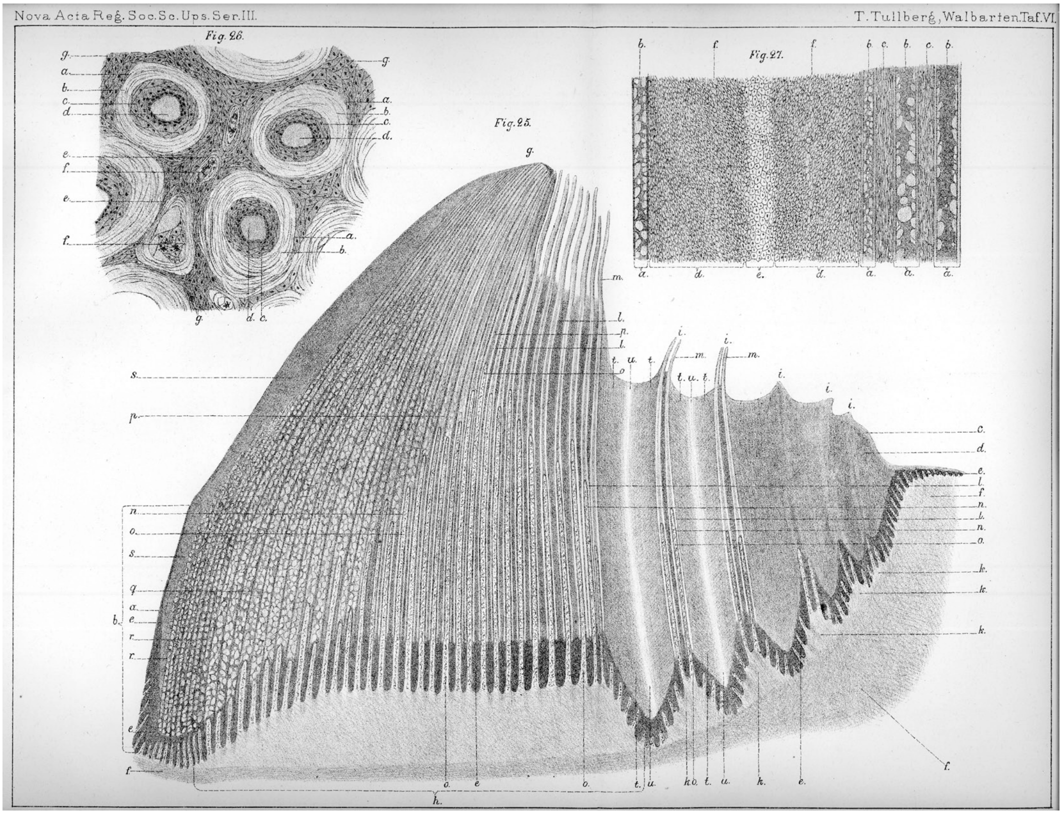

Plate VI. Developing baleen of a 4.55-m-long embryo

Figure 25. Vertical cross section through the most-developed part of the developing baleen—enlarged about four times: a: the outer edge; b: the part of the outer edge that is sunk into the connective tissue; c: remainder of the *stratum corneum*; d: *stratum subcorneum*; e: *stratum mucosum*; f: connective tissue; g: developing main baleen plate; h: the corresponding connective tissue plate; i: developing accessory plates; k: corresponding connective tissue cones; l: tubules, presented as thicker and fewer in number than in reality; m: the free tips of the tubules; n: the inner, soft layer of the tubules; o: elongated connective tissue papillae; p: medullae; q: larger tubules with very large bubble-like cavities in the medullae; r: columns of bubble-like cavities without distinct tubules; s: the firmer part of the developing baleen on the border of the jaw edge; t: side part of the embryonic *Zwischensubstanz*; and u: central part of this substance. **Figure 26.** Horizontal section through a piece of the developing baleen with well-developed tubules, greatly enlarged: a: larger tubules cut below the tips of the papillae; b: the outer, horny layer; c: their inner, soft layer; d: papillae; e: smaller tubules cut above the tips of the papillae; f: medullae; and g: intertubular material. **Figure 27.** Vertical section through tubules and *Zwischensubstanz*, greatly enlarged: a: tubules; b: medullae; c: intertubular material; d: side portion of the *Zwischensubstanz* composed of flattened cells; and e: its central part.

It should be noted that the transverse connective tissue plates do not form a straight line when they are more fully grown but, rather, take on a more S-shaped curve.

The histology of the front part of the developing baleen in this stage resembles the preceding stage, but changes occur as development continues. These changes consist mainly of a stronger development of the connective tissue extensions, especially of the transverse connective tissue plates, elongation of the papillae at the distal edge of these plates and at the end of the cones, a more significant differentiation of the middle layer (*stratum subcorneum*), and the successive pushing away of the outer keratinized layer. To illustrate these changes, I will describe the structure of the most developed part of the baleen during this stage.

