PSEUDOCHLORITIS INSIGNIS – A PECULIAR LARGE LAND-SNAIL FROM THE MIOCENE OF SW GERMANY: TAXONOMIC STATUS AND CENSUS OF MORPHOLOGICALLY RELATED FORMS

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Abstract *The Miocene land gastropod* Pseudochloritis insignis *(von Zieten, 1832) shows a very high variability in size and its systematic designation has been debated for a long time. Statistical analyses reveal no indications for the presence of more than one species. Since the original material is definitely lost, we have defined a neotype. The relationships between P. insignis and the following taxa are discussed: Genus* Ampelita *(Acavidae), genus* Trigonephrus *Pilsbry, 1905 (Dorcasidae), genus* Chloritis *Beck, 1837 (Camaenidae), genus* Liburnica *Kobelt, 1904 (Helicidae: Ariantinae), genus* Dinarica *Kobelt, 1902 (Helicidae: Ariantinae) and* Monacha homalospira *(Reuss, 1860) (Hygromiidae) as well as* Pseudochloritis incrassata *(Klein, 1853) and the family Elonidae Gittenberger, 1979. An assignment to* Ampelita, Trigonephrus, *or* Chloritis *is rejected because of morphologic differences as well as palaeobiogeographic and palaeoclimatic considerations. The species* Monacha homalospira *(Reuss, 1860) is remarkably older than* P. insignis. *Due to teleoconch morphology as well as shape and sculpture of the protoconch, a membership of* insignis *within the fossil genus* Pseudochloritis *C. R. Boettger, 1909 is suggested herein. The stratigraphy of* P. insignis *ranges from late Langhian to early Tortonian (mammal zones MN 7 to MN 9). The suprageneric designation of this genus is, however, problematic. As for the morphological characters, it shows more similarities with the subfamiliy Ariantinae Mörch, 1864 (Helicidae) than with the Elonidae Gittenberger, 1979, but due to the absence of anatomical features this designation remains tentative.*

Key words *Gastropods, Ariantinae, Joossia, Dinarica, Steinheim Basin, microsculpture.*

INTRODUCTION

The Middle to Late Miocene species *Pseudochloritis insignis* (von Zieten, 1832 (Pulmonata, Gastropod) is a large land gastropod from the lacustrine sediments of the Steinheim Basin in SW Germany, a Middle Miocene impact crater lake. It was first described by von Zieten (1832) as *Helix insignis* from Steinheim am Albuch (Baden-Württemberg, SW Germany). Since then, several authors have discussed the phylogenetic relationships of this species. The first was von Kurr (1856), who related *P. insignis* to the South African genus *Trigonephrus* (Dorcasidae), followed by Sandberger (1872), who suggested a relationship with *Liburnica hoffmanni* (Rossmässler, 1836) (Helicidae: Ariantinae). Several authors then made assumptions about the relationship of *P. insignis* and in 1909 O. Boettger saw *P.insignis* as an ancestor of *Monacha homalospira* (Reuss, 1860) and the Madagascan genus *Ampelita* (Acavidae) (see O. Boettger 1909). Gottschick & Wenz (1920) and C.R. Boettger & Wenz (1921) compared it with the extant *Dinarica stenomphala* (Menke, 1830) (Helicidae, Ariantinae) (see also Schileyko 2006). Pfeffer (1929) proposed the new genus *Joossia* for the species *insignis* within the family Eulotidae. Later, Nordsieck (1986) placed it in the family Xanthonychidae. Binder (2008) referred *P. insignis* to the Ariantinae. According to C. R. Boettger (1909), some authors (not mentioned by him) had placed *P. insignis* into the relationship of *Chloritis* (Camaenidae). Miller (1900), C. R. Boettger (1909) and Nordsieck (1986) as well as Binder (2008) saw a strong relationship with the Badenian species *Pseudochloritis incrassata* (Klein, 1853).

This paper presents the first detailed study of *P. insignis* and aims to clarify its taxonomic status with statistical methods and considerations of shell morphology. The geographic distribution as well as stratigraphy and palaeoecology are discussed. After a morphological description with the definition of a neotype, a statistical analysis of shell parameters is presented. Then we compare *P. insignis* with other genera and discuss its attribution to a family.

MATERIAL AND METHODS

The species was first described as *Helix insignis* by von Zieten (1832). The next studies were conducted by Adolph von Klein (1805–1892) in 1846

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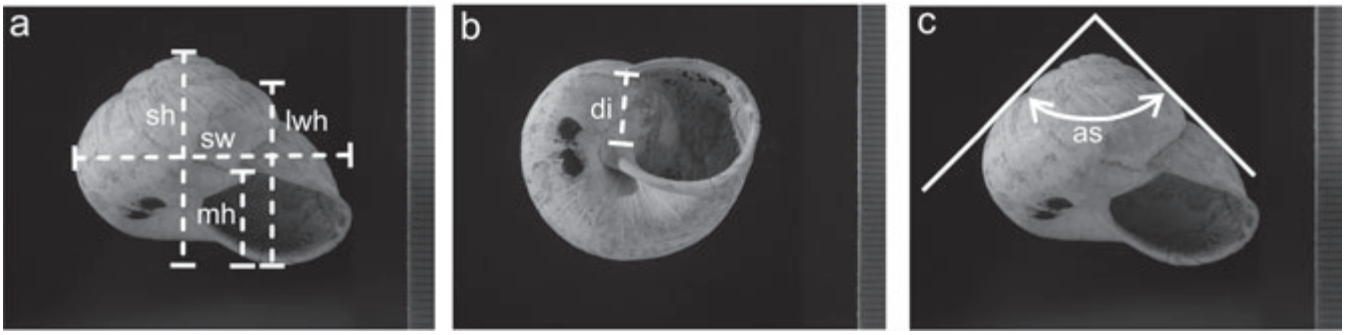


Figure 1 Measurements of the different morphometric features.

and by Miller (1900), the material of whose is present in the collection of Staatliches Museum für Naturkunde Stuttgart (SMNS). A remarkable number of shells also occurs in the collection of Franz Gottschick. He was a forester in Steinheim am Albuch at the beginning of the 20th century and the author of some publications about the fossil snails of Steinheim am Albuch, partly together with the malacologist Wilhelm Wenz. After his death in 1927, his collection came to the SMNS. Another important contemporary collection with a considerable number of unpublished shells of *P. insignis* at the SMNS is that of Carlo H. Jooss (born in 1883).

The collection of the first author Carl Hartwig von Zieten (1785 – 1846) is lost, apart from some Mesozoic material (Cleevely 1983). We searched the SMNS collection intensively and made a survey among other German colleagues and so we can confirm that no relevant material exists. Due to this fact and to delineate it from *Pseudochloritis incrassata* (Klein, 1853) , we are herein defining a neotype in accordance the International Code of Zoological Nomenclature (online version: www.nhm.ac.uk/hosted-sites/iczn/code). The neotype is from the original material of Klein (1846). The front cover of the issue of this journal shows the year 1847, but the pagination within the journal always quotes the year 1846. It is not clear, whether this is because of a typo, but from the beginning (e.g., Klein 1853) this paper was cited as 1846.

