

Cetacean phylogeny and systematics based on the morphogenesis of the nasal skull

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Summary

The morphogenesis of the nasal skull of the cetaceans indicates that the traditional division of the order Cetacea into two suborders, the toothed whales (Odontoceti) and the baleen whales (Mysticeti), is phylogenetically not substantiated. The following conclusions can be drawn on the basis of the presented study. The whales are of a monophyletic origin, with all the extant forms being closely related. The sperm whales are, however, distinct from other odontocetes, with which they are traditionally associated, and seem to be more closely related to the baleen whales. The embryological findings presented here are remarkably consistent with a recent molecular phylogenetic analysis. According to the morphogenesis of the nasal skull the following almost equivalent groupings, which may be considered superfamilies, can be distinguished within the order Cetacea: Balaeopteroidea, Physteroidea, and Delphinoidea. However, no representatives of the families Ziphiidae and Platanistidae were available for the present study.

Introduction

The displacement of the nasal openings from the rostral tip to the parietal pole of the head ranks as one of the most perfect adaptations of the whales to the aquatic way of life. This adaptation is enabled through extensive rebuilding of the skull, involving particularly the morphogenesis of the embryonic cartilaginous nasal skull. We may assume that this important embryonic anlage reflects typical features of the phylogeny of the particular whale groups and is of significance for the systematics.

It is not the purpose of the present study to provide a detailed description of the development of the nasal structures in the Cetacea, as this has been done in the previous papers (Klima & Van Bree, 1985; Klima *et al.*, 1986; Klima, 1987; and a monography by Klima in press); the implications of our findings for systematics and understanding

of phylogeny will be discussed here. Embryological data on the development of the nasal skull challenge the traditional classification of the Cetacea divided into two suborders: Odontoceti and Mysticeti (cf. also Klima & Oelschläger, 1994). The mentioned embryological findings show interesting parallels with the recent results of molecular biology (Milinkovitch, 1992a, 1992b; Milinkovitch *et al.*, 1993) as well as with other studies (Gaskin, 1976, 1982; Heyning & Mead, 1990; Klima, 1990b).

Material and methods

A total number of 72 embryos and fetuses from 11 species of cetaceans were investigated (see Table 1). The specimens were serially sectioned following routine histological methods, except for several large fetuses which were examined by macroscopical dissection. Only the specimen of *Globicephala melas*, which could not be inspected directly, was evaluated after the description in the literature (Schreiber, 1916). Several specimens were selected for modelling or for graphic reconstruction of the nasal skull. For detailed information on the material investigated see earlier papers (Klima & Van Bree, 1985; Klima, 1987, 1990b).

Results

Schematic representation of the embryonic nasal structures in cetaceans

The embryonic nasal skull of cetaceans is markedly different from that in other mammals. While the dermal bones are of no relevance for the discussion, only the elements of the cartilaginous capsule will be considered here (cf. Fig. 1). The latter can be divided according to the topography into three groups.

The median structures (ms) form the nasal septum and include from front to back: rostrum nasi (rn), septum nasi (sn), spina mesethmoidea (spm), and septum interorbitale (sio).

Table 1. List of species evaluated in this study. Collection acronyms are: FRA—Zentrum der Morphologie, Klinikum der J. W. Goethe-Universität, Frankfurt, FRG; SEA—National Marine Fisheries Service, Mammal Laboratory, Seattle, WA, USA; TOK—Department of Anatomy, Faculty of Medicine, University of Tokyo, Hongo, Tokyo, Japan; UTR—Hubrecht Laboratory, International Embryological Institute, Utrecht, The Netherlands

Species	Number of embryos investigated	Total body length in mm	Collection
<i>Balaenoptera acutorostrata</i>	1	455	FRA
<i>Balaenoptera physalus</i>	2	165–400	FRA; UTR
<i>Megaptera novaeangliae</i>	3	37–107	TOK; UTR
<i>Delphinus delphis</i>	8	24–131	FRA
<i>Globicephala melas</i>	1	123	(Schreiber 1916)
<i>Lagenorhynchus albirostris</i>	2	107–115	FRA
<i>Stenella attenuata</i>	14	21–225	FRA
<i>Stenella coeruleoalba</i>	11	17–156	FRA; SEA; TOK
<i>Monodon monoceros</i>	1	137	UTR
<i>Phocoena phocoena</i>	14	25–355	FRA
<i>Physeter catodon</i>	15	19–565	FRA

The anterior side wall structures (fs) lie in front of the nasal passage (N) and include partly isolated, partly fused elements of the original nasal floor, solum nasi. Following structures can be distinguished from front to back: cartilago ductus nasopalatini (cdnp), cartilago paraseptalis (cps), processus lateralis ventralis (plv), and lamina transversalis anterior (lta).

The posterior side wall structures (hs) lie behind the nasal passage (N) and include the fused material of the original elements of the nasal roof, tectum nasi, and the nasal wall, paries nasi. Following structures can be distinguished from front to back: cupula nasi anterior (ca), tectum nasi (tn), paries nasi (pn), commissura orbitonasalis (con), cupula nasi posterior (cp), and processus paraseptalis posterior (psp). Some further structures (which are not mentioned here) can be identified inside the posterior side wall.

Ontogenetic displacement of the nasal structures in cetaceans

Several elements of the original nasal skull of terrestrial mammals are reduced as a consequence of adaptation onto the aquatic way of life. Most reduced are the internal nasal structures, particularly the nasal conchae. Due to the loss of the olfactory function (Oelschläger & Buhl, 1985a, 1985b) the whole nasal capsule simplified. In the earliest stages (as in terrestrial mammals), the nasal openings lie at the tip of the rostrum. During ontogeny they become gradually displaced towards the parietal pole of the head, resulting in the rotation of the nasal capsule from horizontal to a vertical position.

Simultaneously, the septum nasi elongates and projects into the cartilaginous nasal rostrum (rn). This cartilaginous structure together with the original cartilaginous nasal floor (fs), particularly lamina transversalis (lta) and cartilago paraseptalis (cps), forms a basis for dermal bones, especially maxillare and praemaxillare, which develop later. They all participate in building the typical protruding cetacean rostrum, combined from the cartilaginous structures as well as the dermal bones.

The structures of the nasal floor, particularly lamina transversalis anterior and cartilago paraseptalis, rotate, move forwards, and grow. They are, apart from the cartilaginous nasal septum, the only cartilaginous nasal structures which develop progressively. They have lost their original connection to the nasal skeleton and become, both topographically and functionally, the most important part of the combined cetacean rostrum. They persist incidentally even in adult whales as distinct structures, the so-called Meckelian ossicles, or, more precisely, pararostral bones, ossa pararostralia (Klima & Van Bree, 1990; Klima, 1994).

All these transformation processes during embryonic development are part of skull morphogenesis (Kükenthal, 1893; Boeninghaus, 1903; De Burlet, 1916; Honigman, 1917; Eales, 1950; Klima & Van Bree, 1985, 1990; Klima *et al.*, 1986; Klima, 1987). The above studies have shown that the very earliest anlage of the nasal skull in the Cetacea is distinct from that of the terrestrial mammals. In an embryo of about 40 mm body length, all the studied cetacean species reveal the same morphology of the nasal skull. The group-specific modifications appear later, in stages with an embryonic body length of

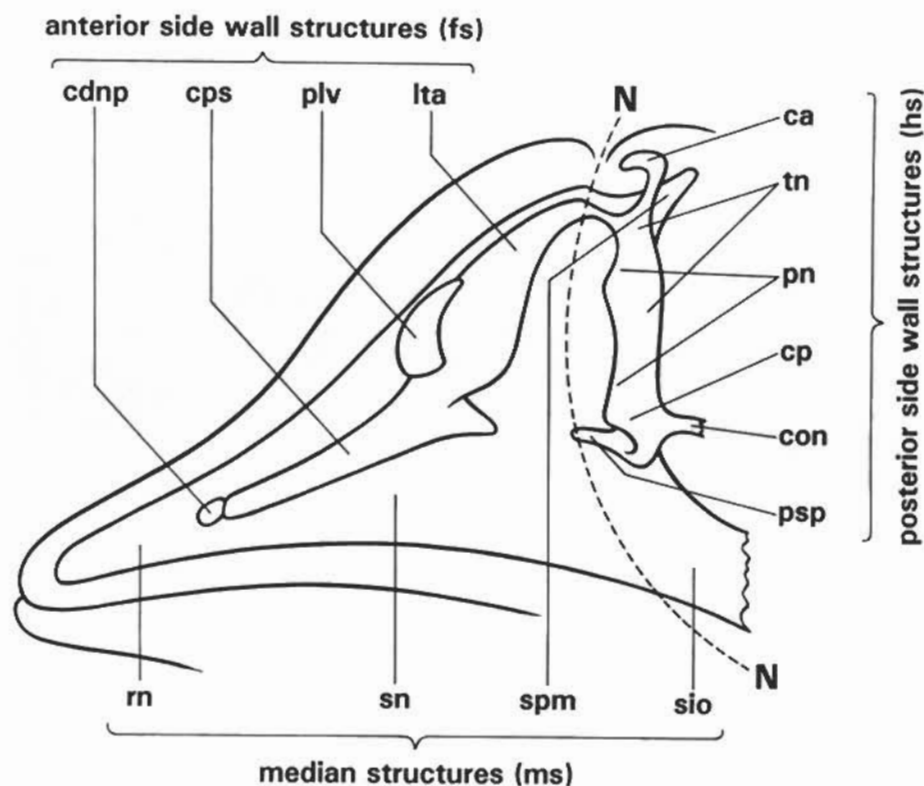


Figure 1. Generalized schematic illustration of embryonic nasal structures in cetaceans seen in left lateral view. For labelling see list of abbreviations.

about 90 mm, when the reconstructive processes have been completed. Three basic types of the nasal skull may be distinguished: (1) baleen whales, mysticetes; (2) sperm whale, *Physeter catodon*, and (3) toothed whales, odontocetes, apart from the sperm whale.

Baleen whales, mysticetes (Fig. 2)

Within the median structures, the nasal septum (sn) is low, the mesethmoidal spina (spm) long and

List of abbreviations: ca, cupula nasi anterior; cad, cupula nasi anterior dextra; cas, cupula nasi anterior sinistra; cdnp, cartilago ductus nasopalatini; con, commissura orbitonasalis; conl, commissura orbitonasalis, lower branch; conu, commissura orbitonasalis, upper branch; cp, cupula nasi posterior; cps, cartilago paraseptalis; fs, front side structures, anterior side wall structures; hs, hind side structure, posterior side wall structures; Ita, lamina transversalis anterior; ms, median structures; N, nasal passage; plv, processus lateralis ventralis; pn, paries nasi, nasal wall; prmx, processus maxillaris; prpe, processus paraethmoidalis; psp, processus paraseptalis posterior; rn, rostrum nasi; sio, septum interorbitale; sn, septum nasi; spm, spina mesethmoidea; tn, tectum nasi, nasal roof.

narrow, projecting steeply upwards. The anterior side wall structures are simplified. The pararostral cartilage (cps) joins the transverse anterior lamina (Ita) to form a slim rod. Other structures are not distinguishable. The posterior side wall structures project moderately at an angle of about 45 degrees to the horizontal plane of the longitudinal axis of the skull. The paries nasi (pn) is massive and broad, with two outer processes, the paraethmoidal process (prpe) and the maxillar process (prmx). The nasal tectum (tn) is relatively wide and long and lies almost horizontally. The anterior nasal cupula (ca) has several small processes that project both forward and upward. The posterior paraseptal process (psp) is small and is completely covered laterally by the paries nasi (pn) and the posterior nasal cupula (cp). Inside the nasal capsule, four lamelles may be distinguished. They are, the semicircular crest, the maxilloturbinal, the frontoturbinal and the first ethmoturbinal cartilages. The nasal skull is connected with the neurocranium via massive paired orbitonasal commissures (con).

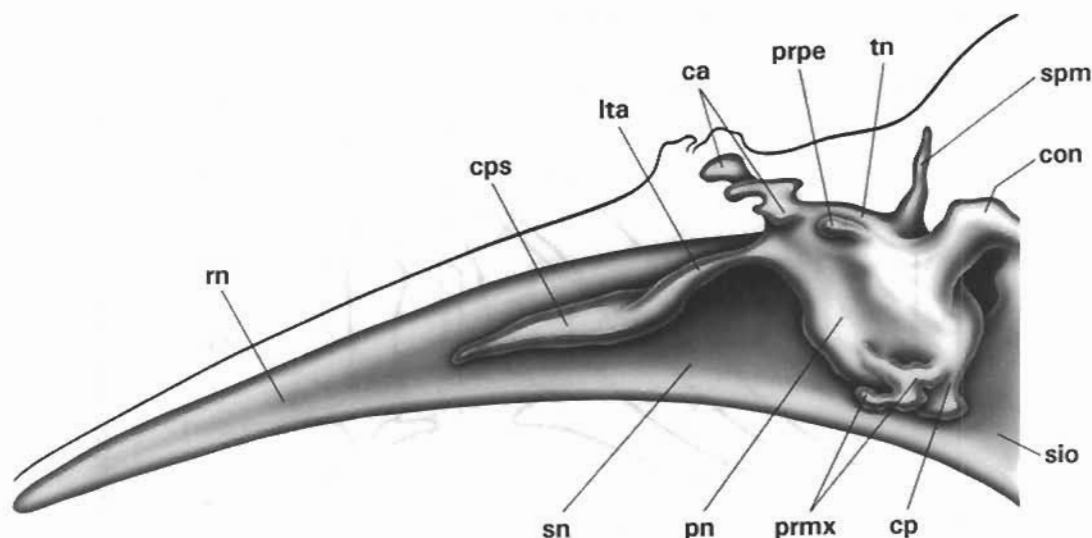


Figure 2. Left lateral view of the nasal skull of *Balaenoptera physalus*, embryo of 156 mm body length. For labelling see list of abbreviations.

Sperm whale, *Physeter catodon* (Figs 3 and 4)

Within the median structures, the nasal septum (sn) is low, except for its hind part which is strongly projecting. The mesethmoidal spine (spm) is long and broad and projects dorsally. The anterior side wall structures form a slim rod, with the boundaries between the transversal anterior lamina (lta), paraseptal cartilage (cps), and the nasopalatal duct cartilage (cdnp) being almost undistinguishable. On the left side (Fig. 3), the anterior side wall structures are separated from the paries nasi, on the right side (Fig. 4), they are connected with it. The posterior side wall structures project anteriorly, forming an angle of about 70 degrees with the horizontal plane of the longitudinal axis of the skull. The paries nasi (pn) is massive and broad, without any projections. The nasal tectum (tn) is elongate and connected to the caudal part of the nasal septum (sn) as well as with the left (cas) and the right (cad) anterior nasal cupula. Together, these structures form an elongate rod which projects anterodorsally across the entire forehead. This characteristic feature of the nasal skull in the sperm whale persists in adults (Behrmann & Klima, 1985; Klima *et al.*, 1986; Klima, 1990a). The posterior paraseptal process (psp) is small and hidden from view beneath the paries nasi (pn) and the posterior nasal cupula (cp). Inside the nasal capsule, the semilunar crest and the maxilloturbinal cartilage may be seen as distinct lamellae. The frontoturbinal and the first ethmoturbinal cartilages are only small. The connection between the nasal skull and the

neurocranium is mediated by an orbitonasal commissure, which is split into upper (conu) and lower (conl) branches.

Non-Physeterid odontocetes (Fig. 5)

Within the median structures, the nasal septum (sn) projects steeply upward between the nasal rostrum (rn) and the interorbital septum (sio). The mesethmoidal spine (spm) is short and pointed backwards. The anterior side wall structures extend forward with several partly or completely isolated structures: the anterior transversal lamina (lta), ventral lateral process (plv), paraseptal cartilage (cps), and the nasopalatal duct cartilage (cdnp). The posterior side wall structures project toward the neurocranium, creating an angle of about 90 degrees with the horizontal plane of the longitudinal skull axis. The paries nasi (pn) is narrow and flattened, without any projections. The nasal tectum (tn) is regressed and narrow with only a single minute variable projection, the anterior nasal cupula (ca). The long posterior paraseptal process (psp) arises from the paries nasi and the posterior nasal cupula (cp) and extends forward. The inside of the nasal capsule is smooth and simplified: only the maxilloturbinal cartilage can be distinguished, all other structures being completely regressed. The nasal skull is connected only incompletely with the neurocranium, or, moreover, the both structures are separated each from other. The orbitonasal commissure (con) is either present as a thin cartilaginous bridge, or is reduced to form a small projection on the back margin of the nasal capsule.

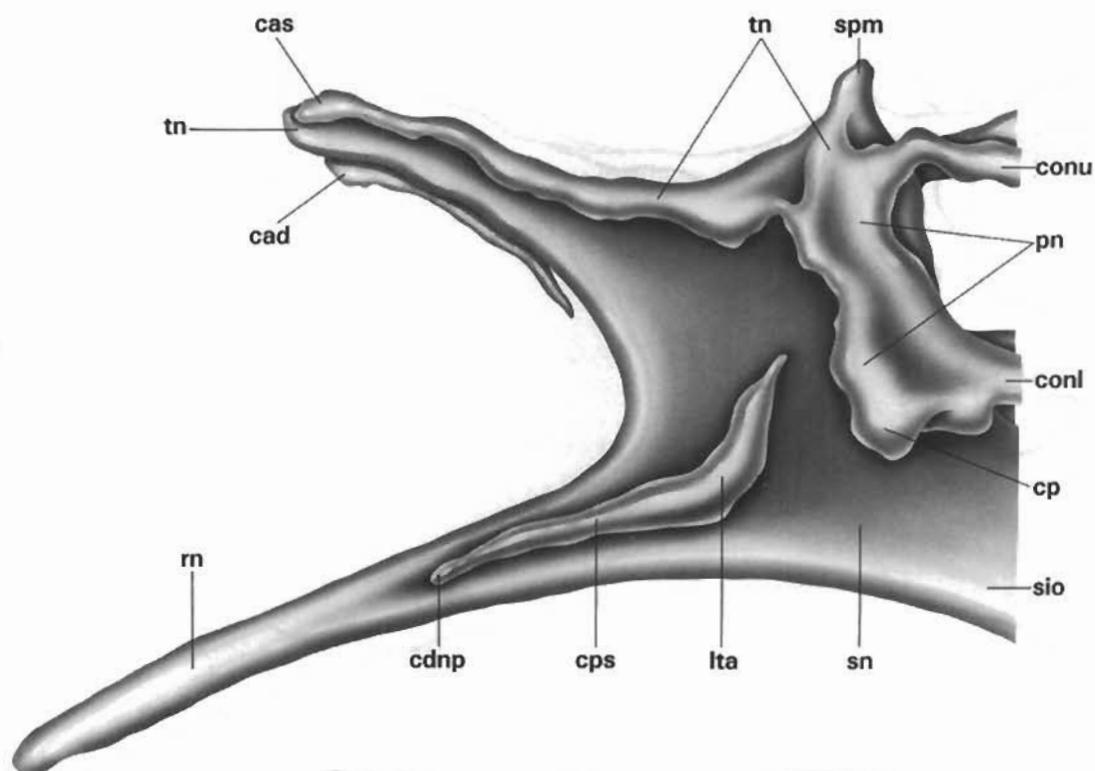


Figure 3. Left lateral view of the nasal skull of *Physeter catodon*, embryo of 102 mm body length. For labelling see list of abbreviations.

Conclusions

The morphogenesis of the nasal skull shows many considerable differences between the Cetacea and the terrestrial mammals. Within the order Cetacea, the nasal skull shows still the same modification. From this point of view "the nasal capsule of the sperm whale shows a conspicuous similarity to that of other odontocetes" (Klima, 1987), as well as to that of the mysticetes examined. The fact that the nasal skull is restructured in the same way in the early stages in all the examined cetaceans points to their common origin and monophyly of the order. The modified nasal skull of the late stages shows similarities and differences which suggests division of cetaceans into three groups (Fig. 6). These groups may be considered superfamilies: Balaeopteroidea, Physeteroidea, and Delphinoidea. There is no clear separation between the mysticetes and the odontocetes according to the above studies. On the contrary, the embryonic skull of the sperm whale shows in many traits a larger similarity to the skull of the baleen whales than to the toothed whales.

Discussion

Until recently, the monophyletic origin of the cetaceans from a single group of terrestrial ancestors was questioned. All the similarities in body structure between the baleen and toothed whales used to be interpreted as convergent adaptations to the aquatic way of life, and the order was considered an artificial taxon of diphyletic or polyphyletic origin (e.g. Slijper, 1962; Yablokov, 1964; Rice, 1967, 1977; Kuzmin, 1976). This hypothesis was based particularly on remarkable differences in the structure of the skull and the dentition, as well as in the presence of a sonar orientation system in the Odontoceti and its absence in the Mysticeti. In spite of these and other differences, the diphyletic origin of the cetaceans could not be established unambiguously.

There is, however, a bulk of evidence for the monophyletic origin of the Cetacea. According to paleontological findings, all whales can be derived from the archaeocetes (family Protocetidae) which, in turn, can be derived from a single group of terrestrial ancestors, the Mesonychidae

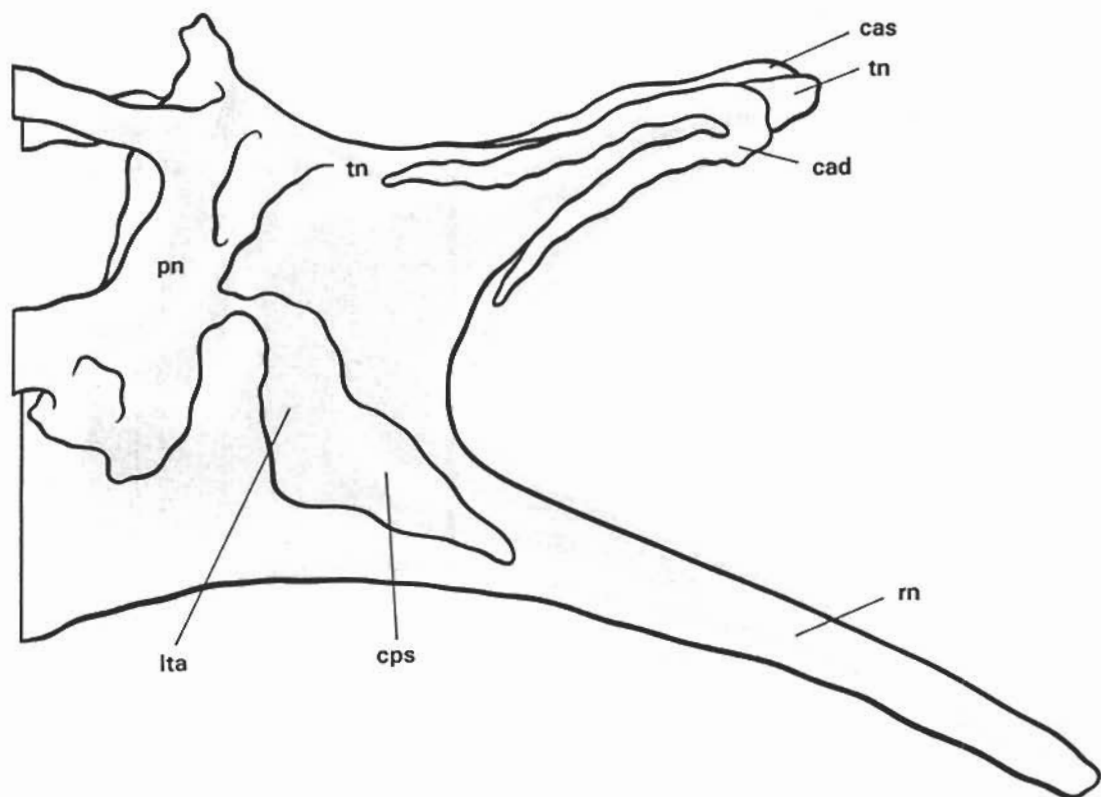


Figure 4. Right lateral view of the nasal skull of *Physeter catodon*. The schematic illustration of the same specimen as in Fig. 3 demonstrates the asymmetry of the anterior side wall structures. For labelling see list of abbreviations.

(Rothausen, 1968; Gaskin, 1976, 1982; Fordyce, 1980, 1988; Barnes, 1984; Barnes *et al.*, 1985). The similar structure within the bony ear capsule, the tympanoperioticum, is unlikely to have developed in parallel and independently in all groups (Archaeoceti, Odontoceti, and Mysticeti). This considered key evidence for monophyly of the order (Van Valen, 1968; Fleischer, 1976, 1978; Oelschläger, 1986a, 1986b, 1987, 1990; Pilleri *et al.*, 1987). Nevertheless, recent studies by Fordyce (1988, 1989) do not support this statement.

The morphology of the brain provides a further clue for the interpretation of the evolution of cetaceans. The conformities between the extant odontocetes and mysticetes can be found in the form of the brain, absence of one occipital pole of the telencephalon hemisphere, and in a massive temporal lobe (Morgane & Jacobs, 1972). The neocortex is relatively thin, yet strongly folded, while the paleocortex (olfactory system) and the archicortex (Hippocampus) are only weakly developed (Schwerdtfeger *et al.*, 1984; Oelschläger & Buhl, 1985a, 1985b; Buhl & Oelschläger, 1988;

Oelschläger, 1989). Further morphological conformities indicating monophyly of the order can be found in the development of the acoustic system, in the form of the cerebellum, and the inferior olive (Morgane & Jacobs, 1972; Oelschläger, 1989).

The cytogenetic studies support, in the same way, the hypothesis of a monophyletic origin of whales (Arnason, 1969, 1970, 1974; Kulu *et al.*, 1972; Arnason & Benirschke, 1973; Arnason *et al.*, 1977). These findings showed many similarities in the morphology of chromosomes, and in the characteristic distribution of heterochromatin (C-banding) that the independent origin of these features seems to be highly improbable. Interesting enough, the sperm whales (Physeteridae) deviate somewhat from this scheme. Arnason (1974) writes: '... *Physeter catodon* and *Kogia breviceps* both deviate in chromosome number and karyology from all other cetaceans so far studied. The Karyotypes of these two species cannot be compared directly with the karyotypes of other odontocetes (Arnason & Benirschke, 1973) even if it has been attempted in the case of *Physeter* (Kulu *et al.*, 1971)'.

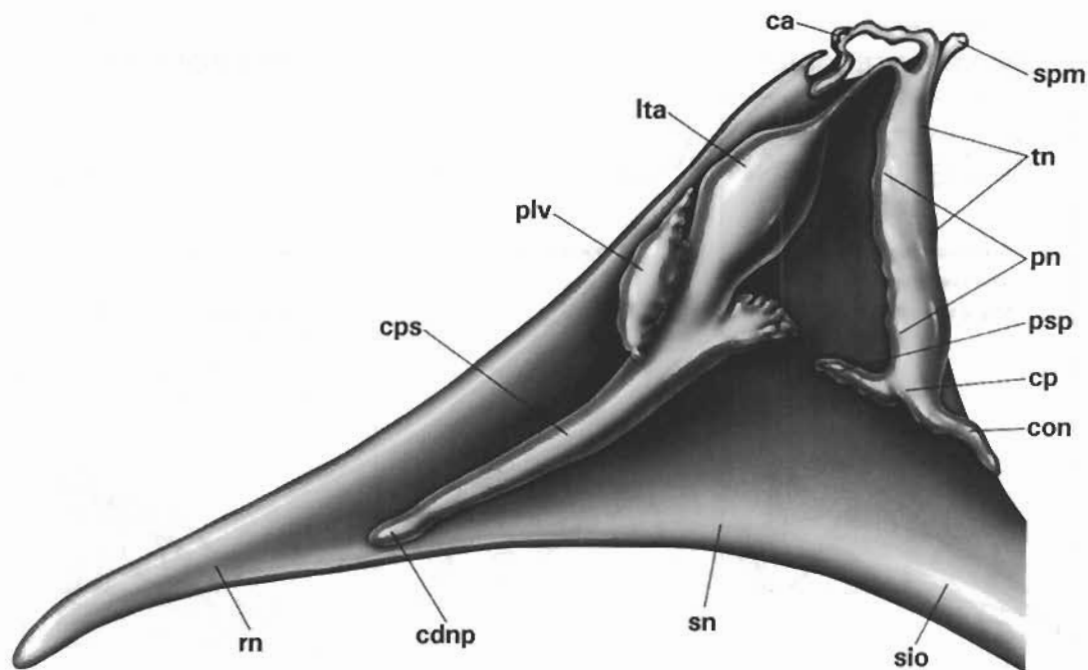


Figure 5. Left lateral view of the nasal skull of *Stenella attenuata*, embryo of 153 mm body length. For labelling see list of abbreviations.

The dentition is treated as being particularly important by the classical systematics of whales. It has been well known for some time (Sainte Hilaire, 1807; Cuvier, 1836) that baleen whales, at least in embryonic and early fetal stages, possess the tooth anlagen. Since the terrestrial origin of whales has never been questioned, the finding should not be surprising. However, the embryonic dentition in baleen whales does not resemble the original, heterodont pattern of terrestrial ancestors but consists of numerous, simply built conical teeth similar to the secondarily polyodont and homodont dentition of the toothed whales (Kükenthal, 1891, 1893; Karlsen, 1962). This fact indicates that the loss of the teeth and formation of the whalebone is only of a younger phylogenetic origin. Again, these findings can be considered as evidence of monophyly of the order.

The embryological studies of the pectoral girdle and the sternum in whales (Klima, 1978, 1990b) indicate the same division of the Cetacea into the three superfamilies as suggested also by the present study (see above). The clavicle does not appear at all during embryogenesis in the mysticetes, and in the sperm whale it appears as a minute remnant in one developmental stage only. On the contrary, in the odontocetes, without the sperm whale, a regular appearance of the clavicle as a temporary rudiment during embryogenesis has been established, and

furthermore, a rudimentary clavicle may occasionally appear also in adults (Behrmann, 1982; Klima, 1990b). However it should be pointed out here that the embryological studies (of the pectoral girdle as well as of the nasal capsule) did not include embryonic materials of river dolphins and beaked whales.

Also the anatomical findings on soft structures of the nasal region, particularly the melon, accessor air sacs and the musculature around the nasal openings give evidence that the sperm whale diverges from other toothed whales, and that the differences between baleen and toothed whales are smaller than expected (Mead, 1975; Heyning, 1989; Heyning & Mead, 1990). Surprisingly, the melon, the adipose structure in front of the blow-opening, which was supposed to occur only in the toothed whales, was found, though less developed, also in the baleen whales. This finding challenges the functional interpretation according to which the melon serves as an acoustic lens focusing the emitted ultrasonic signals (e.g. Norris, 1964; Norris *et al.*, 1971; Evans, 1973). More probably, the fat-rich tissue serves primarily for sealing the air ways, and only secondarily it may have, if at all, become a component of the echolocation system of the toothed whales (Heyning & Mead, 1990). This finding stresses the importance of those hypotheses on the echolocation which are based on cartilaginous or bony structures as sound transmitter over those which are based on the

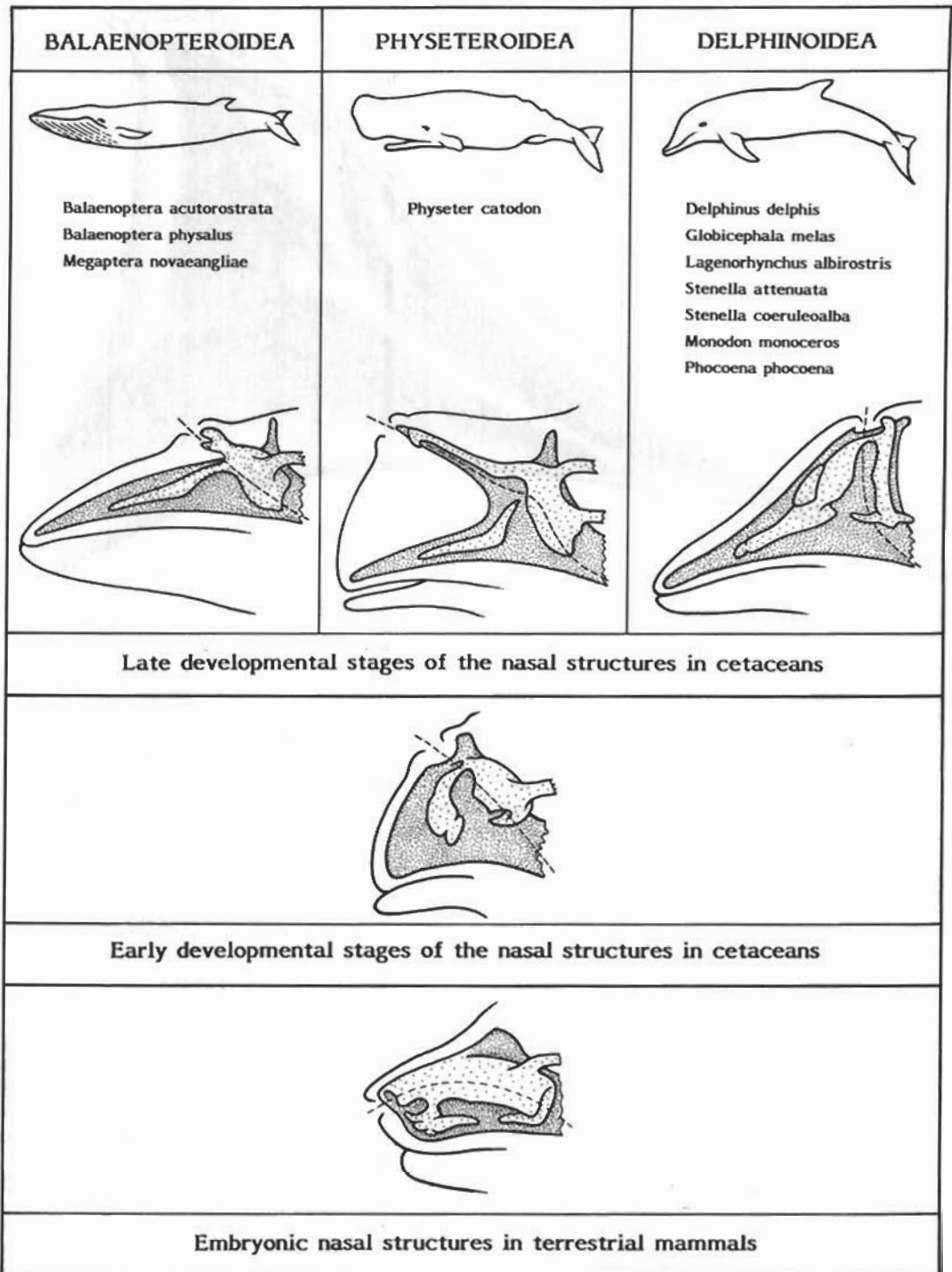


Figure 6. Comparison of embryonic cartilaginous nasal skull in terrestrial mammals and in cetaceans.

analyses of soft tissues (cf. Purves, 1966; Pilleri *et al.*, 1983; Purves & Pilleri, 1983; Pilleri, 1990). Apart from these considerations, the presence of a minute melon in the baleen whales suggests again a much closer relationship between them and the toothed whales than previously assumed.

The most recent molecular phylogenetic investigations (Milinkovitch, 1992a, 1992b; Milinkovitch *et al.*, 1993) brought not only the supportive evidence for the above presented morpho-systematical relationships, but furthermore, they led to some quite unconventional conclusions. The authors have analyzed mitochondrial ribosomal DNA-sequences from two gene segments in 16 cetacean species and have revised phylogeny of whales accordingly (Milinkovitch *et al.*, 1993). The results support a close relationship between the Artiodactyla and the Cetacea, and suggest a monophyletic origin of all the extant superfamilies of whales. In addition, the authors suggest that the sperm whales are more closely related to the baleen than to the other toothed whales. Consequently, the Odontoceti—if including the Physeteridae—have to be considered an artificial taxon and the division of the Cetacea into two suborders, Odontoceti and Mysticeti, would be superfluous. The authors have calculated that the common ancestor of the baleen and sperm whales might have possessed the echolocation system, which was retained by the sperm whales but degenerated in the baleen whales.

The mitochondrial data suggested an arrangement of the Cetacea into four large groups. Again, however, no representative of the river dolphins was investigated. An almost similar taxonomical division was derived also from the analyses of myoglobin sequences in ten species of cetaceans (Milinkovitch *et al.*, 1993).

The division of the Cetacea according to the molecular phylogenetic data is supported by the study based upon the morphogenesis of the nasal skull as presented above. In addition to the three groups (Balaenopteroidea, Physeteroidea, and Delphinoidea), the fourth group of the beaked whales (Ziphiidae) was established according to the mitochondrial and myoglobin data. The representatives of this family were, however, not available for the present embryological examination. There are, nevertheless, some anatomical features which indicate consistently that even according to the morphological criteria, the beaked whales (Ziphiidae) as well as the river dolphins (Platanistidae) probably should be considered separate groups.

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