THE PALAEOTACHEA COMPLEX (GASTROPODA: PULMONATA) IN THE MIOCENE OF SW GERMANY: A MORPHOMETRIC APPROACH

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Abstract *Gastropods in the Obere Süßwassermolasse ("Upper Freshwater Molasse") of Germany formerly referred to the genus Cepaea include five species:* Palaeotachea dentula *(MN 5),* P. silvana *(MN 5),* P. renevieri *(MN 5) as well as* P. turonensis *(MN 5/6),* P. sylvestrina *(MN 7- MN 9-?) and* P. elevata *(MN7). Their taxonomic status is discussed in this study.* Palaeotachea sylvestrina *and* P. silvana *can be differentiated morphologically using statistical methods. The previously recognized subspecies* Palaeotachea sylvestrina sylvestrina *(Schlotheim, 1820),* P. sylvestrina gottschicki *(Wenz, 1919) and* P. sylvestrina geniculata *(Sandberger, 1872) are no longer maintained in the species* Palaeotachea sylvestrina *(Schlotheim, 1820). Likewise, a subspecies* P. silvana malleolata *(Sandberger, 1875) is no longer recognized in the species* Palaeotachea silvana *(Klein, 1853). The taxon* Palaeotachea renevieri elevata *(Berz & Jooss, 1927) is elevated to species rank. The attempt to solve the proposed relationship of* Palaeotachea turonensis *with the* Pliocene Frechenia *and the Recent* Eobania vermiculata *using morphometric features brought no result.*

Key words Cepaea, Megalotachea, Palaeotachea, *Obere Süßwassermolasse, silvana-beds, morphometrics.*

INTRODUCTION

Traditionally, a wide range of helicid landsnail species have been attributed to the genus *Cepaea*, although already Pfeffer (1929) suggested that the fossil forms cannot be related to the extant forms of this genus. Instead, all fossil species-level taxa of this group should be summarized into *Palaeotachea* Jooss 1912 (see also Nordsieck 2014b & c). Members of *Palaeotachea* are among the most abundant and conspicuous landsnails of the Obere Süßwassermolasse (OSM) ("Upper Freshwater Molasse", Middle to Late Miocene). Despite their abundance and although their taxonomic status is problematic in most cases, they have never been subject of detailed studies. Particularly two common species, Schlotheim's (1820) "*Cepaea*" *sylvestrina* and Klein's (1853) "*C.*" *silvana* are problematic due to their high morphological variability. A further problematic genus of this taxonomic complex is *Frechenia*, because its taxonoic status is under debate as well. This paper aims to answer of the following questions: (1.) How many species of *Palaeotachea* were present in the OSM and what is their taxonomic status? (2.) Can a *Frechenia /Palaeotachea* relationship be demonstrated using morphometic features? (3.) Which are the differences between *Palaeotachea silvana* (Klein, 1853) and *P. sylvestrina* (Schlotheim, 1820), and can they be considered as different species? (4.) What is the palaeogeographic distribution of this species complex in Central Europe? The single species are described in detail together with their distinguishing features. Finally, we provide an identification key for the *Palaeotachea* species of the OSM.

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MATERIAL AND METHODS

In order to test for the separation of the two species *Palaeotachea silvana* and *P. sylvestrina,* more than one hundred specimens were measured and statistically analysed. The material comes from Middle Miocene Obere Süßwassermolasse (OSM; "Upper Freshwater Molasse") locations and time equivalent sites in South Germany, which were chosen because they yield the highest numbers of well-preserved specimens. The OSM is a freshwater episode in the North Alpine Foreland Basin (NAFB), which was formed during the Alpine orogeny. Sediments of the NAFB are dived into four units: Untere Meeresmolasse, Untere Süßwassermolasse, Obere Meeresmolasse and Obere Süßwassermolasse. The lake basins of Randeck Maar and Steinheim Basin are time-equivalent developments of the OSM situated on the Swabian Alb. For a detailed overview of the geological background see Geyer & Gwinner (2011).

An important event in the Middle Miocene was the Nördlinger Ries/Steinheim Basin meteorite impact between 14.6 and 15.0 Ma bp (Buchner *et al*. 2013). The gastropods examined in this study are from sediments deposited both before and after the Ries/Steinheim event. All studied material is stored in the Staatliches Museum für Naturkunde Stuttgart (SMNS) and the Senckenberg Museum in Frankfurt am Main. Important complexes are the collections of Adolf von Klein (1805–1892) and Carlo Jooss (1883-?), because they contain type material. The former include the original material of *Palaeotachea silvana* and *Palaeotachea dentula*. The latter hosts the original material of *Palaeotachea elevata*.

The studied material comes from the following localities. (1.) Gastropods labelled as *Cepaea silvana* (Klein, 1853): Zwiefalten, Baden-Württemberg, South Germany (type locality of *C. silvana*), MN5/6: 15 specimens (n =15), Mörsingen (district of Zwiefalten), MN 5 (Esu 1999): 138 specimens (n=138). (2.) Gastropods labelled as *Cepaea sylvestrina* (Schlotheim, 1820): Steinheim am Albuch, Baden-Württemberg, South Germany, MN 7 (Gentry *et al*. 1999): 114 specimens (n=114). Reimlingen, at the Sportplatz, Nördlinger Ries, Bavaria, South Germany, according Bolten (1977) from Post-Ries sediments 44 specimens (n=44).

For morphometric examination of the Pliocene landgastropod genus *Frechenia* Schlickum & Strauch 1971, the following taxa were examined: *Frechenia reichenbachi* (type species) (n= 14), from Frechen near Cologne; *Palaeotachea turonensis* (n=24) from the Miocene of Grund near Vienna; *Eobania vermiculata* (type species) (n=24), from Italy; *Cepaea nemoralis* (type species) (n=24), from France; *Caucasotachea vindobonensis* (n=24) (formerly *Cepaea vindobonensis*, see Neiber & Hausdorf 2015) from Austria. This two species were taken for two reasons: 1. Apart from the distinct outerlip, *Frechenia* has a "*Cepaea*"-like outer morphology and *C. nemoralis* is the type species of the genus. 2. *Caucasotachea vindobonensis* was included, because like *C. nemoralis*, it bears an outer morphology similar to *Frechenia*.

For statistics, the following parameters were measured (Fig. 1): (1.) Shell height (sh), (2.) shell width (sw), (3.) height of the aperture (ah), (4.) height of the last whorl (lwh), (5.) angle of spire (as), (6.) distance of insertions (di). The measurements were made using the software "Image J" (Burger & Burge 2006) and a digital slide gauge as well as a simple goniometer. The following statistical methods were applied to the *Palaeotachea* specimens: (1.) The above parameters were used for a principal component analysis (PCA) (Matrix Variance-covariance) using "PAST" software (see Hammer *et al*. 2001). (2.) The following ratios were calculated from the above parameters: sh/sw; lwh/ah; sh/ah; sh/di; as/ah; as/lwh; as/sh; as/sw; as/di; ah/di; sw/di; lwh/di; sw/ah; as/ah to as/lwh ratio; sh/sw to as/di ratio; as/sh to as/sw ratio; sh/mh to sw/mh ratio; lwh/mh to sh/di ratio; as/ah to as/sh ratio; as/mh to as/sw ratio; as/di to as/ah ratio. The values from all specimens were used to calculate a cluster analysis (euclidean, Ward's method) using PAST software. The analysis of these measured dimensions alone did not provide any reasonable results and is therefore not shown here. In a next step, the arithmetic means of each given ratio were calculated and then used for another cluster analysis. These results are presented below. (3.) In order to test for different growth rates, the size of the first three whorls was measured and compared with the total shell width. These measurements were made using the image analysis software of a Keyence microscope. In addition to the *silvana/sylvestrina* problem, we aimed to test for the taxonomic status of further species