In order to analyse the morphological variability of *P. insignis* and to find potential relationships, the following standard parameters were measured (Fig. 1a–c)**:** shell height (**sh**), shell width (**sw**), height of the aperture (**mh**), and height of the last whorl (**lwh**). Additionally, the angle of spire (**as**) and the distance between the insertions (**di**) were measured. This was done for the species *Pseudochloritis insignis* (n=82), *P. incrassata* (n=82) as well as *Dinarica pouzolzi* (n=77). The two last named species are the type species of their genus. They were chosen, because they represent the morphologically and palaeogeographically closest forms to *P. insignis*. Only adult shells were measured. The measurements were made with a digital slide gauge, a goniometer, and the image analyses software Image J (Burger & Burge 2006). All material is stored in the Staatliches Museum für Naturkunde Stuttgart (SMNS): fossil gastropods in the collection of Tertiary and Quaternary Invertebrates, and modern gastropods in the Malacozoology collection. The numbers and localities of the measured specimens are listed in Appendix 1. For further statistical calculations, the following ratios were calculated (compare Fig. 1): sh/sw, sh/mh, sh/lwh, sh/di, sh/as, sw/mh, sw/lwh, sw/di, sw/as, lwh/mh, mh/di, mh/as, lwh/di, lwh/as. Furthermore, arithmetic mean (A) and standard deviation (SD) were calculated for each ratio (Appendix 2). A cluster analyses (Ward`s method, euclidean) was calculated using all measured ratios mentioned above, and another one using arithmetic means only (Fig. 2b; Appendix 2) using the statistics software "PAST" (Hammer *et al*. 2001). Furthermore, a Principal Component Analysis (PCA; variance-covariance Matrix; Fig. 3) was calculated using the measured single parameters (sh, sw, etc.).

All the measured material of *P. insignis* comes from Steinheim am Albuch. The SMNS also has a relatively large number of specimens from the Late Miocene (MN 9) of Höwenegg near Immendingen (Baden-Württemberg, S Germany). These specimens are, however, mostly deformed and therefore not usable for morphometric methods.

RESULTS

SYSTEMATICS

Pseudochloritis insignis (von Zieten, 1832)
(Figs 4.1, 4.2, 4.7, 4.8; Figs 5.7, 5.8; Figs 6.1–12)

Helix insignis Schübler in von Zieten, 1832: P. 38, Tab. XXIX, Fig. 1 (Steinheim am Albuch (Original material lost).
Helix insignis Schübler – Klein, 1846: P. 65, tab. 1, fig. 2
Helix steinheimensis – Klein, 1846: P. 70, tab. 1, fig. 10
Helix steinheimensis Klein- Sandberger 1872: pl. 28 F. 9, 9a
Helix (Campylaea) insignis var. *steinheimensis* Klein- Sandberger, 1872: 650
Helix (Campylaea) *insignis* Schübler – Sandberger, 1872: P. 650.
Chilostoma (Dinarica) insignis (Schübler) Zieten – Gottschick & Wenz, 1920: P. 44.
Campylaea (*Dinarica*) *insignis* (Zieten) – Wenz, 1923: P. 522 (see there for more synonyms)
Joossia insignis (Zieten) – Pfeffer, 1929: P. 246
Joossia insignis (Zieten 1830) – Binder, 2008: P. 177.

Material A most typical specimen of the Klein collection (Figs 4.1, 4.7, 4.8)) is defined as the neotypus of *Pseudochloritis insignis* (von Zieten, 1832). It is stored at Staatliches Museum für Naturkunde Stuttgart (SMNS), inv. no. SMNS 23910b. The *locus typicus* is the Steinheim Basin (coordinates of the basin center: 48°41'11.8"N 10°03'55.8"E), political district Steinheim am Albuch, Baden-Württemberg, SW Germany. The *stratum typicum* are the "Steinheimer Seeschichten", mammal zone MN7, Middle Miocene.

Description The massive shell has a dextral, helicoid shape, ranging from globular to very depressed. It consists of 4.5 regular whorls. The

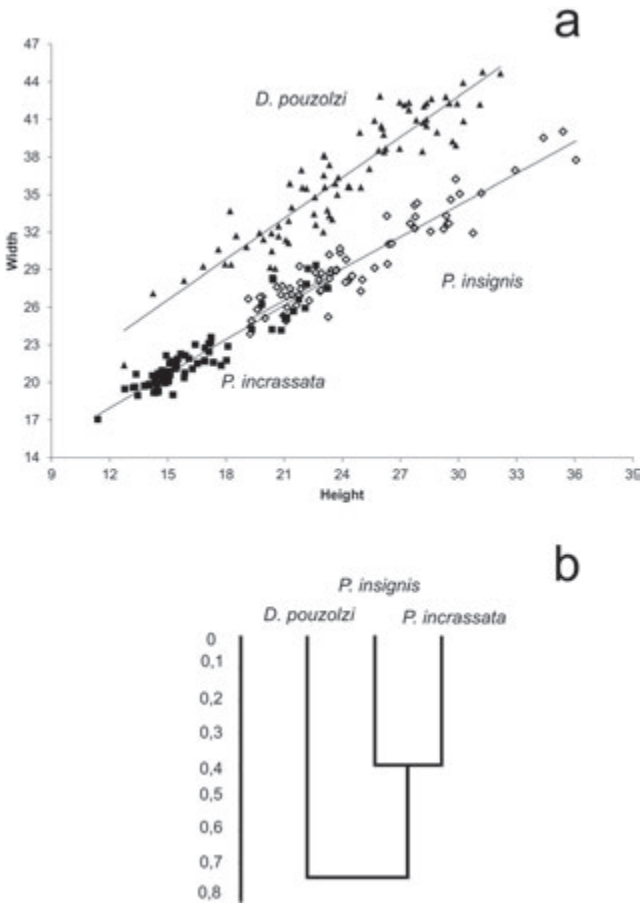


Figure 2a. Diagram with the plotted shell height and shell width. **b.** Cluster analysis with *Pseudochloritis insignis*, *P. incrassata* and *Dinarcia pouzolzi*.

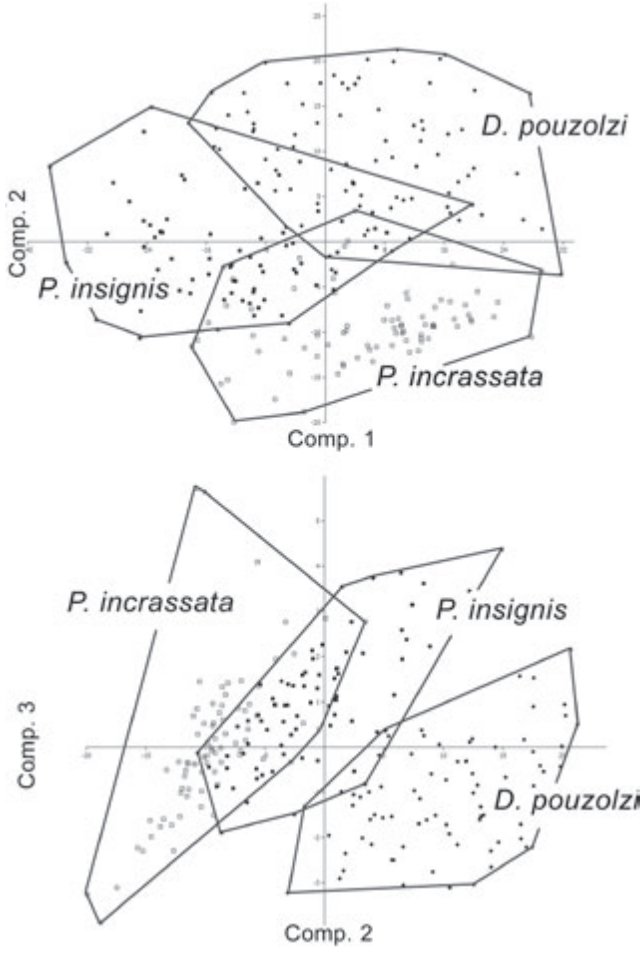


Figure 3 Principal component analysis (PCA) with *Pseudochloritis insignis*, *P. incrassata* and *Dinarcia pouzolzi*.

