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ROWS OF SMALL TEETH IN ZIPHIROID WHALES

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In Ziphioid Whales the toothrows as a rule have been subject to pronounced reduction, so that the number of teeth of fairly large size is restricted to one pair in the lower jaw. Even these often are concealed in the gum and then must be regarded as functionless, though especially in old males the tips of these teeth protrude above the gum and may be used for the capture of the prey. In many species, besides the larger teeth in the lower jaw, rows of smaller teeth have been found in both jaws, often completely hidden in the gum, sometimes with their tips protruding. In *Tasmacetus shepherdi* Oliver these smaller teeth are of fairly large size, they show signs of wear against their antagonists of the other jaw, indicating that here they are functional. The much smaller teeth occurring in rows in both jaws of other Ziphioid Whales generally are regarded as rudimentary, though in one species, *Mesoplodon grayi* Von Haast, they constantly form a so distinct regular row on each side of the upper jaw that they seem to perform a distinct function. Moreover, in this species the tips of the small teeth always protrude above the surface of the jaw, an additional indication of a definite function.

The data concerning the position of the larger teeth in the lower jaw and their size and shape may be summarized as follows.

Hyperoodon. At the tip of the lower jaw as a rule one pair, usually concealed in the gum, in older specimens sometimes with the tips projecting. In some specimens on one or on both sides a second tooth closely behind the first, the second tooth generally slightly smaller than the first. The teeth are conical, sharp pointed, oval in cross section. In a fairly large male the length of the teeth was 38 mm, the long (antero-posterior)

diameter 19 mm, the short (transverse) diameter 12 mm¹). In female specimens the teeth remain smaller than those of the males.

Berardius. Two pairs of teeth at the tip of the lower jaw. The teeth are compressed laterally, roughly triangular in side view. The front teeth may reach a length of 75 mm, the hinder teeth a length of 50 mm¹).

Ziphius. At the tip of the lower jaw a single pair of large, rather bulbous teeth, with rounded or conical crowns, in cross section more or less circular. Length of the teeth in a male specimen 57 mm, diameter 32 mm¹). In female specimens the teeth are more slender and tapering, smaller than those of the males.

Mesoplodon. Two teeth in the lower jaw; position, shape, and size differing in the species. In *M. bidens* (Sowerby) these teeth are found near the hinder end of the symphysis of the lower jaw; in *M. layardi* (Gray) and in *M. grayi* Von Haast they have a corresponding position. In *M. stejnegeri* True and in *M. bowdoini* Andrews the teeth are slightly behind the symphysis. In *M. densirostris* (Blainville) the large teeth are about half way along the lower jaw from the tip. In *M. europaeus* (Gervais) they are found in front of the hinder end of the symphysis. In *M. hectori* (Gray) the teeth are close to the tip of the lower jaw; in *M. mirus* True they are at the very tip of the lower jaw. In the various species there are considerable differences in regard to the shape and the size of the teeth; as an example some data on the teeth of *M. bidens* are noted here. In this species the teeth are flattened laterally, they have a triangular crown and a fairly long root obliquely placed in the jaw; this root may be twice as long as the apex. In an adult male the length of the teeth was 95 mm, the antero-posterior diameter 32 mm; in an adult female the length of the teeth was 44 mm¹).

Tasmacetus. A single pair of large teeth at the tip of the lower jaw. The teeth are bulbous with conical blunt tips, oval in cross section. Their length is 41-42 mm, their antero-posterior diameter 23-24 mm, their transverse diameter 16 mm²).

The smaller teeth of *Tasmacetus* are about half as large as the front teeth of the lower jaw, their length varies from 15 to 27 mm, their antero-posterior diameter from 5 to 13 mm²); their shape corresponds with that of the larger teeth. In all other Ziphioid Whales the smaller teeth are conical, slightly curved, circular or oval in cross section, so that their shape often is entirely different from that of the larger teeth. In most cases they vary in length from 5 to 12 mm, exceptionally they may grow out to a length of 16 mm. The chief data from the literature concerning these teeth are summarized below.

Baussard (1789). In an adult female and in a young specimen of *Hyperoodon rostratus* the upper jaw and the palate showed numerous small hard and sharp pointed excrescences. The figure gives the impression as if in each jaw there was a row of minute teeth.

De Lacépède (1804). Description of the genus *Hyperoodon*. Name based on the alleged occurrence of small teeth on the palate (by mistake the horny excrescences described by Baussard, 1789, regarded as teeth).