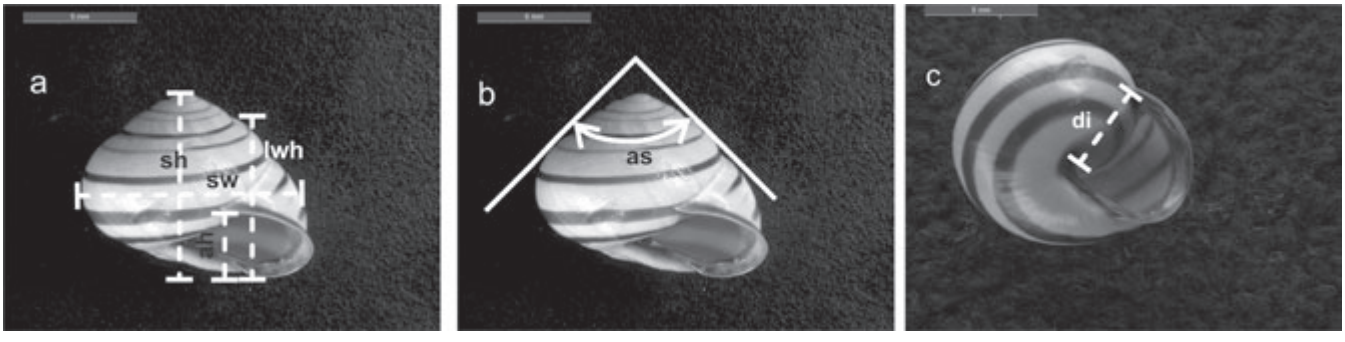


Figure 1 Shell morphometric features mentioned in the text and used for statistics.

that had been attributed to the "*Palaeotachea*"-group. For this purpose we studied all available material of the related species in the Staatlichen Museum für Naturkunde Stuttgart (SMNS) and the Senckenberg Museum in Frankfurt am Main and described it taxonomically. In addition to that, SEM-photos of the protoconches of the different species were made. However, due to incomplete preservation, no distinct features can be identified. According to that, they are not illustrated here. The stratigraphic information for each locality is listed in Table 1. Table 2 lists the localities with verified Mammal zone (MN).

For the examination of *Frechenia* the according ratios were used for two cluster analyses. One with a Paired Group Algorithm and Euclidean Similarity Index, the other with Single Linkage Algorithm and Bray-Curtis Similarity Index. Additionally, two Principal Component Analyses (PCA) were conducted: 1. Correlation matrix, disregard groups, Mean value imputation (PCA1). 2. Variance-covariance Matrix and disregard groups, Mean value imputation (PCA2). Both PCAs have 15 components (PC). The statistics were also calculated using PAST (Hammer *et al*. 2001).

Cepaea and the Palaeotachea complex

Cepaea-type shell morphologies are common among Cenozoic landsnails, but their taxonomic attribution on the genus level is difficult due to a high variability and the discrepancy between taxonomic features used in fossil (morphology), and extant (anatomy, molecular genetics) snails, respectively. According to Zilch (1959–1960), Kerney *et al*. (1983) and Welter-Schultes (2012b), the genus *Cepaea* Held 1837 includes four extant species: *Cepaea nemoralis* (Linnaeus, 1758) (type species) (Fig. 5.4), *C. hortensis* (O.F.Müller, 1774) (Fig. 5.3), *C. silvatica* (Draparnaud, 1801) (Fig. 5.2) and *C. vindobonensis* (Férussac, 1821) (Fig. 5.1). Schileyko (2006) divided the genus into two subgenera: *Cepaea* (*Cepaea*) with the species *hortensis* and *nemoralis* as well as *Cepaea* (*Austrotachea*) with *silvatica* and *vindobonensis*.

Based on nuclear and mitochondrial DNA marker sequences, Cadahia *et al*. (2014) recently suggested that *Cepaea* is a paraphyletic taxon and that *C. nemoralis* and *C. hortensis* are closer related to *Eobania vermiculata* (O.F.Müller, 1774) then to *Cepaea vindobonensis*. In 2015, Neiber & Hausdorf confirmed the polyphyly of *Cepaea*. Following these authors, only *C. nemoralis* and *C. hortensis* remain in *Cepaea*. The species *vindobonensis* is referred to *Caucasotachea,* and *sylvatica* to *Macularia*. In fact, already Pfeffer (1929) has splitted the four extant *Cepaea* species into three different genera according to their different callous columellar plate ("Columellar-Callusplatte") and the shell fine sculpture. He proposed the new genera *Hyalotachea* for *silvatica* and *Austrotachea* for *vindobonensis*, while *nemoralis* and *hortensis* remained in the genus *Cepaea*. The problem with Pfeffer`s work is that he gave no illustrations of his observations and descriptions. As justification for this he wrote that the relevant shell features are not visible in only one view but the shell has to be turned into different directions (Pfeffer, 1929, p. 136). For the extant species, these new genera were not accepted by later authors (Zilch 1959–1960).

The Oligocene and Miocene "*Cepaea*"-like forms are traditionally placed in the genus *Cepaea* (e.g., Wenz, 1920a & b; Schlickum, 1976; Lueger, 1981; Kókay, 2006). Because of the microsculpture and the columellar area, however, Pfeffer (1929) was the opinion that the fossil forms has nothing to do with the extant *Cepaea.* He therefore placed the fossil species in his newly designated genera *Megalotachea and Pachytachea* as well as in the genus *Palaeotachea* Jooss, 1912. The author differentiated the genera according to the microsculpture and the formation of the columellar plate. This was later rejected by Zilch (1959–1960). In 1986, Nordsieck grouped the Oligo-Miocene species of the "*Cepaea*"-group, based on Pfeffer`s observation and stratigraphy, into two genera: *Palaeotachea* Jooss, 1912 and *Megalotachea* Pfeffer 1929 (see Nordsieck 1986). The author saw *Pachytachea* as a synonym of *Megalotachea* and published a comment on the terminology used by Pfeffer (1929) (see Nordsieck 2014a). According to Nordsieck (1986; 2014b; 2014c), the *Palaeotachea* species exhibit radial rib-striae granulated by spiral striae, while the *Megalotachea* species does not. In the *Palaeotachea* species, the end of the columellar plate is mostly in a higher (more umbilical) position than *Megalotachea*. However, Nordsieck (2014c) wrote that the delimitation of both genera proved to be difficult because these differences do not allow a clear separation. For example, *Palaeotachea subcarinata* has a microsculpture like *Palaeotachea* but a columellar plate like *Megalotachea* (Nordsieck 2014c). According

Table. 1 Localities with Miocene land gastropods and their stratigraphic correlation. If exact correlations are known, the appropriate reference is given. Otherwise, the stratigraphic information comes from labels of the SMNS collection.

Locality	Country	Biostratigraphy
Altheim near Ehingen	Baden-Württemberg, Germany	Miocene (collection data)
Aulfingen	Baden-Württemberg, Germany	Miocene, Helicidenmergel (Jooss 1923)
Baach near Zweifalten	Baden-Württemberg, Germany	Miocene (Wenz 1923; collection data)
Bechingen near Riedlingen	Baden-Württemberg, Germany	Miocene (collection data)
Bonladen	Baden-Württemberg, Germany	MN 6 (Sach 1999)
Diepflingen	Switzerland	Miocene (collection data)
Edelbeuren-Mauerkopf	Baden-Württemberg, Germany	MN 5 (Sach 1999)
Edelbeuren-Schlachtberg	Baden-Württemberg, Germany	MN 5/6 (Sach 1999)
Emerberg (a ridge near Zwiefalten)	Baden-Württemberg, Germany	Miocene (collection data)
Faluns de Touraine	France	MN 5 (Ginsburg 2001)
Frechen near Cologne	Nordrhein-Westfalen, Germany	Pliocene (Schlickum & Strauch 1971)
Grund	Vienna, Austria	MN5 (Zorn 2004)
Häder near Dinkelscherben	Baden-Württemberg, Germany	MN 5 (Heizmann 1973, quoted in Ginsburg 1999)
Hard near Densbüren	Switzerland	Miocene (collection data)
Harthausen auf der Scheer	Baden-Württemberg, Germany	Miocene, Helicidenmergel (Jooss 1923)
Herznach	Switzerland	Miocene (collection data)
Heselberg near Ochsenhausen	Baden-Württemberg, Germany	Miocene (Sach 1999)
Heuhof near Oggenhausen	Baden-Württemberg, Germany	MN5 (Böttcher *et al*. 2009)
Hohenhewen	Baden-Württemberg, Germany	Middle to Upper Miocene (Geyer & Gwinner 2011)
Hohenmemmingen	Baden-Württemberg, Germany	Miocene (Gottschick & wenz 1916; collection data)
Hohenstoffeln	Baden-Württemberg, Germany	Middle to Upper Miocene (Geyer & Gwinner 2011)
Höwenegg	Baden-Württemberg, Germany	MN 9 (Hünermann 1989, quoted in Heißig 1999)
Korneuburger Basin	Lower Austria, Austria	MN5 (Harzhauser & Wessely 2003)
Lauchheim	Baden-Württemberg, Germany	Miocene (collection data)
Le Locle, Kanton Neuenburg	Switzerland	MN 7 (Kälin 1993, quoted in Boon-Kristkoiz & Kristkoiz 1999)
Manthelan	Indre-et-Loire, France	MN 5 (Hugueney 1999)
Michalesberg near Dischingen	Baden-Württemberg, Germany	Miocene (collection data)
Mörsingen	Baden-Württemberg, Germany	MN 5 (Esu 1999)
Nebelbergweg near Nunningen, Kanton Solothurn	Switzerland	MN 9 (Kälin & Engesser 2001)
Neuberg	Switzerland	Miocene (collection data)
Nördlinger Ries	Bayern, Germany	Post Ries, probably MN6
Oberwilzingen am Emerberg	Baden-Württemberg, Germany	Miocene (collection data)
Oggenhausen	Baden-Württemberg, Germany	MN5 (Böttcher *et al*. 2009)
Ramsen, Kanton Schaffhausen	Switzerland	Miocene (collection data)
Randecker Maar near Kirchheim Teck	Baden-Württemberg, Germany	MN 5 (Heizmann 1983 quoted in Hellmund & Hellmund 2002; Rasser *et al*. 2013)
Ravensburg	Baden-Württemberg, Germany	MN 5 (van der Made 1999)
Reimlingen at Nördlinger Ries	Bayern, Germany	Post Ries, probably MN6 or later (Bolten 1977)
Riesental near Epfenhofen	Baden-Württemberg, Germany	Miocene, Helicidenmergel (Jooss 1923)
Rognes	Bouches-du-Rhône, France	Miocene (collection data)
Route de la Sagne	Neuchâtel, Switzerland	Miocene (collection data)
Rumpel bei Oltingen	Switzerland	Miocene (collection data)

