Pteropoda (Mollusca, Gastropoda, Thecosomata) from the Eocene/Oligocene boundary interval of three cored boreholes in southern coastal Tanzania and their response to the global cooling event

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ABSTRACT

The Eocene - Oligocene Transition was a period of major climatic and oceanographic change, resulting in widespread biotic overturning. However, the record of many marine organisms remains patchy. Planktic Mollusca (Pteropoda) from three cored boreholes spanning the Eocene/Oligocene boundary (EOB) in southern coastal Tanzania are represented by eight species, three of which are introduced as new: *Heliconoides nikkieae* sp. nov., *Limacina tanzaniaensis* sp. nov. and *Limacina timi* sp. nov. Three of the other species can only be identified in open nomenclature. The two most commonly occurring species, *H. nikkieae* and *L. timi*, straddle the EOB without noticeable loss in abundance. Two species, *Limacina robusta* (Eames, 1952) and *L. tanzaniaensis* disappear before the EOB. The species *Bovicornu* aff. *eocenense* Meyer, 1886 disappears shortly after the EOB. Two species were only found in a single sample each, in the Eocene part of the succession. Response to changing environmental conditions seems to be demonstrated by two or three of the pteropod species that become extinct before or shortly after the EOB.

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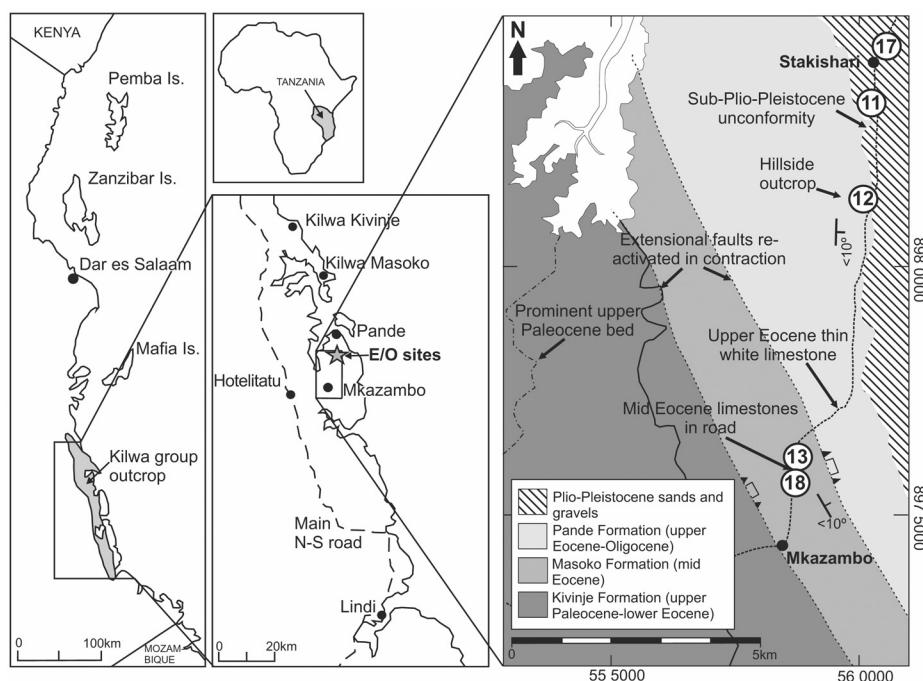
INTRODUCTION

The Eocene-Oligocene transition (EOT) was one of the most dramatic events of the Cenozoic, associated with major climatic disruption and widespread biotic turnover in both marine and terrestrial realms (see Coxall and Pearson, 2007 for review). High-resolution studies of the marine response have been carried out using planktic and benthic foraminifera, and nanno-fossils (e.g., Zachos et al., 1994; Molina et al., 1993; Diester-Haass et al., 2001; Lui et al., 2004; Wade and Pearson, 2008; Cotton and Pearson, 2011; Cotton et al., 2014). However, records of other marine groups are often patchy. Pteropods are planktic gastropods and are increasingly being used in studies of recent ocean records and climate change (Fabry, 1990; Wall-Palmer et al., 2012; Bednaršek and Ohman, 2015; references therein). Their aragonitic shells are susceptible to dissolution, making them excellent model organisms to study ocean acidification. However, palaeoecological data for older pteropod records are relatively uncommon, yet may add important information to the overall understanding of climatic impacts in the marine realm. Pteropods have a well-documented fossil record, but many regions remain understudied, and early well-preserved records are therefore exceptionally important (e.g., Janssen et al., 2016).

The Eocene-Oligocene Transition (EOT) is an extended period of global oceanographic and climatic perturbation spanning between 33.5 - 34 Ma. The Eocene/Oligocene Boundary (EOB) is defined by the last occurrence of the planktic foraminiferal family Hantkeninidae at the Global Boundary Stratotype-Section and Point (GSSP) at Massignano, near Ancona, on the Italian Adriatic coast (Premoli Silva and Jenkins, 1993), which occurs at 33.7 Ma on the timescale of Cande and Kent (1995). However, an unreliable magnetostratigraphy and stable-isotope stratigraphy (Bodiselitsch et al., 2004) and lack of carbonate (macro)fossils (pers. observ. AWJ, August 1992) in the Massignano section prevented global correlation with climatic events. The additional fact that the occurrence of Hantkeninidae is mostly restricted to tropical and sub-tropical environments also made long-distance correlations (e.g., to the North Sea Basin and in particular to the Priabonian stratotype) problematic. Subsequent studies of Deep Sea Drilling Project Site 522, showed that the extinction preceded the most positive oxygen isotopes of the EOT, representing the Early Oligocene Glacial Maximum (Zachos et al., 1994; Liu et al., 2004). More recently this idea has been further refined.

The Kilwa District in southern Tanzania contains an apparently complete succession through the EOT, which was recovered by three Tanzanian Drilling Project boreholes (TDP 11, 12 and 17; Nicholas et al., 2006; Pearson et al., 2008). The dominant lithology consists of hemipelagic clays interspersed with debris flow limestones (Nicholas et al. 2006). These clays contain exceptionally well-preserved calcareous micro- and nannofossils, including aragonitic preservation (Pearson et al., 2008; Wade and Pearson, 2008; Bown et al., 2008). This, coupled with the expanded nature of the sediments, allowed for high resolution stratigraphy chemo-and biostratigraphy to be carried out and precise correlation to global records. This placed, for the first time, the extinction of the Hantkeninidae between the two positive isotope shifts of the transition (Pearson et al., 2008; Wade and Pearson, 2008); the first of which is attributed to temperature change and the second largely to ice-volume (Lear et al., 2008). In addition, the site contains many other exceptionally well-preserved calcareous micro-fossils, including larger benthic foraminifera (Cotton and Pearson, 2011), bryozoans (Martino et al., 2017), dasycladaceae, ostracodes and also benthic molluscs (on which a paper is in preparation), making Tanzania an exceptionally important site for the study of comparatively less ubiquitous fossils across the EOT. Studies of the benthic molluscan record have shown that overall numbers of mollusc shells increase across the boundary. However, that study mainly examined the benthic forms. Here we present a detailed record of occurrences through the EOT interval and taxonomy of specifically the pteropod fauna from TDP 11, 12 and 17 (see Nicholas et al., 2006; Cotton and Pearson, 2011, for details on these boreholes). Though relatively few specimens were found due to the small sample size, the often excellent preservation and well-correlated nature of the record offers a unique insight into a region where no pteropod records were previously known.

FIGURE 1. Location and geological map of the Tanzanian Drilling Project Eocene/Oligocene boundary sites (TDP 11, 12 and 17), additional Tanzanian Drilling Project sites in the area are also shown, modified from Nicholas et al. (2006). After Cotton and Pearson, (2011).

MATERIAL AND METHODS

The Tanzania Drilling Project (TDP) was initiated in 2002 (Pearson et al., 2004; Nicholas et al., 2006, 2007) after preliminary field observations beginning in 1998 (Pearson et al., 2001) on numerous outcrops between the towns of Kilwa and Lindi, southern Tanzania, had demonstrated the presence of well-preserved microfossil assemblages of Cretaceous to Paleogene age. The TDP focused on generating litho- and biostratigraphic, geochemical, micropalaeontological and palaeoclimatic records, and resulted in recovery of over 40 cored boreholes, covering Cretaceous (Aptian) to Paleogene (Oligocene) sediments (Pearson et al., 2004, 2006; Nicholas et al., 2006; Jiminez-Berrucoso et al., 2010, 2012, 2015). These sediments are formally defined as the Kilwa Group and were initially subdivided into four formations: The Nangurukuru, Kivinje, Masoko, and Pande formations (Nicholas et al., 2006), to which a fifth was recently added, the Lindi formation (Jiminez-Berrucoso et al., 2015). The Pande Formation contains an apparently locally conformable succession through the EOT and was recovered in three boreholes drilled approximately along strike of each other; a minor hiatus is inferred at TDP Sites 11 and 17 but TDP 12 appears conformable (Figure 1).