Here, the large connective tissue plates (Figures 23d & 25h) reach a height of 4 mm, and the cones (Figure 25k) a height of 3 mm. The longest papillae in the middle of the connective tissue plates reach a length of 1.5 cm, which is extraordinary in relation to the thickness of the entire epithelium structure, and then decrease in length rapidly inwards and slowly outwards. However, shorter

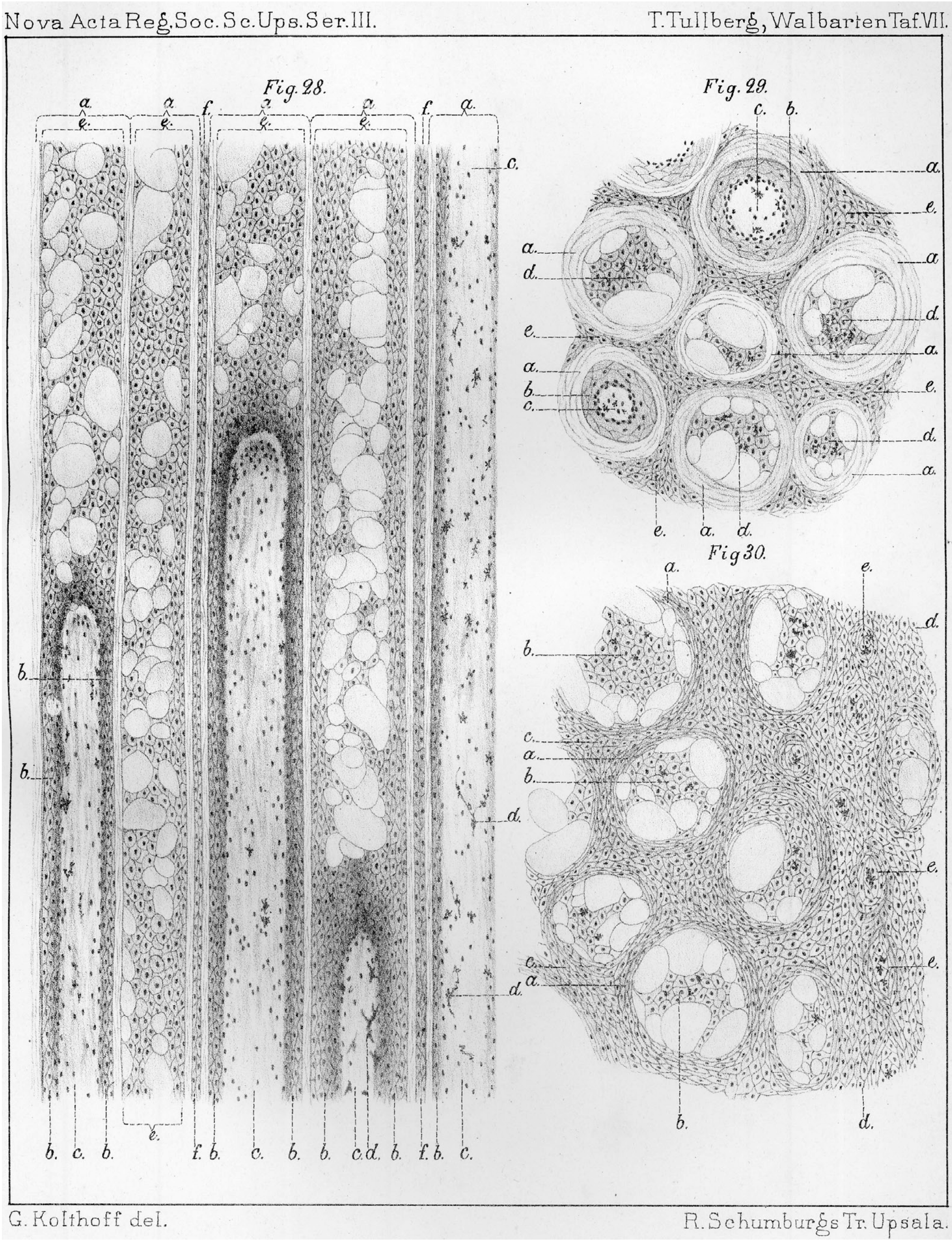

Plate VII. Developing baleen of a 4.55-m-long embryo

Figure 28. Longitudinal section through tubules with thinner walls than depicted in cross section in Figure 26: a: the tubules; b: their inner, soft layer; c: papillae; d: pigment cells; e: medullae with large bubble-like cavities; and f: embryonic intertubular material. **Figure 29.** Horizontal section through approximately the same location as in the previous section; two of the tubules were cut below the tips of the papillae, and the rest were cut above the tips of the papillae: a: the outer layer of the tubules; b: the inner layer; c: papillae; d: medullae with bubble-like cavities; and e: intertubular material. **Figure 30.** Horizontal section through the large, thin tubules on the outer end of a connective tissue plate and through a piece of the embryonic *Zwischensubstanz*: a: tubules; b: medullae; c: intertubular material; d: *Zwischensubstanz*; and e: medullae in the *Zwischensubstanz*.