Locality	Country	Biostratigraphy
Sandelzhausen	Bayern, Germany	MN 5 (Moser *et al*. 2009)
Sansan	Gers, France	MN 6 (Hugueney 1999)
Steinheim am Albuch	Baden-Württemberg, Germany	MN 7 (Gentry *et al*. 1999)
Steubersheim	Baden-Württemberg, Germany	Miocene, Helicidenmergel (Jooss 1923)
Stoffelberg near Ehingen	Baden-Württemberg, Germany	Miocene (collection data)
Tennikerfluh near Tenniken	Switzerland	Miocene (collection data)
Tobel Oelhalde-Nord	Baden-Württemberg, Germany	MN 5/6 (Sach 1999),
Tobel Oelhalde-Süd	Baden-Württemberg, Germany	MN 5 to MN 5/6 (Sach 1999)
Trendel near Öttingen	Bayern, Germany	Post Ries, probably MN6
Undorf near Regensburg	Bayern, Germany	MN 5 (Fejfar (1999)
Wannenwaldtobel	Baden-Württemberg, Germany	MN 5/6 (Sach 1999),
Wirtachtobel at the Pfänder near Bregenz	Vorarlberg, Austria	Miocene (collection data)
Wölflinswil	Switzerland	Miocene (collection data)
Zwiefalten	Baden-Württemberg, Germany	Miocene (collection data)
Zwiefaltendorf	Baden-Württemberg, Germany	Miocene (collection data)

Table 2 List of occurrences of *Palaeotachea* with verified Mammal Neogene Zones (MN).

Locality	Species	Mammal zone (MN)
Mörsingen	*P. silvana*	MN 5 (Esu 1999)
Sandelzhausen	*P. silvana*	MN 5 (Moser *et al*. 2009)
Randecker Maar	*P. silvana*	MN 5 (Rasser *et al*. 2013)
Ravensburg	*P. silvana*	MN 5 (van der Made 1999)
Steinheim am Albuch	*P. sylvestrina*	MN 7 (Gentry *et al*. 1999)
Le Locle, Kanton Neuenburg	*P. sylvestrina*	MN 7 (Kälin 1993, quoted in Boon-Kristkoiz & Kristkoiz 1999)
Höwenegg	*P. sylvestrina*	MN 9 (Hünermann 1989, quoted in Heißig 1999)
Nebelbergweg near Nunningen, Kanton Solothurn	*P. sylvestrina*	MN 9 (Kälin & Engesser 2001)
Faluns de Touraine	*P. turonensis*	MN 5 (Ginsburg 2001)
Korneuburger Becken	*P. turonensis*	MN 5 (Harzhauser & Wessely 2003)
Sansan	*P. turonensis*	MN 6 (Hugueney 1999)
Le Locle, Kanton Neuenburg	*P. elevata*	MN 7 (Kälin 1993, quoted in Boon-Kristkoiz & Kristkoiz 1999)
Oggenhausen	*P. renevieri*	MN 5 (Böttcher *et al*. 2009)
Randecker Maar	*P. renevieri*	MN 5 (Rasser *et al*. 2013)

to this author it is therefore recommendable, to rank both groups only as subgenera of one genus, which means that all Oligo-Miocene "*Cepaea*" group species are classified within the genus *Palaeotachea* (see Nordsieck 2014b & c).

With respect to the generic designation, the current paper follows Nordsieck (2014b & c). However, due to the poor delimitation mentioned above, a separation into subgenera are waived. It is important to note, however, that due to the DNA results from Cadahia *et al*. (2014) and Neiber & Hausdorf (2015) mentioned above, the discussion on "*Cepaea*" relationships is still open.

RESULTS

MORPHOMETRICS AND STATISTICS

The measurements of the relationship between the size of the first three whorls and the total shell width (see Material and methods) provided no differences between the two species *Palaeotachea silvana* and *P. sylvestrina*. However, the cluster analysis (Fig. 2) shows a distinct separation between the specimens from Zwiefalten (type locality of *P. silvana*) and Mörsingen, on the one side, and those of Nördlinger Ries and Steinheim am Albuch (*P. sylvestrina*), on the other. The PCA analysis (Figs 3 & 4) confirms these

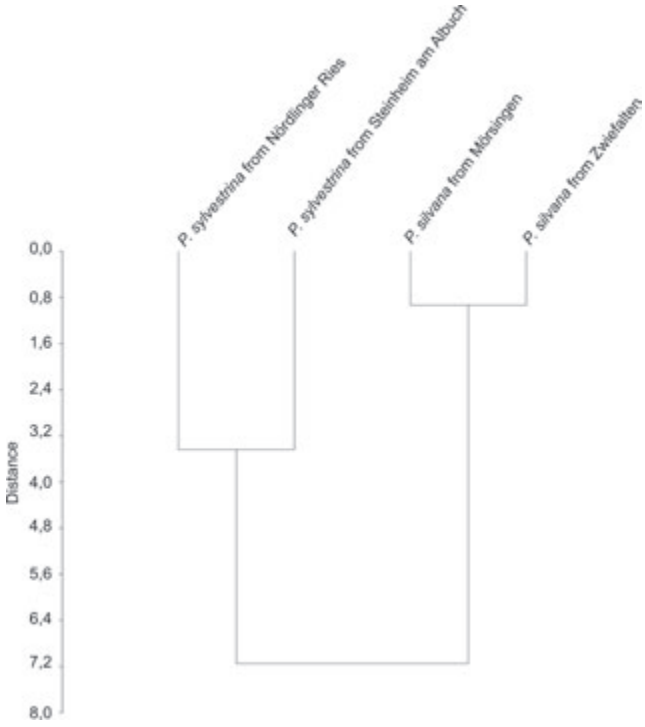


Figure 2 Hierarchical cluster analysis.

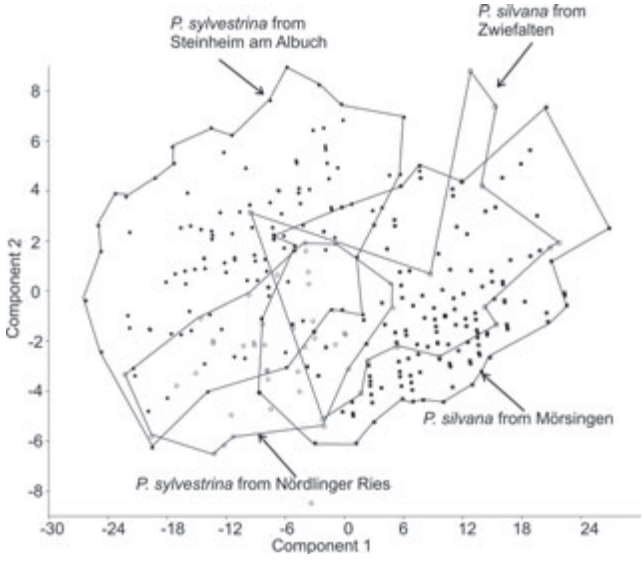


Figure 3 Principal component analysis (PCA). Scatter plot of PC1 and PC2.

