

The Clausiliidae subfamily Phaedusinae (Gastropoda, Pulmonata) in the Balkans.

ALEXANDER REISCHÜTZ, PETER L. REISCHÜTZ & MIKLÓS SZEKERES, Horn - Szeged.-

Summary

This overview assesses the taxonomic information and occurrence data that are currently available on Balkan species of the Clausiliidae subfamily Phaedusinae, and provides descriptions of the new taxa *Sciocochlea cryptica harli* nov. subspec., *Tsoukatosia argolica* nov. spec., *Tsoukatosia nicoleae* nov. spec., and *Tsoukatosia pallgergelyi* nov. spec. from Albania and Greece.

Zusammenfassung

Diese Arbeit soll die derzeit vorhandenen taxonomischen Informationen und Verbreitungsdaten der auf der Balkanhalbinsel vorkommenden Vertreter der Unterfamilie Phaedusinae in der Familie der Clausiliidae zusammenfassen. Die neuen Taxa *Sciocochlea cryptica harli* nov. subspec., *Tsoukatosia argolica* nov. spec., *Tsoukatosia nicoleae* nov. spec. und *Tsoukatosia pallgergelyi* nov. spec. werden aus Albanien und Griechenland beschrieben.

Introduction

Phaedusinae is the widest distributed among the subfamilies of the Clausiliidae, occurring from East and South Asia to Southern and Eastern Europe. In Central Asia its range is interrupted by a gap of 1700 km between Kashmir and the eastern foothills of the Alborz Mountains. In Europe members of the subfamily appeared in the Middle Eocene, and then thrived during most of the Neogene Era (NORDSIECK 2000). But, with the exception of the Mediterranean region, their diversity and presence abruptly decreased with the cooling of the climate toward the end of the Pliocene (NORDSIECK 2013). The latest Phaedusinae fossils in Europe date to the Early Pleistocene (NORDSIECK 2000). By now extant species of the subfamily can only be found sporadically in the Balkan Peninsula and the southern part of Eastern Europe (Figures 1 and 2).

Balkan Phaedusinae occur in the isolated western realm of the subfamily, which extends from the mountainous southern coast of the Caspian Sea to the Northeastern Carpathians. The number of species in this part of the range is much fewer than in the larger eastern part, but they show considerably higher morphological and molecular diversity (NORDSIECK 1978a; UIT DE WEERD & GITTENBERGER 2013). These clausiliids, which are represented by five genera in the Balkans, are seen as Tertiary relicts (NORDSIECK 1978a) that survived the cooling of the climate by adapting to protective habitats. From the 1920s, based on their shell and genital morphology, they were classified as members of the Phaedusinae (LINDHOLM 1924; EHRMANN 1927; WENZ & ZILCH 1959; LIKHAREV 1962). NORDSIECK (1972) adopted the view of WENZ & ZILCH (1959) to regard this group a tribe (Serrulinini), but pointed out that the genital morphology of this so-called *Serrulina* group does not show any characteristic that could justify its separation from the Phaedusinae as a distinct subfamily (NORDSIECK 1973). Later, following up on an idea from EHRMANN (1927), he proposed distinguishing this group as Serrulininae, an independent subfamily (NORDSIECK 1978b). Despite some reservations (e.g. NÉMETH & SZEKERES 1995), this notion became widely accepted. However, a recent molecular phylogenetic analysis found that the Caucasian and Balkan genera are closely related to those of East Asia, supporting their classification within the Phaedusinae. Furthermore, this study also revealed that the genera of the Caucasus and the Balkans do not

even constitute a monophyletic group of the subfamily (UIT DE WEERD & GITTENBERGER 2013).



Figure 1: Distribution of the Balkan Phaedusinae: *Serrulina serrulata* data in the eastern Black Sea and Caucasus regions are not shown.

Except for two wide-spread species, all other Balkan Phaedusinae are highly endemic and confined to subterranean habitats. Shells of these are typically discovered in debris washed to the surface through the openings of deep karst crevices. Due to the difficulties of finding such sites and obtaining the shell material, the studying of these fascinating clausiliids took a late start. Their first representative had been described at the beginning of the 20th century (STURANY 1904), and this was followed by the second only in the early 1980s (RÄHLE 1982). Thereafter increased interest in subterranean snails resulted in the description of three additional species by 2000 (SUBAI 1993; SUBAI & SZEKERES 1999; GITTENBERGER 2000), which were then followed by further five to this date (A. & P. L. REISCHÜTZ 2004, 2009, 2014; HUNYADI & SZEKERES 2009; A., N. & P. L. REISCHÜTZ 2012). These findings greatly increased our knowledge of the Phaedusinae of the Balkans, but they also made clear that a substantial part of this fauna still needs to be discovered. This paper provides an assessment of the currently available information on this group and describes new taxa from Albania and Greece.

The shell material used in this study is in the collections of the Hungarian Natural History Museum, Budapest (HNHM), Muzeul de Istorie Naturală - Kimakowicz collection, Sibiu (MINS-Km), Naturalis Biodiversity Center, Leiden (NNM), Naturhistorisches Museum, Wien (NHMW), and Naturmuseum Senckenberg, Frankfurt am Main (SMF), as well as the private collections of A. and P. L. Reischütz, Horn (RE) and M. Szekeres, Szeged (SZ).

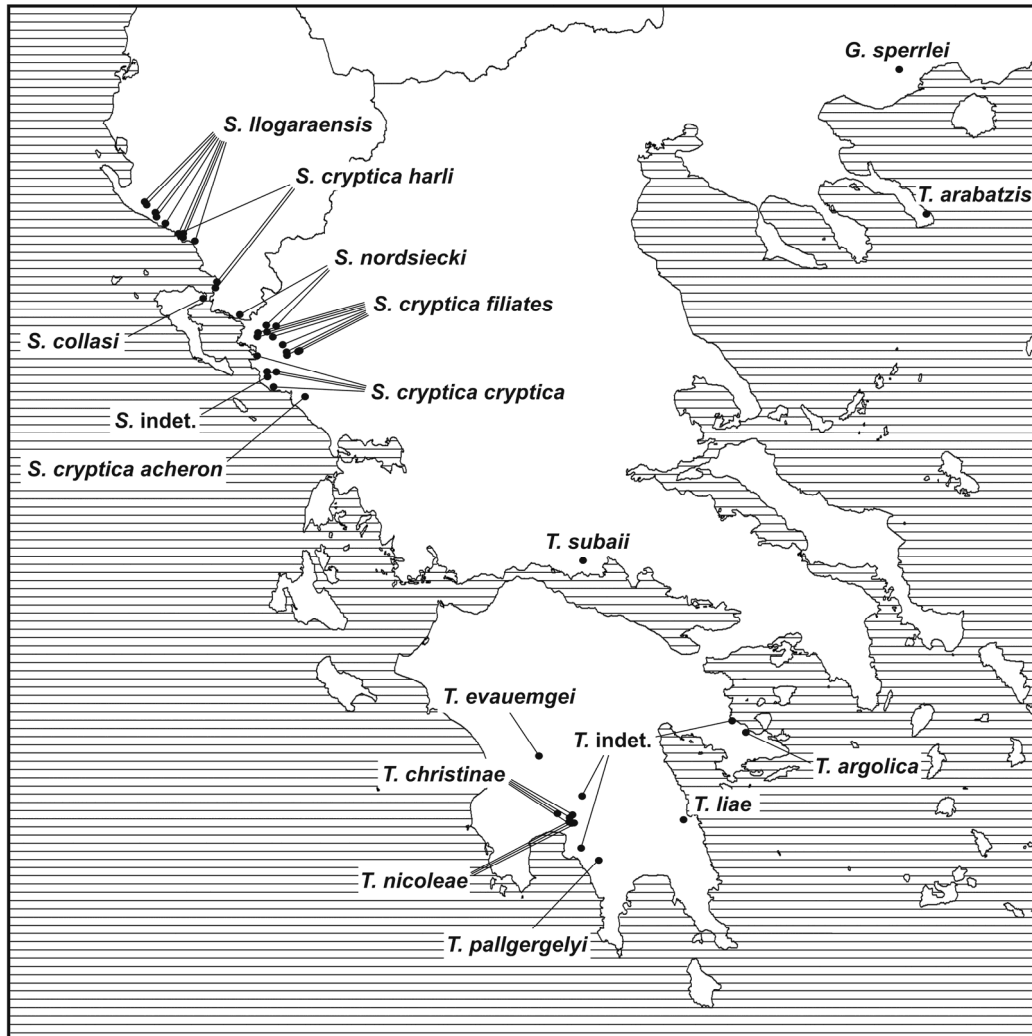


Figure 2: Localities of the *Graecophaedusa*, *Sciocochlea* and *Tsoukatosia* species.

Taxonomic part

Serrulina MOUSSON 1873

Type species: *Clausilia sieversi* PFEIFFER 1871

Diagnosis: The spindle-shaped shell has gradually tapering, pointed apex. The peristome is serrate, at least at its columellar margin. The lamella inferior starts less deep than the spiralis and ends marginally, at the lower third of the aperture. The lamella subcolumellaris is interrupted near its lower end. It also terminates at the peristome margin just below the inferior, often separated from that by a strong plica. Along the lamella spiralis a lamella inserta is present. The short upper and lower palatal plicae at the dorsolateral to lateral side are connected by a weak lunella. The deltoidal clausilium plate with a blunt, backward-bent tip is widest at its middle. The genital system (NORDSIECK 1973 and 1978a) is characterized by an epiphallus having much longer proximal than distal part, elongate penis with broadly attached retractor, and a diverticulum that is longer than the bursa copulatrix plus its distal pedunculus.

Distribution: The geographic range of the genus extends from the northeastern Alborz Mts. of Iran in the east to the Ukrainian Carpathians in the west. Most of the occurrences are known

from the Caucasus and regions along the southern coastlines of the Caspian and Black Seas (LIKHAREV 1962; NORDSIECK 1995). The localities in the western part of the distribution area are shown in Figure 1.

Habitat: *Serrulina* species prefer undisturbed forests, where they live in moist, decaying tree trunks under the bark and even deep in the texture of the wood.

Remarks: *Serrulina* has been erected by MOUSSON (1873) for *Clausilia sieversi*. In addition to this species the genus includes only *Serrulina serrulata* (PFEIFFER 1847).

Serrulina serrulata (PFEIFFER 1847)
(Figure 3a)

Synonymy: *Clausilia erivanensis* ISSEL 1866

Diagnosis: This species is larger and has stronger sculpture than *Serrulina sieversi*. Its peristome margin is usually strongly serrate on both sides, and the palatal plicae are more lateral than in the type species of the genus. The genital organs are described and figured in URBAŃSKI (1960). Dimensions: Hs (shell height) 11.0-16.5 mm, Ws (shell width) 2.6-3.7 mm, Ha (aperture height) 2.3-3.4 mm, Wa (aperture width) 1.9-2.6 mm.

Type material: There is no known type material of *Serrulina serrulata* (SYSOEV & SCHILEYKO 2009).

Locus typicus: "Tauris" (PFEIFFER 1847).

Distribution: The species is widely distributed in the Caucasus, the coastal areas of northern Anatolia, and toward the northwest it has isolated European occurrences as far as the Ukrainian Carpathians (PÁLL-GERGELY & ROIBU 2011). Here only its Balkan localities are listed. In Romania: Mănăstirea Cocoș near Niculițel, W of Tulcea (GROSSU 1981). In Bulgaria: forest of the Longoza Reserve NE of Dolni Chiflik, along the Kamchia (URBAŃSKI 1960); Stara Planina, near Tvârdica (NORDSIECK 1978a); E shore of Lake Vaya at Burgas (URBAŃSKI 1960); Arkutino Swamp at the mouth of the Ropotamo, SE of Burgas (URBAŃSKI 1960); forest along the right bank of the Ropotamo 3 km upstream of the mouth (URBAŃSKI 1960); Strandzha Mts., at the headwaters of the Ropotamo near Novo Panicharevo (leg. H. Gyurkovics & M. Szekeres); Strandzha Mts., 3 km W of Kondolovo along the Michurin (= Tsarevo) to Malko Târnovo road (ERÖSS & FEHÉR 2001); Strandzha Mts., 2.3 km toward Stoilovo from the Zvezdec to Malko Târnovo road (leg. L. Németh). In Turkey: Yıldız Mts. near Demirköy (leg. H. Gyurkovics).

Remarks: Tauris (= Crimea), the locus typicus (PFEIFFER 1847), is apparently an erroneous record as the species does not occur there. It seems possible that PFEIFFER's description, like those of several other Caucasian species (see: RETOWSKI 1887), originated from flotsam deposited by the Black Sea (SYSOEV & SCHILEYKO 2009). Most Bulgarian occurrences of *Serrulina serrulata* are known from the region around the Strandzha Mts. (called Yıldız Mts. in Turkey). Apart from these and the site near Dolni Chiflik there is only one more, vaguely defined and yet unconfirmed record from the Plovdiv area (HESSE 1913) which, therefore, is not shown in the occurrence map in Figure 1. Flotsam data from Varna and Burgas (URBAŃSKI 1960) are also not shown on the map. Intriguingly, in Turkey an isolated form of this species, *Serrulina serrulata amanica* (NÄGELE 1906), occurs in south-central Anatolia, at

the Gulf of Iskenderun along the Mediterranean coast (Figure 1). This large-size subspecies has a shell height of 16 mm (NÄGELE 1906).

Dobatia NORDSIECK 1973

Type species: *Serrulina (Serrulina) goettingi* BRANDT 1961

Diagnosis: The spindle-shaped shell with gradually tapering apex often bends toward the aperture side. Only the columellar margin of the peristome is serrate. The lamella inferior ends marginally at the lower third of the aperture. Inside it starts less deep than the spiralis. The uninterrupted lamella subcolumellaris reaches the peristome margin just below the inferior, often separated from that by a strong plica. There is no lamella inserta. The short, dorsolateral upper and lower palatal plicae are connected by a weak lunella. The deltoid-shaped clausilium plate is widest at the middle, its tip is only slightly backward-bent. Compared to that of *Serrulina*, the genital system (NORDSIECK 1973 and 1978a) has much shorter penis, shorter epiphallus with proximal and distal parts of comparable lengths and narrowly attached retractor, as well as a diverticulum that is shorter than the bursa copulatrix with the distal pedunculus.

Distribution: The geographic range of this monotypic genus is identical with that of *Dobatia goettingi* (BRANDT 1961).

Habitat: *Dobatia* occurs in undisturbed forests, where it is found under leaf litter (BRANDT 1961) and, preferentially, in the underground parts of decaying tree stumps.

Remarks: NORDSIECK (1973) suggested that *Dobatia goettingi* can be a troglomorphic species. Based on this assumption and similarities of the shell structure he raised the possibility of a close relationship between *Dobatia* and *Sciocochlea* C. R. BOETTGER 1935.

Dobatia goettingi (BRANDT 1961) (Figure 3b-c)

Diagnosis: The shell features are those of the genus. Dimensions: Hs 10.5-13.1 mm, Ws 2.2-2.6 mm, Ha 2.1-2.9 mm, Wa 1.7-2.4 mm.

Locus typicus: Lake Abant near Bolu, in NW Anatolia.

Holotype: SMF 163957.

Distribution: The species occurs along the southwestern coastline of the Black Sea between Samsun in northern Turkey and Burgas in Bulgaria (Figure 1). Here only its Balkan localities are listed. Bulgaria: Kiten, S of the mouth of the Ropotamo (URBAŃSKI 1978); Strandzha Mts., 1.7 km W of Kondolovo (leg. L. Németh & B. Páll-Gergely); Strandzha Mts., 3 km W of Kondolovo along the Michurin (= Tsarevo) to Malko Târnovo road (ERŐSS & FEHÉR 2001); Strandzha Mts., 2.3 km toward Stoilovo from the Zvezdec to Malko Târnovo road (leg. L. Németh).

Remarks: Like several other gastropod species of northern Anatolia, *Dobatia goettingi* was also found in flotsam at various locations along the Black Sea coast. The shells from the Crimean coast determined as *Serrulina sieversi* by RETOWSKI (1887) actually belong to this

species (material: MINS-Km 3371), just as the specimen from Poti at the Georgian coast that was figured as *Serrulinella senghanensis* (GERMAIN 1933) (Figure 40d in SYSOEV & SCHILEYKO 2009). It seems likely that the first Balkan record of *Dobatia goettingi* from the Ropotamo Reserve (NORDSIECK 1973) was also based on a sea flotsam specimen. A further dubious locality is in the Peloponnesos (7 km from Vitina toward Langadia, at the junction to the Agion Theodoron Monastery, 37°38'45" N 22°6'34" E, 1100 m), where L. Németh collected nine shells, all from a single decaying trunk of Greek fir (*Abies cephalonica*). It seems that this small population could have resulted from accidental human transfer.

Sciocochlea C. R. BOETTGER 1935

Type species: *Serrulina collasi* STURANY 1904

Synonymy: *Phygas* WAGNER 1914

Diagnosis: The more or less club-shaped shell with broad apex is often bent toward the aperture side. The peristome margin is smooth, or serrate only at its columellar rim. The lamella inferior ends marginally at the lower third of the aperture. Inside it reaches less deep than the spiralis. The uninterrupted lamella subcolumellaris terminates marginally below the inferior, often separated from that by a strong plica. Lamella inserta is not present. The short upper palatal plica is on the dorsolateral side. Below it the lower plica is rudimentary or absent. The narrow clausilium plate with parallel sides is visible through the aperture. The genital system is not known.

Distribution: The genus has a narrow distribution area along the western coastline of the Ionian Sea, between the Bay of Vlorë in Albania and the Ambracian Gulf in Greece (Figure 1). The localities of the species are shown in Figure 2.

Habitat: All known *Sciocochlea* material has been collected from deposits or debris originating from deep limestone crevices that are known, or thought to be, connected to caves. So far no live specimens have been found.

Remarks: *Sciocochlea* was introduced by C. R. BOETTGER (1935) as nomen novum to replace *Phygas*, which had been preoccupied (non TREITSCHKE 1833). In his book on European non-marine molluscs WELTER-SCHULTES (2012) combined all species of the genus under the name *Sciocochlea collasi*. He argued that, considering the limited material that was available from only a few locations and a report of considerable size variation at one of these sites, it seemed questionable dividing the genus into species. By now, however, studies of larger samples from a much higher number of localities provide strong support to the validity of the four *Sciocochlea* species, which have distinct shell characteristics and distribution ranges. The shells of these species differ primarily in their shape, sculpture, and the presence or absence of plicae at the interlamellar peristome margin (Figure 3d-k).



Figure 3: *Serrulina*, *Dobatia* and *Sciocochlea* taxa of the Balkans:

a: *Serrulina serrulata* (PFEIFFER) (Yıldız Mts. near Demirköy), b: *Dobatia goettingi* (BRANDT) (Strandzha Mts., 3 km W of Kondolovo), c: *Dobatia goettingi* (BRANDT) (Peloponnesos, between Vitina and Langadia), d: *Sciocochlea collasi* (STURANY) (syntype), e: *Sciocochlea cryptica cryptica* SUBAI & SZEKERES (Igoumenitsa to Plataria road), f: *Sciocochlea cryptica cryptica* SUBAI & SZEKERES (N of Anthousa), g: *Sciocochlea cryptica acheron* A. & P. L. REISCHÜTZ (Skepasto), h: *Sciocochlea cryptica filiates* A. & P. L. REISCHÜTZ (paratype), i: *Sciocochlea cryptica harli* nov. subspec. (holotype, NHMW 111424), j: *Sciocochlea llogaraensis* A. & P. L. REISCHÜTZ (paratype), k: *Sciocochlea nordsiecki* SUBAI (hermitage 5 km N of of the Mavroneri junction). Scale bar corresponds to 5 mm.

Sciocochlea collasi (STURANY 1904)

(Figure 3d)

Diagnosis: The glossy shell is almost entirely smooth, with only very fine striation over the neck. The interlamellar peristome margin is entirely smooth or has only a few fine, indistinct plicae right above the lamella inferior. The upper palatal plica is very short, the lower one is missing. The rudimentary clausilium plate is very narrow. Dimensions: Hs 8.2-10.9 mm, Ws 2.0-2.6 mm, Ha 1.9-2.5 mm, Wa 1.3-1.6 mm.

Syntypes: NHMW 39544 (specimen figured in STURANY 1904), 44869, 110177, 79000/K/54001, SMF 61458, SZ, RE.

Locus typicus: "Höhle des Monte San Salvatore auf Korfu" (STURANY 1904).

Distribution: So far the species is known only from the locus typicus.

Remarks: *Sciocochlea collasi* had been described by STURANY (1904) from an undefined cave of the Monte San Salvatore in Corfu (= Mt. Pantokratoras in Kerkira, Greece), which was then tentatively identified as the Katsouri Cave near Barbati (= Mparmpati) where the species was re-discovered (GITTENBERGER 1977 and 2000). This locality is at 39°44'34" N 19°55'31" E, 170 m.

Sciocochlea cryptica SUBAI & SZEKERES 1999

Diagnosis: The shell is stout, glossy, finely and densely striate. The protoconch is often almost as broad as the body whorl. From the dorsal side to the peristome there are fine, densely-spaced ribs that become stronger toward the basis. The interlamellar region of the peristome has no or only few (up to four) plicae. The upper palatal plica is short, the lower one is rudimentary. The clausilium plate is much wider than that of *Sciocochlea collasi*.

Sciocochlea cryptica cryptica SUBAI & SZEKERES 1999

(Figure 3e-f)

Diagnosis: The interlamellar part of the peristome is smooth or has only indistinct plicae. The end of the lamella inferior bends strongly and becomes nearly horizontal before reaching the peristome margin. Dimensions: Hs 9.2 mm, Ws 2.7 mm, Ha 2.1 mm, Wa 1.5 mm (holotype), Hs 7.7-9.3 mm, Ws 2.3-2.6 mm, Ha 1.8-2.2 mm, Wa 1.2-1.4 mm (material from all localities).

Holotype: SMF 311778.

Locus typicus: Greece, Epirus, karst slope above the Preveza to Igoumenitsa highway near Karteri, 1 km NW of the Mazarakia junction, 80 m.

Distribution: The subspecies is also known from the following additional localities in Greece, Epirus: cliffs above the Igoumenitsa to Plataria road (39°28'26.4" N 20°14'57.5" E, 200 m) (leg. P. Subai); Greece, Epirus, 8 km W of the crossing between the Perdika to Karteri road with Road 6 (39°22'38" N 20°19'19" E, 320 m) (leg. A., N. & P. L. Reischütz); Greece, Epirus, cliffs N of Anthousa (39°18'1" N 20°22'24" E, 200 m) (leg. A., N. & P. L. Reischütz).

Remarks: The exact position of the type locality given by SUBAI & SZEKERES (1999) is not clear. The holotype was found by P. Subai in soil sample from a small sinkhole of a karst field, which he could not locate at another visit two years later.

Sciocochlea cryptica acheron A. & P. L. REISCHÜTZ 2004
(Figure 3g)

Diagnosis: The shell is larger than those of the other *Sciocochlea cryptica* subspecies. There are three to four fine plicae at the interlamellar part of the peristome. Apart from the marginal plica at its end, the lamella inferior descends in an almost straight line. Dimensions: Hs 9.4-14.0 mm, Ws 2.0 - 2.5 mm, Ha 1.6-2.1 mm, Wa 1.2-1.5 mm.

Holotype: NHMW 103243.

Locus typicus: Greece, Epirus, quarry between Vouvopotamos and Gliki. This likely erroneous record has been corrected in a later paper as Greece, Epirus, Skepasto, quarry along Road 18 at the bridge S of the Kanallaki junction, S of Gliki (A. & P. L. REISCHÜTZ 2009a) (at 39°13'38" N 20°37'14" E, 110 m).

Distribution: So far *Sciocochlea cryptica acheron* is known only from the locality near Skepasto.

Remarks: Meanwhile the site at Skepasto was badly damaged by dumped organic waste (A. & P. L. REISCHÜTZ 2009a), but more recently the subspecies could again be collected there (A., N. & P. L. REISCHÜTZ, 2010b).

Sciocochlea cryptica filiates A. & P. L. REISCHÜTZ 2009
(Figure 3h)

Diagnosis: The interlamellar part of the peristome is mostly without plicae. The neck ribs are stronger and the aperture is less projected than in the nominotypical subspecies. Dimensions: Hs 7.5-10.4 mm, Ws 1.7-2.2 mm, Ha 1.8-2.3 mm, Wa 1.3-1.8 mm.

Holotype: NHMW 106688.

Locus typicus: Greece, Epirus, underneath Filiates, between Filiates and the road junction to Mavroneri.

Distribution: In addition to its locus typicus (39°36'9" N 20°19'5" E, 140 m), the subspecies is also known from the following sites in Epirus: near Smertos along the Sagiada to Filiates road at rkm 29 (mentioned as *Sciocochlea nordsiecki* in A., N. & P. L. REISCHÜTZ 2014b); cliffs on the left side of the Thiamis at the dam near Fragma Kalama (39°34'41" N 20°15'4" E, 50 m) (leg. A., N. & P. L. REISCHÜTZ); at the Thiamis along the Elaia to Pigadoulia road (39°34'16" N 20°21'35" E, 40 m) (mentioned as *Sciocochlea nordsiecki* in A., N. & P. L. REISCHÜTZ 2010b); cliffs above the Thiamis 1.6 km N of Neraida (A., N. & P. L. REISCHÜTZ 2014b) (at 39°32'4" N 20°26'1" E, 60 m); 1.5 km E of the Souli exit of Highway 2 (mentioned as *Sciocochlea* sp. in A., N. & P. L. REISCHÜTZ 2014b) (at 39°30'11" N 20°32'47" E, 680 m); above the Souli exit of Highway 2 (mentioned as *Sciocochlea* sp. in A., N. & P. L. REISCHÜTZ 2014b) (at 39°29'58" N 20°32'16" E, 650 m); Kristallopigi NW of Paramithia (39°29'40" N 20°27'48" E, 270 m) (mentioned as *Sciocochlea nordsiecki* in A., N. & P. L. REISCHÜTZ

2010b); quarry along the Grika to Kristallopigi road (39°28'44" N 20°28'7" E, 230 m) (leg. A., N. & P. L. Reischütz).

Remarks: It has been pointed out that *Sciocochlea cryptica filiates* specimens at the locus typicus show considerable variation in the size, but not the morphology, of the shells (A. & P. L. REISCHÜTZ 2009a). Such diversity might be due to substantial differences between ages of these shells, and thus the environmental conditions under which the corresponding animals lived. In *Sciocochlea cryptica filiates* some morphological dissimilarity can only be seen in the southernmost populations near Kristallopigi, which have specimens with stronger neck sculpture. The northernmost point in the range of this subspecies is less than 5 km south of that of *Sciocochlea nordsiecki*. Remarkably, despite such geographical vicinity, the neighbouring populations of the two *Sciocochlea* species do not show any tendency for morphological transition.

Sciocochlea cryptica harli nov. subspec.

(Figure 3i)

Diagnosis: The shell is very small, with broad apex. The thick peristome has up to two plicae at its interlamellar part. The lamella superior is strong. The end of the lamella inferior descends straight, or bends slightly downward, before turning horizontal at the peristome margin.

Description: The very small shell of 6 to $6\frac{2}{3}$ whorls has rather broad apex. The surface of the whorls is glossy, almost entirely smooth, only the neck has dense regular ribs that become stronger from the dorsal side toward the peristome. The peristome is ovoid, its thick and deflexed margin has up to two interlamellar plicae. The sinulus is large, the lamella superior is strong. The lamella inferior descends straight, or makes a weak downward wave, before becoming horizontal and ending in a strong marginal plica at the lower third of the aperture height. The lamella subcolumellaris also ends marginally, separated from the inferior by a strong plica. The plica principalis starts laterally and spans half a whorl toward the aperture. Of the dorsolateral palatal plicae the upper is short, the lower one residual or absent. The clausilium plate with parallel sides and blunt tip is partly visible through the aperture. Dimensions of the holotype: Hs 7.2 mm, Ws 1.7 mm, Ha 1.8 mm, Wa 1.2 mm, and of the paratypes: Hs 6.2-6.5 mm, Ws: 1.5 mm, Ha 1.5-1.6 mm, Wa 1.1 mm.

Locus typicus: Albania, Vlorë County, S of Sarandë along Highway 81 (39°50'43" N 20°1'28" E, 20 m).

Type material: Holotype (from the locus typicus, leg. A. & P. L. Reischütz 7.2009): NHMW 111424, paratypes (with the same data): RE/1 + 3 body whorls, SZ/1.

Additional material: From Albania, Vlorë County: Gjiri i Llamani, S of Himarë (40°4'55" N 19°46'7" E, 50 m) (leg. A., N. & P. L. Reischütz 9.2013 and 5.2015); cliffs along the Sarandë to Ksamil road (39°47'57" N 20°0'42" E, 60 m) (leg. A., N. & P. L. Reischütz 3.2011).

Derivatio nominis: The new subspecies is dedicated to Josef Harl, a friend and esteemed colleague of the authors.

Remarks: The southernmost locality of the new subspecies is only about 10 km NE of the locus typicus of *Sciocochlea collasi*, which occurs on the opposite side of the Straits of Corfu (Figure 2). In the north, at Gjiri i Llamani, it was found together with multiple shells of

Sciocochlea llogaraensis. Samples of *Sciocochlea cryptica harli* nov. subsp. collected from the locus typicus and the site between Sarandë and Ksamil have already been mentioned in earlier publications as *Sciocochlea* cf. *collasi* (A., N. & P. L. REISCHÜTZ 2010a and 2014b).

Sciocochlea llogaraensis A. & P. L. REISCHÜTZ 2009
(Figure 3j)

Diagnosis: The shell is slender and finely costate. The strength and spacing of the ribs only moderately and gradually increase until the aperture. The interlamellar peristome margin is smooth, or has up to two fine, indistinct plicae at its lower half. The lamella inferior makes a strong downward bend before turning again toward the peristome. The marginal plica at its end is usually much stronger than that joining the lamella subcolumellaris. The palatal plicae and the clausilium are as in *Sciocochlea cryptica*. Dimensions: Hs 7.4-14.5 mm, Ws 1.8-3.1 mm, Ha 1.6-2.7 mm, Wa 1.0-1.8 mm.

Holotype: NHMW 106687.

Locus typicus: Albania, Vlorë County, 500 m SE of the Qafa e Llogarasë, in the direction of Himarë.

Distribution: In addition to the locus typicus (at 40°11'35" N 19°36'8" E, 1010 m), the following other occurrences are known from Albania, Vlorë County: 500 m W of the Dukat junction at the road SH8, S of Vlorë (40°14'52" N 19°32'43" E, 340 m) (A. & P. L. REISCHÜTZ 2009b); Maja e Shën Iliut opposite to Dukat, S of Vlorë (A., N. & P. L. REISCHÜTZ 2014b) (at 40°13'55" N 19°33'28" E, 450 m); cliffs N of Palasë, S of the Qafa e Llogarasë (40°10'30" N 19°36'25" E, 250 m), (leg. A., N. & P. L. Reischütz); gorge S of the Plazhi i Gjipesë bus stop along the road SH8, S of Ilias (40°7'59" N 19°40'21" E, 200 m) (leg. A., N. & P. L. REISCHÜTZ); cliffs along the Kudhës to Pilur road, S of the pass (40°5'7" N 19°47'58" E, 270 m) (leg. A., N. & P. L. Reischütz); cliffs of Gjiri i Llamani, S of Himarë (A., N. & P. L. REISCHÜTZ 2014b) (at 40°4'55" N 19°46'7" E, 50 m); Porto Palermo, cliffs SE of the fortress (40°3'38" N 19°47'53" E, 20 m) (leg. A., N. & P. L. REISCHÜTZ); cliffs S of Borsh (40°3'27" N 19°51'43" E, 150 m) (leg. A., N. & P. L. Reischütz).

Remarks: Like *Sciocochlea cryptica filiates* (see A. & P. L. REISCHÜTZ 2009a), *Sciocochlea llogaraensis* also shows remarkable size range at some of its localities. This is apparent in the samples from Porto Palermo (Hs 7.4-11.4 mm) and Gjiri i Llamani (Hs 9.3-14.5 mm). At the latter site three specimens of *Sciocochlea cryptica harli* nov. subsp. were also collected. In June 2015 the locus typicus of *Sciocochlea llogaraensis* has been destroyed (see Figure 7).

Sciocochlea nordsiecki SUBAI 1993
(Figure 3k)

Diagnosis: The slender shell is glossy, finely and densely striate. The final two-thirds of the last whorl are distinctly costate, the ribs become very strong and wide-spaced on the dorsal side and at the neck. There are at least four strong plicae along the entire interlamellar peristome margin. The palatal plicae and the clausilium are as in *Sciocochlea cryptica*. Dimensions: Hs 6.9-9.7 mm, Ws 1.7-2.4 mm, Ha 1.6-2.3, Wa 1.1-1.4 mm.

Holotype: SMF 309220.

Locus typicus: Greece, Epirus, cave hermitage along the side road to Mavroneri, 5 km from its junction at the Filiates to Igoumenitsa road, 150 m.

Distribution: Apart from the locus typicus (at 39°38'38" N 20°18'49" E, 140 m), the species also occurs at the following localities: Albania, Vlorë County, cliffs 300 m N of Skallë, ESE of Butrint (39°41'49" N 20°7'15" E, 60 m) (leg. A., N. & P. L. Reischütz); Greece, Epirus, Dafni NE of Filiates (39°38'22" N 20°23'41" E, 180 m) (A., N. & P. L. REISCHÜTZ 2010b).

Remarks: The species has a very narrow distribution area, which is surrounded by those of *Sciocochlea cryptica* subspecies.

Unidentified *Sciocochlea*

The two short apical fragments of a *Sciocochlea* from Greece, Epirus, 1,5 km S of Perdika (39°20'55" N 20°19'22" E, 110 m, leg. A., N. & P. L. Reischütz) could not be identified. They possibly belong to *Sciocochlea cryptica cryptica*, as the locality is within the range of that subspecies (see map in Figure 2).

Tsoukatosia GITTENBERGER 2000

Type species: *Tsoukatosia liae* GITTENBERGER 2000

Synonymy: *Tsoukatosia (Agiosspeleikos)* A. & P. L. REISCHÜTZ 2003

Diagnosis: The costate, dextral shell often bends toward the aperture side. The ribs of the last whorl are interrupted by a conspicuous furrow that encircles the basis. The peristome margin is serrate, at least on its columellar side. The weak lamella superior joins a pointed sinulus. The marginally ending lamella inferior initiates as deep as the spiralis. The uninterrupted lamella subcolumellaris also ends marginally, separated from the inferior by a strong plica. There is no lamella inserta. The plica principalis starts lateral-ventrolaterally and extends over half of a whorl. Laterally a short upper palatal plica is fused to a weakly-bent lunella. The narrow clausilium plate has parallel sides and blunt tip.

Distribution: The main distribution area of the genus is in the southern half of the Peloponnesos, but toward the north and northeast isolated occurrences reach Central Greece and the Halkidiki Peninsula (Figure 1).

Habitat: The habitat preferences of *Tsoukatosia* species are the same as those of *Sciocochlea*.

Remarks: The subgenus *Tsoukatosia (Agiosspeleikos)* was erected for *Tsoukatosia christinae* (A. & P. L. REISCHÜTZ 2003), the second species described in this genus. Although some of its shell features markedly differ from those of *Tsoukatosia liae*, the subsequently discovered *Tsoukatosia* species with transitional morphology did not seem to support subgeneric division of the genus. The shells of *Tsoukatosia* species differ mainly in their size, proportions, sculpture, peristome plicae, and the positions of the lamellae (Figs 4a-h and 5).



Figure 4: *Tsoukatosia* and *Graecophaedusa* taxa:

a: *Tsoukatosia arabatzis* A. & P. L. REISCHÜTZ (paratype), b: *Tsoukatosia argolica* nov. spec. (holotype, NHMW 111423), c: *Tsoukatosia christinae* A. & P. L. REISCHÜTZ (paratype), d: *Tsoukatosia evauemgei* A., N. & P. L. REISCHÜTZ (holotype, NHMW 108112), e: *Tsoukatosia liae* GITTENBERGER (between Leonidio and Tsitalia), f: *Tsoukatosia nicoleae* nov. spec. (holotype, NHMW 111421), g: *Tsoukatosia pallgergelyi* nov. spec. (holotype, NHMW 111422), h: *Tsoukatosia subaii* HUNYADI & SZEKERES (holotype, HNHM 96864), i: *Graecophaedusa sperrlei* (Pangaion Mts., N of Hortokopi). Scale bar corresponds to 5 mm.

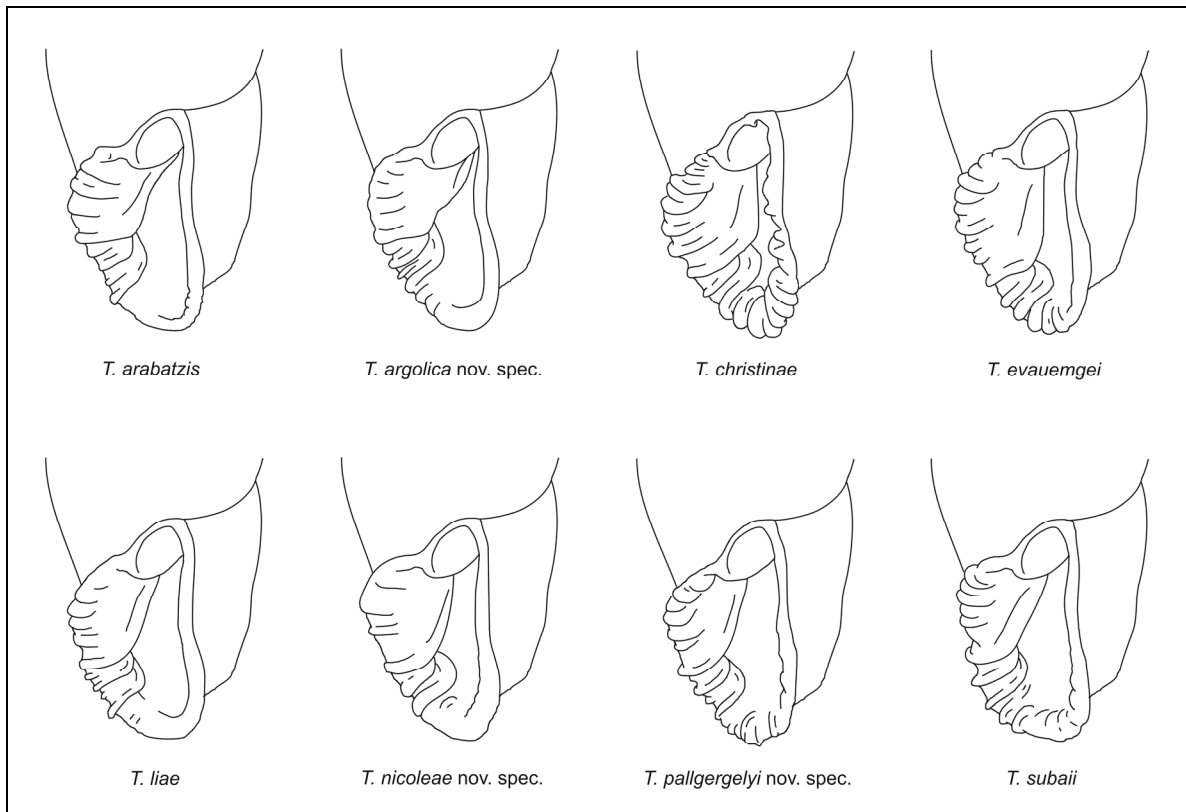


Figure 5: Lamella positions of the *Tsoukatosia* species.

Tsoukatosia arabatzis A. & P. L. REISCHÜTZ 2014
(Figure 4a)

Diagnosis: The slender, finely costate shell has relatively small aperture. The ribs at the neck are somewhat stronger and wider-spaced. The basal furrow is weak, barely visible in front view. The parietal margin of the peristome has only weak, indistinct plicae. The lamella inferior ends with a long, well visible horizontal segment at about mid-height of the aperture. The lamella subcolumellaris terminates farther down, diverging from the inferior and separated from it by not only one major, but also additional minor plicae. Dimensions: Hs 10.0-11.1 mm, Ws 1.8-2.0 mm, Ha 1.8-1.9 mm, Wa 1.6 mm.

Holotype: NHMW 108887.

Locus typicus: Greece, Macedonia, Athos Peninsula, cliffs N of the Megistis Lavras Monastery, 150 m.

Distribution: So far the species is known only from the locus typicus (at 40°10'27" N 24°22'53" E).

Remarks: *Tsoukatosia arabatzis* differs from all other *Tsoukatosia* species (except *Tsoukatosia argolica* nov. spec.: see there) by its weak basal furrow and high-positioned lamella inferior. The species is the northeasternmost representative of the genus, occurring at a distance of more than 250 km from the closest *Tsoukatosia* localities (Figure 2).

Tsoukatosia argolica nov. spec.

(Figure 4b)

Diagnosis: Relatively large species with weak basal furrow that is not visible in front view. The lamella inferior ends at mid-height of the aperture, much higher than the subcolumellaris.

Description: The body whorl fragments of the type material originate from relatively large shells. Their glossy surface is densely costate. The ribs become stronger, but not wider-spaced, at the neck. The weak basal furrow is not visible in front view of the shell. The ovoid peristome has thick margin, which is entirely smooth at its parietal side. The plicae of the columellar margin are uniform, evenly spaced and somewhat diffuse. The weak lamella superior is not much more emerged than the adjacent interlamellar plicae. Toward its end the lamella inferior bends downward before turning again toward the aperture, where it terminates marginally with a horizontal segment at about half height of the peristome. The lamella subcolumellaris is also marginal, its end part diverges from that of the inferior (Figure 5). In addition to a strong marginal plica, there are additional minor plicae between the two lamellae. The palatal plicae are as in the other *Tsoukatosia* species. The clausilium plates of the type specimens have been lost. Dimensions: holotype (fragment with aperture and $1\frac{1}{3}$ whorls): height 5.5 mm, Ws 2.6 mm, Ha 2.4 mm, Wa 1.8 mm, paratype (fragment with aperture and $1\frac{1}{2}$ whorls): height 5.7 mm, Ws 2.5 mm, Ha 2.3 mm, Wa 1.8 mm.

Locus typicus: Greece, Central Greece (NE Peloponnesos Peninsula), along the Neratzia to Hora road, S of the Galatas to Fanari road (37°33'8" N 23°15'42" E, 280 m).

Type material: Holotype (from the locus typicus, leg. A., N. & P. L. Reischütz 5.2015): NHMW 111423, paratype (body whorl with the same data): RE/1.

Derivatio nominis: The new species is named after the Argolis Peninsula, where it was discovered.

Remarks: *Tsoukatosia argolica* nov. spec. resembles *Tsoukatosia arabatzis* that has similarly high-positioned lamella inferior and similar sculpture, but differs from that species by its much larger size, weaker basal furrow, and the absence of parietal peristome plicae.

Tsoukatosia christinae A. & P. L. REISCHÜTZ 2003

(Figure 4c)

Diagnosis: The slender, moderately large and strongly costate shell has relatively small aperture (Hs/Ha >5.5). The neck ribs are strong, sharp and wide-spaced. The strong basal furrow is well visible along the entire last whorl. The peristome margin is strongly and densely serrate on both sides and even in the sinulus. The lamella inferior descends almost vertically, then turns sharply toward the aperture and reaches the margin with a long, horizontal end part at about the lower third of the peristome. The lamella subcolumellaris reaches the margin close and parallel to the inferior, separated from that by a strong plica. Dimensions: Hs 12.2-14.7 mm, Ws 2.6-3.1 mm, Ha 2.4-2.8 mm, Wa 1.8-2.0 mm.

Holotype: NHMW 102674.

Locus typicus: Greece, Peloponnesos, Taigetos Mts., cliff chapel 12 km S of Dirrahio, N of Kalamata.

Distribution: Apart from the locus typicus (at 37°7'45" N 22°6'43" E, 670 m), the species was also collected at the following other sites in Greece, Peloponnesos, Taigetos Mts.: ca. 500 m toward Nedoussa from the junction at Road 82 (A. & P. L. REISCHÜTZ 2004) (at 37°7'17" N 22°12'25" E, 450 m); along Road 82 between the Karveli and Nedoussa junctions (A. & P. L. REISCHÜTZ 2004) (at 37°6'28" N 22°11'22" E, 440 m); 2 km SE of the Karveli junction of Road 82 (37°5'0" N 22°11'1" E, 530 m) (leg. A., N. & P. L. Reischütz).

Remarks: *Tsoukatosia christinae* inhabits the western side of the Taigetos Mts., N and NE of Kalamata. Toward the south it reaches the range of *Tsoukatosia nicoleae* nov. spec. and occurs together with it at the site 2 km SE of the Karveli junction (A., N. & P. L. REISCHÜTZ 2010b).

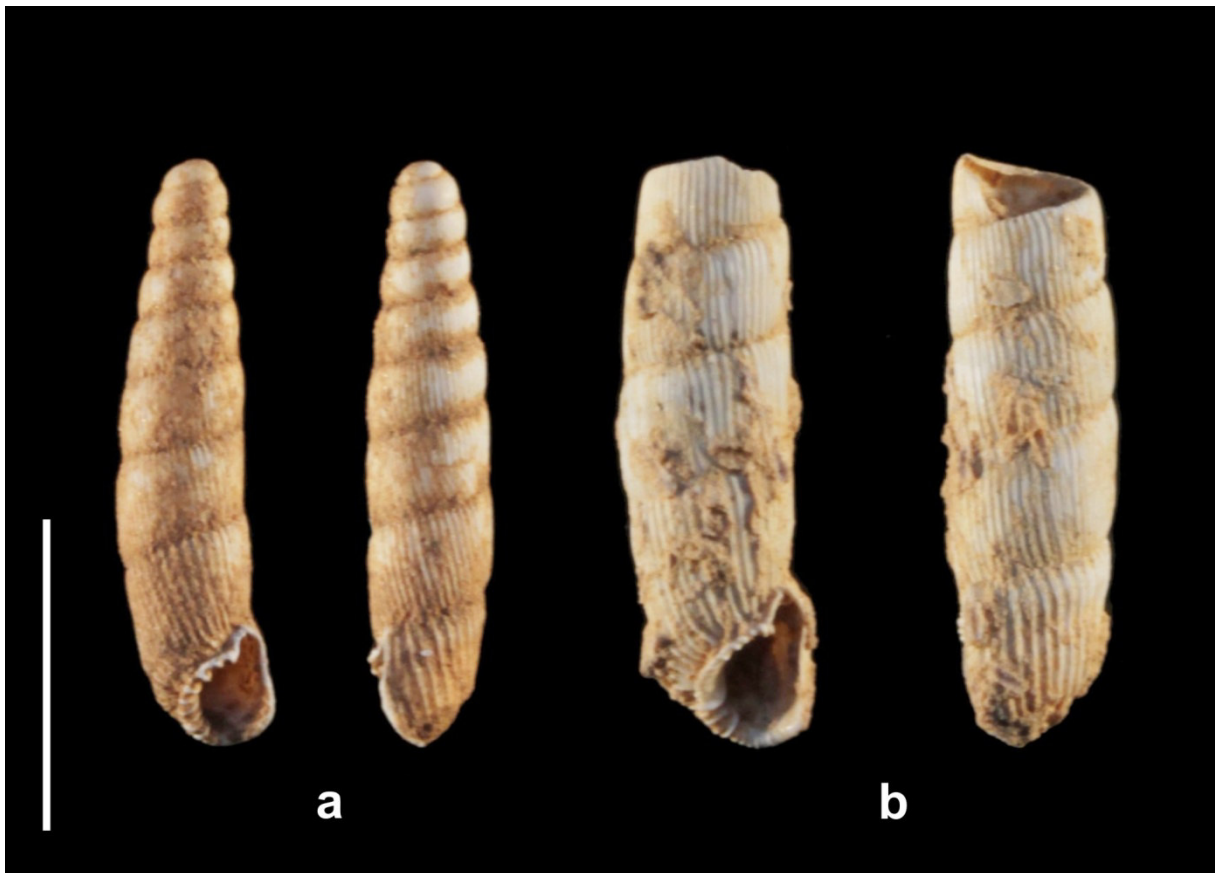


Figure 6: Two *Tsoukatosia* species occurring at the same locality
a: *Tsoukatosia nicoleae* nov. spec. (paratype) and b: *Tsoukatosia christinae* A. & P. L. REISCHÜTZ from the Taigetos Mts., 2 km SE of the Karveli junction of Road 82. Scale bar corresponds to 5 mm.

Tsoukatosia evauemgei A., N. & P. L. REISCHÜTZ 2012
(Figure 4d)

Diagnosis: The shell with a broad apex and relatively large aperture ($H_s/H_a < 4.5$) is densely costate. The ribs toward and at the neck become stronger and sharper, but only slightly wider spaced. The basal furrow encircles almost the entire last whorl. The lower half of the parietal peristome margin has a few indistinct plicae. The lamella inferior descends straight deep in the aperture, then turns sharply and reaches the margin horizontally at about the third of the peristome height. The marginal lamella subcolumellaris terminates below the interior,

separated from it by a strong plica. Farther there are some more strong marginal plicae down to the basis of the peristome. Dimensions: Hs 9.8 mm, Ws 2.5 mm, Ha 2.2 mm, Wa 1.8 mm.

Holotype: NHMW 108112.

Locus typicus: Greece, Peloponnesos, Taigetos Mts., W of the mountain pass along the Neda to Lykaio road, W of Megalopoli, 200 m downstream of a roadside spring.

Distribution: So far the species is known only from the locus typicus (at 37°25'15" N 21°58'26" E, 890 m).

Remarks: Of *Tsoukatosia evauemgei* only the holotype is known. Within one year from its discovery the collection site was destroyed by road construction. The site is near the northern end of the Taigetos range and represents one of the farthest *Tsoukatosia* occurrences from the coast (Figure 2).

Tsoukatosia liae GITTENBERGER 2000
(Figure 4e)

Diagnosis: The stout shell with broad apex is finely and densely costate. The ribs become stronger and sharper, but not denser, at the neck. The basal furrow encircles almost the entire last whorl. The parietal margin of the peristome is smooth. The lamella inferior descends straight, then bends gradually toward the peristome. It reaches the margin at about the lower third of the aperture, parallel to the also marginal end of the lamella subcolumellaris, which is separated from it by one large and up to two minor plicae. Dimensions: Hs 10.5-11.6 mm, Ws 2.8-3.0 mm, Ha 2.2-2.3 mm, Wa 1.6-1.7 mm.

Holotype: NNM 75727.

Locus typicus: Greece, Peloponnesos, 3.95 rkm toward Tsitalia from the junction at the Leonidio to Plaka road, 310 m.

Distribution: So far the species is known only from the locus typicus (at 37°8'35" N 22°52'47" E, 300 m).

Remarks: *Tsoukatosia liae* of the southeastern Peloponnesos shares the smooth parietal peristome only with *Tsoukatosia argolica* and *Tsoukatosia arabatzis*, which also mark the eastern border of the *Tsoukatosia* range. It differs from *Tsoukatosia arabatzis* by its stout shape, and from both species by the lamella inferior that ends lower and closer to the subcolumellaris.

Tsoukatosia nicoleae nov. spec.
(Figure 4f)

Diagnosis: A species with stout, densely costate shell, indistinctly serrate parietal peristome, and retracted lamella subcolumellaris that bends smoothly at its end.

Description: The stout shell with broad apex consists of $8\frac{1}{3}$ to 9 whorls. The surface of the whorls is densely costate. Toward the neck there are stronger, sharper and wider-spaced ribs (9 to 12 over the quarter whorl behind the peristome). The basal furrow encircles the entire

last whorl. The relatively large peristome (Hs/Ha 4.61-4.95) has drawn-out sinulus and recessed basis. The peristome is serrate on both sides, but the plicae are weak and diffuse on the parietal margin where they are confined mostly to its lower half. The weak lamella superior is not better emerged than the adjacent plicae of the columellar margin. The upper part of the obliquely descending lamella inferior is retracted, partly hidden behind the columella. The end part of the inferior bends in a smooth arch as it reaches the margin at about the lower third of the peristome height. The broadly-bent, also marginal lamella subcolumellaris is separated from the inferior by a strong plica (Figure 5). The palatal plicae are as in the other *Tsoukatosia* species. The clausilium plate could not be observed. Dimensions of the holotype: Hs 10.2 mm, Ws 2.6 mm, Ha 2.2 mm, Wa 1.7 mm, and of the paratypes: Hs 9.4-10.7 mm, Ws 2.4-2.6 mm, Ha 2.0-2.2 mm, Wa 1.6-1.7 mm.

Locus typicus: Greece, Peloponnesos, Taigetos Mts., 2 km SE of the Karveli junction of Road 82 (37°5'0" N 22°11'1" E, 530 m).

Type material: Holotype (from the locus typicus, leg. A., N. & P. L. Reischütz 7.2009): NHMW 111421, paratypes (with the same data) RE/4, SZ/1.

Additional material: In Greece, Peloponnesos, Taigetos Mts. the new species was also collected at the following localities: between Karveli and the Karveli junction at Road 82 (37°4'54" N 22°11'40" E, 510 m) (leg. A., N. & P. L. Reischütz 7.2010 and 4.2014); along the Karveli to Lada road at rkm 16 (37°4'50" N 22°13'4" E, 590 m) (leg. A. & P. L. Reischütz 7.2004); NW of Karveli (37°4'39" N 22°12'22" E, 600 m) (leg. A., N. & P. L. Reischütz 7.2010).

Derivatio nominis: The new species is dedicated to Nicole Steiner-Reischütz, who participated in several field trips and drove tens of thousands of kilometres on Balkan roads.

Remarks: At the locus typicus the new species occurs together with *Tsoukatosia christinae* (A., N. & P. L. REISCHÜTZ 2010b; Figures 2 and 6). Compared to that species, *Tsoukatosia nicoleae* nov. spec. has smaller, stouter shell, finer sculpture and denser neck ribs (9-11 at the last quarter whorl, whereas 7-9 in *Tsoukatosia christinae*), finer, less distinct parietal peristome plicae that do not reach the sinulus, and more retracted, not vertically descending lamella inferior with smoothly bending terminal part (Figure 5).

Tsoukatosia pallgergelyi nov. spec.
(Figure 4g)

Diagnosis: A *Tsoukatosia* species with very large, slender, strongly costate shell, serrate parietal peristome rim, and obliquely descending lamella inferior with smoothly bending terminal part.

Description: The large, slender shell of $10\frac{1}{3}$ whorls has relatively small aperture (Hs/Ha >5.5). The whorls are strongly costate. The height and spacing of the ribs increase gradually from the apex toward the basis. There are 11 ribs over the quarter whorl behind the peristome. The basal furrow encircles almost the entire last whorl. The ovoid peristome is strongly serrate all around, except for the sinulus. The lamella superior is weak, not more emerged than the adjacent peristome plicae of the columellar side. The lamella inferior descends obliquely, close to the columella. Its terminal part bends smoothly toward the aperture and reaches the margin at the lower third of the peristome height. The lamella subcolumellaris also ends marginally, parallel to the inferior and separated from it by a strong plica (Figure 5).

The palatal plicae and the clausilium plate could not be examined. Dimensions of the holotype: Hs 16.0 mm, Ws 3.6 mm, Ha 2.9 mm, Wa 2.2 mm.

Locus typicus: Greece, Peloponnesos, Taigetos Mts., pass between Mt. Mavrovouna and the Panagia Giatrissa Monastery, ESE of Kampos (36°53'21" N 22°20'53" E, 1410 m).

Type material: Holotype (from the locus typicus, leg. A. & P. L. REISCHÜTZ 7.2004): NHMW 111422.

Derivatio nominis: The new species is dedicated to Barna Páll-Gergely, a much-valued friend and colleague of the authors.

Remarks: Of *Tsoukatosia pallgergelyi* nov. spec., the southernmost representative of its genus (Figure 2), only the holotype is known. In an earlier publication (A. & P. L. REISCHÜTZ 2004) it was identified as *Tsoukatosia christinae*, which seems to be its closest relative. The new species differs from it by the much larger shell, weaker neck sculpture and peristome serration, as well as the obliquely descending lamella inferior with smoothly-bent end part.

Tsoukatosia subaii HUNYADI & SZEKERES 2009
(Figure 4h)

Diagnosis: The stout shell with broad apex has relatively large aperture (Hs/Ha <4.5). The fine ribs of the whorls become stronger, but not denser, toward and at the neck. The moderate basal furrow peters out before encircling the entire last whorl. The peristome is strongly serrate on its columellar side, but much less distinctly at the parietal margin. The well-emerged lamella inferior descends straight before turning toward the aperture with a short, arched end part. It reaches the margin at the lower third of the aperture. The lamella subcolumellaris also terminates marginally, parallel to the inferior and separated from it by a strong plica. Dimensions: Hs 10.4 mm (holotype), Ws 2.2-2.4 mm, Ha 2.2-2.6 mm, Wa 1.7-2.1 mm.

Holotype: HNHM 96864.

Locus typicus: Greece, Central Greece, right side of the road from Eratini to Lidoriki at 800 m N of the first Malandrino junction (38°25'13" N, 22°14'32" E, 700 m).

Distribution: So far the species is known only from the locus typicus.

Remarks: Of this species only the holotype was collected as complete shell, the rest of the type material consists of fragments. *Tsoukatosia subaii* occurs in Central Greece, close to the Gulf of Corinth, just north of the Peloponnesos Peninsula (Figure 2). It resembles *Tsoukatosia liae*, but differs from that by its less flattened whorls, weaker sculpture, and the serrate parietal peristome margin.

Unidentified *Tsoukatosia* samples

The limited *Tsoukatosia* material from three localities of the Peloponnesos Peninsula did not allow unambiguous identification. The samples are from the following sites:

(1) SE of Palaia Epidavros, along the road to Ano Fanari (37°36'33" N 23°10'34" E, 100 m), leg. A., N. & P. L. Reischütz 5.2015. The two apical fragments of less than 6 whorls were

found just about 10 km NE of the locus typicus of *Tsoukatosia argolica* nov. spec. and, based on their size, may also belong to that species.

(2) Taigetos Mts., cliffs along the Longanikos to Agoriani road (37°13'13" N 22°15'28" E, 800 m), leg. A., N. & P. L. Reischütz 4.2014. Two apices of a large species (3.1-3.5 mm, corresponding to $3\frac{1}{3}$ to $3\frac{1}{2}$ whorls). The locality is NE of those of *Tsoukatosia christinae* and *Tsoukatosia nicoleae* nov. spec. Unlike those, it occurs on the eastern side of the Taigetos and quite far, about 25 km away, from the coast (Figure 2).

(3) Taigetos Mts., between Kentro and Anatoliko, NE of Kampos (36°57'17" N 22°15'12" E, 640 m), leg. A. & P. L. Reischütz 7.2004. The collection site is between the range of *Tsoukatosia nicoleae* nov. spec. and the locus typicus of *Tsoukatosia pallgergelyi* nov. spec. (Figure 2). In an earlier paper (A. & P. L. REISCHÜTZ 2004) the single broken specimen without an apex (10.1 mm, $5\frac{1}{2}$ whorls) was identified as *Tsoukatosia christinae*, which shows apparent resemblance. The locality, however, is quite far from those of *Tsoukatosia christinae* and, based merely on the only available shell with larger size and somewhat differing morphology, the relation to this species is difficult to judge.

Graecophaedusa RÄHLE 1982

Type species: *Graecophaedusa sperrlei* RÄHLE 1982

Diagnosis: The slender, strongly costate shell with gradually tapering apex often bends toward the aperture side. The ovoid peristome with large sinulus has strongly serrate columellar and smooth parietal sides. The weak lamella superior is not much more emerged than the adjacent peristome plicae. The lamella inferior initiates deeper than the spiralis and ends just below mid-height of the aperture, higher than in most other Balkan Phaedusinae. The uninterrupted lamella subcolumellaris ends marginally below the inferior, separated from it by a strong marginal plica. There is no lamella inserta. The plica principalis runs from the ventral to the dorsal side. The ventrolaterally positioned short upper and slightly longer lower palatal plicae are connected by a weak lunella. The clausilium plate could not be examined.

Distribution: This monotypic genus is known only from the locus typicus of the type species (Figures 1 and 2).

Habitat: The habitat preferences of *Graecophaedusa* are the same as those of *Sciocochlea* and *Tsoukatosia*.

Remarks: Based on the high-ending and beyond the spiralis originating lamella inferior RÄHLE (1982) raised the possibility that *Graecophaedusa* might be closer related to some Phaedusinae of the Caucasus (e.g. *Pravispira* LINDHOLM 1924) than to those of the Balkans. The taxonomic value of these shell characters, however, seems questionable. A molecular phylogenetic study from UIT DE WEERD & GITTENBERGER (2013) revealed that *Dobatia* is closer related to *Pravispira* than to *Serrulina*, with which it shares similar inferior lamella structure. Furthermore, in some recently discovered Balkan species (e.g. *Tsoukatosia arabatzis* and *Tsoukatosia argolica* nov. spec.) this lamella ends almost as high as in *Graecophaedusa*.

Graecophaedusa sperrlei RÄHLE 1982

(Figure 4i)

Diagnosis: The shell features are those of the genus. Dimensions: Hs 11.2 mm (holotype), Ws 2.3-2.4 mm, Ha 2.1-2.2 mm, Wa 1.6 mm.

Holotype: SMF 254918.

Locus typicus: Greece, Macedonia, Pangaion Mts., "Pilaf Tepé, unterhalb des Gipfels dieses Berges in ca. 1900 m Höhe" (RÄHLE 1982).

Distribution: In 2006 the species was found in Greece, Macedonia, Pangaion Mts., along the road ascending from Hortokopi, 7 km upward from the Ipapantis tou Christou Monastery (40°55'0" N 24°11'27" E, 890 m) (leg. A. & P. L. REISCHÜTZ & FISCHER).

Remarks: *Graecophaedusa sperrlei* was described on the basis of a single intact shell, of which the exact locality was not known. Following several failed attempts the species was re-discovered only 25 years later at a site that is believed to be very close to the actual locus typicus (A. & P. L. REISCHÜTZ & FISCHER 2008). So far the holotype is the only available well-preserved specimen of this taxon.

Zoogeographical considerations

Cooling and drying of the climate during the Pliocene and Early Pleistocene caused a dramatic decrease in the diversity of the Phaesusinae in Europe and the entire western range of the subfamily (NORDSIECK 2013). The survival of the extant genera through these periods was ensured by their special biotope preferences, as well as by favourable local climatic conditions. The species of all these genera, except those of *Serrulina* and *Pravispira* that can hibernate deep inside decaying wood, are confined to temperate coastal regions with narrow yearly fluctuation of the temperatures (SUBAI & SZEKERES 1999; GITTEBERGER 2000).

Among the Phaesusinae of the Balkans *Serrulina serrulata* and *Dobatia goettingi* are forest-dwelling species that have their main distribution area farther to the east (LIKHAREV 1962; NÉMETH & SZEKERES 1995). Most likely they were not present in the Balkans before the Holocene period. By contrast, *Sciocochlea*, *Graecophaedusa* and *Tsoukatosia* species are highly endemic Tertiary relicts (NORDSIECK 1978a; RÄHLE 1982; GITTEBERGER 2000), which occur in so-called shallow subterranean habitats (JUBERTHIE, DALAY & BOUILLON 1981; CULVER & PIPAN 2009) that are often connected to caves. Their persistence under the increasingly unfavourable climate of the Mediterranean region, namely the colder winters and drier summers, was ensured by these microrefuges that provided balanced temperatures and humidity all year round (SUBAI & SZEKERES 1999; GITTEBERGER 2000). Trogllobiont populations are confined to their particular cave systems. These small communities and the lack of reproductive contacts between them provide favourable conditions for rapid speciation, which can result in many endemic taxa with small geographic ranges within relatively short periods of time (BARR & HOLSINGER 1985). Such circumstances could contribute to the diversity of *Sciocochlea* and *Tsoukatosia* species. No such effect is seen among the subterranean Phaesusinae along the permanently humid Caspian and Black Sea coasts. *Serrulinella senghanensis* (GERMAIN 1933), *Pontophaedusella ofensis* NORDSIECK 1994, and *Nothoserrulina subterranea* NÉMETH & SZEKERES 1995, which inhabit only 20-50 cm deep crevices without cave connections, all belong to monotypic genera.

The phylogenetic position of these subterranean *Phaedusinae* genera is uncertain. As live material of these could never be collected, their taxonomy is based solely on shell morphology. The difficulty of their classification is further aggravated by uncertainties regarding the age of the available shells. In their karst environments the shells can remain well preserved and even translucent over thousands of years, thus it is not clear whether they originate from extant populations or represent merely subfossil specimens. It is also uncertain if distinct species found at the same locality are/were truly sympatric, or inhabited the biotope during different periods of time. A clear indication for considerable age differences is seen in the wide size range of *Sciocochlea* shells at some of the localities.

Acknowledgements

The authors are grateful to Edmund Gittenberger, Henrik Gyurkovics, László Németh, Nicole Steiner-Reischütz and Peter Subai for their valuable contributions to this work, as well as to Anita Eschner, Zoltán Fehér and Ronald Janssen for granting access to the public collections at their care. Thanks are also due to Márta Börcsök S. for her help in preparing the photographic material, and to the providers of the Biodiversity Heritage Library database (<http://www.biodiversitylibrary.org/>) for making early zoological literature available.

References

- BARR T. C. & J. R. HOLSINGER (1985): Speciation in cave faunas.- *Annual Reviews of Ecology and Systematics* 16:313-337, Palo Alto (CA).
- BOETTGER C. R. (1935): Exploration biologique des cavernes de la Belgique et du Limbourg Hollandais. 22e Contribution: Mollusca.- *Mitteilungen der Höhlen- und Karstforschung* 1935:49-63, Berlin.
- BRANDT R. A. (1961): Diagnosen neuer Clausiliiden.- *Archiv für Molluskenkunde* 90:1-20, Frankfurt am Main.
- CULVER D. & T. PIPAN (2009): Superficial subterranean habitats - gateway to the subterranean realm.- *Cave and Karst Science* 35:5-12, Buxton, Derbyshire.
- EHRMANN P. (1927): Zur Systematik der Clausiliiden, besonders der ostasiatischen.- *Sitzungsberichte der Naturforschenden Gesellschaft zu Leipzig* 49-52:18-59, Leipzig.
- ERŐSS Z. & Z. FEHÉR (2001): *Dobatia goettingi* BRANDT, 1961 (Gastropoda: Clausiliidae) in Bulgaria.- *Opuscula Zoologica* 33:139-142, Budapest.
- GITTENBERGER E. (1977): Cave snails from Corfu, Greece. *Comunicacions del 6è Simposium d'Espeleologia*.- *Bioespeleologia* 1977:47-53, Terrassa.
- GITTENBERGER E. (2000): Serrulininae in Greece, there may be more (Gastropoda, Pulmonata, Clausiliidae).- *Basteria* 64:81-87, Leiden.
- GROSSU A. V. (1981): *Gastropoda Romaniae*, vol. 3. Suprafamiliile Clausiliacea și Achatinacea.- pp. 269, Universitatea din București, București.
- HESSE P. (1913): Zur Kenntnis der Molluskenfauna von Ostrumelien, 2.- *Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft* 45:1-16, 69-74, Frankfurt am Main.
- HUNYADI A. & M. SZEKERES (2009): *Tsoukatosia subaii* spec. nov. (Gastropoda: Pulmonata: Clausiliidae), a third representative of a relict genus from Greece.- *Schriften zur Malakozoologie* 24:1-4, Cismar, Ostholstein.
- ISSEL A. (1866): *Catalogo dei molluschi raccolti dalla missione italiana in Persia*.- *Memorie della Reale Accademia delle Scienze di Torino, Serie 2* 23:387-439, Torino.
- JUBERTHIE C., B. DALAY & M. BOUILLON (1981): Sur l'existence d'un milieu souterrain superficiel en zone calcaire.- *Mémoires de Biospéologie* 8:77-93, Saint Girons.
- LIKHAREV I. M. (1962): *Fauna SSSR, Mollyuski*, 3/4 (Clausiliidae).- pp. 317, Academic Press, Moskva, Leningrad (in Russian).

- LINDHOLM W. A. (1924): A revised systematic list of the genera of the Clausiliidae, recent and fossil, with their subdivisions, synonymy and types.- Proceedings of the Malacological Society of London 16:53-80, London.
- MOUSSON A. (1873): Coquilles recueillies par M. le Dr. SIEVERS dans la Russie méridionale et asiatique. - Journal de Conchyliologie 21:193-230, Paris.
- NÄGELE G. (1906): Einiges aus Vorderasien.- Nachrichtenblatt der Deutschen Malakozoologischen Gesellschaft 38:25-30, Frankfurt am Main.
- NÉMETH L. & M. SZEKERES (1995): New and little known species of the *Serrulina* group from northern Turkey (Gastropoda: Pulmonata: Clausiliidae).- Archiv für Molluskenkunde 124:93-96, Frankfurt am Main.
- NORDSIECK H. (1972): Fossile Clausilien, 1. Clausilien aus dem Pliozän W-Europas.- Archiv für Molluskenkunde 102:165-188, Frankfurt am Main.
- NORDSIECK H. (1973): Zur Anatomie und Systematik der Clausilien, 12. Phaedusinae, 1: Phaedusen aus Nepal und ihre systematische Stellung innerhalb der Unterfamilie.- Archiv für Molluskenkunde 103:63-85, Frankfurt am Main.
- NORDSIECK H. (1978a): Zur Anatomie und Systematik der Clausilien, 20. Die rezenten Arten der Serrulininae und der Gattung *Caspiophaedusa*.- Archiv für Molluskenkunde 109: 91-101, Frankfurt am Main.
- NORDSIECK H. (1978b): Zur Anatomie und Systematik der Clausilien, 19. Das System der Clausilien, I: Taxonomische Merkmale und Gliederung in Unterfamilien.- Archiv für Molluskenkunde 109:67-89, Frankfurt am Main.
- NORDSIECK H. (1995): Iranische Clausiliidae: Die Arten in Gilan und Mazandaran (mit Beschreibung neuer Taxa) (Gastropoda: Stylommatophora).- Stuttgarter Beiträge zur Naturkunde, Serie A 527:1-27, Stuttgart.
- NORDSIECK H. (2000): Annotated check-list of the fossil (pre-Pleistocene) Clausiliidae (Gastropoda: Stylommatophora) from central and western Europe.- Mitteilungen der Deutschen Malakozoologischen Gesellschaft 65:1-15, Frankfurt am Main.
- NORDSIECK H. (2013): Clausiliidae from the Villafranchian site Monte Serampoli (Lower Valdarno, Tuscany, Italy) (Gastropoda: Pulmonata: Stylommatophora).- Archiv für Molluskenkunde 142:237-244, Frankfurt am Main.
- NORDSIECK H. (2014): Annotated check-list of the genera of fossil land snails (Gastropoda: Stylommatophora) of western and central Europe (Cretaceous - Pliocene), with description of new taxa.- Archiv für Molluskenkunde 143:153-185, Frankfurt am Main.
- PÁLL-GERGELY B. & C.-C. ROIBU (2011): Land snail fauna of the Humosu Secular Forest (Suceava County, Romania); a new locality of *Serrulina serrulata* (L. PFEIFFER, 1847) (Gastropoda: Pulmonata: Clausiliidae).- Malacologica Bohemoslovaca 10:48-50, Bratislava.
- PFEIFFER L. (1847): Diagnosen neuer Heliceen.- Zeitschrift für Malakozoologie 4:12-16, 31-32, 65-71, 81-84, Kassel.
- RÄHLE W. (1982): *Graecophaedusa sperrlei* n. gen., n. sp.: ein bemerkenswertes Tertiärrelikt aus Griechisch-Mazedonien.- Archiv für Molluskenkunde 112:45-48, Frankfurt am Main.
- REISCHÜTZ A. & P. L. REISCHÜTZ (2003): Helleniká pantoía, 3: Die Schönste von allen. *Tsoukatosia (Agiosspeleikos) christinae* nov. subgen., nov. spec. (Clausiliidae: Pulmonata: Gastropoda).- Nachrichtenblatt der Ersten Vorarlberger Malakologischen Gesellschaft 11:1-3, Rankweil.
- REISCHÜTZ A. & P. L. REISCHÜTZ (2004): Helleniká pantoía, 9: Zur Verbreitung der Serulininae (Clausiliidae: Gastropoda) in Griechenland.- Nachrichtenblatt der Ersten Vorarlberger Malakologischen Gesellschaft 12:5-6, Rankweil.

- REISCHÜTZ A., P. L. REISCHÜTZ & W. FISCHER (2008): Helleniká pantoía, 15: Kein Ende abzusehen - Zur Kenntnis der Gattung *Balcanodiscus* RIEDEL & URBANSKI 1964 (Gastropoda: Pulmonata: Zonitidae).- Nachrichtenblatt der Ersten Vorarlberger Malakologischen Gesellschaft 15:11-13, Rankweil.
- REISCHÜTZ A. & P. L. REISCHÜTZ (2009a): Helleniká pantoía, 23: Ein Beitrag zur Kenntnis der Verbreitung von *Sciocochlea* C. R. BOETTGER 1935 (Gastropoda: Clausiliidae) im Epirus (Griechenland).- Nachrichtenblatt der Ersten Vorarlberger Malakologischen Gesellschaft 16:33-35, Rankweil.
- REISCHÜTZ A. & P. L. REISCHÜTZ (2009b): Es muss nicht immer Griechenland sein: *Sciocochlea* C. R. BOETTGER 1935 (Gastropoda: Clausiliidae) in Albanien, und andere malakologische Notizen.- Nachrichtenblatt der Ersten Vorarlberger Malakologischen Gesellschaft 16:47-49, Rankweil.
- REISCHