# A late Miocene balaenopterid petrotympanic from Liessel (The Netherlands)

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In 2020 a new fossil species of rorqual (Balaenopteridae) was described as *Archaeobalaenoptera liesselensis* Bisconti, Munsterman, Fraaije, Bosselaers & Post, 2020 from a sandpit in Liessel (Province of Noord-Brabant, The Netherlands) based on a skull stored in the Oertijdmuseum in Boxtel. The collection of Museum Klok & Peel in Asten (The Netherlands) holds a well preserved unidentified rorqual petrotympanic from the same sandpit. A comparative study of this important skull element showed that it probably belongs to the same species. Our comparison also proved again that during the late Tortonian at least two, maybe even more, different rorqual species were already frequenting the southern North Sea Basin.

KEY WORDS: Balaenopteridae, petrotympanic complex, Tortonian, dinoflagellate cysts, southern North Sea Basin

## Introduction

In late Miocene times the southeastern provinces of the Netherlands were largely covered by a shallow sea. During the last decades many fossils of Tortonian age have been found in several sandpits in the area as a result of subaqueous quarrying activities, that were carried out by dredging (Liessel) and suction-dredging (Liessel and Mill) (Peters 2009, 2013) (Fig. 1).

These fossils comprise a variety of terrestrial remains (plant seeds and fruits) as well as marine species such as molluscs, bony fishes and sharks, but also numerous isolated remains of baleen whales and toothed whales (Peters, 2009, 2013). By the nature of the sand extraction at the pit, all are ex-situ finds, but many of the fossils are embedded in a sandy matrix which permits an age determination.

A few fossil whales originating from glauconitic sands in the southern part of the Netherlands and the northern part of Belgium were described during the last few years. *Metopocetus hunteri* Marx, Bosselaers & Louwye, 2016 from Liessel (Marx *et al.* 2016) and *Herentalia nigra* Bisconti, 2014 from Herentals (Belgium) (Bisconti, 2014) are taxa belonging to a now extinct family Cetotheriidae. The geological age of both taxa was dated at c. 9 - 7.6 Ma. Representatives of Cetotheriidae were probably the most common mysticetes in the late Tortonian, while the rorquals became the dominant mysticetes during Pliocene up to recent times. From Liessel also a rorqual is described: *Archaeobalaenoptera liesselensis* Bisconti,

Munsterman, Fraaije, Bosselaers & Post, 2020 (8 Ma, Bisconti *et al.*, 2020), and a very large and much younger specimen awaits publication (*c*. 5 Ma; unpublished data Munsterman TNO).

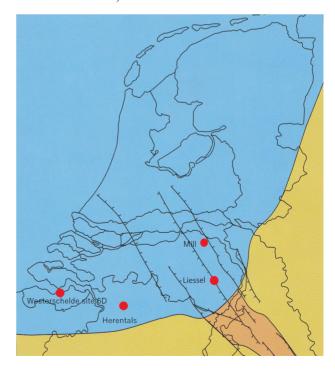


Figure 1. Southern North Sea Basin in late Miocene times.

Considering the fact that at least ten partial skulls discovered in Liessel belong to cetotheres and only two to rorquals it is plausible that the bulk of other fossil remains of mysticetes (vertebrae, ribs, pectoral appendages) originate from cetotheres as well, although some big mandibular fragments and vertebrae obviously are associated with whales of large dimensions, possibly early rorquals. Looking at the geological age of *Metopocetus hunteri* (Marx *et al.*, 2016) and *Archaeobalaenoptera liesselensis* (Bisconti *et al.*, 2020), it seems plausible to suggest that representatives of both families lived contemporarily in the Liessel environment during the late Tortonian.

Here a bulla and partial petrosal (petrotympanic complex according to Ekdale *et al.*, 2011) from the sandpit in Liessel are described and compared with the same elements of some relevant rorquals. Late Miocene bullae of balaenopterids are rare, so any new find such as this well-preserved specimen from Liessel can add important information to our knowledge.