Figure 31. Baleen plates from humpback (left) and sei (right) whales showing the triangular shape of the main plates, the smooth labial edge, and the fringed lingual edge; small minor plates are visible at the lingual margin of the main plates in both species. The white tissue that acts as a spacer between adjacent plates is the *Zwischensubstanz*, which is best understood as a type of soft keratin. The width of the plates from both baleen series is about 20 cm.

papillae also occur among the longer papillae, a circumstance that corresponds completely with the structure in fully grown baleen where, as mentioned above, longer and shorter bristles alternate. The papillae on the connective tissue cones are far smaller than the papillae on the plates, and reach a length of 1 cm on the cone closest to the plate. On the cones lying inside, the papillae gradually decrease in size until they are only slightly higher than the papillae coming from the connective tissue between the extensions. At this stage, these papillae are not higher than in the preceding stage, just as the corresponding papillae in the *Zwischensubstanz* of a fully grown animal are also insignificant in size. However, only the papillae at the bases of the furrows between the extensions remain so small. At the sides of the extensions, the papillae enlarge gradually from the base of the extension distally, where the longer papillae mentioned above arise. At the side of the developing baleen facing the edge of the jaw, where it is sunk into the connective tissue (Figure 25b), there are also papillae, of which the most inner ones are of considerable size, but the outer ones are very small. Also, towards the inner edge of the developing baleen, the papillae decrease until they merge with papillae in the mucosa at the border.

Here, as in the preceding developmental stage, it is possible to differentiate among the three layers in the epithelium structure. The most inner or the mucosa layer (Figures 23b & 25e), which is stained most strongly by carmine and hematoxylin, entirely fills the spaces between the extensions and, on the other side, the spaces between the papillae. It also stretches over the distal part of the extensions, where the much-enlarged papillae are attached. However, here it is only the spaces between the parts on the bases of the papillae that are filled by this layer. On the other hand, one can say that this continues over the elongated papillae and covers them up to their tips like a thin membrane (Figures 24g & 25n). Accordingly, the mucosa of the developing baleen at this stage corresponds entirely with the inner layer of the *Zwischensubstanz*, the inner layer of the covering layer, and the inner layer of the tubules in fully grown baleen plates. At the outer

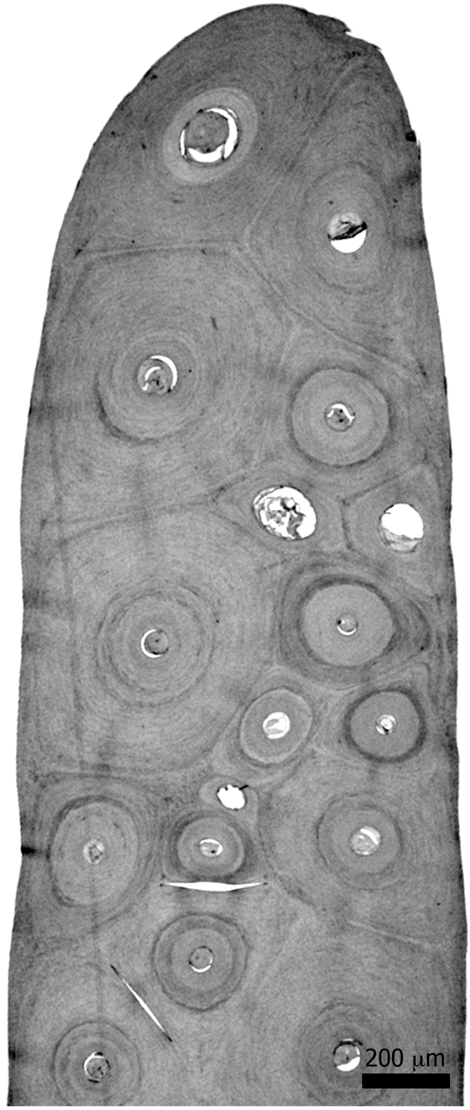

Figure 32. H&E stained section of the labial edge of a minke whale baleen plate; compare with the drawing in Figure 5 from Tullberg.