Cuvier (1836). In a specimen of *Mesoplodon bidens* on each side three small teeth behind the larger tooth in the lower jaw (same specimen later described by Gervais, 1859, 1880). In Cuvier's figure the small teeth are drawn too large.

Wesmael (1840). No traces of the hard and sharp points on the palate of a specimen of *Hyperoodon rostratus*, as these were mentioned by Baussard (1789).

1) Measurements from Fraser (1948).

2) Measurements from Oliver (1937).

Bellingham (1843). In the specimen examined, belonging to *Hyperoodon rostratus*, no horny tubercles (cf. Baussard, 1789).

Eschricht (1845). In a specimen of *Hyperoodon rostratus* thirteen small teeth in the right upper jaw, two of these with their tips protruding from the gum; probably the same number in the left upper jaw, one protruding from the gum. Eleven small teeth in the right ramus of the lower jaw; the number of small teeth in the left lower jaw not noted; two small teeth in the lower jaw protruding from the gum. Small teeth rather strongly curved, length 3.2 to 5.9 mm, thickness 1.6 mm.

Vrolik (1848). A specimen of *Hyperoodon rostratus* had six rudimentary teeth in the gum of the anterior part of the left ramus of the lower jaw. Length of these teeth 2 to 4 mm.

Duvernoy (1851). Rudimentary teeth may occur in *Hyperoodon rostratus* in both jaws. A few rudimentary teeth in the right ramus of the lower jaw of a specimen of *Mesoplodon bidens* (same teeth later described by Gervais, 1859, 1880).

Gervais (1859). Figure of six maxillary teeth of *Ziphius*, one from the tip of the jaw 11 mm long, the remaining teeth smaller. In the text mention is made of several small teeth in the upper jaw concealed in the gum (the foremost partly above the jaw?). The teeth appear to be coated with a thick layer of cement. Figure of skull of *Mesoplodon bidens* with four small teeth behind the larger tooth in the lower jaw (specimen previously figured by Cuvier, 1836).

Burmeister (1866 a). In the gum of a specimen of *Ziphius cavirostris* on each side of the upper jaw twenty-five teeth, in each ramus of the lower jaw thirty to thirty-two; length of the teeth 3 to 5 mm.

Burmeister (1866 b). Notes on the small teeth mentioned in the previous paper.

Gray (1866). Mentions the small teeth discovered by Eschricht (1845) in *Hyperoodon rostratus*.

Burmeister (1868). Elaborate description of the rows of twenty-five small teeth in each half of the upper jaw, of thirty to thirty-two in each ramus of the lower jaw, in a specimen of *Ziphius cavirostris*, all completely hidden in the gum; length of the small teeth 5 to 6 mm.

Von Haast (1876 a). Description of *Mesoplodon grayi*, based on three heads. The specific character of the new species is a row of minute slightly curved teeth on each side of the upper jaw, with their roots embedded in the gum, and with their tips freely protruding. The number of teeth on each side of the jaw in the three specimens was from seventeen to nineteen. Length of the small teeth 5 to 10 mm. These teeth are regarded as functional.

Von Haast (1876 b). Four additional specimens of *Mesoplodon grayi* proved to possess, on each side of the upper jaw, rows of minute teeth, varying in number from seventeen to nineteen in one row. On account of this constant occurrence of rows of teeth partly protruding above the gum the author proposes to place the species in a separate genus, *Oulodon*, characterized by the peculiar rows of small functional teeth.

Von Haast (1876 c). Same data as in the two previous papers.

Hector (1878). Mentions Von Haast's discovery of rows of minute maxillary teeth in *Mesoplodon grayi*. Remarks that similar teeth have been found in *Ziphius cavirostris*.

Flower (1879). A specimen of *Mesoplodon grayi* with nineteen small teeth on each side of the upper jaw, the crowns of the largest protruding 4 mm above the gum. Whole length of the small teeth, including crown and root, up to 12 mm, greatest thickness $2\frac{1}{2}$ mm.

Gervais (1880). In the lower jaw of a specimen of *Mesoplodon bidens* four small teeth in the right ramus, two in the left, behind the larger tooth of each side. Length of the small teeth not over 5 mm. Description of the skeleton of a specimen of *Mesoplodon grayi* with eighteen maxillary teeth on the left side and seventeen on the right.

Southwell (1881). "Recently, a row of small teeth, of determinate number and definite form, has been discovered in many individuals of a species of *Mesoplodon*" (p. 99). Apparently reference to Von Haast (1876 a, b).

Southwell & Clarke (1886). Refer to the occurrence of rudimentary functionless teeth in the gum of the upper and lower jaws of *Mesoplodon bidens*, and to the apparently constant rows of maxillary teeth in *M. grayi*.

Turner (1886). Description of five or six rudimentary teeth in each ramus of the upper and lower jaws of a specimen of *Hyperoodon rostratus*; the small teeth partly embedded in the gum, partly protruding with their tips.

Weber (1886). Found rudimentary teeth in the gum of a specimen of *Hyperoodon rostratus*; total number of these teeth about thirty, length 5 to 5.5 mm.

Van Beneden (1888). Mentions the occurrence of rows of small teeth in *Mesoplodon bidens*, *M. grayi*, and *Ziphius cavirostris*; data based on previous literature.

Ogilby (1892). Specific character of *Mesoplodon grayi*: a series of small conical teeth set in the gum of the upper jaw, commencing opposite the lower tooth and extending nearly to the gape of the mouth.

Beddard (1900). In Ziphioid Whales there may occur in both jaws, in addition to the functional teeth, a number of small teeth. *Mesoplodon grayi* has nineteen small teeth on each side of the upper jaw. In *Mesoplodon bidens* similar teeth may be found in both jaws. *Hyperoodon rostratus* has numerous small teeth. In *Ziphius cavirostris* besides the larger teeth smaller functionless teeth may be present.

Kükenthal (1900). States that in embryos of *Hyperoodon rostratus* there are more rudiments of teeth than in adults. In a small embryo there were twenty-eight in each half of the jaws; in a larger specimen seventeen in the lower jaw and twelve in the upper.

Millais (1906). In female and young individuals of *Hyperoodon rostratus* often five or six rudimentary teeth are present along each side of the upper jaw. In the lower jaw there are sometimes similar undeveloped teeth.

True (1910). Rudimentary teeth have been noted in various specimens of *Ziphius cavirostris*. There were two such teeth in the mandible of one specimen, one of these is described. This tooth is cylindrical and moderately curved, long 16 mm, diameter 2 mm.

Turner (1912). Rudimentary teeth in the upper and lower jaws of *Hyperoodon rostratus*, some projecting through the gum, others in tooth sacs in the gum. Figures from Turner (1886).

Cabrera (1914). In Ziphioid Whales some rudimentary small teeth embedded in the gum of the upper jaw.

Heck (1915). In embryos of *Hyperoodon rostratus* there are a fairly large number of teeth, pointing to a resemblance to dolphins.

Harmer (1918). In *Hyperoodon rostratus* several vestigial teeth may occur in the lower jaw and near the front end of the upper jaw.

Abel (1919). In recent genera of Ziphioid Whales there are rudiments of teeth concealed in the gum.

Oliver (1922). *Mesoplodon grayi* has seventeen to nineteen small conical teeth in each side of the upper jaw.

Wood-Jones (1925). Mentions the maxillary teeth of *Mesoplodon grayi*, and remarks that in all Beaked Whales small, functionless teeth appear to be present in the gum of the upper jaw.

Harmer (1927). In the right ramus of the lower jaw of a specimen of *Mesoplodon bidens* a row of six vestigial teeth; one vestigial tooth in the left ramus.

Vinciguerra (1927). In a specimen of *Ziphius cavirostris* no rudimentary teeth in either jaw.

Wollebaek (1927). In *Mesoplodon bidens* some rudimentary teeth in each ramus of the lower jaw.

Van Deirse (1931). A row of about twenty small teeth on each side of the upper jaw of a specimen of *Mesoplodon bidens* (later proved to be *M. grayi*). Eighteen small teeth in the right upper jaw, fifteen in the left upper jaw; twelve small teeth in the right lower jaw, ten in the left lower jaw of a specimen of *Hyperoodon rostratus* (these teeth figured Pl. XIV of the present paper).

Hale (1932). Portion of skin of rostrum of *Mesoplodon grayi* with fifteen small conical teeth on right side of upper jaw (skin of left side of upper jaw decayed).

Brazenor (1933). *Mesoplodon grayi* is characterized by having a number of vestigial teeth (up to nineteen on each side) embedded in the gum of the upper jaw.

Degerbøl (1935). No teeth in the upper jaw of *Mesoplodon bidens*, or a number of insignificant teeth of the size of a pinhead, loosely implanted in the skin; similar small teeth in the lower jaw. In upper and lower jaws of *Hyperoodon rostratus* small degenerating teeth, covered by the skin.

Fraser (1936). In the three specimens of *Ziphius cavirostris* examined, vestigial teeth were found concealed in the gum. In one specimen (the lower jaw only was available) fourteen small teeth in the right ramus, twelve in the left; length of the largest of these teeth 8.5 mm. In the second specimen one vestigial tooth and seven empty follicles in the left lower jaw (the right lower jaw not available). In the left upper jaw eight small teeth and six or seven additional follicles; in the right upper jaw seven small teeth and seven empty follicles. Of the third specimen one ramus of the lower jaw was available, with twenty-eight vestigial teeth, the longest of which was 3.9 mm.

Fraser (1937). In the upper and lower jaws of Ziphioid Whales frequently there are series of vestigial teeth, to as many as thirty-two in one row. *Hyperoodon rostratus* may have a series of small vestigial teeth along the upper and the lower jaws, completely concealed in the gum. In *Ziphius cavirostris* vestigial teeth are not uncommon; twenty-eight to thirty in a row in young animals and reduced numbers in older ones. *Mesoplodon grayi*: "This form is said to be characterized by the row of small teeth on each side of the upper jaw, but as similar teeth are to be found occasionally in several other species as well it is not a very indicative character for this one" (p. 281).

Raven (1937). Occurrence of numerous peg-like teeth in alveolar groove noted for *Mesoplodon grayi*.

Arné (1937). On the gum of the lower jaw of a specimen of *Ziphius cavirostris* small excrescences, height 1 to 2 mm, very hard but not calcified. These seem to represent the vestiges of rudimentary teeth; there were fifteen on the left side, fourteen on the right.

Oliver (1937). Description of *Tasmacetus shepherdi*, a Ziphioid Whale with one large tooth in the tip of each ramus of the lower jaw, nineteen smaller teeth in each half of the upper jaw, and twenty-six to twenty-seven smaller teeth in each ramus of the lower jaw. The smaller teeth functional, varying in length from 15 to 27 mm.

Cabrera & Yepes (1940). Mention the small maxillary teeth, seventeen to nineteen in number, as a specific character of *Mesoplodon grayi*.

Fraser (1945). Vestigial teeth in the upper jaw of a specimen of *Hyperoodon planifrons*. On each side there were about twenty, length of the small teeth 4 to 14 mm.

Fraser (1946). Reference to the small teeth of three specimens of *Ziphius cavirostris*, dealt with in a previous paper (Fraser, 1936).

Glauert (1947). No traces of vestigial teeth found in a specimen of *Mesoplodon grayi* from Western Australia. This does not prove that these have not been present, as identification took place after the skull had been cleaned.

Fraser (1948). Same data as in Fraser (1937).

Boschma (1950). Description of a row of fifteen small teeth or empty follicles on the right side, and four small teeth on the left side of the upper jaw of a specimen

of *Hyperoodon rostratus*. Account of twenty-two maxillary teeth on each side of the skull of a specimen of *Mesoplodon grayi*.

Brazenor (1950). In *Mesoplodon grayi* there are about nineteen minute teeth embedded in the gum of the upper jaw, but they are not attached to the bone.

Not all the data in this list are references to small teeth. Those of Bausard (1789), De Lacépède (1804), Wesmael (1840), and Bellingham (1843) are dealing with horny papillae that might be mistaken for teeth. Perhaps the observation by Arné (1937) belongs in the same category.

The small teeth occurring in *Hyperoodon*, in *Ziphius*, and in *Mesoplodon bidens* undoubtedly are rudimentary and functionless. In the majority of the cases described the whole rows of small teeth were concealed in the gum, exceptionally a few small teeth were found to protrude with their tips above the gum, but they were so loosely attached that they easily fell out of their follicles. Moreover, in none of the animals mentioned above small teeth were found that still possessed open pulp cavities; invariably the roots were closed by a bulbous mass of cement that often formed a root-like extension beyond the original basis of the tooth (Fraser, 1945; Boschma, 1950).

On the other hand the small teeth of *Mesoplodon grayi* do not appear as entirely functionless. In this species they invariably occur in a regular row of seventeen to twenty-two on each side of the upper jaw just behind the large tooth in the lower jaw. Here the small teeth are as regularly spaced as those of the Common Dolphin, each tooth is slightly curved in such a manner that the concavity is on the palatal side, and each tooth with its sharp point protrudes for 2 to 3 mm above the gum. The regularity of the toothrows and the shape and the position of the small teeth of *Mesoplodon grayi* indicate that in this species these teeth have a function for capturing or holding the prey. In this connexion it is interesting that in a drawing by Von Haast (1876a) the minute teeth of *M. grayi* are shown to have a squarely cut off basal part of the root, indicating that the teeth were still in full growth.

As compared to those of *Mesoplodon grayi* the small teeth of *Hyperoodon rostratus* (Müller) usually form rather irregular rows, especially as far as concerns the distances between the individual teeth. In this respect the rows of small teeth figured in the present paper (Pl. XIV) form an exception.

The specimen is a young male of *Hyperoodon rostratus* (Müller), length 4.20 m, captured in November 1927 off Texel. The skeleton is in the Leiden Museum (reg. no. 1633), the parts of the gum containing the rows of small teeth are in their original position, adhering to the skull. Van Deirse (1931) made mention of the fact that in this specimen there are eighteen small teeth in the right upper jaw, fifteen in the left upper jaw, twelve in the right lower jaw, and ten in the left lower jaw.

In the left upper jaw the row of small teeth commences at a distance of 133 mm from the tip of the jaw, it ends at 214 mm from this point. The three teeth in the foremost part of the row are slightly smaller than the twelve following, the latter have a length of up to 7-8 mm. The last tooth of the row is completely hidden in the gum, faintly visible in the figure.

The row of small teeth in the left lower jaw begins at a distance of 159 mm from the tip of the jaw, it ends at 231 mm from this tip. The six teeth in the front part of the row are very small, the four following are distinctly larger, up to 6 mm in length.

The row of small teeth in the right upper jaw begins at a distance of 123 mm from the tip of the jaw, the last tooth is 218 mm from this tip. The three teeth in the foremost part of the row (one only shown in the figure) are very small, the four following are slightly larger, and the remainder of the row, eleven in number (the second of these broken off) again are larger, reaching a length of 7 to 8 mm.

In the right lower jaw the row of small teeth stretches from 163 mm from the tip of the jaw to 242 mm from this tip. Most of these teeth are comparatively small, the largest are the three at the posterior end of the row, reaching a length of up to 6 mm.

All these small teeth, those in the maxillary rows as well as those in the mandibular rows, are slightly curved, their concave side being turned towards the palatal or lingual side of the jaws. They are conical, more or less sharp pointed, though often the tips are coated with an irregular layer of cement. The greatest breadth of the small teeth is in their lower half; from this region the root gradually narrows to the closed end that usually terminates in a small bulbous mass of cement.

The figures show that in the toothrows the individual teeth are implanted at rather regular intervals. It is unknown how many of these teeth with their tips were protruding from the gum. In the specimen the teeth are fixed in the gum for a small part of the roots only or for a considerable distance; it remains unknown whether the situation in respect to the gum as shown at present corresponds with that found in the fresh animal or is the result of dissection. At least partly owing to the drying of the tissues all the small teeth now are firmly adhering to the gum.

In another male specimen of *Hyperoodon rostratus* of which strips of the gum of each side of the upper jaw were available (Boschma, 1950) there were twelve small teeth and three empty follicles in the right upper jaw, and four teeth in the left upper jaw. As the total length of this specimen was 7.5 m, the smaller number of minute teeth as compared to those of the specimen dealt with above might form an indication for the fact that

the number of small teeth progressively diminishes with age. This corresponds with Kükenthal's (1900) statement, who reported upon rows of twenty-eight teeth in each half of the jaws in a small embryo, and seventeen in the lower jaw and twelve in the upper of a larger embryo. On the other hand Fraser (1946) found in a fairly large specimen of *Hyperoodon planifrons* Flower (length 6.5 m) in each jaw rows of about twenty small teeth.

The small teeth in *Hyperoodon* undoubtedly are rudimentary and functionless. As a rule they remain hidden in the gum, and when their tips are protruding above the gum they may easily become lost. In the specimen described by Eschricht (1845) the few small teeth protruding above the gum soon became detached from the jaw. Moreover, the empty follicles in the specimen of 7.5 m (Boschma, 1950) indicate that here recently small teeth had been lost from their place of attachment.

The reduction of the toothrows of *Hyperoodon* has gone so far that as a rule the majority of the small teeth does not grow out above the gum. In *Ziphius* the reduction of the toothrows has gone even farther, as here it appears to be a common condition that all the small teeth remain completely concealed in the gum.

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Plate XIV

Upper figure. *Hyperoodon rostratus* (Müller), specimen from off Texel, rows of small teeth in left upper and lower jaws.

Lower figure. Same specimen, rows of small teeth in right upper and lower jaws (except the foremost maxillary teeth).

Approximately natural size.