## Material and methods

The left bulla and partial petrosal from Liessel was found during dredging activities in sandpit Hoogdonk during the late 1990's (Peters, 2009). Since then it has been stored in Museum Klok & Peel (Asten, The Netherlands), collection number Li 2153. Preceding the current investigation, glauconitic sand of the matrix was removed to reveal some more details of the petrosal. The extracted sand was preserved for examination of its dinoflagellate cyst content.

For a better insight into the anatomy of the bulla as well as the periotic the two parts of the complex were separated.

In this study two left bullae stored in the collection of the Natural History Museum in Rotterdam (The Netherlands) were used for morphological comparison with Li 2153: NMR 3410 is the bulla of a recent *Balaenoptera acutorostrata* (Lacépède, 1806) that at first glance shows a strong resemblance to the fossil Li 2153. The second bulla, NMR 16975 is of a late Miocene rorqual, that was recently dredged from the Western Scheldt (Westerschelde). Its age has been dated to about 8 Ma., the same age as the Liessel specimen.

# Palynological preparation and analysis

Twenty grams of fine-grained glauconitic sands from the matrix of the current balaenopterid petrotympanic were prepared for palynological analysis by Palynological Laboratory Services (PLS, UK). The standard sample processing procedures were used, which involves HCl and HF treatment to dissolve the carbonates and the silicates, heavy liquid separation (ZnCl<sub>2</sub>) and sieving over an 18 µm mesh sieve (Janssen & Dammers, 2008). The organic residue was mounted on microscopic slides with glycerine jelly. A quantitative palynological analysis was carried out at the Geological Survey of the Netherlands (TNO) following standard procedures. A Leica light-microscope was used with 500x magnification. In total, a targeted minimum of c. 200 dinoflagellate

cysts, spores and pollen (palynomorphs) were counted. The First Occurrence Datum (FOD) and Last Occurrence Datum (LOD) of dinoflagellate cysts were used for the age interpretation of the matrix sample. Species important for stratigraphical and/or sedimentary facies analysis are mentioned in the dedicated section of this paper. The dinoflagellate taxonomy follows Fensome *et al.* (2019).

The palynological interpretation is based on key references relating to the palynostratigraphy of the Miocene from the North Sea region: Anthonissen (2012), Dybkjaer & Piasecki (2010), Köthe (2012), Kuhlmann *et al.* (2006), Louwye (2002), Louwye and De Schepper (2010), Munsterman & Brinkhuis (2004) and Powell (1992). The zonation of Munsterman & Brinkhuis (2004) is followed in this study, since it is generally used in the Netherlands. The zonation is recalibrated to the Geological Time Scale sensu Ogg *et al.*, 2016 (Munsterman *et al.*, 2019).

## Palynological results

#### **Palynofacies**

The preservation of the palynomorph (sporomorph and dinoflagellate cyst) association recovered from the green-sands associated with the balaenopterid petrotympanic fossil is good. The remainder of the slides were scanned for rare taxa. The number of dinoflagellate cysts, as well as the number of other microfossils (e.g., Botryococcus, chambers of foraminifers, acritarchs, Pediastrum) is shown in the distribution table (Table 1).

Marine dinoflagellate cysts (66 %) outnumber the total sum of dinoflagellate cysts and sporomorphs (spores and pollen). Bisaccate pollen (86 %) dominate the sporomorph category. Bisaccate pollen are formed by gymnosperms (Gymnospermae). These are usually considered to flourish in a relatively dry environment, such as higher pine forests. Bisaccate pollen grains however have a high buoyancy in both water and air, hence can be easily transported over large distances to distal marine, even oceanic, settings, excluding any spores (Abbink, 1998). Spores are present in low numbers (14 % of the total sum sporomorphs), and represented exclusively by simple trilete spores (ferns). The highest numbers of dinoflagellate cysts are represented by the genus Spiniferites (54 % of the dinocysts sum). This genus is present in neritic conditions, but when dominating the assemblage, this points to relatively open-marine (neritic) influence (Brinkhuis, 1994). Operculodinium centrocarpum (9 %) is a cosmopolitan, opportunistic taxon, hence influenced by multiple ecological factors (Hennissen et al., 2017). The coastal marine taxon Lingulodinium machaerophorum is also relatively well-represented (7 % of the dinocyst sum). The heterotrophic genera, like Barssidinium, Lejeunecysta and Selenopemphix are also included (13 % of the dinocyst sum) in the microflora indicating nutrient-rich influence. The variety of dinocyst species is relatively high. All indicators combined can be interpreted as relatively open-marine neritic nutrient-rich conditions. Reworking is very rare.

Liessel 2153							
	Lithostratigraphy	Chronostratigraphy	Dinoflagellate Cysts	SP	MP		
Samples			Absolute abundance Analyst(s): DMU	*1 *2	*1		
			Achomosphaera andalousiensis Barssidinium graminosum Barssidinium graminosum Barssidinium pilocenium Cordosphaeridium minimum Dapsilidinium pseudocolligerum Habibacysta fectata Hadanlium miocenicum Heteraliusacysta spp. Homotryblium spp. Homotryblium spp. Homotryblium spp. Homotryblium spp. Lingulodinium tuncatum Lejeunecysta spp. Lingulodinium machaerophorum Operculodinium centrocarpum sensu Wall & Dale Operculodinium janduchenei Operculodinium janduchenei Operculodinium janduchenei Sperculodinium sensu Wall & Dale	Systematoprora piacacantria Bisaccantris Bisaccantris (and histoprotes)	(exti. Disaccates)		
Samples in Discipline(s) : Paly	Formation	Age	Achomosphaera andalous Barssidinium grammosum Barssidinium grammosum Barssidinium pilocenium Cordosphaerdium minimu Dapsildinium pseudocoliith Hadinium micanicum Heradinium micanicum Heradinium micanicum Heradinium micanicum Labyninhodrium spp. Homotryblium spp. Lingulodinium machaerop Meliasphaeridium chroard Operculodinium machaerop Operculodinium centrocard Operculodinium ianduchei Operculodinium ianduchei Operculodinium ochrocardium paralecaniella spp. Polysphaeridium zohayi Raticulatosphaera actinoc Reworking dinocysts Selenopemphix brevispinc Selenopemphix dionaesec Selenopemphix inephroide Spiniferites spp.	Bisaccates Sporomorpho	Acritarchs Foraminifera		
Samples			888888888888888888888888888888888888888	3 % 8	P M M		
● LI 2153	Diessen	late Tortonian, Zone SNSM 13	2 5 5 1 2 1 + 1 1 3 2 10 5 12 1 1 + 2 1 1 1R2 2 1 73	2 61 1	0 1 13		

Table 1. Distribution table of palynomorphs in sediment from sample Li 2153.

#### Age assessment

Age diagnostic taxa are the dinoflagellate cysts Labyrinthodinium truncatum and Systematophora placacantha. The former taxon has a LOD in the late Miocene, late Tortonian, Zone SNSM14 (Munsterman & Brinkhuis, 2004). This event is also used to define the DN9 Zone by De Verteuil & Norris (1996) for the East coast of the USA and followed in Belgium and Germany (Köthe, 2012). In addition, the LOD of Systematophora placacantha is defined in slightly older late Miocene, late Tortonian, Zone SNSM13 (Munsterman & Brinkhuis, 2004). Zone SNSM13 comprises the lower part of Zone DN9 as recorded by De Verteuil & Norris (1996) and is correlated to the Hystrichosphaeropsis obscura Zone on- and offshore Denmark by Dybkjaer & Piasecki (2010). Marker species indicating possibly older zones, for example Palaeocystodinium golzowensis (LOD in Zone SNSM12) are missing. The presence of Operculodinium janduchenei with a FOD in the Tortonian confirms the dating. The occurrence of Headinium miocenicum also fits the age interpretation. In conclusion, the age assessment of the present palynospectrum is late Miocene, late Tortonian, Zone SNSM13, c. 8.7-8.1 Ma (Munsterman et al., 2019).

## **Description**

General: successive preparation of the Liessel petrotympanic complex provided a more complete picture of the bulla and revealed some details of the periotic, previously hidden in the matrix. Unfortunately, the anterior part of the periotic is severely damaged and the posterior part is missing. Description of the periotic therefore is incomplete and comparison of the preserved fragment with ear bones of other taxa is difficult. In the preparation process not only the periotic but also the malleus was isolated from the complex.

In Fig. 2 the petrotympanic complex is shown before the isolation of the different parts, in Fig. 3 tympanic bulla Li 2153 is shown in four views (photographs) with elucidation.

Bulla Li 2153 is rather small, its dimensions are about the size of recent *Balaenoptera acutorostrata* (Lacépède, 1806) (see Table 2).

Its overall shape is ovoid, in ventral view all sides except the lateral are convex. The lateral furrow is transversely oriented, relatively deep and thereby roughly divides the bulla into anterior and posterior parts, the anterior lobe slightly shorter than the posterior one. Anteriorly there is



Figure 2. Petrotympanic complex Li 2153 in lateral view.

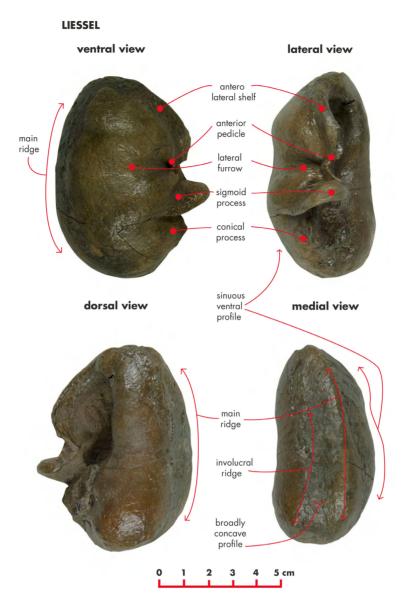


Figure 3. Isolated bulla Li 2153 in ventral, lateral, dorsal and medial views.

	Li 2153	NMR 3410	NMR 16975
length (mm)	87.2	87.5	94.9
width over sigmoid process (mm)	66.6	66.1	74.1
height (mm)	48.3	48	51.9

**Table 2.** Dimensions of bullae Li 2153, NMR 3410 and NMR 16975.

a shallow anterolateral shelf, its lateral margin is curved. The sigmoid process is 31 mm in length, measured from its origin to the apex; towards the apex it curves slightly in anterior direction. The apex of the conical process is more or less rectangular. The anterior pedicle is missing, but the position where it was attached to the periotic is clearly visible, the posterior pedicle before the separation of bulla and periotic was present and (in ventral view) located behind the conical process. The eustachian outlet

is bordered by a thick crest that runs posteriorly along the anterolateral shelf up to the anterior pedicle. Due to the relatively deep lateral furrow (leaving a depression in the profile), in lateral view the ventral side of the bulla is undulated. The main ridge and the involucral ridge on the medial side of the bulla diverge from the anterior to the posterior end of the bulla, leaving a widening interprominential area in between, which is concave and deepening towards the posterior end (Figs 3 & 4). Interestingly this is a character of the bulla that is commonly noted in cetotheres, but not in rorquals.

Three views of the incomplete periotic are shown in Fig. 5. Anterior and posterior processes are missing for the most part, but the pars cochlearis is well preserved, broadly attached to (the rest of) the anterior process, and shows the characteristic shape of the pars cochlearis of a balaenopterid. The length of the pars cochlearis is 41.6 mm. The fenestra rotunda is rounded; in ventral view it is obscured by the pointed caudal tympanic process of the pars coch-

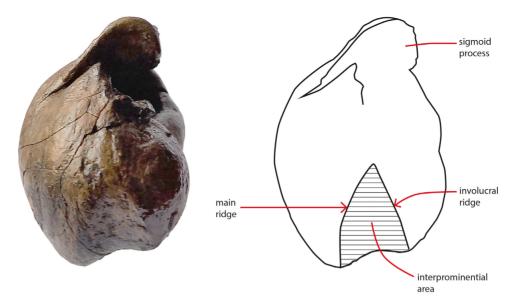


Figure 4. Bulla Li 2153 in posterior view: a. photograph b. line drawing.

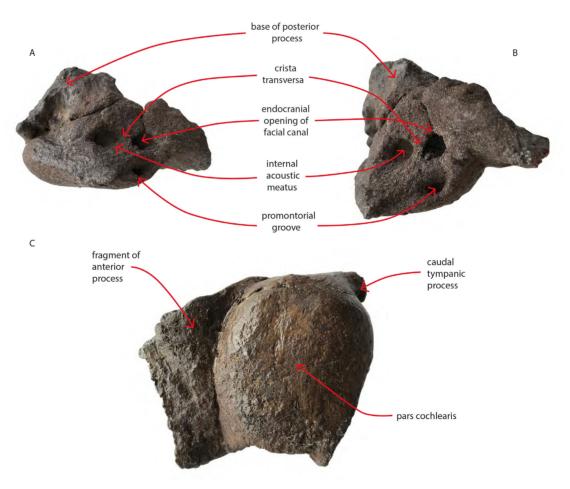


Figure 5. Periotic of complex Li 2153 in three views, lateral (A), cranial (B) and central (C).

learis. Two differences between the periotic of Li 2153 and recent *Balaenoptera acutorostrata* are notable in lateral view (Fig. 6): the steepness of the slope towards the posteromedial border and the more acute-angled side of the pars cochlearis (see dashed lines in Fig. 6).

The head of the malleus is rounded and its position within

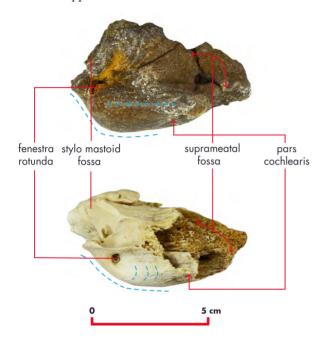
the original complex was clearly visible anterodorsally from the sigmoid process. After its isolation from the complex the malleus could be observed from different angles. In posterior view (Fig. 7) the head is carrying the two incudal facets, perpendicularly arranged. The vertical facet is twice as large as the horizontal one. The head

is confluent with the manubrium that is narrowing and ends in an obtuse tip.

## Comparison

For several of its characters bulla Li 2153 is compared with a recent bulla of *Balaenoptera acutorostrata* (NMR 3410) and with a yet undescribed bulla of a 7.5 - 8 Ma old rorqual from the Western Scheldt (NMR 16975).

In overall appearance and dimensions Li 2153 resembles



**Figure 6.** Periotic of complex Li 2153 and recent *Balaenoptera acutorostrata* (Lacépède, 1806) in lateral view.

NMR 3410, but its size is distinctly smaller than NMR 16975 (Table 2).

In medial view (Fig. 8) all three bullae are more or less oval in profile, yet the outline of Li 2153 is more rounded with respect to the other two. The bulla of B. acutorostrata is slightly higher than Li 2153 and NMR 16975. Differences are most prominently exposed in the anterior halves of the bulla. In Li 2153 this area is rounded and convex, in NMR 3410 the anterior margin is more oblique and even slightly concave. In bulla NMR 16975 this area is oblique, slightly convex but more flattened than in Li 2153 (Fig. 8, solid line arrows). The lateral furrow in NMR 3410 is located about the middle of the bulla, transversely oriented and less deep than in Li 2153. In NMR 16975 the lateral furrow is also transversely oriented and deep, but located somewhat more towards the anterior half of the bulla. In lateral view the profile of bulla Li 2153 therefore is different from the two other specimens (Fig. 9, broken line arrows and solid lines)

The relatively deep and diverging concave groove between the main ridge and the involucral ridge in Li 2153 marks another significant difference between this bulla and the other two (Fig. 8, solid lines). In the recent bulla this interprominential area is very shallow to flat, in the Western Scheldt bulla there is no groove.

The antero-lateral shelf of bulla Li 2153 is strikingly curved in dorsal direction, a character clearly different from this margin in recent bulla NMR 3410 and fossil bulla NMR 16975, where the margin is more or less straight (Figs 3 & 9). The sigmoid process of bulla Li 2153 is 31 mm in length, measured from its origin to the apex; towards the apex it curves slightly in anterior direction. In extant *Balaenoptera acutorostrata* NMR 3410 the sigmoid process measures 28.4 mm. in length, curves in

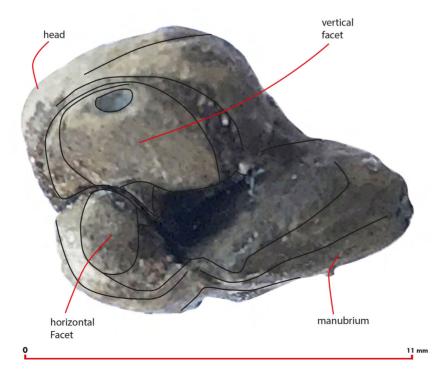


Figure 7. Malleus of complex Li 2153 in posterior view.

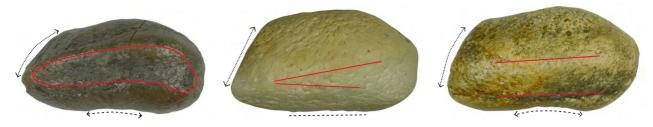


Figure 8. Bullae Li 2153 (l), NMR 3410 (m) and NMR 16975 (r) in medial view.

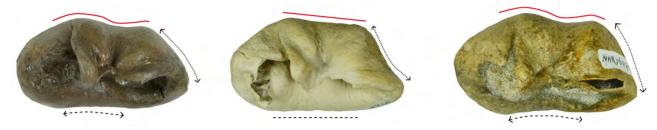


Figure 9. Bullae Li 2153 (l), NMR 3410 (m) and NMR 16975 (r) in lateral view.

the same way but the tip bends backwards. The sigmoid process of bulla NMR 16975 is 37.7 mm. in length. The outline is straighter and the orientation perpendicular to the longitudinal axis of the bulla. In recent Balaenopteridae the sigmoid process is orientated more obliquely (posteriorly inclined). The conical processes in the three bullae differ in the vertical angle of the apex. In Li 2153 the apex is about rectangular, while in *B. acutorostrata* it is obtuse and in NMR 169075 the apex is acute-angled.

# Discussion

Worldwide, remains of rorquals dated to late Miocene times are relatively rare. In the last decades just a few balaenopterid whales with an age of over 7 Ma have been described. A European example is *Plesiobalaenoptera quarantellii* Bisconti, 2010 from Northern Italy, estimated Tortonian in age (11-7 Ma). Another taxon is a Californian balaenopteroid, age between 7.6 and 7.3 Ma, assigned in 1922 by Kellogg to the genus *Megaptera* Gray, 1846; redescribed and renamed as *Norrisanima miocaena* Leslie, Peredo & Pyenson, 2019. A third Miocene rorqual is *Incakujira anillodefuego* Marx & Kohno, 2016 from the Peruvian desert dated at 8–7 Ma.

Recently in the Netherlands several interesting whale fossils were dredged from the Western Scheldt, one of them a balaenopterid (*Nehalaennia devossi* Bisconti, Munsterman & Post, 2019). That species has been dated to approximately 8.1–7.5 Ma. From the same sediments stems bulla NMR 16975, part of an undescribed skull, used for comparison in this article.

The bulla and periotic of *Plesiobalaenoptera quarantellii* are well known. The bulla differs in many aspects from Li 2153: in morphology as well as in dimensions. Its anterior border is abruptly depressed, which is not the case in Li 2153, the sigmoid process is described as high and short, different from our Liessel specimen, and the area between main ridge and the involucral ridge also is clear-

ly different in shape. Moreover, bulla Li 2153 is distinctly smaller than the bulla of *P. quarantellii*. The tympanic bulla of *Norrisanima miocaena* differs in many aspects from Li 2153, such as its overall rectangular shape in dorsal view, the position of the sigmoid process and the lateral furrow, the area between main ridge and involucral ridge and the absence of an anterolateral shelf. Compared with Li 2153, the bulla of the Peruvian whale *Incakujira anillodefuego* shows more similarities in morphology as well as in dimensions. But in at least one aspect the two are clearly different: the diverging and deepening area between main ridge and involucral ridge, so characteristic for Li 2153, is absent in *I. anillodefuego*.

Differences between the Western Scheldt bulla NMR 169075 and the Liessel bulla 2153 were described earlier in this article.

## Conclusion

We identify Li 2153 as a petrotympanic complex from a rorqual (Balaenopteridae) that lived in the southern North Sea Basin, 8.1-8.7 Ma ago. Based on its geological age, the specific morphology of the bulla (differing from other known late Miocene rorquals), and the presence of a synchronous rorqual from the same sandpit in Liessel, we consider it highly probable that Li 2153 stems from an individual of the species *Archaebalaenoptera liesselensis*. The presence of a contemporaneous bulla from the Western Scheldt, although with other characters and dimensions, proves that in Tortonian times at least two different rorquals lived in the Southern North Sea.

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## References

- Abbink, P. 1998. Palynological investigations in the Jurassic of the North Sea region. PhD study, University of Utrecht.
- Anthonissen, E. 2012. A new Miocene biostratigraphy for the northeastern North Atlantic: an integrated foraminiferal, bolboforma, dinoflagellate and diatom zonation. Newsletters on Stratigraphy 45: 281-307.
- Bisconti, M. 2010. A new balaenopterid whale from the late Miocene of the Stirone River, Northern Italy (Mammalia, Cetacea. Mysticeti). Journal of Vertebrate Paleontology 30 (3): 943-958.
- Bisconti, M. 2014. Anatomy of a new cetotheriid genus and species from the Miocene of Herentals, Belgium, and the phylogenetic and palaeobiogeographical relationships of Cetotheriidae s.s. (Mammalia, Cetacea, Mysticeti), Journal of Systematic Palaeontology 13(5): 1-19. https://doi.org/ 10.1080/14772019.2014.890136
- Bisconti, M., Munsterman, D.K. & Post K. 2019. A new Balaenopterid whale from the Late Miocene of the Southern North Sea Basin and the evolution of balaenopterid diversity (Cetacae, Mysticeti). PeerJ 7: e6915. https://doi. org/10.7717/peerj.6915
- Bisconti M., Munsterman D.K., Fraaije, R.H.B., Bosselaers, M.E.J. & Post, K. 2020. A new species of rorqual whale (Cetacea, Mysticeti, Balaenopteridae) from the Late Miocene of the Southern North Sea Basin and the role of the North Atlantic in the paleobiogeography of Archaeobalaenoptera. PeerJ 8: e8315. https://doi.org/10.7717/peerj.8315
- Brinkhuis, H. 1994. Late Eocene to Early Oligocene dinoflagellate cysts from the Priabonian type-area (northeast Italy); biostratigraphy and palaeoenvironmental interpretation. Palaeogeography, Palaeoclimatology, Palaeoecology 107: 121-163. https://doi.org/10.1016/0031-0182(94)90168-6
- De Verteuil, L. & Norris, G. 1996. Miocene dinoflagellate stratigraphy and systematics of Maryland and Virginia. Micropaleontology Supplement 42: 1-172.
- Dybkjaer, K. & Piasecki, S. 2010. Neogene dinocyst zonation for the eastern North Sea Basin, Denmark. Review of Palaeobotany and Palynology 161: 1-29.
- Ekdale, E.G., Berta, A. & Deméré, T.A. 2011 The comparative osteology of the petrotympanic complex (ear region) of extant baleen whales (Cetacea: Mysticeti). Plos One 6: e21311. https://doi.org/10.1371/journal.pone.0021311
- Fensome, R.A., Williams, G.L. & MacRae, R.A. 2019. The Lentin and Williams Index of fossil dinoflagellates 2019 edition. AASP Contributions Series, 50: 1173 pp.