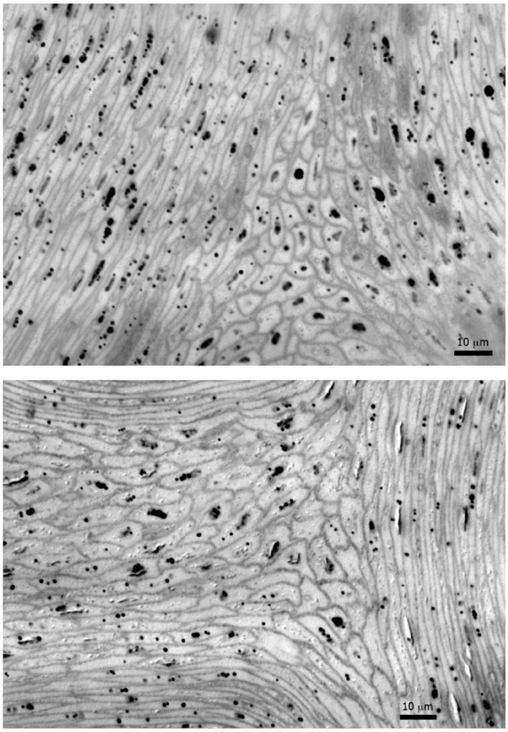

Figure 33. H&E stained sections from humpback baleen (top) and sei baleen (bottom); note the two tissue phases that are evident in these pictures: (1) tubular horn, which is made up of flattened cells oriented circumferentially around the tubule axis, and (2) intertubular horn, which consists of keratinized cells between the tubules.

Figure 34. Anterior (left) and posterior (right) margins of the left baleen rack from a minke whale, viewed from the underside that faces the dermis; note the striking resemblance to Tullberg's Figures 12 & 13. In Tullberg's figures, there is a clear trend in the developing baleen of collinear dermal cones merging into the corresponding main dermal plate. Here, we see a similar pattern that is not a developmental gradient but, rather, a morphological one in which the main plates get progressively smaller toward the anterior and posterior ends. At the extremes, there are no plates at all, only stiff hairs (to use the terminology of Williamson, 1973). These developmental and morphological patterns are consistent with a hypothesis put forth by Demere et al. (2008), suggesting that early mysticetes had both teeth and rudimentary baleen, which most likely consisted of stiff bristles only.

depression at the edge of the developing baleen, the mucosa decreases in thickness in the same way that the papillae decrease, which also occurs at the inner edge. The outer layer (*stratum corneum*) is lacking entirely at the part of the surface of the developing baleen where the transverse plates and the cones have started to separate into bristles. In a cut through the most developed part of the developing baleen, such a layer (Figures 25c) can only be observed at the edge, and it also seems that the outer parts are about to detach. This layer, which is not stained by carmine and hematoxylin, covers the newly formed ridges as well as the parts lying in between these. Thus, it is clear that they do not break through this layer while appearing at the surface.

At this stage, the middle and largest layer (Figures 23a & 25d) in the epithelium structure, as mentioned, is more differentiated than in the previous stage. To begin with, we can observe the tubules themselves here (Figures 23e, 24d, 24e, 25l, 26a, 27a, 28a & 29a). As we saw previously, there were early indications in the previous stage, but here the tubules are significantly more developed. They surround the enlarged papillae (Figures 23h, 24f, 25o, 26d, 28c & 29c), and a few mm away from their bases (i.e., where the actual mucosa ends), the beginning of the formation of tubules can be seen (Figures 23 & 25). The cells, however, are still insignificantly keratinized and are stained relatively strongly by carmine and hematoxylin. Further along, they become increasingly more keratinized, and their staining becomes correspondingly weaker. The tubules push against the mucosa with their bases, and between them and the papillae is the continuation of the mucosa mentioned above or "the inner layer of the tubule" (Figures 23g, 24g, 25n, 26c, 28b & 29b), consisting of less flattened epithelium cells which are stained strongly by carmine. Beyond the end of the papilla, this tubule is filled by a medulla (Figures 23i, 25p, 28e & 29d) in which epithelial cells of