results. The first component accounts for a variance of 92.21%, followed by the second one with 7.24% variance. The remaining four components range between 0.21% and 0.06% variance. The scatter plot of PC 1 (Eigenvalue 134.83) and PC2 (Eigenvalue 10.58) (Fig. 3) shows a remarkable differentiation of the specimens from Mörsingen and Zwiefalten (*P. silvana*) on the one side, and from Nördlinger Ries and Steinheim am Albuch

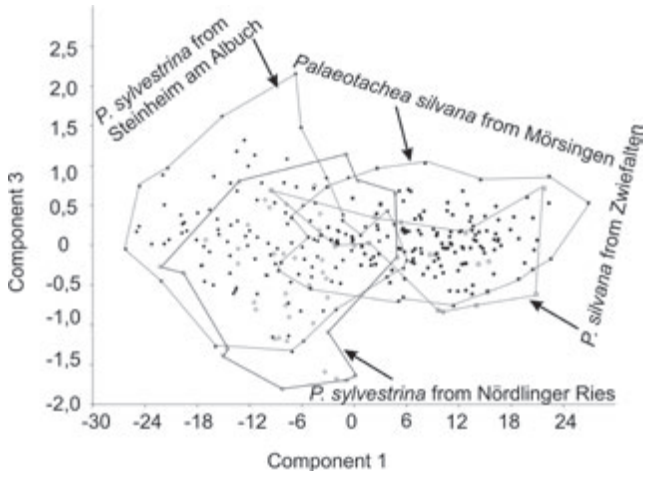


Figure 4 Principal component analysis (PCA). Scatter plot of PC1 and PC3.

(*P. sylvestrina*), on the other. The scatter plot of PC1 and PC3 (Eigenvalue 0.31) (Fig. 4) shows the same separation. In both scatter plots there is a remarkable overlapping zone of the four different localities.

The cluster analyzes as well as the principal component analyzes (PCA) did not reveal any morphological relationships between *Frechenia* and one of the other measured taxa. According to that, an illustration of the diagrams was waived.

TAXONOMY

Palaeotachea silvana (Klein, 1853)
(Figs 5.1–5; Figs 6.3 & 6.4)

Helix silvana Klein, 1853: 205, Pl. V, fig. 2.
Helix sylvana- Sandberger 1872: Pl. XXIX, figs. 13a–d [non Fig. 13b]
Helix (Macularia) sylvana- Sandberger 1875: 592–594 (ref. Pl. XXIX, figs.13a,13c–d)
Helix malleolata Sandberger, 1875: 594.
Cepaea silvana silvana (Klein)-Wenz 1923: P. 667–679. See here for the very large number of synonyms.
Cepaea silvana malleolata (Sandberger)-Wenz 1923 679–680.
Megalotachea silvana KLEIN-Pfeffer 1929: 146–147.
Palaeotachea silvana (Klein)-Nordsieck 2014b: 21

Material examined 100 specimens, including a syntype, see Material and Methods section.

Type locality The locality quoted on the collection label of the syntype is Zwiefalten,

Baden-Württemberg, South Germany. According to Klein's (1853) description, it comes from freshwater limestones south of Zwiefalten, the so-called Tautschbuch. In this forested area north of river Danube, several limestones of the so-called *silvana*-limestones are still outcropping in old quarries.

Description The syntype is 12.3mm high and 17.1mm wide. The height of the aperture is 9.2mm and of the last whorl 10.3mm. The height/width ratio is 0.75. The shell appears to have three colour bands. The height ranges from 10.1 to 16.8mm and the width from 14.7 to 21.0mm. The shell has a typical helicoid, dextral "*Cepaea*"-like form with all transitions between the lower and the higher measures. The 4 ¼ convex whorls are growing regularly. The last whorls often show an indistinct keel. It usually disappears ca. 0.5 whorls prior to the aperture. Shortly before reaching the aperture, the last whorl obliquely turns the abapical direction.

The aperture has an oblique-oval shape and the two intersections are connected by a thin callus. The peristome is turned backwards (see Figs 5.4 & 5.5). At the lower margin, there is a slight callosity folding near the umbilicus region. This can be more or less pronounced in the individual specimens. The umbilicus is covered by a parietal callus. The sutures are moderately deep. The protoconch, which consists of ca. 1.5 whorls is almost entirely smooth and without a sculpture. It has a diameter of ca. 3.6mm. The teleoconch is covered by very fine and regular growth lines or collabral striation (Fig. 6.3). On the outer side of the lower peristome, there are tiny knobs that are difficult to identify even under higher magnification (Fig. 6.4).

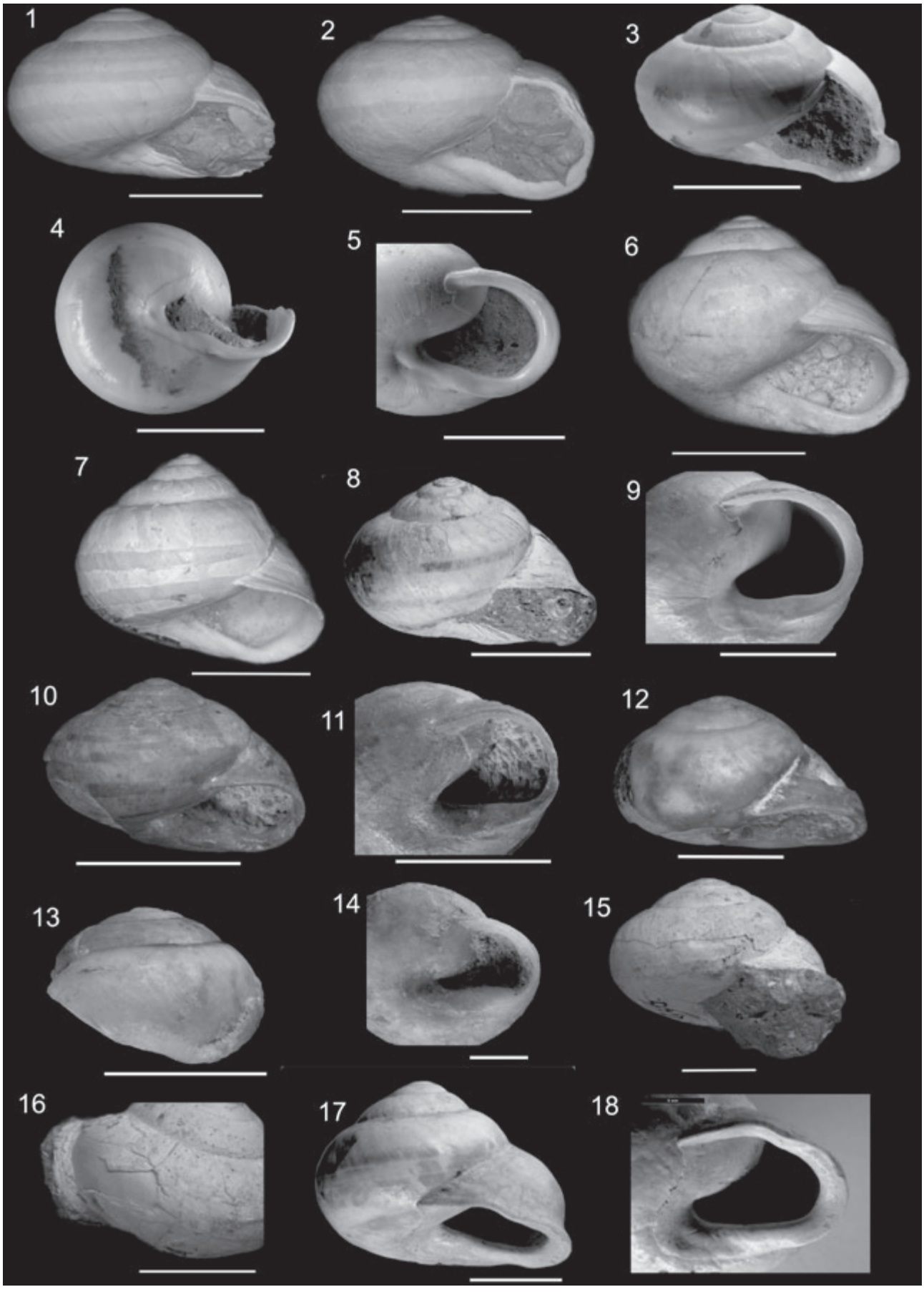
Discussion Sandberger (1874) designated a species from Altheim near Ehingen, Baden-Württemberg, Germany as *Helix malleolata*. According to Wenz (1923), this is a subspecies of *C. silvana*. Sandberger (1874) gave no illustration of his species. An investigation of a specimen from the SMNS-Jooss collection from this locality revealed no notable differences to *C. silvana* from any of the other localities. For this reason we suggest to emend the subspecies *C. silvana malleolata*.

Distribution Wenz (1923 &1924) mentioned several Miocene localities in Baden-Württemberg, Bavaria and Oberhessen (Germany) as well as in Switzerland. Also some places in Poland near Krakow and in the Ukraine ("Ostgalizien") were listed. Additionally, Wenz (1923) quoted some questionable Pliocene deposits in France. It is not very likely that Wenz has reviewed all of the identifications in the quoted literature. For this reason, only examined collection material (SMNS and the Senckenberg Museum in Frankfurt am Main) is considered for the distribution herein. Mörsingen (district of Zwiefalten), Randecker Maar near Kirchheim Teck, Heuhof near Oggenhausen, Häder near Dinkelscherben. Ravensburg, Sandelzhausen, Michaelsberg near Dischingen, Bechingen near Riedlingen, Altheim near Ehingen, Hohenmemmingen Zwiefalten, Zwiefaltendorf (district of Riedlingen), Emerberg (ridge near Zwiefalten). Undorf near Regensburg (Sandberger 1872, pl. XXIX, fig.13c) According to Sach (1999): Edelbeuren-Mauerkopf, Bonladen, Edelbeuren-Schlachtberg, Wannenwaldtobel, Tobel Oelhalde-Süd, Tobel Oelhalde-Nord, Heselberg near Ochsenhausen. However, the according gastropods collected by Sach (1999) are often deformed so the Identification is uncertain.

Mammal zone (MN) range MN5 (Prae-Ries-sediments).

Palaeotachea sylvestrina (Schlotheim, 1820)
(Figs 5.6–9; Fig. 6.5)

Helicites sylvestrinus Schlotheim, 1820: 99.
Helix silvestrina nobis, Zieten 1832: 38, pl. 29 figs.2a–c
Helix geniculata Sandberger, 1872: 629, pl. XXVI, fig. 23–23b
Helix platychelodes Sandberger, 1875: 626.
Helix geniculata -Sandberger, 1875: P. 629,
Cepaea gottschicki Wenz, 1919a: 70.
Cepaea sylvestrina- Wenz 1920: 19–20, fig. 1–2 (Syntype Schlotheim 1820)
Cepaea gottschicki Wenz-Gottschick 1920: 49.
Cepaea sylvestrina gottschicki Wenz-Wenz 1920b: 156, figs. 7–8.
Cepaea sylvestrina sylvestrina (Schlotheim)-Wenz 1923: 690–691. See here for additional synonyms.
Cepaea sylvestrina geniculata (Sandberger)-Wenz 1923: 691–693.
Cepaea sylvestrina gottschicki Wenz-Wenz 1923: P. 693–695.
Megalotachea silvestrina Schlot.-Pfeffer 1929: 147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Material examined > 100 specimens, see Material and Methods section.

Description The dextral shell has helicoid typical *Cepaea*-like form and consists of 4 ½ whorls. It has a maximum width of ca. 27.3mm and a maximum height of ca. 22.5mm. The size is extremely variable. Like in *P. silvana*, both higher and lower forms exist. The average ratio between shell height and height of aperture is ca. 1.6. The regularly growing whorls are convex and the sutures is moderately deep. Before reaching the aperture, the last whorl turns in abapical direction. The degree of inclination can also be different. It ranges from a relatively abrupt down-turning, to a more shallow dip. The aperture is oblique-oval with a slightly turned back periostome (see Fig. 5.9). The first part of the upper margin runs more or less straight and parallel to the lower one. The lower margin of the aperture shows a small callous thickening, the distinctiveness of which is variable between the different shells. The umbilicus is covered by a parietal callus. Also the intersections are connected by a thin callous layer. The teleoconch is covered with a very fine, irregularly radial striation which is not visible on all specimens (Fig. 6.5). Also more or less regularly arranged fine spiral lines can be seen on very well preserved shell. The protoconch, which consists of ca. 1 ¼ whorls, is smooth. The according whorls have a more bulbous shape.

Discussion Originally described by Schlotheim (1820) as *Helicites sylvestrinus*, the author mentioned the following distribution: Buschweiler (today`s name Bouxviller, Alsace) and Ermreuth, Bavaria, as well as the Kanton Basel ("Jurakalk") in Switzerland. Von Zieten (1832) then described this species from Steinheim am Albuch as *Helix sylvestrina* nobis. Already in 1830, Schübler wrote in a letter to the "Journal de Géologie par MM", that the reference of the according Steinheim am Albuch specimens to the species *Helicites sylvestrinus* sensu Schlotheim is doubtful (p. 301, "Correspondance et Variétés"). Also Wenz (1919) suggested that the according gastropods from Steinheim do not fit with the description of Schlotheim and erected for the Steinheim specimens the new species *Cepaea gottschicki* n. nom Wenz, 1919. In the same year he visited the Geological-Palaeontological Institute in Berlin in order to study the original material of Schlotheim (1820), because he had strong doubts about the accuracy of Schlotheim's geographic information. Already Miller (1900) had claimed that Schlotheim (1820) mixed different species together under the name *Helicites sylvestrinus*.

After closer examination, Wenz (1920a) came to the conclusion that this material originated from the Nördlinger Ries, Bavaria, Germany, and that Schlotheim (1820) had made a mistake in the geographic distribution. Following Wenz (1920a), *Helicites sylvestrinus* is also identical with *Helix platychelodes* from the Nördlinger Ries, designated by Sandberger (1875). Wenz (1920a) determined a "Typus" from the Schlotheim collection. In 1920b, he designated his *C. gottschicki*

Figure 5 Shells of *Palaeotachea* species **5.1**. *P. silvana* (Klein, 1853). Middle Miocene, Scale 10mm. Zwiefaltendorf, Baden-Württemberg, Germany. Inv. Nr. SMNS 106768. **5.2.** *P. silvana* (Klein, 1853). Middle Miocene. , Scale 10mm. Zwiefaltendorf, Baden-Württemberg, Germany. Inv. Nr. SMNS 106769. **5.3 & 5.4.** P. *silvana* (Klein, 1853). Middle Miocene. Scale (both figures) 10mm. Zwiefalten, Baden-Württemberg, Germany. Syntype. Inv. Nr. SMNS 22738. **5.5** *P. silvana* (Klein, 1853). Middle Miocene. Scale 10mm. Mörsingen, Baden-Württemberg, Germany. Inv. Nr. SMNS 105.005. **5.6. & 5.7.** *P. sylvestrina* (Schlotheim, 1820). Middle Miocene. Scale (both figures) 10mm. Steinheim am Albuch, Baden-Württemberg, Germany. Inv. Nr. SMNS 106766 (Fig. 6); Inv. Nr. SMNS 106767 (Fig. 7). **5.8.** *P. sylvestrina* (Schlotheim, 1820). Middle Miocene. Scale 10mm. Trendel near Öttingen im Ries, Bavaria, Germany. Original material to Wenz (1920a & b). Inv. Nr. SMNS 105.000. **5.9**. *P. sylvestrina* (Schlotheim, 1820). Middle Miocene. Scale 10mm. Steinheim am Albuch, Baden-Württemberg, Germany. Inv. Nr. SMNS 15.817–129. **5.10 & 5.11.** *P. renevieri* (Maillard, 1891). Middle Miocene. Scale (both figures) 10mm. Harthausen auf der Scheer, Baden-Württemberg, Germany. Original material to Jooss (1923). Inv. Nr. SMNS 105.001. **5.12.** *P. dentula* (Quenstedt, 1867). Middle Miocene. Scale 5mm. Emerberg near Zwiefalten, Baden-Württemberg, Germany. Paratype of *Helix pachyostoma* Klein, 1853. Inv. Nr. 105.004. **5.13 & 5.14**. *P. dentula* (Quenstedt, 1884). Middle Miocene. Scale: Fig. 5.13: 10mm; Fig. 5.14: 5mm. Emerberg near Zwiefalten, Baden-Württemberg, Germany. Holotype of *Helix pachyostoma* Klein, 1853. Inv. Nr. 105.004. **5.15** & **5.16** *P. elevata* Berz & Jooss, 1927. Middle Miocene. Scale (both figures) 5mm. Near Le Locle, Kanton Neuch?tel, Switzerland. Holotype. Inv. Nr. SMNS 105.002. **5.17** &5.**18** *P. turonensis* (Deshayes, 1831). Middle Miocene. Scale Fig. 16: 5mm; fig. 17: 10mm. Manthelan, Dept. Indre-et Loire, France. Original material to Wenz (1920b). Inv. Nr. SMNS 105.003.

as a subspecies of *C. sylvestrina* (see Wenz 1920a and 1920b), and defined three subspecies: *C. sylvestrina sylvestrina* (Schlotheim), *C. sylvestrina gottschicki* (Wenz) and *C. sylvestrina geniculata* (Sandberger). In the same year, Gottschick (1920) put C. gottschicki back into the species rank. The taxa *geniculata* was originally designated by Sandberger (1872) as *Helix geniculata* Sandberger. According Sandberger, it is abundant in the Gypsum and Limestones of the Hohenhewen. This is the only locality named for this taxa by the author.

Distribution Steinheim am Albuch, Höwenegg, Hohenstoffeln, Lauchheim, Reimlingen at Nördlinger Ries, Trendel near Öttingen, Nördlinger Ries. Hohenhewen (Sandberger 1872) Switzerland: Nebelbergweg near Nunningen Le Locle, Ramsen.

Mammal zone (MN) range MN6-MN9-? (Post-Ries-sediments).

Palaeotachea dentula (Quenstedt, 1867)
(Figs 5.12–14; Fig. 6.1)

Helix pachyostoma Klein, 1853: 207, Pl. V, Fig. 4.
Helix dentula Quenstedt 1867: 482, pl. XLV, fig. 6.
Cepaea lepida Wenz, 1919a: 70.
Cepaea dentula (Quenstedt)-Wenz 1919b: 64.
Pachytachea dentula Quenst.-Pfeffer 1929: 146.

Material examined Four specimens (SMNS105004) including the holotype of *Helix pachyostoma* Klein, 1853, figured in Figs 5.13 & 5.14.

Description The dextral helicoid shell has a maximum width of ca.14.2mm and a maximum height of ca. 9.2mm. The height of the aperture is in average 51% of the shell height. Like in other "*Cepaea*"-group species, there are different forms with a high or a very low spire. The species has 3 ¾ regularly growing and moderately deep whorls. The protoconch consists of ca. 1.5 whorls. The first teleoconch whorl is relatively flat. The last one is more bulbous and forms with low spires can be slightly subangulate. Shortly before the aperture, the last whorl strongly descends. The columellar margin is more or less straight. The peristome is slightly thickened (see Figs 5.13 & 5.14). On the columellar margin, there is also a callous thickening. This extends to the point where the columellar margin passes arc-shaped to the convex upper one. The parietal callus is well developed. Also the umbilicus is covered by this parietal callus. The Protoconch is smooth. On the teleoconch, there are barely visible, regularly arranged and slightly S-curved growth lines.

Discussion Discussion: Wenz (1919a) discovered that a senior homonym *Helix pachystoma* Hombron & Jacquinot 1841 existed, and therefore he changed the name of Klein's species into *Cepaea lepida* n. nom. Later, Wenz (1919b) discovered that *Cepaea dentula* (Quenstedt, 1867) is identical with *Helix pachystoma* Klein, 1853. Because of being the next younger synonym, *Palaeotachea. dentula* is the valid name for the species designated by Klein, 1853.

P. dentula is with a maximum width of ca. 14.2mm the smallest *Palaeotachea* species in the OSM. *P. sylvestrina* and *P. turonensis* are significantly larger than *P. dentula*. *P. silvana* has a peristome that is more expanded. The aperture of both species is noticeable different. At *P. dentula* the abapical margin runs more straight. The adapical one goes steeper downward than it is the case at *P. silvana*. *P. dentula* differs from *P. renevieri* by a more or less straight lower periostome margin, an earlier downward flexing of the upper periostome margin, and a less convex last whorl.

Distribution The original material comes from the Miocene of Ober-Wilzingen am Emerberg near Zwiefalten. According to Wenz (1923) it occurs also in the Miocene of Baach near Zwiefalten and of Wirtachtobel at the Pfänder near Bregenz, Austria.

Mammal zone (MN) range MN5 (Prae-Ries-sediments).

Palaeotachea renevieri **(**Maillard**, 1891)**
(Figs 5.10 & 5.11)

Helix (Macularia) renevieri, Maillard, 1891: 43, Pl. 3, fig. 18
Cepaea renevieri (Maillard)-Jooss 1923: 198–200, Pl. XI, fig. 18–23
Cepaea renevieri (Maillard)-Wenz 1923: 652–653 (see there for further synonyms)
Cepaea renevieri renevieri (Maillard)-Berz & Jooss 1927: 203
Cepaea renevieri coniuncta Berz & Jooss, 1927: 203
Palaeotachea renevieri Maillard-Pfeffer 1929: 143

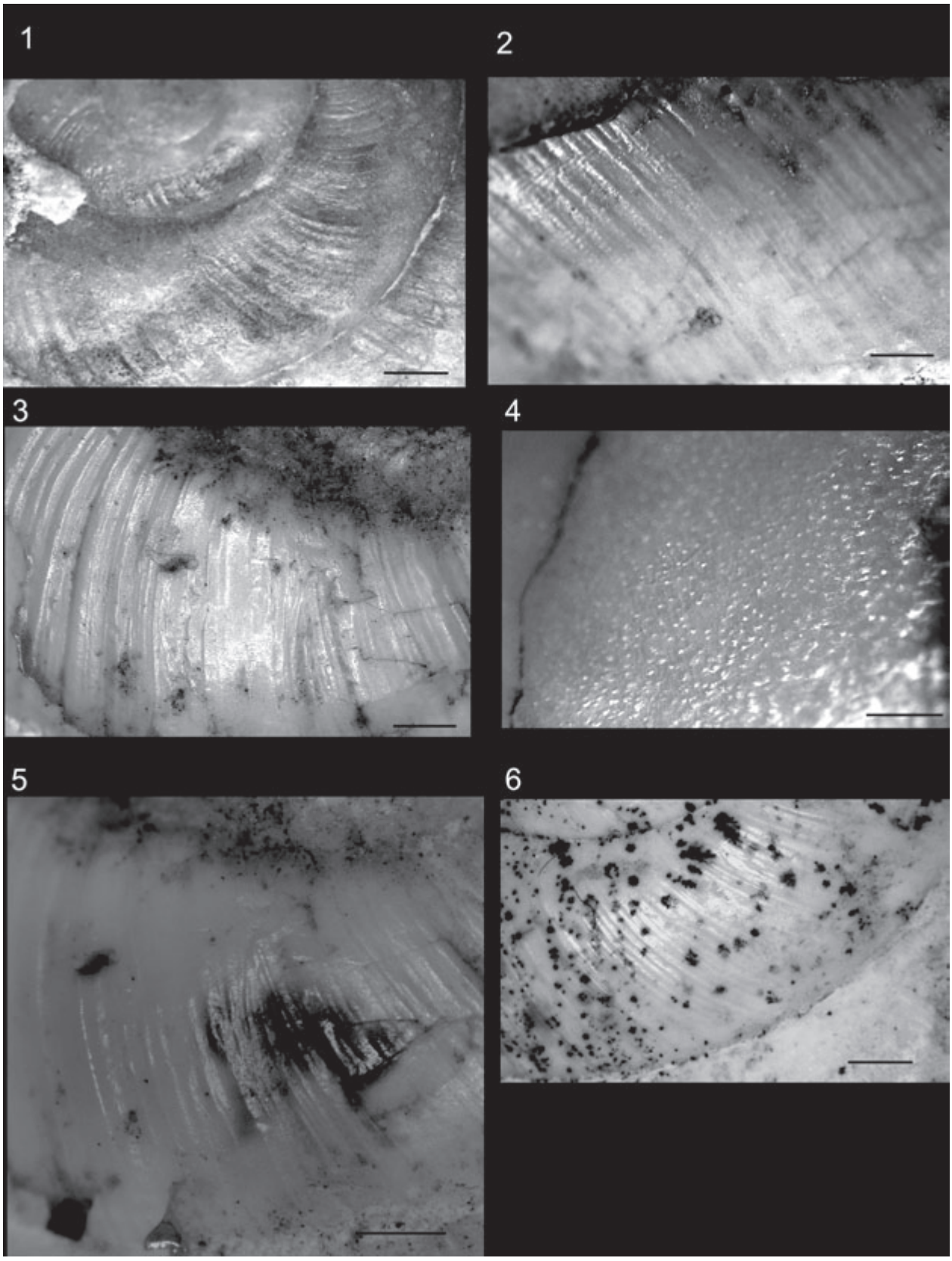

Figure 6 Sculptural details of the shells *Palaeotachea* species **6.1** Detail of Fig. 5.12. Scale 1mm. **6.2** Detail of Figs 5.15 & 5.16. Scale 0.5mm. **6.3 & 6.4** Detail of Figs 5. 3 & 5.4. Scale 0.5mm. **6.5** Detail of Fig. 5.6 Scale 0.5mm. **6.6** *Palaeotachea turonensis* (Deshayes, 1831). Middle Miocene. Mörsingen, Baden-Württemberg, Germany. Scale 1mm. Inv. Nr. SMNS J66.799.