neotype is 28mm high and 32mm wide. The aperture is 18mm high and the last whorl 24mm. The protoconch of the neotype is ca. 2.5mm in diameter. Height and width measures of the different shells are extremely variable. The average height /width ratio is ca. 0.81, that of the neotype is ca. 0.89. The whorls are convex with moderately deep sutures. Before reaching the periostome, the last whorl runs downwards obliquely. The aperture has an oblique-ovate shape. The peristome is deflected. The insertions are connected by a thin callous layer .The umbilicus is deep and half covered by a columellar callus. There are very distinct and regular prosocline growth lines on the whorls. Their strengths differ between individuals. The microsculpture consists of little hair pits on the first teleoconch whorls (Figs 5.7, 5.8), which disappear on the later whorls. The protoconch consists of ca. 1.5 whorls and has a remarkably bulbous shape. The microsculpture of the protoconch consists of little pustulae and little pits (Fig. 6.10), which was also described by Gottschick & Wenz (1920) and Binder (2008). These are visible on the neotype even at low magnification. Likewise, fold-like ribs can be found on the protoconch. The thickness and strength of these folds are variable. A few specimens bear traces of a brown band near the periphery of the last whorl just like *Pseudochloritis incrassata* (Klein, 1846) (see also C. R. Boettger 1911; Binder 2008). The secondary ribs on the last whorl as described by Binder (2008), are hardly visible in the studied material. In some specimens, also very weak traces of spiral lines can be seen. In the collection of the SMNS, the largest specimen has a width of 40mm. Most of the shells widths range between 24 and 36mm. The maximum diameter according to Miller (1900) is 43mm, but he also wrote that the specimen figured in von Zieten (1832) has 44mm. Quenstedt (1884) mentioned 47mm for the specimen figured by von Zieten. Unfortunately, the original description of von Zieten (1832) contains no size specification and the material is lost.

Statistics The sh/sw diagram (Fig. 2a) for *P. insignis* and *P. incrassata* reveals a linear function between shell height and width. The measured A and SD values are listed in App. 2. *Pseudochloritis insignis* and *P. incrassata* show the highest SD in the sw/di division. This ratio seems to be the most variable one among shells of *P. insignis*. This species has the lowest SD of the sh/lwh ratio with 0.03, which means that the relationship between shell height and height of the last whorl seems to be relatively constant. *D. pouzolzi* has the highest SD of the lwh/di ratio. The cluster analysis of the arithmetic mean values (A) (Fig. 3) shows a closer affinity between *P. insignis* and *P. incrassata* than between the former and *D. pouzolzi*. The first three components of the PCA (Fig. 3) account for 66.73%, 31.69% and 0.94%, respectively. Both a scatter plot of PC1 (Eigenvalue 193.40) and PC 2 (91.85), and one of PC 2 and PC 3 (2.72), respectively, reveal clear separation of the three species. Most overlaps occur between *P. incrassata* and *P. insignis*, on the one hand, and between *P. insignis* and *D. pouzolzi*, on the other.

Palaeogeographic distribution *Pseudochloritis insignis* has a relatively limited geographical distribution in Baden- Württemberg, SW Germany. Most of the specimens in the collections come from Steinheim am Albuch (48°41'16.6"N 10°03'35.6"E). The other locality with a higher number of shells is Höwenegg near Engen (47°54'41.2"N 8°44'30.9"E). Besides that, only one specimen from Böttingen (48°24'44.5"N 9°33'10.0"E) is known. Several other localities are mentioned by Wenz (1923), but none of these findings could be confirmed among the studied collections. Therefore, these records should be treated with caution. A confusion with the species *P. incrassata* is possible.

Palaeoecology Since direct descendants are unknown, the ecological preferences of *P. insignis* are difficult to reconstruct. According to Goodfriend (1986), larger snails are frequently associated with relatively moist conditions. The presence of hairs would also indicate a moist environment (see Pfenninger *et al*. 2005).

Stratigraphy The species is reported from Middle Miocene (mammal zone MN 7, Steinheim am Albuch; summary in Rasser 2013) to Late Miocene (mammal zone MN 9; Höwenegg; summary in Munk *et al*. 2007). The stratigraphy of the locality Böttingen is not supported sufficiently, but assumed to be Middle Miocene (Rosendahl *et al*. 2003). According to Gottschick & Wenz (1920), *P. insignis* occurs in Steinheim am Albuch in the *trochiformis*-beds and in the *kleini*-beds as well as in the layers above them (review

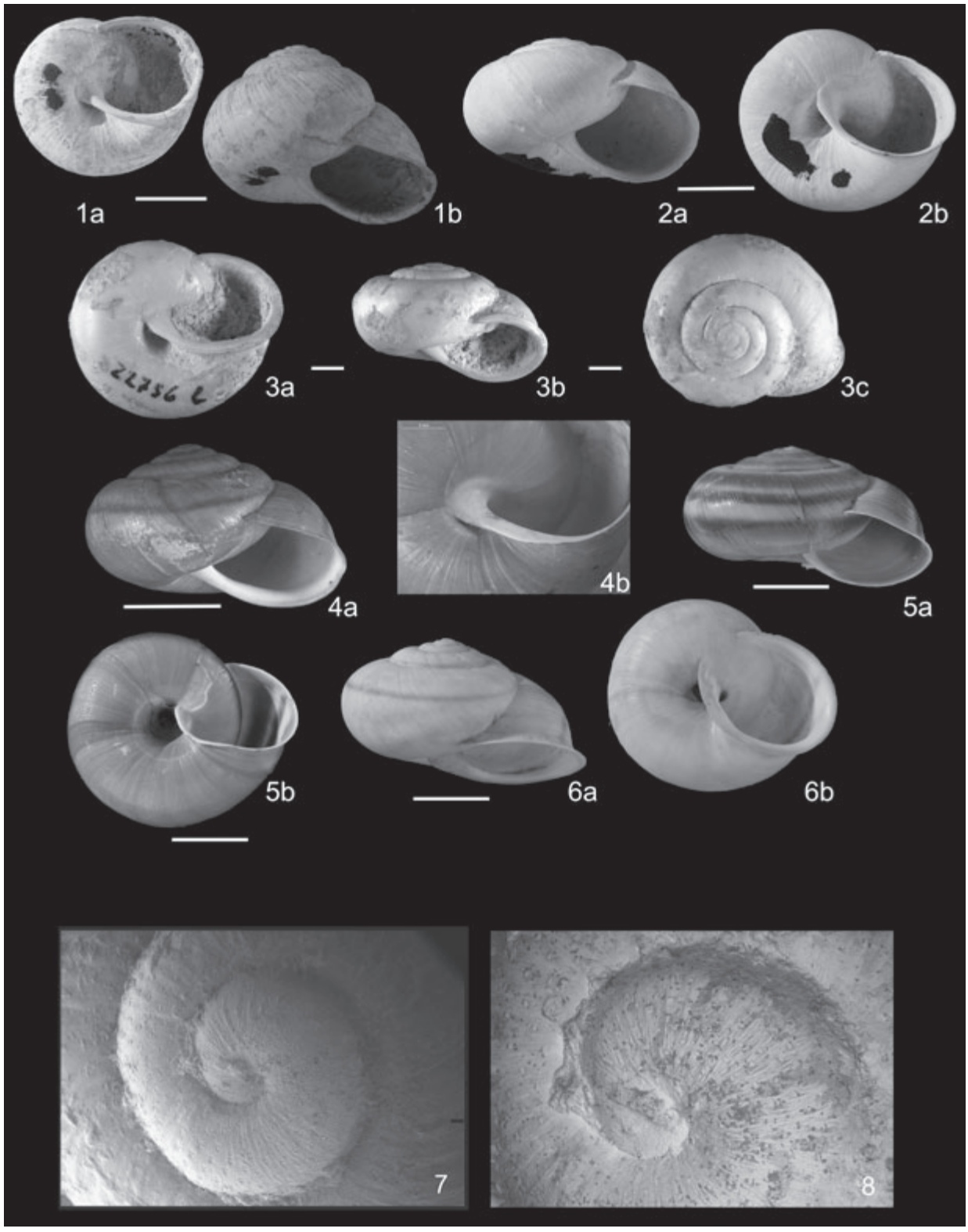


Figure 4.1 *Pseudochloritis insignis* (von Zieten, 1832), Steinheim am Albuch, Miocene, Neotype, Scale 10mm, SMNS 23910b. **4.2** *P insignis*, Steinheim am Albuch, Miocene, Scale 10mm, SMNS 101666. **4.3** *P. incrassata* (Klein, 1853), Zwiefalten, Miocene, One of the original material of *Helix inflexa* Klein, 1846. Scale 10mm. SMNS 101525. **4.4** *Dinarica stenomphala* (Menke, 1830) SMNS-ZI0078280. Welebit, Croatia. Scale: a=5mm, b=2mm. **4.5** *D. pouzolzi* (Deshayes, 1832) SMNS-ZI0078278, Aleksina Medja near Trebinje, Bosnia and Herzegovina, Type species of *Dinarica*. Scale 10mm. **4.6** *Liburnica hoffmanni* (Rossmässler, 1836), SMNS-ZI78279, Dalmatia. Scale 10mm. **4.7** *P. insignis*, Protoconch of Fig. 1, Neotype, Scale 200µm. **4.8** *P. insignis* , Detail of Fig. 7, Neotype, Scale 100µm.

