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WHALES ALLIED TO BALÆNOPTERA

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THE GENERA OF FOSSIL WHALEBONE WHALES
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By FREDERICK W. TRUE

In preparing to study and identify the remains of Tertiary whalebone whales contained in the collections of the United States National Museum, I had occasion four years ago to examine the literature relating to these forms, and also the type-specimens of North American species, so far as they were available. The two principal works relating to extinct finback whales are Van Beneden's "Description of Fossil Remains from the Vicinity of Antwerp" ¹ and Brandt's "Fossil and Subfossil Cetacea of Europe." ²

I studied Van Beneden's work attentively, and endeavored by means of comparative tables, composed of data extracted from the accounts of the various genera, to form diagnoses by which they could be discriminated. This undertaking, though it involved much labor, proved unremunerative, for the reason that the information given by Van Beneden is inexact, conflicting, and insufficient. While the text of this work is thus very unsatisfactory, the illustrations which accompany it are of the highest excellence and importance.

¹ VAN BENEDEN, P. J.—Description des Ossements Fossiles des Environs d'Anvers. Brussels, 1877-1886. Folio.

Pt. 1. Pinnipèds ou Amphithériens. Ann. Mus. Roy. Hist. Nat. Belg., ser. Paleont., vol. 1, 1877. Pls. 1-18.

Pt. 2. Genres *Balænula*, *Balæna* et *Balanotus*. *Op. cit.*, vol. 4, 1880. Pls. 1-39, 1878.

Pt. 3. Genres *Megaptera*, *Balanoptera*, *Burtinopsis*; et *Erpetocetus*. *Op. cit.*, vol. 7, 1882. Pls. 1-109.

Pt. 4. Genre *Plesiocetus*. *Op. cit.*, vol. 9, 1885. Pls. 1-30.

Pt. 5. Genres *Amphicetus*, *Heterocetus*, *Mesocetus*, *Idiocetus* et *Isocetus*. *Op. cit.*, vol. 13, 1886. Pls. 1-75.

² BRANDT, J. F.—Untersuchungen über die fossilen und subfossilen Cetaceen Europa's. Mém. Acad. Imp. Sci. St. Petersburg, ser. 7, vol. 20, no. 1, 1873, pp. i-viii, 1-372, pls. 1-34.

Ergänzungen zu den fossilen Cetaceen Europa's. *Op. cit.*, vol. 21, no. 6, 1874, pp. i-iv, 1-54, pls. 1-5.

They constitute, indeed, the only comprehensive series of good illustrations of fossil whalebone whales thus far published.

Brandt's work, unlike the foregoing, is in large measure critical and exact, but is, nevertheless, somewhat unsatisfactory on account of its discursiveness, its numerous supplements, and its more or less involved and indefinite system of classification. It suffers also from its very badly drawn plates, which, in many instances, are entirely useless for critical comparisons.

On account of the obscurity in which the subject was involved, I finally determined to disregard the literature, and to endeavor to form diagnoses directly from the illustrations furnished by American and European authors, including those already mentioned, together with such specimens as were available for study. The resulting diagnoses based on characters of the skull, which are given below, were completed May 1, 1909. A few months afterwards I received a copy of Dr. Winge's paper on *Plesiocetus* and *Squalodon* from Denmark,¹ which contains very valuable critical remarks on the fossil genera under consideration, though no attempt is made to formulate diagnoses of them. His opinions are, however, in close accord with my own, and as the article is written in Danish, it has seemed to me desirable to present a translation of his remarks in this place, in so far as they relate to the American forms. (See p. 5.)

A summary of his conclusions is as follows:

VALID GENERA OF FOSSIL WHALEBONE WHALES, ACCORDING TO WINGE²

<i>Aulocetus</i>	<i>Cetotherium</i>	<i>Megaptera</i>
<i>Balænoptera</i>	<i>Herpetocetus</i>	<i>Plesiocetus</i>

GENERA OF DOUBTFUL VALIDITY, ACCORDING TO WINGE

<i>Cetotheriomorphus</i>	<i>Pachycetus</i>	<i>Tretulias</i>
<i>Mesoteras</i>	<i>Rhegnopsis</i>	<i>Ulias</i>
<i>Metopocetus</i>	<i>Siphonocetus</i>	

The complete list of genera considered by Winge, with his opinion and my own regarding each, is as follows:

¹ WINGE, H.—Om *Plesiocetus* og *Squalodon* fra Danmark. Vidensk. Meddel. fra den naturhist. Foren. i Kjøbenhavn for 1909, pp. 1-38, pls. 1, 2, 1910.

Separately published, April 20, 1909.

² The genera of Right whales and the genus *Rhachianectes* are not included.

	WINGE	TRUE
<i>Amphicetus</i> Van Ben.	Equals <i>Plesiocetus</i> Van Ben.	Concurrence.
<i>Aulocetus</i> Van Ben.	Valid.	Concurrence.
<i>Balænoptera</i> Lacép.	Valid.	Concurrence.
<i>Burtinopsis</i> Van Ben.	Equals <i>Megaptera</i> Gray.	Equals <i>Plesiocetus</i> ?
<i>Cetotherium</i> Brandt.	Valid.	Concurrence.
¹ <i>Cetotheriophanes</i> Brandt.	Equals <i>Plesiocetus</i> Van Ben.	Concurrence.
<i>Cetotheriopsis</i> Brandt.	Equals <i>Aulocetus</i> Van Ben.	Concurrence.
<i>Cephalotropis</i> Cope.	Equals <i>Plesiocetus</i> Van Ben.	Valid ?
<i>Cetotheriomorphus</i> Brandt.	Doubtful.	Concurrence.
¹ <i>Eucetotherium</i> Brandt.	Equals <i>Cetotherium</i> Brandt.	Concurrence.
<i>Herpetocetus</i> Van Ben.	Valid.	Probably equals <i>Plesiocetus</i> .
<i>Heterocetus</i> Van Ben.	Equals <i>Plesiocetus</i> Van Ben.	Concurrence.
<i>Isocetus</i> Van Ben.	Equals <i>Plesiocetus</i> Van Ben.	Concurrence.
<i>Idiocetus</i> Capellini.	Equals <i>Plesiocetus</i> Van Ben.	Concurrence.
<i>Mesocetus</i> Van Ben.	Equals <i>Plesiocetus</i> Van Ben.	Concurrence.
<i>Metopocetus</i> Cope.	Probably equals <i>Plesiocetus</i> Van Ben.	Valid ?
<i>Mesoteras</i> Cope.	Doubtful.	Concurrence.
<i>Megaptera</i> Gray.	Valid.	Concurrence.
<i>Megapteropsis</i> Van Ben.	Equals <i>Megaptera</i> Gray.	[Not studied.]
<i>Plesiocetus</i> Van Ben.	Valid.	Concurrence.
¹ <i>Plesiocetopsis</i> Brandt.	Equals <i>Plesiocetus</i> Van Ben.	Concurrence.
<i>Pachycetus</i> Van Ben.	Doubtful.	Concurrence.
<i>Rhegnopsis</i> Cope.	Probably equals <i>Cetotherium</i> .	Doubtful.
<i>Siphonocetus</i> Cope.	Probably equals <i>Cetotherium</i> .	Doubtful.
<i>Tretulias</i> Cope.	Doubtful.	Concurrence.
<i>Ulias</i> Cope.	Doubtful.	Concurrence.

The subjoined diagnoses of the genera are, as already mentioned, based only on characters of the skull, as a full comparison of the remainder of the skeleton is not feasible at this time. It is recognized that they are incomplete and subject to revision, but it is thought that they may be of use as a basis for a fuller characterization of the genera.

DIAGNOSES OF GENERA OF FOSSIL WHALEBONE WHALES ALLIED TO
BALÆNOPTERA

BALÆNOPTERA Lacépède. 1805²

Orbital plates of frontal on a lower level than vertex, much produced anteriorly. Maxillæ produced proximally in a narrow extension at side of nasals. Proximal end of premaxillæ narrow, scarcely

¹ Subgenus.

² *Megaptera* cannot be distinguished from *Balænoptera* generically by the skull alone.

reaching superior surface; ending opposite distal end of nasals, or as a narrow slip of bone on each side of them. No temporal ridge. Parietals scarcely appearing on vertex. Frontals very short on vertex. Nasals moderate. Tympanic bone with a ridge on inner side (that is, on the border nearest the median line of the skull). Alveolar groove and dental canal of mandible as in *Plesiocetus*. Proximal end of mandible solid. Orifice of dental canal small. Alveolar groove roofed.

AULOCETUS Van Beneden. 1861

Orbital plate of frontal less descending than in *Balænoptera*, not so much produced anteriorly, and with a trace of a temporal ridge. Form of maxillæ proximally, and form of parietals and frontals on vertex, as in *Balænoptera*. Nasals very long. Proximal end of premaxillæ as in *Balænoptera*, but broader and more superiorly placed. Tympanic bone with a ridge on internal border (that is, on the border nearest the median line of the skull). Maxillæ very broad. Premaxillæ expanded distally and inserted between maxillæ and nasals proximally. Mandible not very convex externally at posterior end, nor emarginate toward inferior border; not deeply concave internally (hence, as in *Balænoptera*). Alveolar groove and dental canal as in *Plesiocetus* (?). Alveolar groove roofed.

PLESIOCETUS Van Beneden. 1859

Orbital plate of frontal not abruptly on a lower level than vertex, trumpet-shaped, not produced anteriorly; with a distinct or indistinct temporal ridge. Parietals on vertex long or moderate; frontals the same. Nasals long. Maxillæ rather narrow, without a proximal nasal branch, or extension. Proximal end of premaxillæ broad, superiorly placed, and articulating with frontals by a very coarse and deep interdigitating suture. Tympanics flat or concave on internal border (that is, on the border nearest the median line of the skull). Proximal end of mandible convex externally, with a more or less pronounced emargination near inferior border; internally, very concave. Alveolar groove and dental canal confluent, the former roofed over. Gingival foramina on the inner side (?).

NOTE.—The vertex of *Plesiocetus* does not seem to be well-known, but as Van Beneden's figures of other parts correspond to those of *Heterocetus*, etc., it may be safe to assume that the vertex has the same form as in those nominal genera. The genus *Plesiocetus* may be regarded as including *Heterocetus* Van Ben., *Amphicetus* Van Ben., *Mesocetus* Van Ben., *Idiocetus* Capellini, *Isocetus* Van Ben., and probably also *Herpetocetus* Van Ben. and *Burtinopsis* Van Ben.

CETOTHERIUM Brandt. 1843

Orbital plate of frontals, and parietals and frontals on vertex, as in *Plesiocetus*. Posterior nasal extension, or process, of maxillæ as in *Balænoptera*, but broader, more triangular, and less distinctly marked off. Maxillæ narrow. Premaxillæ inserted between maxillæ and nasals proximally as in *Balænoptera*; not expanded distally (?). Nasals moderate. Tympanic bone rounded internally (that is, on the edge nearest the median line of the skull). Alveolar groove and dental canal as in *Plesiocetus* (?). Alveolar groove roofed.

CEPHALOTROPIS Cope. 1896

Differs from *Plesiocetus* only in having the apex of the supra-occipital very rugose and deeply pitted.

METOPOCETUS Cope. 1896

Differs from *Plesiocetus* only in having the parietals on the vertex rather shorter and the nasals also short.

GENERA BASED ON MANDIBLES

SIPHONOCETUS Cope. 1895

Alveolar groove and dental canal distinct. Groove roofed over and perforate.

NOTE.—I suspect that these characters are of no value and that *Balænoptera*, *Aulocetus*, *Cetotherium*, and *Plesiocetus* are all alike as regards the canal and groove.

ULIAS Cope. 1895

“Alveolar groove and dental canal confluent in a gingivodental canal.” Canal open. No gingival canals.

TRETULIAS Cope. 1895

Similar to *Ulias*, but with gingival canals at the sides of the mandible.

WINGE'S CRITICISMS OF COPE'S GENERA

Winge's comments on Cope's genera are appended.

Siphonocetus Cope.—“To Cope's account [of this genus] two objections have to be made. In the first place, it is certain that Cope's interpretation of the canals in the lower jaw is incorrect. To conclude from his figures, representing diagrammatically a section of the

lower jaw, it appears that the *sulcus alveolaris*,—the furrow in the upper border of the mandible in which the embryonic rudimentary teeth are lodged (which ordinarily disappears in adult finback whales),—fills up almost entirely with bony tissue; that the *canalis mandibularis*,—the canal in the interior of the jaw, in which the third branch of the *nervus trigeminus* and the accompanying blood-vessels run,—is divided into an upper and a lower branch, while, as a rule, it is undivided. From the upper branch—Cope's 'alveolar groove,' *sulcus alveolaris*—proceed, on each border, *foramina mentalia*, which are simply orifices of side branches from the *canalis mandibularis*.

"As regards the second objection, the mandible in *Cetotherium* shows in section an entirely similar figure to Cope's *Siphonocetus*. Brandt figures it in the type of the genus, *C. ratkai*. On the score of the canals of the lower jaw, there was no ground for establishing a new genus. *Siphonocetus* is, therefore, much in need of new proofs." (*Op. cit.*, p. 25.)

Ulias Cope.—"The characters of the genus are that the *canalis mandibularis* and *sulcus alveolaris* are not separated, and together form a broad, wide-open canal in the upper border of the mandible, which may, however, be closed near the anterior end of the jaw; and that the *foramina mentalia* are wanting, except at the very front. Cope believed that *Ulias*, when adult, retained characters which are found elsewhere in embryonic Right whales. But Cope's interpretation is certainly not correct. The lack of the *foramina mentalia* alone is so extraordinary that it gives grounds for questioning whether the upper border of the jaw in the specimen concerned is really undamaged. From the figure, which represents a diagrammatic section, one gets an impression of the jaw that is very far from reminding one of an embryo of a Right whale; that it is as in the fully grown Finbacks, but that the upper border is broken off, so that the bottom of the *canalis mandibularis* has become visible. This explanation is, however, a guess, but it may be right, nevertheless. It should also be remembered that it is very difficult in a weathered bone to distinguish broken surfaces from natural surfaces. In order that the genus *Ulias* may be accepted, there must be presented a far more carefully prepared account of it than that which Cope has given." (*Op. cit.*, pp. 26-27.)

Tretulias Cope.—"*Tretulias* was established by Cope from two pieces of the lower jaw from the North American Miocene, one piece 'in fairly good preservation,' the other 'considerably worn.' The single species is *T. buccatus*. The characters of the genus are that the *canalis mandibularis* is 'obliterated' and that the *sulcus alveolaris* is open, without a bony roof, except along the inner border, where there are found 'gingival canals and foramina.' Cope's interpretation cannot be correct. That the *canalis mandibularis* should be 'obliterated' is inconceivable. What he calls the 'dental groove'—*sulcus alveolaris*—is clearly enough the *canalis mandibularis*, to judge from the figure, a diagrammatic section of the jaw. As in *Ulias*, it is sure that a piece of the upper border of the jaw is broken

off, but that the inner wall has remained further back than in *Ulias*." (*Op. cit.*, p. 27.)

Metopocetus Cope.—“*Metopocetus* was established by Cope on a much-damaged skull from the Miocene of North America. The species is called *M. durinasus*. Cope himself thought that it might be the same genus as *Ulias* and *Tretulias*, which are known from the lower jaw. The genus probably stands near *Cetotherium* (with *Plesiocetus*), but differs especially in that the nasals are short and almost ankylosed together and with the frontals. In addition, there is a difference in the temporal crest, which, however, to judge by the figure, is not distinct. The skull on which the genus is founded is so much damaged that the relation of the frontals and nasals cannot be clearly seen, and the length of the nasals cannot be correctly guessed. If Cope was right in his opinion that the bones were ankylosed, that would not be sufficient ground for establishing a new genus. Ankylosis may result from advanced age, or from pathologic conditions. Nearly ankylosed nasals are figured by Cope himself in *Cetotherium megalophysum*. From the figure, which, however, is only an outline of the skull seen from above, *Metopocetus* agrees so well with *Plesiocetus* that a generic difference is not probable.”¹ (*Op. cit.*, pp. 27-28.)

Cephalotropis Cope.—“*Cephalotropis* was established by Cope from a very imperfect skull from the Miocene of North America. The single species is *C. coronatus*. Cope himself thought that it might be the same genus as *Ulias* or *Tretulias*. From *Cetotherium* (with *Plesiocetus*) it is supposed to differ in having temporal ridges, or angles, which are lacking in *Cetotherium*; but that is an error. The anterior part of the temporal crest, that which is referred to, is essentially the same in all extinct Finbacks. To judge from the figure, there is no ground for separating *Cephalotropis* from *Plesiocetus*.” (*Op. cit.*, p. 28.)

Rhegnopsis Cope.—“*Rhegnopsis* was founded by Cope on a fragment of a mandible from the Miocene of North America. On the same piece Leidy established his *Balæna palæatlantica*, which later, without any further explanation, was transferred to a new genus, *Protobalæna*. That generic name, however, was not valid, as Cope pointed out, since it had already been used by Van Beneden in another sense, and Cope adopted the name *Rhegnopsis* instead. The only ground for the separation of *Rhegnopsis* from *Cetotherium*, or other allied Finbacks, is the presence of a ‘Meckelian fissure,’ a slit which extends from the inner side of the jaw deep in through the interior of the bone. In reference to the slit, Cope wrote in 1865 (p. 145): ‘I am inclined to doubt whether it is normal in adult animals. When the rami of recent *Balænidæ* dry, they sometimes split along the line of the primitive Meckelian groove, but not

¹ I would remark as regards the nasals, which I have examined in the type-specimen, that they are complete anteriorly as shown in Cope’s figure, and hence quite short.

always. It remains to be seen whether this is the origin of the fissure in the present species.' Cope does not say whether he had investigated the question when he established the genus *Rhegnopsis* in 1896, though an investigation was much to be desired. From the figures, which are diagrammatic sections of jaws, it appears that Cope's 'Meckelian fissure' in *Tretulias* and *Rhegnopsis* is nothing more than an artificial crack. It is, at all events, entirely different from the 'Meckelian fissure,' *sulcus mylohyoideus*, which, as a shallow canal, follows more or less the lower border on the inner side of the jaw in various Right whales. *Rhegnopsis* is, in any case, of very doubtful validity." (*Op. cit.*, pp. 28-29.)