TDP 11. South of Stakishari (Tanzania, Kilwa region), coordinates UTM 37L 560250 8983211; pteropod specimens are available from four samples TDP11.26.2, 64-74 cm, to TDP11.33.2, 74-84 cm.

TDP 12. South of Stakishari (Tanzania, Kilwa region), coordinates UTM 37L 560222 8981309; pteropods are available from 16 samples TDP12.11.4, 20-26 cm, to TDP12.29.2, 20-30 cm.

TDP 17. Stakishari (Tanzania, Kilwa region), coordinates UTM 37L 560539 8984483; pteropod specimens available from 36 samples 17.15.1, 50-63 cm, to 17.41.3, 0-15 cm.

Based on micropalaeontological event correlations the three sections were given "composite depths" to enable direct comparison of results between the three sites (Pearson et al., 2008). These composite depths are specified in the distribution tables following the systematical part.

The meters added are, for TDP 17 cores 1-35: 0 m; for TDP17 cores 36-42: 12 m; for TDP11 cores 1-28: 17 m, and for TDP11 cores 29-36: 20 m.

The Eocene Tanzanian shelf is thought to have been narrow, much like today, and the three boreholes are estimated to be approximately 50 km from the palaeo-shoreline (Kent et al., 1971; Nicholas et al., 2006, 2007). Based on the sedimentary facies and smaller benthic foraminiferal

assemblage the palaeo-depth is estimated to be approximately 300-500 m, although it is possible it is deeper than this (Nicholas et al., 2006; 2007). The dominant sediment is dark green-grey clay with < 10% CaCO$_3$.

The half-round core-samples of the hemi-pelagic clays, varying in length from 1.5 to 15 cm, were washed through a 63 μm sieve and the residues dried (Lear et al., 2008; Pearson et al., 2008; Wade and Pearson, 2008). Pteropods were then picked using a paintbrush under a binocular microscope.

The Kilwa Group is characterised by excellent preservation of its carbonate microfossils, this extends to the pteropods, which is related to the high clay content and shallow maximum burial depth (Pearson et al., 2001; Van Dongen et al., 2006; Bown et al., 2008). However, the condition of pteropod specimens varies from perfect shell preservation to shells filled with pyrite and specimens preserved as pyritic internal moulds with partly or completely dissolved aragonitic shell material. Local dissolution may be related to pyritisation. Some specimens are badly deteriorated and indeterminate. Specimens are housed in the fossil holoplanktic mollusc collection of Naturalis Biodiversity Center, Leiden (The Netherlands), registered with RGM-registration numbers.

Scanning Electron Microscopy

SEM micrographs were made by Renate Helwerda from uncoated specimens at 1.000 kv with a Jeol Field emission scanning electron microscope type: JSM-7600F at Naturalis Biodiversity Center, Leiden, The Netherlands.

Micro-Computed Tomography

Micro-computed tomography (Micro-CT or X-ray microtomography) scanning of the three holotypes (RGM 777415a, RGM 777428b and RGM 1007748b) was carried out by Dirk van der Marel, of Naturalis Biodiversity Center in Leiden, the Netherlands, using a Bruker SkyScan 1172 micro-CT scanner. 1601 projections of 3 -15 sec exposure were collected with a 2000x1336 detector, using a source voltage of between 80 and 140 kV. No filtration was used, and the scan provided a reconstructed dataset with 0.8 – 1.4 μm voxels.

The pteropod shells were segmented in Avizo 9.0.0. and surface files exported as .wrl. The files were subsequently edited in Meshlab 1.3.3. Laplacian smoothing was applied and Quadric Edge collapse Decimation used, reducing the polygon count by approximately a factor of 10. Files were saved as .ply and u3d for viewing as three dimensional PDFs.

SYSTEMATICS (AWJ)

Phylum MOLLUSCA Linnaeus, 1758
Class GASTROPODA Cuvier, 1795
Subclass HETEROBRANCHIA Burmeister, 1837
Superorder PTEROPODA Cuvier, 1804
Order THECOSOMATA de Blainville, 1824
Suborder EUTHECOSOMATA Meisenheimer, 1905
Superfamily LIMACINOIDEA Gray, 1847
Family LIMACINIDAE Gray, 1847
Genus ALTASPIRATELLA Korobkov, 1966 (= *Plotophysops* Curry, 1982)

Type species. *"Limacina elongatoides"* [*sic*] (Aldrich), by original designation of Korobkov (1966, p. 74) = *Physa elongatoidea* Aldrich, 1887 = *Altaspiratella elongatoidea* (Aldrich, 1887) (Eocene, early Ypresian, Wilcox Group, Hatchetigbee Formation, Bashi Member; Zone NP 10).

Altaspiratella bearnensis (Curry, 1982)
Figure 2.1-2

*v   1982   *Plotophysops bearnensis* Curry, p. 40, pl. 1, figure 9a-c.

v.   (1986)   *Spiratella tutelina* Curr. – Merle, p. 43 (*non* Curry).

v.   1990b   *Altaspiratella bearnensis* (Curry 1981) – Janssen, p. 68.

?   1992   *Altaspiratella bearnensis* (Curry) – Hodgkinson et al., p. 13, pl. 1, figures 1-2.

·   (1996)   *Altaspiratella bearnensis* (Curry, 1981) – Kunz, p. 164, pl. 30, figures 1-3.

v.   2010   *Altaspiratella bearnensis* (Curry, 1982) – Cahuzac and Janssen, p. 24, pl. 2, figures 1-4, pl. 3, figure 1.

v.   2013   *Altaspiratella bearnensis* – King et al., p. 192, 193.

Material examined. TDP 12.28.1, 66-76 cm, depth 90.91-91.01 m below surface, composite depth 148.91-149.01 m; RGM 777374 (1 specimen, Figure 2.1-2, H = 1.36, W = 0.80 mm).

Description. Only available specimen with high conical shell, 1.7 times higher than wide, and apical angle of *c*. 40°. Four and a half slightly convex and comparatively high whorls, regularly increasing in diameter and separated by incised, oblique suture. Whorls attach below periphery of preceding whorl. Specimen incomplete, last whorl missing, in shell preservation, but filled with pyrite.

Discussion. Two closely resembling *Altaspiratella* species are currently known. *Altaspiratella elongatoidea* (Aldrich, 1887) occurred during the earliest

FIGURE 2. *Altaspiratella bearnensis* (Curry, 1982); RGM 777374; 1: apical view, 2: apertural view. Bar equals 100 *µ*m.

Eocene (Ypresian, nannoplankton Zones NP 9 and 10) of the USA (Hodgkinson et al., 1992; Janssen et al., 2016); *A. bearnensis* (Curry, 1982), introduced from the Ypresian (zone NP 12/13) of SW France, is also known from the USA (with some

doubt) in rocks of middle Eocene, Lutetian age (Zone NP 15). These two species differ only very slightly in the proportions of their early whorls. Of *A. elongatoidea* no specimens preserving apertural structures are known, so there might be differences in that respect as well.

In the single available specimen from Tanzania apertural structures are missing, and its apical whorls take a position in between the two known species mentioned above. This could be an indication that these two taxa represent a single, long-ranging species. However, as long as apertural structures cannot be compared it seems better to keep them apart and the one available Tanzanian specimen is here considered, for the time being, to be the youngest representative of the *A. elongatoidea - A. bearnensis* lineage. The specimen extends the vertical range to the Priabonian (Zones P 16-17, NP 19-20; Nicholas et al., 2006, figure 16).

Genus HELICONOIDES d'Orbigny, 1835

Type species. *Atlanta inflata* d'Orbigny, 1834, by subsequent designation of Herrmannsen (1846, p. 514) = *Heliconoides inflatus* (d'Orbigny, 1834) (Recent).

Heliconoides nikkieae sp. nov.
Figures 3.1-5, 4

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Type material. Holotype RGM 777415a (Figure 3.1); paratypes1-2, RGM 777415b-c (Figure 3.3, 3.5) from the type locality. Kilwa Group, Pande Formation (upper Eocene, Priabonian), Zones P 18 and NP 21; paratype 3, RGM 777 381 (Figures 3, 4), from TDP 17.21.1, 9-20 cm, Kilwa Group, Pande Formation (early Oligocene, Rupelian), biozones P18 and NP 21.

Additional specimens. TDP 11 (2 specimens), 12 (1 specimen) and 17 (49 specimens, some of which with a query because of poor preservation) (Tables 1-3).

Type locality. Stakishari (Tanzania, Kilwa region), cored borehole TDP 17, sample 17.36.1, 10-25 cm, 104.00-104.10 m below surface, composite depth 116.00-116.10 m.

Etymology. Named after Nikkie Elert, the author's second granddaughter. At age six she is, in many respects, more up-grown than many grown-ups. *Heliconoides* gender masculine (ICZN 1992, art. 30.1.4.4).