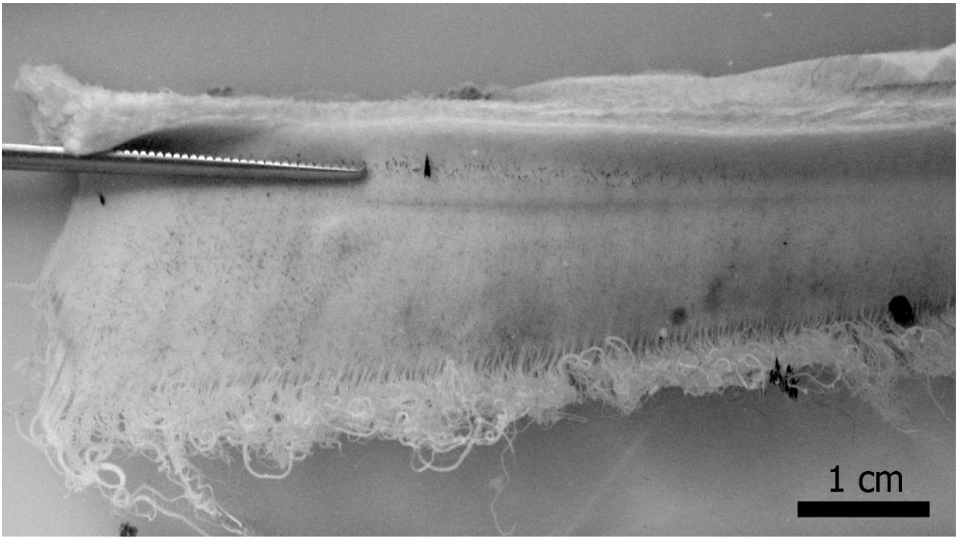

Figure 35. Dermal plate pulled away from a sei whale main baleen plate; note the numerous elongated dermal papillae. In the intact structure, the papillae are long and straight, but these papillae have curled up in the absence of support from the baleen keratin. On the labial side, the papillae are about 7 cm long in this specimen.

Figure 36. Portion of the left baleen rack from a humpback whale, viewed from the underside facing the dermis; the labial side is on the left, and the lingual side is on the right. Anterior is toward the top and posterior is toward the bottom.

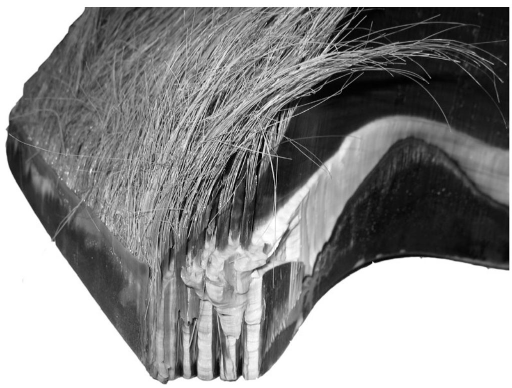

Figure 37. Close-up of the humpback baleen plates shown in Figure 31, displaying the transition from the main plates to the minor plates as well as the white *Zwischensubstanz*.

usual size with distinct nuclei alternate with large bubble-like cavities containing a fine, granular substance in which I could not see a distinct nucleus (Figures 28 & 29). Here, one has the best opportunity to see that the formation of medullae in baleen bristles does not come from the papillae but from the epithelium at the end of the papillae. As these tubules are the beginning of developing bristles, the cell columns enclosed in the tubules are nothing less than the beginning of medullae in the developing bristles, and it is easy to see in this stage (Figure 28) that these medullae do not derive from the papillae, which is evident from their entire structure. These tubules within the epithelium structure are naturally the continuation of the ones seen in earlier stages, although these were by far less developed, had thinner walls, and no bubble-like cavities in their medullae.

As indicated above, these tubules belong only to the parts in the middle layer that correspond to the outer parts of the connective tissue extensions since the enlarged papillae originate only from here and the tubules are formed only around those papillae. The tubules are held together, as in earlier stages, with a sort of intertubular material (Figures 26g, 28f & 29e). But at this stage, the cells forming this intertubular material are few in number, and, thus, the tubules generally lie close together. The division into bristles of the extensions protruding on the surface of the developing baleen is naturally based on the fact that this intertubular material is gradually destroyed, whereby the tips of the tubules become independent from each other (Figures 23f & 25m). The notion that the bristles are united during their first appearance at the surface and then separated in this manner is proven by the fact that they are still connected after they have already emerged a certain distance from the epithelium structure. This is in contrast to bristles protruding from the bases in fully grown baleen plates, which emerge individually from the epithelium. This becomes even clearer when one considers that the bristles have already started to separate at their tips in some of the newly formed baleen plates, while they are still held together by cells between the bristles near the tips. Also, the newly formed bristles are entirely uneven, which is a consequence of intertubular cells that did not completely detach.[30]

Before we leave the group of tubules, we must direct our attention to the enlarged papillae on the parts of the connective tissue plates that lie closest to the edge of the developing baleen. They are larger in diameter than those that come from the part of the plates lying further back (Figure 25). The tubules surrounding them (Figures 25q & 30a) are consequently wider than the ones lying more inside. Also, these tubules are provided with thinner walls and with much bigger bubble-like cavities.

When we consider the cell mass lying between the groups of tubules in the middle layer, we find that this is significantly more developed than in the previous stage and further differentiated. Since this cell mass corresponds best with the *stratum subcorneum* in the *Zwischensubstanz* of fully grown baleen, it is reasonable to call this material adjacent to the underlying parts of the mucosa "the embryonic *Zwischensubstanz*." I have discussed the mucosa previously, so now we will deal with the *stratum subcorneum* of this substance.