in Rasser 2013). Finger (1998) also mentioned "*Dinarica*-fragments" (probably *P. insignis*) in the basal *kleini* beds. For most specimens, however, detailed stratigraphic information is lacking. Following Binder (2008), the related *P. incrassata* is restricted to the Badenium (Langhian of the International Chronostratigraphy), which incorporates mammal zones MN5 and MN6 (Berger *et al*. 2005; Hilgen *et al*. 2012).

Discussion of the systematic position

The specimens of *P. insignis* show a distinct variability in height and width. They range from very flat forms to relatively high ones. However, morphometric analyses reveal no evidence for the presence of more than one species. Originally, the species *insignis* was placed within the genus *Helix* Linnaeus, 1758, like many of other terrestrial gastropods in the 18th and 19th century. Since this time, different proposals for the systematic position of P. *insignis* were made, which are discussed herein.

Helix Linnaeus, 1758
P. insignis clearly differs from *Helix* (compare Schileyko 2006) by the following points: (1.) height/width ratio, (2.) growth development of the protoconch and (3.) lack of sculpture on the protoconch.

Trigonephrus Pilsbry, 1905 (Dorcasidae)
According to von Kurr (1856), no European species is comparable to *P. insignis*. He assumed that it is related with the South Africanp secies *Trigonephrus rosaceus* (Müller, 1774), because of its funnel-like umbilicus. This genus is known from SW Africa since the Eocene (Wenz & Zilch 1960). Today it is limited to the vicinity of the coastline and rivers in the desert regions of SW Africa (Wenz & Zilch 1960). Following Schileyko (1999), however, the embryonic whorls of *Trigonephrus* are smooth, which is in opposite to *P. insignis*. This fact and the geographic distance between them is an argument against this relationship.

Monacha homalospira (Reuss, 1860) (Hygromiidae)
O. Boettger (1909) suggested that *Pseudochloritis insignis* is a "mixed-type" ("Mischtypus"), being the ancestor of the madagassian genus *Ampelita* (family Acavidae) and of *Helix homalospira* Reuss, 1860 (*Monacha homalospira* according to Wenz 1923). O. Boettger (1909) did, however, not specify his hypothesis. Following Sandberger (1872), the last named species occurs only in Tuchořice and Lipno/Czech Republic. The stratigraphic correlation of these localities is Early Miocene (MN 3b; Harzhauser *et al*. 2014), which is much older than the *stratum typicum* of *P. insignis*. Therefore, *insignis* can hardly be the ancestor of *homalospira*.

Ampelita Beck, 1837 (Acavidae)
O. Boettger (1909) suggested that *P. insignis* is the ancestor of the *Ampelita* Beck, 1837. *Ampelita* contains several species with varying shell morphologies. The genus is known since the Pleistocene (Wenz & Zilch 1960) and is restricted to Madagascar (Schileyko 1999). The type species of the genus is *A. lanx* (Férussac, 1821), which differs significantly from the gastropods discussed herein. The only species within the genus that is morphologically comparable with *P. insignis* is *A. robillardi* (Angas, 1876). Nevertheless, there are two arguments against O. Boettgers hypothesis: (1.) *Ampelita* has smooth embryonic whorls (Schileyko 1999) and (2.) the palaeogeography: when *P. insignis* first appeared in the Miocene, Madagascar was already isolated from the continent.

Chloritis Beck, 1837 (Camaenidae)
Another group with a *P. insignis*- like morphology is the Camaenid genus *Chloritis* Beck, 1837, which includes *Austrochloritis* Pilsbry, 1891 and *Nannochloritis* Iredale, 1938, whose taxonomic rank is under discussion (Schileyko 2003; Dharma 2005; Stanisic *et al*. 2010). The species *Nannochloritis layardi* (Gude, 1906), illustrated in Stanisic *et al*. (2010), has a similarly shaped protoconch and the same pustulated sculpture as *P. insignis*. From the overall outline *Chloritis (Austrochloritis) argillacea* (Férussac, 1821), illustrated in Dharma (2005, Pl. 89), is comparable with *P. insignis*. It has a reflected lip and a half covered umbilicus like *P. insignis*. The Camaenidae are widespread in the tropics (Richardson 1985, cited in Harzhauser *et al*. 2008). It is a very large group with many different shell forms (Dharma 2005 or Abbott 1989). They are, however, a polyphyletic group and need to be revised, because the American forms are closely related to the Helicidae and Helminthoglyptidae, while the Australasian ones are a sister group to the Bradybaenidae (Scott 1996). According to this

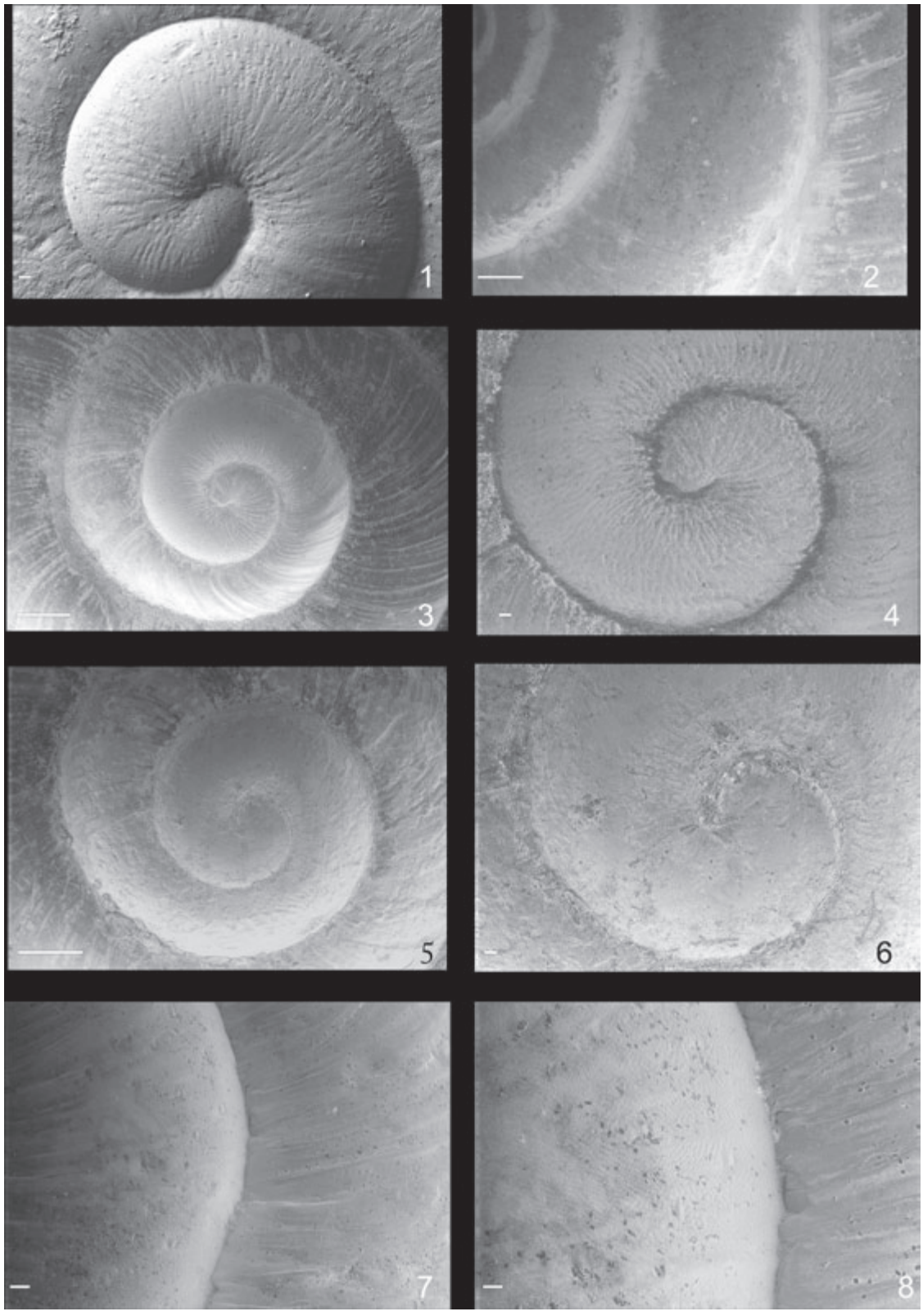


Figure 5.1 *Pseudochloritis incrassata* (Klein, 1846), Protoconch of Fig. 4.3, Scale 100 µm. **5.2** *P. incrassata*, Zwiefalten, Miocene, One of the original material of *Helix inflexa* Klein, 1846, Detail of the teleoconch, Scale 1mm. SMNS 101525. **5.3** *Dinarica pouzolzi* (Deshayes, 1832), Dubrovnik, Croatia. Subadult, Protoconch, Scale 1mm, SMNS-ZI78281. **5.4** *D. pouzolzi* (Deshayes, 1832), Detail of Fig. 3 Scale 100 µm. **5.5** *D. stenomphala* (Menke, 1830), Protoconch of Fig. 4.4. Scale 1mm. **5.6** *D. stenomphala* (Menke, 1830), Detail of fig. 5. Scale 100 µm. **5.7 & 5.8** *P. insignis* (von Zieten, 1832), Steinheim am Albuch, Detail of the teleoconch, Neotype, SMNS 101.524. Scale fig. 7: 200 µm, fig. 8: 100 µm.

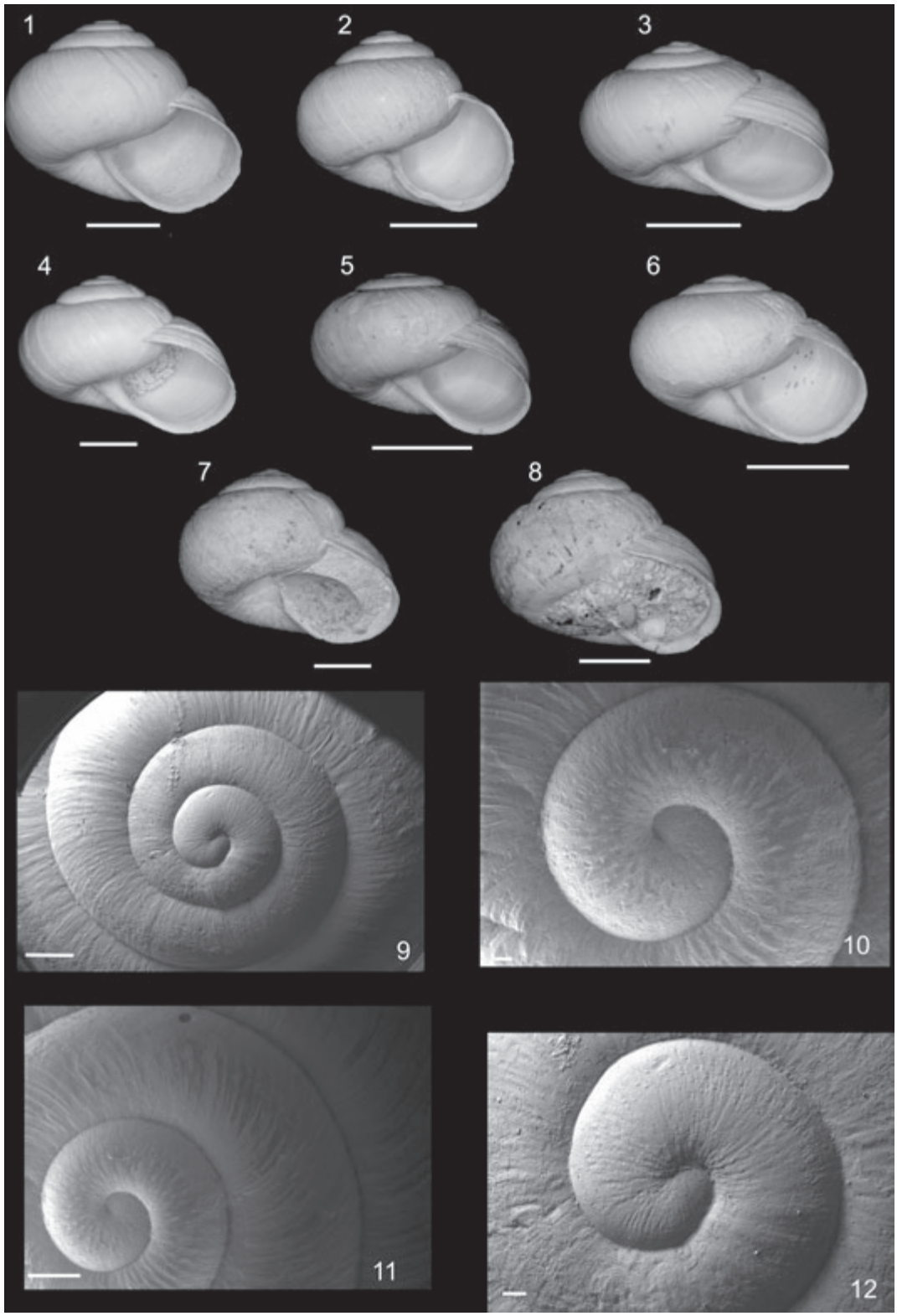
author, the family Camaenidae was defined only by anatomical features (lack of a dart sac and glands). Therefore, an affiliation of a fossil taxon to this family is problematic. Also the "*Chloritis*-group" within the Camaenidae seems to be in need to revision.

Dinarica Kobelt, 1902 (Helicidae, Ariantinae)
Gottschick & Wenz (1920) and C. R. Boettger & Wenz (1921) compared *P. insigins* with the Recent species *Dinarica stenomphala* (Menke, 1830) (Fig. 4.4; Figs 5.5–5.6). The genus *Dinarica* occurs in the Balkan region (Knipper 1939) and the type species is *Dinarica pouzolzi* (Deshayes, 1830) (Fig. 4.5; Figs 5.3–5.4). Following the descriptions of Gottschick & Wenz (1920), however, there are remarkable differences: (1.) Teleoconch: *D. stenomphala* has up to six whorls. The first whorls of *P. insignis* are wider and more massive and the last whorl is more bulbous. The umbilicus in *D. stenomphala* is more covered than that of *P. insignis.* (2.) Embryonic whorls: *D. pouzolzi* and *D. stenomphala* lack the little knobs that occur on the embryonic whorls of *P. insignis*. The growth development of the protoconch is different. The size increases faster in *P. insignis* . (3.) Shells of *Dinarica* are hairless (Subai 2002). (4.) Morphometrics suggest clear separation of the type species *Dinarica pouzolzi* and of *P. insignis* (Figs 2, 3).

Liburnica Kobelt, 1904 (Helicidae, Ariantinae)
Sandberger (1872) placed *P. insignis* close to *Liburnica hoffmanni* (Rossmässler, 1836) (Fig. 4.6), which corresponds particularly with the low-spired forms of *P. insignis*. *L. hoffmanni* has little hair pits on the first whorls (Subai 2002), but the presence of hairs can be different among the single populations and individuals (Knipper 1939). Gottschick & Wenz (1920) have already pointed out the differences between *P. insignis* and *L. hoffmanni*. These are: (1.) The forms of *P. insignis* are lower spired and the peristome is more strongly reflected. (2.) The last whorl is a little more descending and the aperture is not that oblique; *L. hoffmanni* has a thin callus-ledge on the basis of the aperture. (3.) The insertions are remarkably closer to each other in *L. hoffmanni*. (4.) The radial growth lines of *P. insignis* are much stronger. (5.) According to Schileyko (2006), the genus *Liburnica* has mostly smooth embryonic whorls, or they are very finely granulated.

Joossia Pfeffer, 1929 (Eulotidae)
Based on morphology and sculpture, Pfeffer (1929) concluded that *P. insignis* cannot be related to the Ariantinae. Instead, he placed *P. insignis* in his newly designated genus *Joossia* within his also redefined family Eulotidae Möllendorff 1898 (valid name Bradybaenidae Pilsbry 1934 (1898), see Bouchet & Rocroi 2005: 38, 269). This decision was based on a comparison between *P. insignis* and *Dinarica pouzolzi*. However, the differences he described, can even be found between the members within the Ariantinae. Since these arguments are insufficient to place *P. insignis* in the family Bradybaenidae, Wenz & Zilch (1960) and Schileyko (2006) considered *Joossia* a synonym of *Dinarica*.

Pseudochloritis C. R. Boettger, 1909 (Helicidae, Ariantinae)
C. R. Boettger (1909) placed *P. insignis* in his new genus *Pseudochloritis* within the Ariantinae. The most recent work on *Pseudochloritis* was published by Binder (2008). He confirmed the placement within the Ariantinae. Whether *Pseudochloritis* is a subgenus of *Tropidomphalus* or a separate genus, is still debated in literature. We follow Binder (2008) who designated *Pseudochloritis* as a separate genus. Gittenberger (1979) saw *Tropidomphalus*/*Pseudochloritis* as a possible "connection" between the extant *Elona quimperiana* (Férussac, 1821) and *Norelona pyrenaica* (Draparnaud, 1805). Based on anatomical features, he united these two species into the new family Elonidae. Nordsieck (1986) then assumed that *Pseudochloritis* belongs to the Eloninae (= Elonidae *sensu* Gittenberger 1979) as well, but not to the Ariantinae. Later, however, Binder (2008) argued that the similarities between *Pseudochloritis* and *Elona* as well as *Norelona* are only superficial. Binder suggested a relationship with the Ariantinae, which he strongly supported by documenting the similarities in shell microsculpture with the modern species *Helicigona (Campylaea) lefeburiana* (C.Pfeiffer 1828), and we can confirm this with our study. From the discussed geographic distribution, the general shell morphology and the microsculpture of the embryonic whorls, *Pseudochloritis* fits with the Ariantinae. Both *P. insignis* and *P. incrassata* show the same "pattern" of morphological variability as *Arianta arbustorum*, the type species of the Ariantinae (see Fechter & Falkner 1989, p. 227, fig. 3–9).



Figures 6.1–6.3 *Pseudochloritis insignis* (von Zieten, 1832), Miocene, Steinheim am Albuch, *trochiformis*-strata, Collection Jooss. SMNS J66159, Scale 10mm. **6.4** *P. insignis*, Steinheim am Albuch, *trochiformis*- strata, Miocene, Collection Jooss. SMNS J66162, Scale 10mm. **6.5–6.6** *P. insignis*, Steinheim am Albuch, *trochiformis*-strata, Miocene, Collection Jooss. SMNS J66156. Scale 10mm. **6.7–6.8** *P. insignis* , Steinheim am Albuch, *trochiformis*-strata, Miocene, Collection Jooss. SMNS 66161. Scale 10mm. **6.9** *P. insignis* , Protoconch of Fig. 4.2. Inv. No. 101666. Scale 1mm. **6.10** *P. insignis* , Detail of fig. 9. Scale 200µm. **6.11** *P. incrassata*, Protoconch of Fig. 4.3. Scale 1mm. **6.12** *P. incrassata*, Detail of fig. 11. Scale 200µm.

As the type species for his new genus *Pseudochloritis*, C.R. Boettger (1909) chose *Helix inflexa* sensu Klein, 1846, non Zieten 1832, for which the valid name is *Pseudochloritis incrassata* (Klein 1853) according to Binder (2008). The specimens shown in Fig. 4.3; Figs 5.1–5.2; Figs.6.11–6.12 are from the published material of Klein (1846). C.R. Boettger (1911) described *Pseudochloritis* as follows (translated from Latin): "Shell spherical-depressed to conical-depressed, half covered umbilicus, solid to massive, often with one band; low spira, apex in most cases blunt, convex basis; distinct suture. 4.5–5.5 convex whorls, radial ribs and also equipped with pits. The last whorl runs downwards to the tight aperture. Aperture oblique, sickle-shaped, peristome callous thickened, extensively reflected. The columellar region is extended to the outside".

Sandberger (1872) and Miller (1900) pointed to the similarities between *Helix insignis* (i.e., *P. insignis*) and *Helix zelli* Kurr 1856 (i.e., *P. incrassata* according to Binder (2008)). According to our studies, *P. insignis* and *P. incrassata* reveal the following similarities: (1.) The development of the whorls are comparable; because of this, the large forms of *P. incrassata* have often been confused with *P. insignis* (see also Wenz 1923). (2.) Following the sh/sw plot (Fig. 2a), the cluster analysis (Fig. 2b), and the PCA (Fig. 3), *P. insignis* is more related to *P. incrassata* than to the type species of *Dinarica*, *D. pouzolzi*. (3.) The growth of the protoconch is similar (see Fig. 5.1 and Figs 6.9–6.12). (4.) The protoconch of both species bears the same pustulae and hair-pits (see Fig. 4.7; Fig. 5.1; Figs 6.10–6.12). For these reasons a membership of the species *insignis* in *Pseudochloritis* C. R. Boettger, 1909 is suggested herein.

The main differences between *P. insignis* and *P. incrassata* are: (1.) *P. insignis* is larger. (2.) *P. incrassata* has a stronger reflected peristome. (3.) *P. insignis* bears more prominent prosocline radial growth lines. (4.) Despite a certain overlap, morphometrics suggest a separation into two different species (Figs 2, 3).

Conclusion

Based on shell characters and morphology, as well as protoconch development and sculpture, *insignis* is placed into the genus *Pseudochloritis*. Regarding shell morphology, variability pattern and protoconch sculpture, *Pseudochlorits* fits more with the subfamily Ariantinae within the Helicidae, than with the Elonidae. Due to the limited amount of differentiating shell characters, and the tendency to convergent morphologies of land snails, however, a final decision may remain tentative for fossil material. The proposal of von Kurr (1856) about a membership within the Dorcasidae with the genus *Trigonephrus* is impossible due to palaeobiogeographic considerations. The same is true for the assumption of O. Boettger (1909) that *P. insignis* is the ancestor of the Madagascan genus *Ampelita*. According to Schileyko (1999), both genera have smooth protoconchs, which is in contrast to the sculptured protoconch of *Pseudochloritis*. The Camaenidae with *Chloritis*, which O. Boettger (1909) brought into discussion, is a problematic group. Some members of the Australian genus/subgenus *Austrochloritis* are similar to *P. insignis*. The Camaenidae are a very large, and according to Scott (1996), obviously a polyphyletic group that needs to be revised. Therefore, an assignment of fossil land-snails to the Camaenidae remains uncertain.

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References

ABBOTT RT 1989 *Compendium of Landshells: A Full-Color Guide to More than 2,000 of the World's Terrestrial Shells.* American Malacologists, Melbourne, Florida, 240 pp.

BERGER J–P, Reichenbacher B, Becker D, Grimm M, Grimm K, Picot L, Storni A, Pirkenseer C, Derer C & Schaefer A 2005 Paleogeography of the Upper Rhine Graben (URG) and the Swiss Molasse Basin (SMB) from Eocene to Pliocene. I*nternational Journal of Earth Sciences* **94**(4): 697–710.

BINDER H 2008 The systematic positions of the genera *Pseudochloritis* C. Boettger 1909 and *Joossia* Pfeffer 1929. *Archiv für Molluskenkunde* **137** (2): 167–193.

BOETTGER CR 1909 Ein Beitrag zur Erforschung der europäischen Heliciden. *Nachrichtsblatt der deutschen Malakozoologischen Gesellschaft* **41**(1), 1–19.

BOETTGER CR 1911 Einige Worte zu: Noch einmal „Die Verwandtschaftsbeziehungen der Helix Arten aus dem Tertiär Europas". *Nachrichtsblatt der deutschen Malakozoologischen Gesellschaft* **43**(3): 113–133.

BOETTGER CR & WENZ W 1921 Zur Systematik der zu den Helicidensubfamilen Campylaeinae und Helicinae gehörigen tertiären Landschnecken. *Archiv für Molluskenkunde* **53**: 6–55.

BOETTGER O 1909 Noch einmal „Die Verwandtschaftsbeziehungen der Helices-Arten aus dem Tertiär Europas". *Nachrichtsblatt der deutschen Malakozoologischen Gesellschaft* **41**(3): 97–118.

BOUCHET P & ROCROI J–P 2005 Classification and nomenclature of Gastropod families. *Malacologia* **47** (1–2): 1–397.

BURGER W & BURGE MJ 2006 *Digitale Bildverarbeitung: Eine Einführung mit Java und ImageJ*. Springer, Berlin & Heidelberg.515 pp.

CLEEVELY RJ 1983 *World Palaeontological Collections.* British Museum, London, 365 pp.

FECHTER R & FALKNER G 1989 *Weichtiere*. Mosaik Verlag Gmbh, München.287 pp.

DHARMA B 2005 *Recent & Fossil Indonesian Shells*. ConchBooks, Hackenheim, 424 pp.

FINGER I 1998 Gastropoden der kleini-Schichten des Steinheimer Beckens (Miozän, Süddeutschland). *Stuttgarter Beiträge zur Naturkunde,* Serie B, **259**: 1–51.

GITTENBERGERR E 1979 On *Elona* (Pulmonata, Elonidae fam. nov.). *Malacologia*: **18**: 139–145.

GOODFRIEND GA 1986 Variation in land-snail shell form and size and its causes: A review. *Systematic Zoology* **35** (2): 204–223.

GOTTSCHICK F & WENZ W 1920 Die Land- und Süßwassermollusken des Tertiärbeckens von Steinheim am Albuch. 3. Fortsetzung. *Archiv für Molluskenkunde* **52** (1): 33–48.

HAMMER Ø, HARPER DAT & RYAN PD 2001 PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* **4**(1): 1–9.

HARZHAUSER M, GROß M & BINDER H 2008 Biostratigraphy of Middle Miocene (Sarmatian) wetland systems in an Eastern Alpine intramontane basin (Gratkorn Basin, Austria): the terrestrial gastropod approach. *Geologica Carpathica* **59** (1): 45–58.

HARZHAUSER M, NEUBAUER TA, GEORGOPOULOU E, HARL J 2014 The Early Miocene (Burdigalian) mollusc fauna of the North Bohemian Lake (Most Basin). *Bulletin of Geosciences* **89**: 819–908.

HILGEN FJ, LOURENS LJ, & VAN DAM JA 2012 *The Neogene Period.* In: *The geologic time scale (29)* (Gradstein FM, Ogg JG, Schmitz M & Ogg G), pp. 923–978, Elsevier Verlag, München.

KLEIN A VON 1846 Conchylien der Süsswasserformation Württembergs. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg* **2**: 60–116.

KLEIN A VON 1853 Conchylien der Süsswasserformationen Württembergs. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg* **9**: 203–223.

KNIPPER H 1939 Systematische, anatomische, ökologische und tiergeographische Studien an südosteuropäischen Heliciden (Moll. Pulm.). *Archiv für Naturgeschichte*, N. F. **8** (3/4): 327–517.

KURR JG VON 1856 Die Land- und Süsswasserconchylien der Tertiärformation Oberschwabens. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg* **12**: 38–43.

MILLER K 1900 Die Schneckenfauna des Steinheimer Obermiozäns. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg* **56**: 385–406.

MUNK W, BERNOR RL, HEIZMANN EPJ & MITTMANN HW 2007 Excavations at the Late Miocene MN9 (10.3 Ma) Locality of Höwenegg (Hegau), Southwest-Germany, 2004–2006. *Carolinea* **65**: 5–13.

NORDSIECK H 1986 Das System der tertiären Helicoidea Mittel- und Westeuropas (Gastropoda: Stylommatophora). *Heldia*: **1**(4): 109–120.

PFEFFER G 1929 Zur Kenntnis tertiärer Landschnecken. *Geologische und Paläontologische Abhandlungen*, N. F., **17**(3): 151–380.

PFENNINGER M, HRABÁKOVÁ M, STEINKE D & DÈPRAZ A 2005 Why do snails have hairs? A Bayesian inference of character evolution. *BMC Evolutionary Biology* 2005 **5**: 59.

QUENSTEDT FA 1881–1884 *Peterfaktenkunde Deutschlands. Der ersten Abteilung, siebenter Band. Gasteropoden. Teil 1.* Fues`s Verlag, Leipzig, 440 pp.

RASSER MW 2013 Evolution in Isolation: The *Gyraulus* species flock from Miocene Lake Steinheim revisited. *Hydrobiologia* **717**: 3–20.

ROSENDAHL W, LÓPEZ CORREA M, GRUNER C & MÜLLER T (Hrsg. 2003). *Der Böttinger Marmor. Bunter Fels aus heißen Quellen*. Staatsanzeiger Verlag, Stuttgart, 56 pp.

SANDBERGER F 1872 *Die Land-und Süßwasserconchylien der Vorwelt.* C. W. Kreidelsverlag, Wiesbaden; livr. 6–**8**: 161–256, pl: 21–32.

SCHILEYKO AA 1999 Treatise on Recent Terrestrial Pulmonate Molluscs. Part 4. *Ruthenica* **Supplement 2**: 437–564.

SCHILEYKO, AA 2003 Treatise on Recent Terrestrial Pulmonate Molluscs. Part 11. *Ruthenica* **Supplement 2**: 1467–1626.

SCHILEYKO AA 2006 Treatise on Recent Terrestrial Pulmonate Molluscs. Part 13. *Ruthenica* **Supplement 2**: 1765–1906.

SCOTT B 1996 Phylogenetic relationships of the Camaenidae (Pulmonata: Stylommatophora: Helicoidea). *Journal of Molluscan Studies* **62**: 65–73.

STANISIC J, SHEA M, POTTER D & GRIFFITHS O 2010 *Australian Land Snails,* Volume 1. Bioculture Press, Mauritius, 591 pp.

SUBAI P 2002 Revision der Ariantinae. 2. Die Helicigona-Untergattung Liburnica (Gastropoda: Pulmonata: Helicidae). *Archiv für Molluskenkunde* **131** (1/2): 1–65.

WENZ W 1923 *Fossilium Catalogus I: Animalia. Gastropoda extramarina tertiaria*. - XVIII, W. Junk, Berlin, 736 pp.

WENZ W & ZILCH A 1960 Gastropoda Teil 2, Euthyneura. *In*: Schindelwolf OH (Ed.), *Handbuch*

der Paläozoologie, 6. Gebrüder Borntraeger, Berlin, 834 pp.

ZIETEN CH VON 1832 *Die Versteinerungen Württembergs.* V. Verlag & Litographie der Expedition des Werkes unserer Zeit, Stuttgart, 8 pp.

APPENDIX 1: MEASURED SPECIMENS: THEIR LOCALITIES AND NUMBERS.

Dinarica pouzolzi

Herzigowina, Aleksina Medja bei Trebinje. Original to Pl. 1, fig. 5; Pl. 2, fig. 3 & 4 (**1**): Ragusa (6): location? 24084 (**1**): Ragusa 738 (**1**): Dalmatia (2): Herzigowina, Biléca (**1**): Dalmatia 39830 (**2**): Dalmatia 14943 (**2**): ?Krivorizc 14906 (**2**): Makarska, Dalmatia (**2**): Serbia (**1**): Dubrovnik-Gruz, Dalmatia (**3**): At Sentarisee (3): Dalmatia 2249 (**2**): Cattaro (**1**): Dalmatia 36746 (**2**): Dubrovnik-Gruz, Dalmatia HN 2550 (**2**): Cattaro (**5**): Dalmatia, Dubrovnik-Lapad (**3**): Cetinje (**1**): Bosnia (**2**): Gravosa, Dalmatia (**2**): Dalmatia (**1**): ?Herticea 14934 (**2**): Dubrovnik, Dubrovacko-neretvanska ZI0086291 (**2**): Dubrovnik, Dubrovacko-neretvanska ZI0086292 (**2**): Nasic, Bosnia 39837 (**2**): Ogram (**2**): Bosnia and Herzegowina, Federacija Bosnc i Herzegovine, Hercegovacko-neretvanski, Mostar, Neretva-Valley ZI0086294 (**2**): ?Zvezda, Serbia (**1**): Serbia and Montenegro, Crna Gora Lovcen ZI0086293 (**1**): Jablaniko, Herzegowina, 39832 (**3**): Cattaro (**12**).

Pseudochloritis incrassata

Mörsingen/Germany, Miocene. Coll. JOOSS. SMNS 66.206 (**11**): Mörsingen/Germany, Miocene. Coll. JOOSS. SMNS 68.532 (**3**): Michelsberg near Dischingen/Germany, Miocene. Coll. JOOSS. SMNS 66.214 (**4**): Schauenberg near Hohenmemmingen/Germany, Miocene. Coll. JOOSS. SMNS 66.213 (**4**): Friedingen/Germany. Miocene. Coll. JOOSS. SMNS 66.224 (**2**): Mörsingen/Germany. Miocene. Coll. Bechter 4443/2008. (**16**): Mörsingen/Germany. Miocene. Coll. Bechter 4341/2008 (**4**): Mörsingen/Germany. Miocene. Coll. Bechter 4444/2008 (**18**): Coll. Jooss. 66.221 location ? (**1**): Andelfingen/Germany. ? Miocene. ?Holotype to Helix zelli VON KURR, 1856. IMDAS If. Nr. 38992/2005 (**1**): Mörsingen/Germany, Miocene. Coll. JOOSS. SMNS 66.234 (**1**): Scheuenberg near Hohenmemmingen/Germany. Miocene. Coll. JOOSS. SMNS 66.227 (**1**): Nunningen, Kanton Solothurn, Switzerland. ? Miocene. Coll. Jooss SMNS 66.150 (**1**): Zwiefalten/Germany. ?Holotype of Helix incrassata KLEIN, 1853. IMDAS If. Nr.25251/2005 (**1**): Rein, Steiermark/Austria, Miocene. Coll. JOOSS. SMNS 66.235 (**2**): Zwiefalten/Germany. Miocene. Originals of Helix incrassata KLEIN, 1853. IMDAS Nr. If. 41555/2005 (**1**): Friedingen/Germany, Miocene. Coll. JOOSS. SMNS 66.224 (**2**): Hof, Nebelberg near Munningen Kanton Solothurn/ Switzerland, Miocene. Coll. JOOSS. SMNS 66.164 (**4**): Hof, Nebelberg near Munningen Kanton Solothurn/Switzerland, Miocene. Coll. JOOSS. SMNS 66.165 (**2**): Zwiefalten/ Germany. Miocene. Original material of Helix inflexa Klein, 1853. Inv. No. 101525 (**3**).

Pseudochloritis insignis

Steinheim am Albuch/Germany. Miocene (MN7). Neotype. Original to KLEIN, 1847. Inv. No. 23910b (**1**): Steinheim am Albuch. Original to KLEIN 1847. IMDAS If. Nr. 25138/2005 (**1**): Steinheim am Albuch. Original to MILLER 1900. IMDAS Ifd. Nr. 38305/2005 (**2**): Steinheim am Albuch. Original to Helix steinheimensis Klein, 1847. IMDAS If. 25227/2005 (**1**): Steinheim am Albuch. Coll. JOOSS. SMNS 66.159 (**5**): Steinheim am Albuch. Coll. JOOSS. SMNS 66.158 (**4**): Steinheim am Albuch. Coll. JOOSS. Original material to Pl. 1, fig. 2; Pl. 3, fig. 8; Pl. 4, fig. 5, 6, 9 & 10. SMNS 66.156 (**7**): Steinheim am Albuch. Coll. JOOSS. SMNS 66.161 (**5**): Steinheim am Albuch. Coll. JOOSS. SMNS 66.162 (**1**): Steinheim am Albuch. Coll. Bechter. 12409/2008 (**3**): Steinheim am Albuch. Coll. Bechter. 12410/2008 (**4**): Steinheim am Albuch. Coll. Bechter. 12411/2008 (**5**): Steinheim am Albuch. Coll. Bechter. 12192/2008n (**2**): Steinheim am Albuch. Coll. Bechter. 12414/2008 (**4**): Steinheim am Albuch. Coll. Bechter. 12413/2008 (**4**): Steinheim am Albuch. Syntype. Original to Pl. 1, fig. 2. Inv. No. 101666 (**1**): Steinheim am Albuch. Coll. Degenfeld (5): Steinheim am Albuch. 15873/2007 (**3**): Steinheim am Albuch. Coll. Hermann. 12131/2008 (2): Steinheim am Albuch. 12133/2008 (**5**): Steinheim am Albuch. Leg. KAPITZKE 1986. Original material to Pl. 2, fig. 7 & 8 (**1**).

APPENDIX 2. MEAN VALUES (MV) AND STANDARD DEVIATION (SD) OF THE DIFFERENT RATIOS.

Morphometric ratios	*P.insignis* (mv)	*P. insignis* (sd)	*P. incrassata* (mv)	*P. incrassata* (sd)	*D. pouzolzi* (mv)	*D. pouzolzi* (sd)
sh/sw	0.828	0.052	0.742	0.049	0.658	0.048
sh/mh	1.411	0.086	1.356	0.067	1.387	0.08
sh/lwh	1.526	0.032	1.54	0.032	1.197	0.042
sh/di	2.222	0.221	1.904	0.174	2.023	0.184
sh/as	0.235	0.056	0.138	0.033	0.195	0.046
sw/mh	1.706	0.072	1.831	0.092	2.114	0.115
sw/lwh	1.396	0.076	1.562	0.098	1.826	0.113
sw/di	2.691	0.239	2.56	0.224	3.079	0.237
sw/as	0.281	0.052	0.185	0.034	0.293	0.055
lwh/mh	1.226	0.057	1.175	0.049	1.159	0.046
mh/di	1.583	0.127	1.402	0.115	1.458	0.099
mh/as	0.165	0.033	0.101	0.022	0.14	0.029
hlw/di	1.94	0.175	1.649	0.152	1.69	0.135
hlw/as	0.204	0.047	0.119	0.029	0.162	0.038