Diagnosis. Very small limacinid of 2.5 whorls in low-conical spiral, about as high as wide, with large aperture, apertural margin externally thickened and internally doubled in some specimens (Figure 3.2),

FIGURE 3. *Heliconoides nikkieae* sp. nov.; 1: **Holotype**, RGM 777415a, apertural view; 2: apertural view, specimen lost; 3: **paratype 1**, RGM 777415b, umbilical view; 4: **paratype 3**, RGM 777 381, umbilical view; 5: **paratype 2,** RGM 777415c, apical view. Figure 3-1, -2, -3 and -5 from the type locality, TDP 17.36.1, 10-25 cm; Figure 3-4 from TDP 17.21.1, 9-20 cm. Bar equals 100 *μ*m.

FIGURE 4. *Heliconoides nikkieae* sp. nov.; **holotype**, RGM 777415a, 3dPDF. For animation see: http://palaeo-electronica.org/content/2017/2024-pteropoda-from-tanzania.

basal margin with denticle. Apertural margin preceded by about 10 fine, margin parallel riblets.

Description. Strikingly small limacinid of 2.5 whorls, height/width-ratio variable between *c.* 1.19 (holotype H = 0.62, W = 0.52 mm, Figure 3.1) and 0.89 (e.g., H = 0.50, W = 0.56 mm, Figure 3.2), with depressed, low conical spire and distinct, incised suture. Shell surface smooth and shiny, growth lines invisible. Last whorl large, occupying almost entire shell height. Aperture relatively large, slightly higher than wide to almost circular, occupying 4/5th of entire shell height. Apertural margin externally thickened by narrow ridge, running all around margin, flexuous at base of shell, reaching umbilicus, internally (Figure 3.2) in some specimens. Protruding denticle on basal part of margin (Figure 3.3-4). Marginal thickening preceded by

about 10 fine, margin parallel orthocline riblets. Shell base regularly rounded, umbilicus very narrow, *c.* 1/20th of shell diameter.

Discussion. In general shape the new species resembles somewhat the holotype of *Limacina wechesensis* Hodgkinson (1992, p. 21, pl. 5, figures 4-6) from the Lutetian of Texas, USA, but that species has one whorl more and reaches double the size of *H. nikkieae*, does not have the apertural structures of that species and its umbilicus is considerably wider.

Size and apertural structures of the new species form a unique combination and cannot be compared to any limacinid currently known. The holotype was chosen from the sample with most specimens (13) of Priabonian age, but the species continues, in low numbers, well into the Rupelian part of the TDP 17 section.

Genus *LIMACINA* Bosc, 1817

Type species. *Clio helicina* Phipps, 1774 by monotypy = *Limacina helicina* (Phipps, 1774) (Recent).

Limacina robusta (Eames, 1952)
Figures 5, 6

*1952 *Aplexa robusta* Eames, p. 152, pl. 6, figure 149.

Type material. Holotype (Figure 6) in the Natural History Museum, London, NHMUK BM 68457, presented by the Burma Oil Co. Ltd., March 1950; Eames (1952) furthermore recorded 19 paratypes from the type locality.

Type locality. Rahki Nala (Pakistan, western Punjab), 255' above base, local zone 9. Lower Chocolate Clays; according to Afzal et al. (2009, p. 20) nowadays indicated as Kirthar Formation of late Lutetian - Priabonian age.

TABLE 1. Distribution of pteropod species in core TDP 11.

TDP Core section	Depth interval (cm)	Subsurface depth (m)	Composite depth (m)	*Heliconoides nikkieae*	*Limacina robusta*	*Limacina timi*	*Bovicornu* aff. *eocenense*
11.26.2	64-74	82.14	98.14	1	-	-	-
11.32.1	33-40	89.63	109.63	-	1	-	-
11.32.3	64-72	91.94	111.94	1	-	1	-
11.33.2	74-84	94.04	114.04	-	-	-	2

TABLE 2. Distribution of pteropod species in core TDP 12.

TDP Core section	Depth interval (cm)	Subsurface depth (m)	Composite depth (m)	*Altaspiratella bearnensis*	*Heliconoides nikkieae*	*Limacina robusta*	*Limacina timi*	*Limacina* sp. 2	Limacinidae indet.	*Bovicornu* aff. *eocenense*
12.11.4	20-26	38.20	96.20	-	-	-	1	-	-	-
12.12.1	23-31	38.23	96.23	-	1	-	-	-	-	-
12.14.1	47-48,5	44.47	102.47	-	-	-	-	-	-	2
12.14.1	51-53	44.51	102.51	-	-	-	-	-	-	1
12.14.1	56-58	44.56	102.56	-	-	-	-	-	-	1
12.14.3	23-31	46.23	104.23	-	-	-	-	-	-	1
12.18.3	65-76	58.65	116.65	-	-	-	1	-	-	-
12.19.1	22-34	59.22	117.22	-	-	-	1	-	-	-
12.21.1	37-48	65.37	123.37	-	-	-	1	-	-	-
12.23.3	89-96	73.89	131.89	-	-	-	-	-	-	1
12.24.3	0-10	76.30	134.30	-	-	-	-	-	1?	-
12.26.2	54-62	81.79	139.79	-	-	-	1	-	-	-
12.27.1	35-45	89,60	147,60	-	-	1	1	1	-	-
12.28.1	66-76	90.91	148.91	1	-	-	-	-	-	2
12.29.1	25-35	91.90	149.90	-	-	-	1	-	-	-
12.29.2	20-30	92.85	150.75	-	-	-	-	-	-	

Material examined. TDP 11 (1 specimen), TDP 12 (1 specimen), TDP 17 (16 specimens, all from the Priabonian), see Tables 1-3 for specification.

Description. Most available specimens are juveniles and most in pyritic internal mould preservation. Largest and best preserved specimen (Figure 5) higher than wide (H = 0.94, W = 0.72 mm) with four convex whorls rapidly increasing in diameter. Aperture large, oval, occupying more than half shell height. Base of shell regularly rounded with narrow umbilicus.

Discussion. Most of the available specimens are poorly preserved and juvenile, but the illustrated Tanzanian specimen (Figure 5) has a shell height of 0.94 mm, whereas the holotype of *Limacina robusta* has a shell height of 0.75 mm. Some of the smaller specimens have a somewhat wider apical angle than the illustrated specimen. In spite of these small differences the Tanzanian specimens are thought to represent the same species as the Pakistanian *L. robusta*, which has a comparable age and was described from a pre-eastern-Paratethys locality under influence of the Indian Ocean.

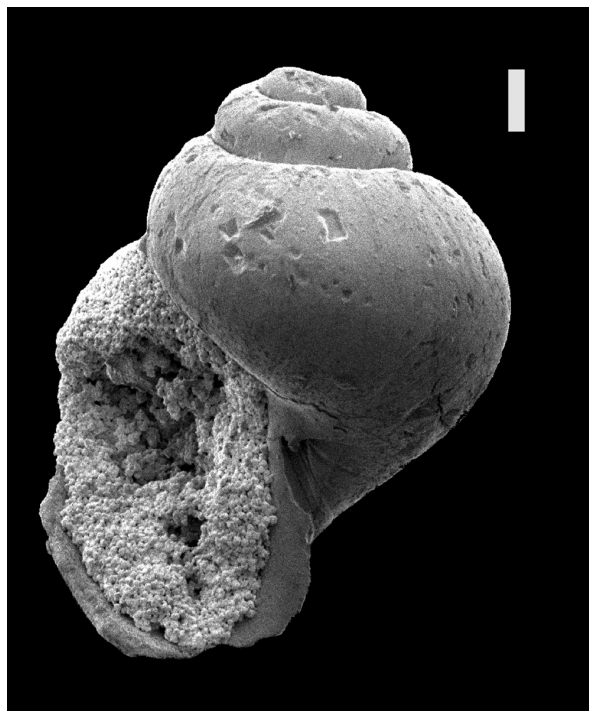Initially the Tanzanian specimens were thought to represent *Limacina conica* (von Koenen, 1892, p. 994, pl. 62, figures 5-6), a species described from the "early Oligocene" of two localities (Atzendorf, Unseburg) in the eastern part of Germany. However, specimens from Atzendorf (NP 21 interval), made available by Arnold Müller (Leipzig, Germany) differ in shape and reach far larger dimensions. Their apical angle is smaller, the whorls are more convex and the aperture remains smaller than half shell height.

Several species described by Hodgkinson et al. (1992), from the Paleogene of the United States also resemble the Tanzanian shells. Especially similar is *Limacina smithvillensis* Hodgkinson (*in* Hodgkinson et al., 1992, p. 19, pl. 3, figure 16) from the Lutetian of Texas. However, that species reaches a shell height of 1.5 mm, has less convex whorls, a wider apical angle, and its aperture occupies just half the shell height. Finally, that species is considerably older (Lutetian, NP 15) than the Priabonian (NP 21) specimens from Tanzania. At first glance also *L. stenzeli* Garvie (*in* Hodgkinson et al., 1992, p. 19, pl. 4, figure 1) from the NP13-14 interval (Ypresian) of Texas is similar. However, that species should be included in the genus *Heliconoides*, because of its reinforced apertural margin.

TABLE 3. Distribution of pteropod species in core TDP 17 (question mark denotes poorly preserved specimens).

TDP Core section	Depth interval (cm)	Subsurface depth (m)	Composite depth (m)	*Heliconoides nikkieae*	*Limacina robusta*	*Limacina tanzaniaensis*	*Limacina timi*	*Limacina* sp. 1	*Limacina* sp. 2	Limacinidae indet.	*Bovicornu* aff. *eocenense*
17.15.1	50-63	47.95	47.95	2	-	-	-	-	-	-	-
17.17.2	0-14	54.45	54.45	2?	-	-	-	-	-	-	-
17.18.3	10-25	58.55	58.55	2	-	-	1	-	-	-	-
17.21.2	9-20	62.87	62.87	1	-	-	-	-	-	-	-
17.23.2	0-10	66.57	66.57	-	-	-	1?	-	-	-	-
17.23.3	0-13	67.54	67.5	2?	-	-	-	-	-	-	-
17.23.3	99-105	68.56	68.56	2	-	-	-	-	-	-	-
17.24.1	20-35	68.30	68.30	5	-	-	-	-	-	-	-
17.24.2	0-15	69.10	69.10	-	-	-	1	-	-	-	-
17.25.1	0-15	71,40	71.40	2	-	-	-	-	1	-	-
17.25.1	50-60	71.90	71.90	1	-	-	-	-	-	-	-
17.25.2	48-58	72.88	72.88	1	-	-	1	-	-	-	-
17.26.3	10-25	77.90	77.90	2	-	-	-	-	-	-	-
17.31.1	20-35	89.10	89.10	2?	-	-	-	-	-	-	-
17.31.2	0-15	89.90	89.90	1	-	-	-	-	-	-	-
17.31.3	0-15	90.90	90.90	3?	-	-	-	-	-	-	-
17.31.4	0-12	91.90	91.90	1?	-	-	-	-	-	-	-
17.32.1	10-25	92.00	92.00	2?	-	-	-	-	-	-	-
17.32.2	0-15	92.90	92.90	3	-	-	-	-	1	1?	1
17.32.4	14-20	95.04	95.04	1	-	-	-	-	-	-	1
17.33.1	3-18	95.93	95.93	1	-	-	-	-	-	-	2
17.33.3	0-15	97.90	97.90	3	-	-	1	-	-	-	1
17.34.1	0-7	98.90	98.90	4?		-	2	-	-	3?	1
17.34.2	91-99	100.81	100.81	-	-	-	-	-	-	-	2
17.36.1	0-5	103.90	115.90	1	-	-	1	-	2?	1?	2
17.36.1	5-13	103.95	115.95	-	-	1	-	-	-	-	-
17.36.1	10-25	104.00	116.00	11	-	7	-	-	-	-	3
17.36.2	52-59	105.42	117.42	-	1	-	-	-	-	3?	-
17.36.2	80-95	105.70	117.70	3+5?	2	1	2?	-	-	2?	-
17.37.1	0-13	106.90	118.90	-	6	-	-	5	-	-	-
17.37.1	32-47	107.22	119.22	-	1	-	-	-	-	-	-
17.38.1	25-35	110.15	122.15	-	-	5	1	-	-	-	-
17.38.2	22-29	111.12	123.12	-	1	2	-	-	—	-	-
	62-70	113.52	123.52	-	-	-	1	-	-	-	-
17.41.1	8-18	119.48	131.48	-	-	1	2?	-	-	-	-
17.41.3	0-15	121.40	133.40	-	1	1	-	-	-	-	-

FIGURE 5. *Limacina robusta* (Eames, 195); RGM 777423b, apertural view. Bar equals 100 *μ*m.

FIGURE 6. *Limacina robusta* (Eames, 1952), **Holotype,** Natural History Museum, London BM 68457. Rahki Nala (Pakistan, western Punjab); Kirthar Formation, Lower Chocolate Clays (late Lutetian – Priabonian); 1: apical, 2: apertural, 3: lateral view. Bar equals 100 *μ*m.

Limacina tanzaniaensis sp. nov.
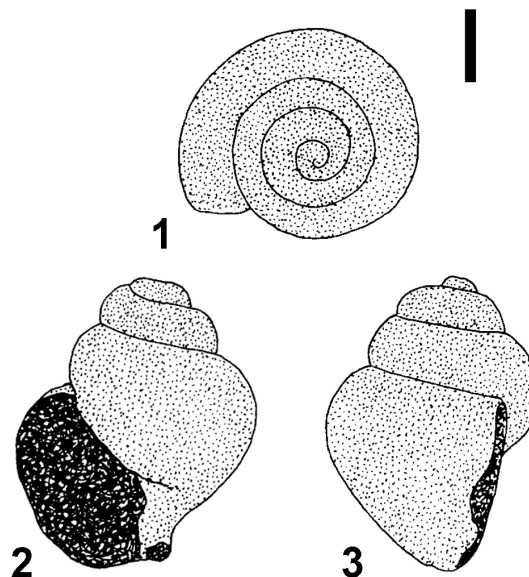Figures 7.1-4, 8

zoobank.org/8C1AB54C-4643-4D30-9455-97C37B793992

Type material. Holotype (Figure 7.1) RGM 777428b; paratype 1 (Figure 7.2), RGM 777438; paratypes 2 and 3 (Figure 7.3-4) RGM 777416b-c. Kilwa Group, Pande Formation (Eocene, Priabonian, biozones P 18 and NP 21).

Additional specimens. Fourteen specimens from TDP 17 (Table 3), all from the Priabonian part of the section. Most specimens poorly preserved as pyritic internal moulds.

Type locality. Stakishari (Tanzania, Kilwa region), cored borehole TDP 17, sample 38.2, 22-29 cm, 111.12-111.19 m below surface = 123.12-123.19 m composite depth.

Diagnosis. Spherical limacinid of almost four whorls, apex flattened. Last whorl inflated, 95% of total shell height, aperture *c.* 75% of total shell height, margin simple, base of shell umbilicate.

Description. Limacinid of spherical shape, measurements of holotype H = 0.92, W = 1.00 mm, consisting of 3.75 moderately convex whorls with convex tangent. First two whorls flattened, last whorl very large, inflated, occupying 95% of total shell height. Aperture large, about 75% of total shell height, attaching on (holotype, Figure 7.1) or
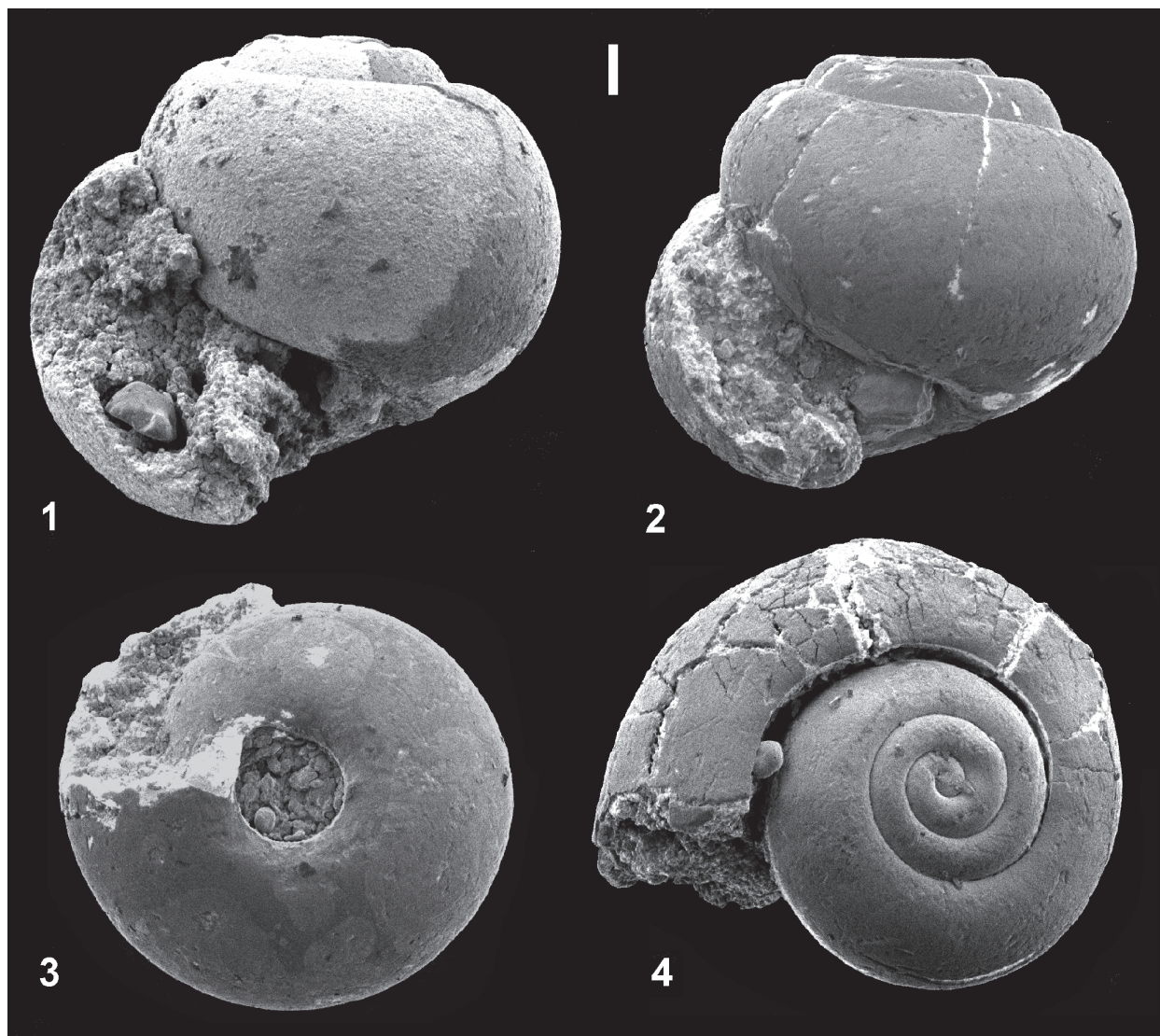
slightly below (paratype 1, Figure 7.2) periphery of penultimate whorl. Apertural margin simple, semi-circular, inner margin and columella invisible as all specimens are in pyritic internal mould preservation. Base of shell regularly rounded, umbilicus present, 20-25% of shell diameter.

Discussion. The available specimens demonstrate variability in height of the apex, in some the initial flattening continues to the third whorl, resulting in an only slightly raised apical shell part. There is some resemblance to the Ypresian species *Limacina heatherae* Hodgkinson *in* Hodgkinson et al. (1992, p. 17, pl. 2, figures 15-18). In that species, however, the whorls attach higher on the foregoing whorl, the aperture is narrower and its umbilicus smaller.

Limacina timi sp. nov.
Figures 9.1-4, 10

zoobank.org/E5DC43EC-4F67-4173-890D-0145DEBEC0B6

Type material. Holotype (Figure 9.1), RGM 1007748b; paratype 1 (Figure 9.2), RGM777408a, from TDP 17.34.1, 0-7 cm, 98.90-98.97 m below surface and composite depth; paratype 2 (Figure 9.3), RGM 777408b, TDP 17.34.1, 0-7 cm; paratype 3 (Figure 9.4), RGM 777414m TDP 17.36.1, 0-5 cm. Kilwa Group, Pande Formation (Eocene,

FIGURE 7. *Limacina tanzaniaensis* sp. nov. 1: **Holotype**, apertural view, RGM 777428b, TDP 17.38.2, 22-29 cm; 2: **paratype 1,** apertural view, RGM 777438, TDP 17.36.2, 80-95 cm; 3: **paratype 2**, umbilical view, RGM 777416b, TDP 17.36.1, 10-25 cm; 4: **paratype 3**, apical view, RGM 777416c, same data as 3. Bar equals 100 µm.

Priabonian); planktic foraminefera zone P 16-17, calcareous nannoplankton zone NP 19-20.

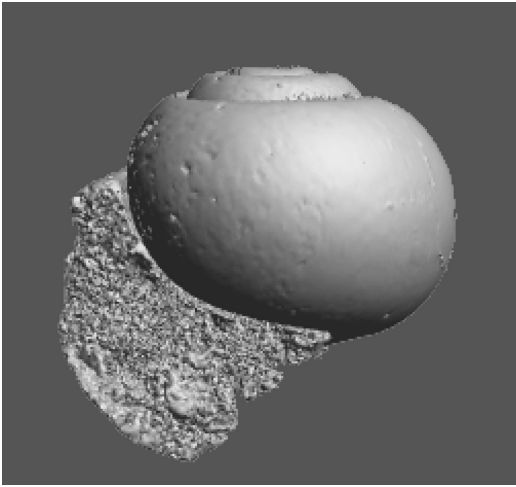**Additional specimens.** Boreholes TDP 11, 12 and 17: 15 specimens (see Tables 1 and 3).

Type locality. South of Stakishari, Tanzania, Kilwa Region, cored borehole TDP 12, coordinates UTM 37L 560222-8981309, sample TDP 12, sample 27.1, 35-45 cm = 89.60-89.70 m below surface = 147.60-147.70 m composite depth.

Etymology. Named after Tim Janssen, the author's six year old second grandson. For him life is nonstop fun. Keep it that way, my friend!
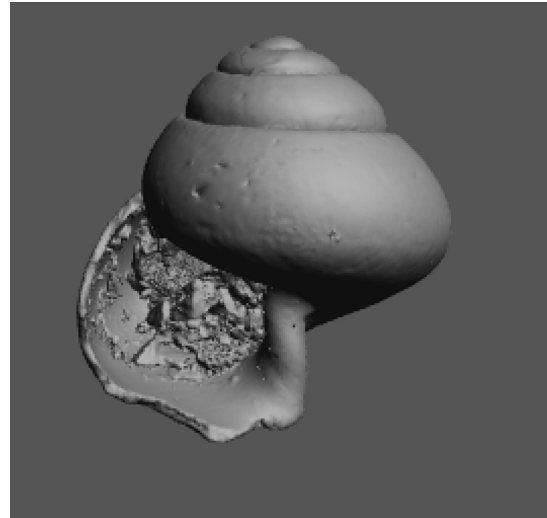
Diagnosis. Small limacinid of 3.75 whorls, slightly higher than wide. Whorls rounded angular in juve-niles, more regularly rounded in adults. Aperture lunate, somewhat higher than half shell height. Base imperforate.

Description. Holotype (H = 1.04, W = 1.00 mm) a small, regularly coiled, conical limacinid of 3.75 slightly convex whorls, separated by incised suture. Last whorl occupying 80% of shell height, slightly angular at periphery. Shell surface smooth, growth lines invisible. Aperture large, lunate, 65% of shell height, no apertural reinforcements pres-ent. Columellar side of aperture smooth, slightly concave internally, straight externally. Base of shell regularly convex, umbilicus absent in holotype, extremely small or absent in juveniles. Angularity

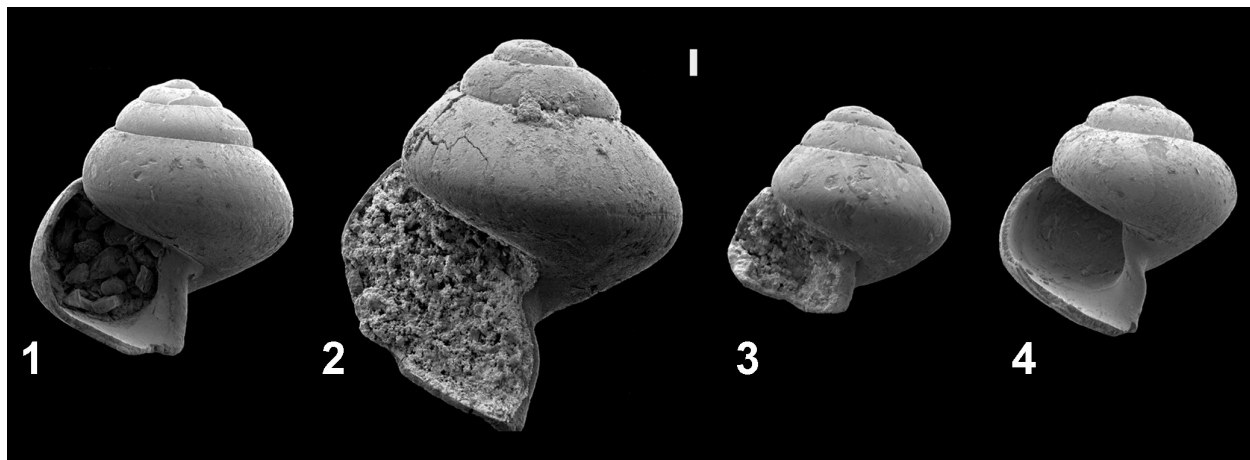**FIGURE 8.** *Limacina tanzaniaensis* sp. nov.; **holotype**, apertural view, RGM 777428b, 3dPDF. For animation see: http://palaeo-electronica.org/content/2017/2024-pteropoda-from-tanzania.

FIGURE 10. *Limacina timi* sp. nov.; **holotype**, RGM 1007748b, 3dPDF. For animation see: http://palaeo-electronica.org/content/2017/2024-pteropoda-from-tanzania.

of whorls more clearly developed in juvenile specimens, resembling a rounded keel, but covered by following whorls attaching at the place of angularity, almost disappeared in adults. Juvenile specimens wider than high, in some of these the keel is rather strong and the apical angle wider (RGM 777425).

Discussion. The angularity of especially juvenile specimens is not very clearly visible in the SEM images given here in Figure 9.3-4, but under light microscope, with illumination from left above it cannot be overlooked.

Limacina timi resembles somewhat the Ypresian species *L. gormani* (Curry, 1982) described

from the Marnes de Gan Formation, of Gan, SW France (Curry, 1982; Cahuzac and Janssen, 2010). The same species or a closely related form was also described from the Stone City and Cook Mountain formations (Lutetian/Bartonian) of Texas, USA (Hodgkinson et al., 1992, p. 19, pl. 3, figures 14-15) as *Limacina pygmaea* (*non* Lamarck, 1805), in which also the juvenile whorls are angular and the base imperforate. The adult shell, however, reaches one and a half times the size of *L. timi*, has a different, more spherical shape and a distinctly wider apical angle. Subsutural crests (Cahuzac

FIGURE 9. *Limacina timi* sp. nov.; 1: **holotype**, RGM 1007748b; 2: **paratype 1**, RGM 777408a; 3: **paratype 2**, RGM 777408b; 4: **paratype 3**, RGM 777414 m; . Apertural views. Bar equals 100 μm.

and Janssen, 2010, pl. 11, figure 2) as seen in *L. gormani* are not present in *L. timi*.

Adult specimens of *Limacina timi* also resemble *Heliconoides nemoris* (Curry, 1965), described from the Bartonian of the UK and also recorded from the Priabonian of Biarritz, SW France by Curry (1982) and Cahuzac and Janssen (2010). That species belongs to the genus *Heliconoides* because of its apertural reinforcements that are apparently absent in *L. timi,* but also its apex is flattened and juvenile specimens have no angular periphery. *Limacina timi* straddles the Eocene/Oligocene boundary.

Limacina sp. 1
Figure 11.1-2

Material examined. Five specimens, all from the same sample TDP 17.37.1, 0-13 cm; 106.90-107.03 m below surface, 118.90-119.03 composite depth; RGM 777440a-c (Table 3).
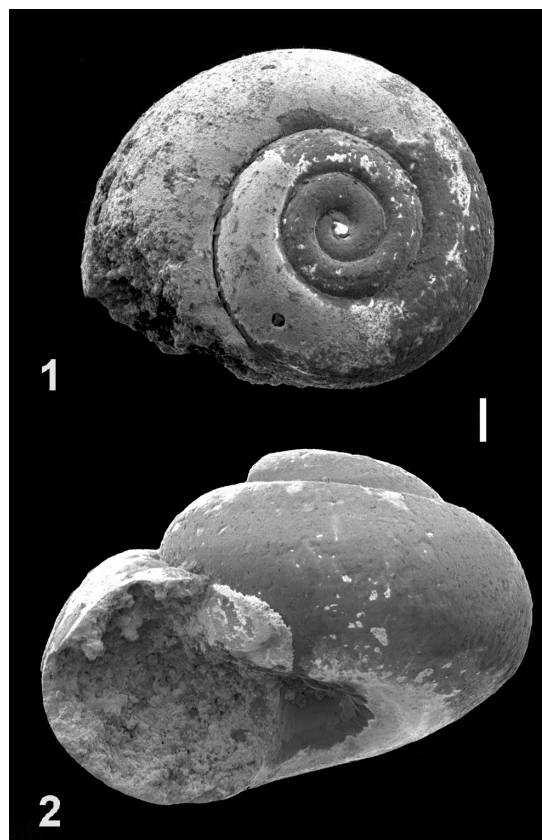
Description. Low conical limacinid of 3.75 moderately convex whorls attaching on periphery of foregoing whorls. Aperture semicircular, slightly more than half shell height, Base regularly rounded, umbilicus *c.* 1/6th of shell diameter.

Discussion. Three of the available specimens are juveniles in poor preservation. In specimen RGM 777440b (Figure 11.2) the first whorl is missing. The two more adult specimens show a striking resemblance with a limacinid illustrated by Lokno and Kumar (2008, figure 3-2) from the Upper Disang Formation (Bartonian - Priabonian) of the Phek District, south-central Nagaland (Assam - Arakan Basin), northeastern India, indicated by these authors as "Limacinidae type A." As these specimens were recorded from Indian Ocean Basin rocks of more or less similar age they could very well represent the same species as the Tanzanian ones. However, the material is insufficient for a reliable identification. Lokno and Kumar compared their specimens with "*Limacina pygmaea,*" as illustrated by Hodgkinson et al. (1992, pl. 3, figures 14-15), correctly stating that that name "most certainly is incorrect," as Hodgkinson et al.'s species seems to be closely related to *L. gormani* (Curry, 1982) (see above) and not to *Limacina pygmaea*.

Limacina sp. 2
Figure 12.1-4

Material examined. One specimen from TDP 12 (Table 2); 4 poorly preserved and presumably juvenile specimens in pyritic internal mould preservation, from TDP 17 (Table 3).
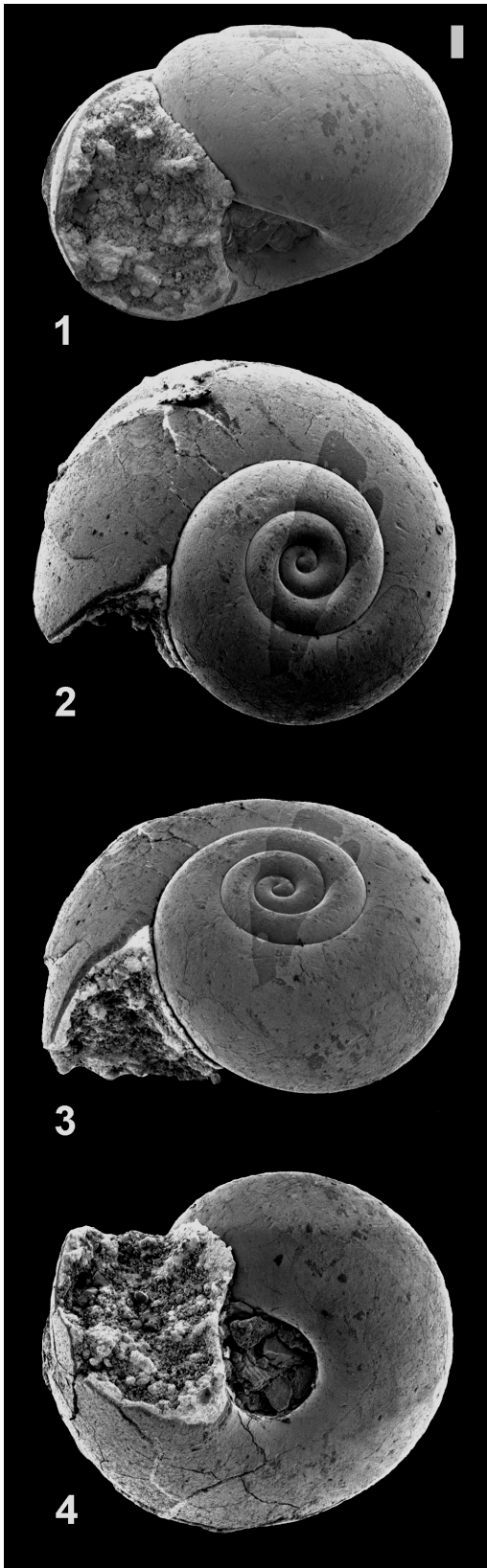

FIGURE 11. *Limacina* sp. 1. 1: RGM 777440c; apical view; 2: RGM 777440b; apertural view. Bar equals 100 *μ*m.

Description. Limacinid of very low conical shape with almost flat, slightly raised, or slightly concave apical plane. Width of illustrated specimen 1.20 mm, height 0.86 mm. Whorls 3.75, regularly increasing in diameter. Aperture semicircular, occupying *c.* 80% or more of total shell height, reaching to far beyond base of preceding whorl. Apertural structures absent or not preserved. The apparently present groove along the apertural margin, as vsible in Figure 13.2-3, is considered to be caused by damage of the mould. Base perforated by umbilicus of 1/5th to 1/7th of shell diameter.
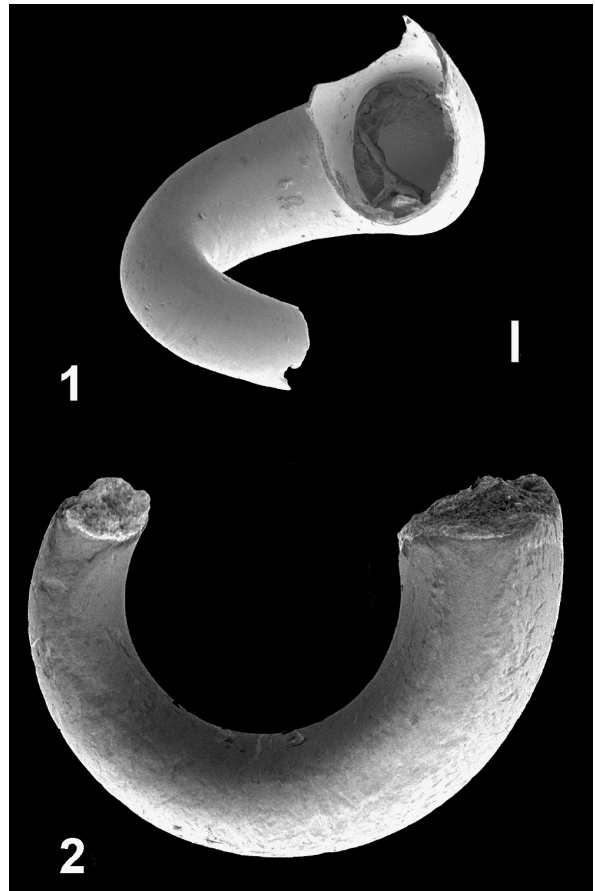
Discussion. Several limacinids with an almost planorboid shell shape are known from the Eocene-Oligocene interval in Europe, Asia and the USA. Some of these are characterised by having a slightly concave apical plane, or, in other cases, by an irregular development of early whorls. In the present specimens, however, the whorls are in a regular spiral and the apical plane is a bit raised, with the first 1.5 whorls flattened (Figure 12.3).

Very similar is a species from the early Oligocene of Japan, described as *Limacina karasawai*

FIGURE 13. *Bovicornu* aff. *eocenense* Meyer, 1886; 1: RGM 777370, apertural view; 2: RGM 1007784, basal view. Bar equals 100 *µ*m.

Ando (2011, p. 248, figures 3.1-2. This species was said to have three quarters of a whorl more than the Tanzanian specimen illustrated here, but we fail to see that from Ando's photographs. Also closely similar is *Limacina canadaensis* Hodgkinson (*in* Hodgkinson et al., 1992, p. 16, pl. 2, figures 4-6), but its last whorl seems to be relatively lower. This species was collected from downhole contaminated cutting samples and could be anything between early Eocene and early Oligocene. An occurrence of similar age (earliest Oligocene) was described from the North Sea Basin and is also known from contemporaneous rocks (base of Viborg Formation) in Jylland, Denmark, as *Limacina mariae* Janssen (1989, p. 111, pl. 4, figures 2-5), but that species always has a concave apical spiral, has a somewhat wider umbilicus and reaches to over 2 mm shell width. Finally, as yet unpublished similar material is available from the Eocene - Oligocene interval in the NE United States and from the eastern part of Germany.

FIGURE 12. *Limacina* sp. 2, RGM 777373,; 1: apertural, 2: apical, 3: oblique apical, and 4: umbilical views. Bar equals 100 *µ*m.

A reliable interpretation of all these forms depends on a larger material for comparisons and therefore the present specimens, apart from the illustrated specimen in poor condition, are left in open nomenclature.

Limacinidae indet.

Material examined. One specimen from TDP 12.24.3, 0-10 cm; 10 specimens from TDP 17 (see Table 3).

Description. These specimens are in internal pyritic mould preservation, more or less strongly deteriorated and cannot be identified any further.

Superfamily CAVOLINIOIDEA Gray, 1850 (1815)
[= Hyalinea Rafinesque, 1815]
Family CRESEIDAE Rampal, 1973
Genus BOVICORNU Meyer, 1886

Type species. *Bovicornu eocenense* Meyer, 1886, by monotypy (early Oligocene, USA).

Discussion. Shortly after its introduction by Meyer (1886) the validity of the genus *Bovicornu* was denied by Dall (1892, p. 302), who considered both species introduced in that genus by Meyer (1886, 1887) to belong to the caecid (benthic) genus *Meioceras* Carpenter, 1858. Dall's point of view was followed, with doubts, by Cossmann (1912, p. 154-155), but rejected by later authors (Collins, 1934, p. 212; van Winkle Palmer, 1947, p. 464; Hodgkinson et al., 1992, p. 24). Indeed, in *Meioceras* the shell wall is considerably thicker and its protoconch is utterly different, whereas in *Bovicornu* the shell is thin-walled and the larval parts agree with species of the pteropod genus *Creseis*. Zilch (1959, p. 49) followed Collins and included *Bovicornu* with a query in the cavoliniid pteropods, considering it a possible synonym of *Euchilotheca* Fischer, 1882, which is also a creseid genus, but its type species, *E. succincta* (Defrance, 1828), shows only very faint traces of spiralisation. We agree with Hodgkinson et al. (1992) that *Bovicornu* should be considered an independent genus in Creseidae.

Bovicornu species demonstrate a certain resemblance with *Hameconia edmundi* Janssen, 2008, described from the late Oligocene (Chattian) of SW France. In that species the bilaterally symmetrical shell has a curvature of *c.* 180°, but it is curved in one plain, not in a spatial spiral. The curvature is dorso-ventral, as is clear by the presence of lateral carinae. Its larval stage differs from *Bovicornu* in having separate protoconchs 1 and 2. Janssen and Maxwell (*in* Janssen, 1995, p. 164), Janssen (2008, p. 160) and Cahuzac and Janssen

(2010, p. 111) included the genus *Hameconia* in the Sphaerocinidae family.

Bovicornu aff. *eocenense* Meyer, 1886
Figures 13.1-2

cf 1886	*Bovicornu eocenense* Meyer, p. 79, pl. 3, figure 12 (not figure 2).
cf 1892	*Meioceras eocenense* (Meyer) – Dall, p. 302.
cf 1912	*Bovicornu eocænense* [*sic*] Meyer – Cossmann, p. 155.
cf 1934	*Bovicornu eocenense* Meyer – Collins, p. 212, pl.9, figure 3, pl. 13, figure 5.
cf 1959	*Bovicornu eocenense* O. Meyer – Zilch, p. 49, figure 164.
cf 1992	*Bovicornu eocenense* Meyer – Hodgkinson et al., p. 24, pl. 7, figures 9-10 (with additional synonymy).

Type material. Holotype (H = 2,8, W = 0,7 mm) United States Natural Museum (Smithsonian Institution) nr. 644596.

Type locality. Red Bluff, USGS locality 5264, Mississippi, USA (Red Bluff Clay; Oligocene, Rupelian, NP 21).

Material examined. Only fragments were found, 2 from TDP 11, 9 from TDP 12, and 11 from TDP 17 (see Tables 1-3 for details).

Description. Spatially spiralised tube with free volutions. Transverse section of tube circular, no surface ornamentation or growth lines visible. Only smaller fragments are available among which no complete aperture or protoconch. Diameter of tube doubles in about half a volution.

Discussion. Two species of the genus *Bovicornu* are currently known and both are exclusively recorded from the USA. The older one of these, *B. gracile* Meyer, 1887 (p. 9, pl. 2, figure 17), of the Moodys Branch Formation, Texas, has an age of Bartonian (NP 17). The other species, *B. eocenense* Meyer, 1886 (p. 79, pl. 3, figure 12), from the Red Bluff Formation of Mississippi, USA occurred during the Priabonian and early Rupelian (NP19-21) (Hodgkinson et al., 1992, figure 3). In both species the shell is creseid, but instead of being straight or slightly curved, as in *Creseis* species, the tube demonstrates clear twisting in a wide spatial spiral that was said to be stronger in *B. gracile*. Hodgkinson et al. (1992), however, collected numerous specimens at both type localities and noted that in many specimens of both species the twisting is stronger and that the species cannot be distinguished on the degree of twisting. There is, however, a clear difference in protoconch morphology: an inflated bulb in *B. eocenense* and a more cylindrical shape in *B. gracile*. The holotypes of

FIGURE 14. Holotypes of *Bovicornu eocenense* Meyer, 1886 (1, 2) and *B. gracile* Meyer, 1887 (3, 4). Shell height of 1 = 2.8 mm, of 2 = 2.7 mm; 2 and 4 are magnifications of 1 and 3, respectively. Photographs after Hodgkinson et al. (1992, pl. 7, figures 9-12).

both species were re-illustrated in Hodgkinson et al. (1992, pl. 7, figures 9-10 and 11-12), reproduced herein as Figure 14.1-4.

Although the few larger fragments from Tanzania seem to indicate a considerably stronger spirally twisted shell than in either of the holotypes it is preferred to indicate the Tanzanian species as related to the younger of the two American species and is indicated here as *Bovicornu* aff. *eocenense*. Once specimens preserving their protoconch become available this position might be revised.

RESULTS

The number of specimens per species/per sample are specified in Tables 1-3. Vertical ranges of the species in the three Tanzanian sections are shown together in Figure 15.
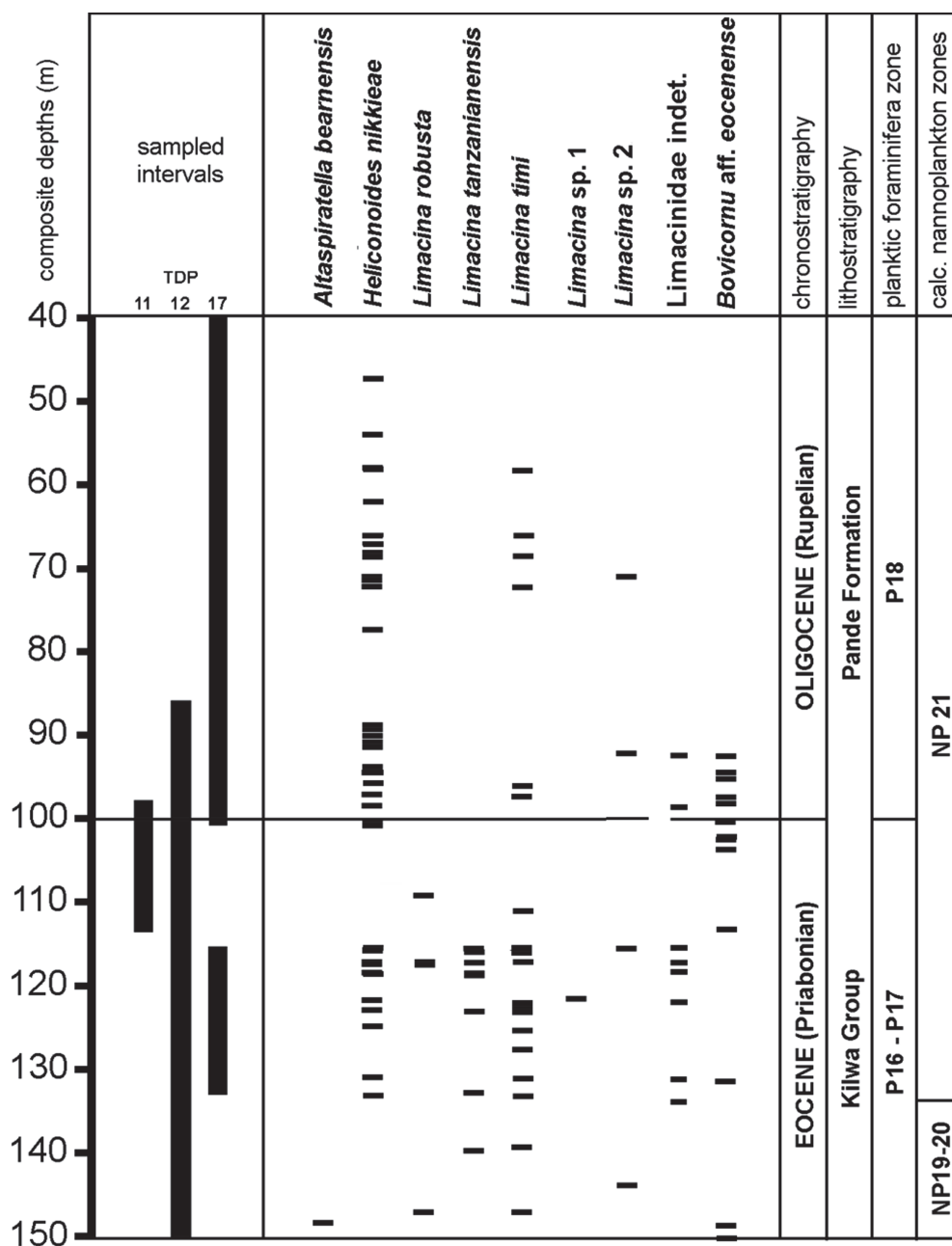
Eight pteropod species are recognised, seven of them belonging to the Limacinidae and one (*Bovicornu*) to the Creseidae. Three of the limacinids are represented by a single or very few specimens only. Three species could only be identified in open nomenclature. Three of the limacinid species are described as new.

The stratigraphic ranges are remarkable. The two most commonly occurring species, *Heliconoides nikkieae* and *Limacina timi* (both introduced herein), and the less frequently represented *Limacina* sp. 2 occur in comparable numbers both

below and above the EOB and do not seem to be influenced by changing environmental conditions. Two other species, *Limacina robusta* and *L. tanzaniaensis*, on the contrary, disappear some 10 m below the EOB, at a level close to the extinction of the *Turborotalia cerroazulensis*-group of planktic foraminifera and the first oxygen isotope step (Step 1 of Pearson et al., 2008; Lear et al., 2008) although improved sampling could of course extend the ranges up to the EOB or beyond. One species, *Altaspiratella bearnensis*, was found as a single specimen only in one of the lowermost samples. Finally, a single species (*Bovicornu* aff. *eocenense*), is irregularly distributed in the Eocene part of the sections, but disappears in the basal 10 m of the Oligocene. No pteropods are found exclusively in the Oligocene part of the record.

DISCUSSION

The newly described taxa, as well as species recorded in open nomenclature, do not present clues that can be applied in long distance correlations. The present material from Tanzania furthermore originates from a very large area from which Paleogene pteropods have never been recorded previously. From the African continent only a late Eocene occurrence is known from Nigeria (Bende Ameki; Curry, 1965 and Naturalis collection) and some Eocene (Ypresian, Bartonian) material was

FIGURE 15. Range chart of pteropods, combined data of TDP 11, 12 and 17, calibrated to composite depths. Basic stratigraphical data mainly from Pearson et al. (2008, figure 16).

collected from Egypt (Valley of the Kings) by the late Chris King (Naturalis Biodiversity Center collections, unpublished).

The presence of *Altaspiratella bearnensis* is quite unexpected. That species is only known from the Aquitaine Basin in SW France (type locality, Ypresian) and from the southern USA (Ypresian and Lutetian). Its presence in the Tanzanian Priabonian is surprising. The record, however, is based on a single incomplete specimen and better pre-

served material might prove that another species is involved.

The occurrence of *Limacina robusta* is interesting. That species was originally described from Pakistan, a locality under the influence of the Indian Ocean, which is equally the case for the Tanzanian material. If *Limacina* sp. 1 is indeed closely related to or even identical with "Limacinidae type A" as described by Lokho and Kumar (2008) from northern India it similarly represents an

interesting palaeogeographical occurrence on the Indian Ocean.

The creseid species *Bovicornu eocenense* is to date exclusively known from the United States and its vertical distribution includes the Priabonian and the Rupelian transition, which is consistent with its range in the Tanzanian material. However, the Tanzanian material is poorly preserved and better specimens might lead to another specific interpretation.

When compared with previous isotope and microfossil data from the Tanzanian material it may be concluded that three pteropod species (*Heliconoides nikkieae, Limacina timi* and *Limacina* sp. 2) do not show clear response following the drastic climatic cooling at the EOB, but two species (*Limacina robusta* and *L. tanzaniaensis*) seem to disappear close to the cooling related step of the EOT, perhaps indicating a temperature sensitivity if a true disappearance. The last occurrence of these two taxa precedes that of the planktic foraminiferal family Hantkeninidae and the extinction level of the larger benthic foraminifera (Pearson et al., 2008; Wade and Pearson, 2008; Cotton and Pearson, 2011). However, it is similar to the last occurrence of the planktic foraminifera *Turborotalia cerroazulensis* Cole, 1928, and related species (Pearson et al., 2008; Wade and Pearson, 2008). In addition, the nannofossil assemblage has shown an increase in nutrient loving taxa close to the onset of the EOT (Dunkley Jones et al., 2008), suggesting nutrient increase in the water column as a potential contributing factor.

There are currently plans to re-core the EOB of Tanzania with wide diameter boreholes (Pearson and Hudson, 2014). Much larger samples and denser sampling may shed further light on the pteropod record across the EOB in the region.

CONCLUSION

Here we have shown a small but important insight into pteropod fauna from both an under-represented geological time and geographic region. Eight species were recognised , three of which were new. Two of the taxa show an apparent, at least, local extinction close to the first major cooling step of the EOT whilst the others seem unaffected, or have too few occurrences to tell. The occurrences of several taxa are surprising with *Altaspiratella bearnensis,* and *Bovicornu* only previously known from Europe and the USA, and from the USA, respectively. The occurrence of *Limacina robusta*, which is only previously known from Pakistan, suggests an Indo-Pacific connection. This therefore underlines the need for increased studies of Paleogene pteropod occurrences, particularly in regions that may be under-sampled but have good preservation potential. Furthermore it shows the importance of carrying out studies of less conventional micro-fossils on cores generally used for foraminiferal or nannoplankton studies.

ACKNOWLEDGEMENTS

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