As in the middle layer of the *Zwischensubstanz* of the fully grown baleen plates, the nuclei of the cells here are also small round bodies with approximately the same appearance as a nucleolus. I was not able to see clearly any evidence of spines on these cells. The cells in the parts that are closest to the groups of tubules are slightly compressed from the side (Figures 27d & 30d), whereas the cells in the middle between the groups of tubules (Figure 27e) are not compressed but are approximately as high as they are wide, just as they are in the preceding stage. However, in the previous stage, there was only a first indication of such a formation in the inner parts, whereas it is distinct here and extends all the way up to the surface. Consequently, the entire, more developed part of the baleen divides into several compartments separated by vertical walls (Figures 23k, 25u & 27e), which are formed by cells that are not compressed and lie in the middle between the connective tissue extensions and the groups of tubules. And since these cells stain less strongly than the ones that are compressed, which occur on the sides, they form a bright, relatively distinct stripe (Figure 24k) in horizontal cuts that are stained with picrocarmine[31] and well-rinsed. This stripe lies between compartments of the developing baleen that are formed by the groups of tubules (Figures 24b & c) and by the flattened cells (Figure 24l) surrounding these. These parts, consisting of more flattened cells as well as the middle part, indicate the formation of columns (Figures 24i, 27f & 30e) arising from the ends of papillae in the mucosa below. The cells in these columns deviate little from those surrounding them, and these columns are characterized mainly by the occurrence of clumps of pigment in them, and by the fact that their cells are slightly more intensively colored than the surrounding tissue. In the *Zwischensubstanz*, an indication of tubule formation is only found at the border next to the group of tubules. The columns in the parts in the middle between the groups of tubules are the least distinct.

Bubble-like cavities are sparsely distributed within the *Zwischensubstanz* and correspond to the cavities inside the medullae of the tubules. However, a large number of such bubble-like cavities can be found arranged in columns (Figures 24m & 25r) in the part of this cell mass that lies next to the outer ends of the groups of tubules arising from the transverse connective tissue plates. These arise from the underlying connective

[30] The discussion here raises the interesting question of how a balance is struck between the coherence of the tubules within the baleen plate and their separation into bristles at the plate lingual margin since the same intertubular material responsible for the former eventually degrades to allow for the latter. Our observations of baleen from sei, minke, and humpback whales suggest that differences in calcification may be involved in the regulation of plate coherence and dissolution into bristles. Pautard (1963) suggested a similar mechanism.

[31] Picrocarmine is a histological dye that is used to stain keratohyaline granules, which are typically found within the *stratum granulosum* of epidermis. The granules most likely consist of high sulfur proteins that eventually form the protein matrix that surrounds the fibrous intermediate filament component within keratinized cells.

tissue papillae in the same way that the medullae form. We therefore also have a region of bubble-like cavities at this stage, although they are much thinner than in the younger stage. Outside this region, on the other hand, is another even thinner compartment (Figures 24n & 25s), which does not contain any bubble-like cavities and only shows subtle formation of columns. This is certainly formed above the connective tissue that limits the outer edge of the developing baleen and whose inner part as mentioned above is occupied by relatively large papillae.

In this stage, there is still no indication of the formation of the covering layer, but naturally this is formed by the parts of the embryonic *Zwischensubstanz* lying next to groups of tubules.

The pigment also occurs in branching cells around the connective tissue papillae in this stage, but they are larger here and more branched out than in the previous stage, and their extensions form networks. A collection of pigment clumps also occurs here beyond the tip of each papilla, and these can also be found, as already mentioned, dispersed in the medullae coming from the tips of the papillae in both the ones containing bubble-like cavities and in the other ones.

Summary

Now that I have described the structure of fully grown baleen in *Balaenoptera musculus* and the baleen at two developmental stages, I will now summarize the conclusions to which these examinations have led regarding the origin and development of the baleen plates. The first change that can be detected in the mucosa of the upper jaw is that the epithelium at the edges of the jaw becomes thicker and the connective tissue papillae become elongated. This thicker part is delineated outwards by a wrinkle in the mucosa. This change, which may start when the embryo is approximately 2 m long, probably starts from the middle part of the edge of the jaw and spreads from there towards the anterior and the posterior. Here, the outer layer of the mucosa differentiates into a thin, completely keratinized layer and an adjacent semi-keratinized layer, which gradually increases in thickness. In contrast, the mucosa increases in thickness more slowly. The connective tissue lying below the epithelium rises gradually into diagonal lengthwise rows of small conical extensions on slightly elevated ridges. These extensions gradually arrange themselves into transverse rows, and since the outermost extensions in these rows merge through the elevation of the connective tissue between them, transverse ridges develop, which form the first indication of the transverse connective tissue plates. On the edges of these plates and on the tips of the conical extensions within, the papillae become gradually larger. With the increase of the surrounding cells and the growth of the papillae, the outer cells become compressed and flattened and tubules develop, which are indistinct in the beginning and become more pronounced as the papillae grow.