- Hennissen, J.A., Head, M.J., De Schepper, S. & Groeneveld, J. 2017. Dinoflagellate cyst paleoecology during the Pliocene-Pleistocene climatic transition in the North Atlantic, Palaeogeography, Palaeoclimatology, Palaeoecology 470: 81–108. https://doi.org/10.1016/j.palaeo.2016.12.023
- Janssen, N. & Dammers, G. 2008. Sample processing for the pre-Quaternary palynology. Internal TNO report.
- Köthe, A. 2012. A revised Cenozoic dinoflagellate cyst and calcareous nannoplankton zonation for the German sector of the southeastern North Sea Basin. Newsletters on Stratigraphy 45(3):189-220. https://doi.org/10.1127/0078-0421/2012/0021
- Kuhlmann, G., Langereis, C.G., Munsterman, D.K., Van Leeuwen, R.-J., Verreussel, R., Meulenkamp, J.E. & Wong, Th.E. 2006. Chronostratigraphy of Late Neogene sediments in the southern North Sea Basin and paleoenvironmental interpretations. Palaeogeography, Paleoclimatology, Palaeoecology 239: 426-455.
- Leslie, M.S., Peredo, C.M. & Pyenson, N.D. 2019. Norrisanima miocaena, a new generic name and redescription of a stem balaenopteroid mysticete (Mammalia, Cetacea) from the Miocene of California. PeerJ 7: e7629. https://doi. org/10.7717/peerj.7629
- Louwye S. 2002. Dinoflagellate cyst biostratigraphy of the Upper Miocene Deurne Sands (Diest Formation) of northern Belgium, southern North Sea Basin. Geological Journal 37: 55-67.
- Louwye, S. & De Schepper, S. 2010. The Miocene-Pliocene hiatus in the southern North Sea Basin (northern Belgium) revealed by dinoflagellate cysts. Geological Magazine 147 (5), 2010, pp. 760-776. https://doi.org/10.1017/ S0016756810000191
- Marx, F.G., Bosselaers, M. & Louwye, S. 2016. A new species of Metopocetus (Cetacea, Mysticeti, Cetotheriidae) from the Late Miocene of the Netherlands. PeerJ 4:e1572. https:// doi.org/10.771/peerj.1572
- Marx, F.G. & Kohno, N. 2016. A new Miocene baleen whale from the Peruvian desert. Royal Society open science 3: 160542. https://doi.org/10.1098/rsos.160542
- Munsterman, D.K. & Brinkhuis, H. 2004. A southern North Sea Miocene dinoflagellate cyst zonation. Netherlands Journal of Geosciences 83: 267-285.
- Munsterman, D.K., Ten Veen, J.H., Menkovic, A., Deckers, J., Witmans, N., Verhaegen, J., Kerstholt-Boegehold, S.J., Van de Ven T. & Busschers, F. 2019. An updated and revised stratigraphic framework for the Miocene and earliest Pliocene strata of the Roer Valley Graben and adjacent blocks. Netherlands Journal of Geosciences 98; e8. https:// doi.org/10.1017/njg.2019.10
- Ogg, J.G., Ogg, G. & Gradstein, F.M. 2016. A Concise Geologic Time Scale. Elsevier, Amsterdam: 240 pp.
- Peters N. 2009. Brabant tussen walvissen en mastodonten. Nationaal Beiaard- en Natuurmuseum Asten & Oertijdmuseum Boxtel: 110 pp.
- Peters N. 2013. Van reuzenhaai tot Chalicotherium. Oertijdmuseum de Groene Poort Boxtel: 158 pp.
- Powell, A.J. 1992. Dinoflagellate cysts of the Tertiary System. In: Powell, A.J. (ed.). A stratigraphic index of dinoflagellate cysts, British Micropalaeontological Society Series: 155-272.