Material examined Ten specimens.

Description Dextral helicoid shell with typical "*Cepaea*"-form. Maximum height ca. 11.4mm, maximum width ca. 14.9mm. Shell-height to height of the aperture relationship is ca. 1.5. It consists of 3 ¾ to 4 ¼ regularly growing whorls and moderately deep sutures. The last whorl is subangulate and becomes rounded ca. ¼ whorls before reaching the aperture. Right before the aperture, the last whorl turns slowly in abapical direction. The aperture has an oval form and the margins are only very slightly thickened and expanded (see Fig. 5.11). The adapical margin runs more or less straight before it goes over a very slight bend in the arched lateral margin. This straightness is a relatively variable feature. On some specimens this adapical margin is slightly curved. The abapical margin is slightly sloping downward. The insertions are connected by a thin callus. This parietal callus completely covers the umbilicus. Neither the teleoconch nor the protoconch sculpture is preserved. The protoconch is hardly recognizable. It consists of ca. 1 ¾ whorls, which are relatively flat. On one specimen (Fig. 5.7) four spiral pigment bands are well visible.

Discussion Berz & Jooss (1927) designated the subspecies *Cepaea renevieri coniuncta* nov. var. The original material is stored in the SMNS (Inv. Nr. SMNS 101369). The differences to *P. renevieri* are insufficient and also Berz & Jooss (1927) wrote that the nominal species and the subspecies are connected by transitions and are often difficult to differentiate. According to this the subspecies *Cepaea renevieri coniuncta* Berz & Jooss, 1927 is emended. *P. renevieri* differs from *Palaeotachea silvana*, *P. sylvestrina* and *P. turonensis* by the remarkably smaller shell size. For *Palaeotachea dentula* and *P. elevata* see there.

Distribution Harthausen auf der Scheer, Oggenhausen. According to Jooss (1923) also Steubersheim, Riesental near Epfenhofen, Aulfingen, Hard near Densbüren, Herznach, Wölflinswil, Rumpel bei Oltingen, Diepflingen, Neuberg and Tennikerfluh near Tenniken. In the Jooss collection there are several specimens where an exact determination is not possible because of the incomplete preservation. Therefore, the above list of Jooss must be treated with caution. For other localities see also Maillard (1891). Two well preserved specimens from the Jooss collection come also from the Zipfelbachschlucht of Randecker Maar.

Mammal zone (MN) range MN5 (Prae-Ries-sediments).

Palaeotachea elevata Berz & Jooss, 1927
(Figs 5.15 & 5.16; Fig. 6.2)

Cepaea renevieri elevata Berz & Jooss, 1927: 204.

Material examined 3 specimens, original material of Berz & Jooss (1927).. SMNS105002. Internal numbers of the Joss collection: 246 (the specimen shown in Figs 5.15 & 5.16), 247, 248.

Description Dextral, helicoid shell with regularly growing whorls, in the outline very similar to *P. renevieri*. It has 4 ¼ rounded whorls with moderately deep sutures. The shell is ca. 14.6mm wide and 12.1mm high. The sh/mh ratio is 1.6. Shortly before the aperture, the last whorl turns slowly downwards. The aperture is of oval shape with a turned-back peristome. The upper aperture margin runs slightly oblique before it passes into the arched lateral margin. The length of this upper one is variable. The lower margin passes obliquely downward. The insertions are connected by a parietal callus which also covers the umbilical region completely. The protoconch is slightly bulbous and without any sculpture. It consists of 1 ¼ whorls. The teleoconch bears more or less regularly arranged growth lines, which are only visible at higher magnifications.

Distribution According to Berz & Jooss (1927) the species occurs in the *sylvestrina*-beds of Le Locle and Route de la Sagne.

Mammal zone (MN) range MN7-? (Post-Ries-sediments).

Diagnostic features *Palaeotachea turonensis*, *P. silvana* and *P. sylvestrina* differ remarkably in size. In the same size range is *Palaeotachea dentula*. *P. elevata* differs in the following points from *P. dentula*: (1.) More rounded last whorl. (2.) More strongly reflected peristome. (3.) At. *P. dentula* the lower aperture margin runs more or less straight. (4.) The aperture of *P. dentula* is more laterally

tapered. (5.) At *P. dentula* the last whorl is going down more strongly and abrupt shortly before the aperture. (6.) Due to 5, the upper aperture edge of *P. dentula* seems to be pulled more forward than that of *P. elevata*.

As mentioned further above, the outline of *Palaeotachea renevieri* is very similar to *P. elevata*. The differences are: (1.) *P. elevata* has a more strongly turned-back peristome (see Fig. 5.16). (2.) The upper aperture margin runs more obliquely in *P. elevata* than in *P. renevieri*. (3.) The last whorl of *P. elevata* is not as "keel-like" rounded as it is the case for *P. renevieri.* (4.) *P. elevata* has a more bulbous protoconch.

Palaeotachea turonensis (Deshayes, 1831)
(Figs 5.17 & 5.18; Fig. 6.6)

?Helix asperula Deshayes 1830 or 1832*:* 251 (see Welter-Schultes 2012a).
?Helix duvauxi Deshayes 1830 or1832*:* 252 (see Welter-Schultes 2012a).
Helix turonensis Deshayes 1830 or 1832: 252 (see Welter-Schultes 2012a)
Helix turonensis Deshayes, 1831: 39–40. pl. 1, fig. 1–2
Helix larteti de Boissy, 1840: II, p. 75
Helix eversa Deshayes in Férussac, 1851: I, p. 395, pl. 1, fig. 5–7
Cepaea eversa eversa (Deshayes)-Wenz 1920b: 156, fig. 1–2
Cepaea eversa larteti (Boissy)-Wenz 1920b: 156, fig. 3–6.
Cepaea eversa eversa (Deshayes)-Wenz 1923: 617–619
Cepaea eversa larteti (Boissy)-Wenz 1923: 619–625
? *Cepaea eversa baumbergeri* Jooss, 1923: 200–204, pl. XI, fig. 24–27
Megalotachea turonensis Desh.-Pfeffer 1929: 147, Pl.. II, fig. 30–31
Megalotachea turonensis (Deshayes, 1831)-Truc 1971: 284–293, pl. 15, fig. 1–3. (See here for further synonyms)
Cepaea larteti (Boissy, 1844)-Fischer 2000:147, fig. 25a–c, 26a-c.

Material examined 5 specimens.

Description Relatively large, distinctly massive dextral helicoid shell with typical "*Cepaea*-form". The whole shell looks much more bulbous than that of all the other species. It is up to ca. 24mm wide and ca. 20mm high. The shell height to height of the aperture relationship is 1.7. It consists of 4 ¾ to 5 convex, regularly growing whorls. Sutures are moderately deep. Before reaching the aperture, the last whorl runs obliquely downward. The aperture has an oval shape stretched in width. The first part of the upper margin runs more or less straight and the lower one goes obliquely downward. The periostome are turned backwards and are remarkably thickened on the inner side. The insertions are connected by a relative thick parietal callus. The umbilicus region is completely covered by this callus. The smooth protoconch consists of ca. 1 ¼ relative flat whorls. The teleoconch bears fine regularly arranged growth lines. On some specimens traces of up to three bands are preserved.

Discussion According Kadolsky (pers. comm., 2015) there are taxonomic and nomenclatorial uncertainties considering the taxa *P. turonensis*, *Helix asperula* Deshayes, 1830 or 1832 and *Helix duvauxi*, Deshayes, 1830 or 1832. Also the publication dates are not sure (see Welter-Schultes 2012). For a clear solution of this problem it is indispensable to examine the original material of Deshayes. However, this would go beyond the scope of this paper. Following Truc (1971), *Helix larteti* de Boissy, 1840 and *Helix eversa* Deshayes in Ferussac, 1851 are synonym with *Palaeotachea turonensis* (Deshayes, 1831). Jooss (1923) designated a species *Cepaea eversa baumbergeri* from the Helicidenmergel. It is only a steinkern, but with traces of a remarkable reflected and distinct periostome. However, due to the incomplete preservation, no definitive identification is possible. The shell is also a little stretched in width. The remarkable inner thickened aperture especially the thickened columellar makes *P. turonensis* uniquely identifiable.

Distribution Hohenmemmingen, Stoffelberg near Ehingen, Emerberg, Grund near Vienna. Sandelzhausen (Gall 1972), Korneuburger Basin (Binder 2002), Sansan (Fischer 2000), Manthelan (Wenz 1920b), Faluns de Touraine (Truc 1971), Rognes (Schlickum & Strauch 1971). For other localities see Wenz 1923, p. 619 & 624–625).

Mammal zone (MN) range MN5-MN6.

Discussion

How many genera?

Our morphometric considerations confirmed that *P. silvana, P. sylvestrina, P. dentula, P. renevieri, P. elevata* and *P. turonensis*, formerly attributed to *Cepaea*, are morphologically closely related to each other and can be attributed to *Palaeotachea*. Yet, all of them could be confirmed to represent valid species.

In 1971, Schlickum & Strauch designated the genus *Frechenia* for Pliocene, helicoid land snails with a remarkable reflected and distinct outer lip/palatal margin. The type locality is a coal pit in Frechen near Cologne, Germany. As type species, they defined *Frechenia reichenbachi*. Due to the distinct palatal margin, the authors assumed a possible relationship with the Miocene *Palaeotachea turonensis* (Deshayes, 1830) and the Recent *Eobania vermiculata* (O.F.Müller 1774), which have similar morphological characters. They also wrote, however, that they had not enough appropriate material to resolve this question. Later, Truc (1971) postulated that *Frechenia* is a side branch that has developed from *Megalotachea* (=*Palaeotachea*), which he in turn interprets as the ancestor of the Recent, monospecific genus *Eobania*. According to Nordsieck (2014c), *Frechenia* may be related to *Cepaea*. Our morphometric analysis suggests that *Frechenia* does not show any relationship with the species studied herein.

Differences between P. silvana and P. sylvestrina

It is important to note that a qualitative comparison of the measurements (see Methods and Results sections) does not allow spearation between *P. silvana* and *P. sylvestrina*. This reflects a problem that is frequently addressed in literature. Cluster and PCA analysis do, however, confirm the separation into two species. In summary, the younger *P. sylvestrina* differs in the following morphological aspects from *P. silvana*:

1. *P. sylvestrina* is usually larger.
2. *P. sylvestrina* is usually more spherical and higher.
3. *P. silvana* has a flatter spire and is more stretched in width.
4. The outline of the last whorl of *P. silvana* is stronger curved and can be indistinctly subangulate. Also some specimens of *P. sylvestrina* can have a very slight angulation on the last whorl, but it is usually less distinct than in *P. silvana*.
5. *P. sylvestrina* has a deeper suture.
6. The protoconch of *P. sylvestrina* is a bit flatter than that of *P. silvana*.
7. In *P. silvana*, the periostome region is generally more thickened.
8. The peristome of *P. silvana* is more expanded (see Figs 5. 6, 5.7 & 5.9).
9. The angle of spire around 117°in *P. silvana* and around 100°in *P. sylvestrina*.

Until today, the two species names *gottschicki* and *sylvestrina* were used in different manner in literature. Already Wenz (1920a & 1920b) has mentioned that there are no distinct boundaries between these subspecies and they could only be seen as graphical races ("lokale Rassen"). In fact, there are no clear dividing lines, not even in the statistical charts, which would justify a division into subspecies. The range of morphological disparity is comparable to that of the extant species *Cepaea nemoralis* and *C. hortensis*. For this reason, the subspecies *Palaeotachea sylvestrina sylvestrina*, *P. sylvestrina gottschicki* and *P. sylvestrina geniculata* are herein emended and summarised into the species *Palaeotachea sylvestrina*.

The silvana and sylvestrina beds

In literature about the geology of Southern Germany, the term "*silvana*-Schichten" is often used. In some publications, such as Miller (1871), the same sediments were named "*sylvestrina*-Schichten". In 1921, Wenz postulated a differentiation between older *silvana* beds and the younger

Table 3 Different angle of spire at *P. silvana* and *P. sylvestrina*.

	Locality	Angle of spire Minimum value	Angle of spire Maximum value	Angle of spire Mean value
P. silvana	Zwiefalten	105°	130°	117,6°
P. silvana	Mörsingen	100°	135°	117,1°
P. sylvestrina	Steinheim am Albuch	84°	116°	99,5°
P. sylvestrina	Reimlingen, Nördlinger Ries	88°	113°	100,9°

Table 4 The *silvana* beds, named after *Palaeotachea silvana*, and their subdivision.

Upper *silvana*-beds	With *Palaeotachea silvana* (formerly *Cepaea silvana malleolata*), known as "Malleolatakalk".
Middle *silvana*-beds	Dominated by *Palaeotachea silvana* and *Palaeotachea turonensis* as well as *Pseudochloritis incrassata*.
Lower *silvana*-beds	*Larteti-Palaeotachea turonensis*) beds "Flammenmergel" with *Palaeotachea dentula* as index fossil.

sylvestrina beds. According to him, only the beds containing *Palaeotachea silvana* should be named *silvana* beds. Following Wenz (1924) the OSM starts with this unit. Our taxonomic results in fact confirm the differentiation between *Palaeotachea silvana* and *P. sylvestrina* and accordingly the presence of two different horizons (*silvana* beds and *sylvestrina* beds). After Wenz (1924), the name-giving species is rare to find in the lower part of the *silvana*-beds. Due to the lack of current outcrops, one has to rely to a large extent on the stratigraphic information of Wenz (1919; 1920; 1921) and Jooss (1923). They presented a subdivision of the *silvana*-bed as shown in Table 4. *Palaeotachea silvana* is often associated with *Pseudochloritis incrassata* (Klein, 1853), *P. sylvestina* often with *Granaria schuebleri* (Klein, 1846) and *Pseudochloritis insignis* (von Zieten, 1832).

Relevant traits and identification key

The traits that are most important for the identification of Miocene *Palaeotachae* species are: (1) shell size, particularly the width; (2) shape of the last whorl; (3) shape of the protoconch (4) margin of periostome, including grade of deflection and thickness; (5) angle of spire; (6) sutures and convexity of whorls.

This key to the identification of *Palaeotoachea* on the species level is based on the morphometric aspects as demonstrated above. Some further considerations that can be helpful are: (1) *P. silvana* and *P. sylvestrina* are the most abundant species in all studied associations. (2) *P. dentula*, *P. renevieri* and *P. elevata* are relative small, while *P. silvana, P. sylvestrina* and *P. turonensis* are remarkably larger. (3) The most difficult case is the differentiation between *P. silvana* and *P. sylvestrina*, but measuring the angle of spire can help (see descriptions above and Nr. 3in the key). (4) *P. silvana* can be associated with *P. turonensis*, *P. dentula* as well as *Pseudochloritis incrassata*, while *P. sylvestrina* is associated with *P. elevata*, *P. turonensis*, *P. dentula*, *P. renevieri* as well as *Pseudochloritis insignis*.

1. Shell >15mm wide?
   Yes: go to **2**
   No: go to **4**
2. Peristome remarkably thickened (see Fig. 5.18)?
   Yes: *Palaeotachea turonensis*
   No: go to **3**.
3. Angle of spire on an average 100°
   Yes: *P. sylvestrina*
   No: *P. silvana*
4. Shell ca. 9mm high or less?
   Yes: *P. dentula*
   No: go to **5**
5. Last whorl "keel-like rounded?
   Yes: *P. renevieri*
   No: *P. elevata*

CONCLUSIONS

Several species of the"*Cepaea*-type" genus *Palaeotachea* were described from the Miocene of the North Alpine Foreland Basin and its adjacent smaller basins. This taxonomic complex can now be separated into six species: *Palaeotachea silvana* (Klein, 1853), *P. sylvestrina* (Schlotheim, 1820), *P. dentula* (Quenstedt, 1867), *P. renevieri* (Maillard, 1891), *P. elevata* Berz & Jooss, 1927 and *P. turonensis* (Deshayes, 1831). These species can be separated using morphological features, which could be partly confirmed by the statistical analyses of morphometric indices. The most difficult differentiation is that between *Palaeotachea silvana* and *P. sylvestrina*, but they are clearly two different species from two different stratigraphic levels. As a consequence, the historical differentiation between *silvana* beds and *sylvestrina* beds could be confirmed. In total, only 13 verified locations with defined Mammal Neogene zones (MN) are known. For this reason, the exact biostratigraphic range of the single species is hard to determine with certainty. The potential relation between *Palaeotachea turonensis* and the Pliocene genus *Frechenia* as well as the Recent *Eobania vermiculata*

mentioned in literature, cannot be solved with morphometric features.

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