These tubules, which form around the papillae, naturally push above them during the growth of the epithelium structure in the same way that the epithelium structure pushes over the papillae in ordinary horn. As the tubules push forward, they become filled by cells, which must form at the tip of the papilla by division of the epithelial cells there. These cells do not flatten, and a number of larger gaps filled with fine granular material develop between them. A similar compression of cells occurs around the larger connective tissue extensions, and here the cells also gradually become flattened. In contrast, the cells between the extensions as well as those outside of the region formed by the extensions remain uncompressed. The development continues until the epithelium structure has reached a certain thickness and an indication of ridges starts to appear at the surface of the developing baleen. These ridges correspond to the connective tissue extensions and therefore have the same arrangement as these. The beginning of these ridges, however, is not formed in the way that the more differentiated parts of the epithelium lying above the connective tissue extensions break through the remaining mass. Instead, this mass becomes abandoned, which becomes evident in that the ridges are covered with a keratinized layer in the beginning. During continued strong growth of the papillae on the edges of the connective tissue extensions and of the epithelium surrounding these, the tubules arising from the papillae gradually reach the surface of the developing baleen. This might occur partly via the repulsion of the epithelium structure lying above the group of tubules and partly by being pushed aside by the advancement of stiffer groups of tubules.[32] Meanwhile, the papillae become significantly longer and penetrate a considerable distance into the middle layer; now the tubules formed around them start to become keratinized. As this group of tubules rises above the epithelium structure in the form of transverse plates or cones, the tubules gradually separate via

[32] Here, Tullberg implies that the tubules reach the surface of the developing baleen by pushing through overlying layers. He presents no evidence for this, and in light of what we now know about keratin development, it is very unlikely. A more plausible scenario is that tubules are eventually exposed at the surface via the wearing away of overlying layers of cells.

the destruction of the cells between them, and the first bristles appear on the newly formed small baleen plates. At this point, the developing baleen is divided into mostly developed tubules coming off the connective tissue extensions and the cell mass surrounding the extensions (i.e., the embryonic *Zwischensubstanz*).

Due to a lack of appropriate material, I was not able to study the next developmental stage, but it is not difficult to infer most of the changes that are likely to take place based on our knowledge of the previous stages and the fully grown baleen. Keratinization occurs in the connective tissue extensions and in the slightly flattened cells around the group of tubules in a manner that resembles how the cells of the tubules around the papillae begin to keratinize. In an almost full-term fetus of *Balaena mysticetus*, Eschricht found a thin keratinized layer over the main baleen plates. It is possible that the papillae coming from the sides of the connective tissue extensions had already disappeared and were replaced by ridges as found in the fully developed animal, but it is more likely that keratinization also started earlier. Since the papillae disappear, the mostly distinct medullae arising from them also disappear, and the keratinized layer that surrounds the connective tissue extensions and group of tubules becomes more homogenous like the covering layer in a fully grown baleen plate. Because the connective tissue extensions, which have been compressed almost from the beginning, eventually move away from each other as the animal grows, the space between them becomes filled by the *Zwischensubstanz*. Since the papillae persist here, papilla tips and corresponding medullae pass through the filler cell mass as well as the embryonic *Zwischensubstanz*.

As development continues, the papillae enclosed in the bases of the tubules also elongate more and more, while the parts of these tubules outside the epithelium structure become harder and harder. Hereby it is clear that the papilla, when it has come out of the *Zwischensubstanz*, becomes surrounded by a solid tubule. From this moment on, a shifting between the papilla and the tubule should not occur, but, according to all my observations, the papilla has to keep the same pace in its development as the bristle.[33] The papillae in the tubules of fully grown baleen plates are surrounded by a layer of cells that is not keratinized to the same degree as the outer layer of the tubules. However, these tubule cells are keratinized enough that it is hard to imagine that any cell division could occur. Furthermore, cell division within this long, uniform tubule could not occur without the tubule being broken up.[34] It is difficult to imagine a mechanism in which the tubules are pushed away from the papillae that does not involve cell division on the surface of the entire papilla.[35] If the tubule were nevertheless able to push forward ahead of the papilla, the formation of new medulla cells would naturally need to occur at the tip of the papilla, or else a large cavity would form there. Such a large cavity does not exist at the tip, and the smaller cavities which occur there are too small and irregular to have been formed in such a way. Furthermore, a formation of new medulla cells is unthinkable because the tip of the papilla, as shown above, is destroyed regularly. One could argue that the destroyed blood at the top of the papilla would fill this space. Although I cannot say with certainty what distance this yellow substance covers in the longest bristles, this distance seems to be too insignificant to fill in the space that would form via a shifting between the tubule and papilla. If such a shift occurred after the hardening of the tubule, it would need to occur during the entire growth of the tubule and, consequently, the tubule could push a considerable distance forward.

It is clear that the papillae must reach far into the tubules in the baleen to be able to securely attach the heavy baleen plates, which are attached by relatively short connective tissue plates through the wreath-ligaments and the *Zwischensubstanz*. If the papillae were short and conical, and only surrounded by a soft cell layer, as is the case, for instance, in the horns of Cavicornia,[36] these soft cells, which would connect the firmer keratinized tissue with the papillae alone, would not be strong enough to attach the baleen plates.[37]

Eschricht made the observation that the number of baleen plates in newborn young of *Balaena*

[33] While it is likely that tubule growth and papilla elongation go hand in hand during development, as Tullberg suggests here, it is also likely that in fully grown baleen, new tubule material grows off papillae of fairly constant length. See Bragulla (2003) for more information on how this process occurs in hard α-keratin structures that arise from a papillary epidermis such as horse hoof.

[34] Here, Tullberg is trying to reason through where cell division is likely to occur, and he concludes correctly that it is unlikely to occur within the hard keratinized cells of the tubular horn.

[35] Tullberg comes to the correct conclusion that growth of tubular horn arises mainly from the basal epithelial cells on the surface of the papillae. What might have been difficult for Tullberg to grasp at the time is that the growth rate of cells off the steep sides of the papillae must be considerably slower than the rate of growth off flatter portions of the basal epithelium in order for the structure to grow at a constant rate overall.

[36] See footnote 13 for an explanation of this term.

[37] Here, Tullberg is musing over the significance of the extreme length of the papillae in baleen, and he suggests

mysticetus is the same as in older individuals and thus the baleen plates do not increase in number after birth. This was demonstrated by the fact that newborns possess 240 connective tissue plates, whereas fewer connective tissue plates were present in the developing baleen. On the other hand, the baleen plates themselves should continue to grow throughout the entire life of the animals, as Eschricht also assumes, partly by formation of new material at the bases of the plates and partly by a continued formation of new baleen plates at the inner edge of the baleen. The baleen plates, therefore, increase in width by incorporating new accessory plates, as Eschricht has proven, and which I can confirm. This occurs in the same way that the small connective tissue plates merge with the connective tissue cones in the embryo (i.e., the connective tissue between the connective tissue plates of a main plate and its next accessory plate rises to connect both). To be able to provide a more complete picture of this, however, one would need to examine a greater number of fresh or preserved baleen plates than I was able to. Once the baleen plates have approached each other, no *Zwischensubstanz* is formed any more, and when the ridge that connects the connective tissue plates has reached the same height with them, the formation of a covering layer between the baleen plates also ceases. In this way, they merge into a single baleen plate, which is, of course, still divided distally. Furthermore, through continual splitting of the unmerged parts, the original accessory plate is broken up into bristles. As the baleen plate grows continually from its base, it will surely be split up at the inner edge. The bristles may otherwise be destroyed through wear and should be very short in older animals, but I did not find any evidence for this.

In spite of this, however, the growth in older animals does gradually decrease in intensity and could possibly stop almost entirely in very old animals. Compared to other horny structures in mammals, baleen is distinguished by several unique characteristics. These include the overall form, the division of the plates into bristles at the inner edge, the covering layer that surrounds the layer of tubules, the extremely elongated papillae, the connective tissue plate that invades the plate at the base, and finally the peculiar *Zwischensubstanz* between the basal parts of the plates. Tubule formation in baleen is extreme, as mentioned above, and this they share with the chewing plate in *Rhytina* and rhinoceros horn. The structure of the covering layer is most similar to nails and claws since they lack medullae.

From a morphological perspective, baleen plates are most closely related to the callus in the palate of certain mammals (i.e., ruminants), although they differ significantly in the fully developed stage. At the fully developed stage, when the ridges start to protrude on the surface of the developing baleen, the baleen plates have a striking similarity to the formations mentioned above, although the epithelium structure in the developing baleen is considerably thicker. In both cases, there are protruding connective tissue extensions with groups of elongated papillae, and in both cases the connective tissue extensions correspond to the ridges on the surface of the mucosa. Whereas these ridges remain at this stage in ruminants, they continue their development in baleen plates in the way I described above.

[37] (continued)
quite convincingly that this may be partly explained by the fact that the hardened parts of the baleen are connected to the softer parts below that give rise to them. Longer papillae translate into more surface area for attachment and lower shear stresses overall at the boundary between hard and soft parts. This is likely very important for baleen, which must be capable of withstanding substantial hydrodynamic forces, especially in the lunge-feeding rorquals like *B. musculus*.

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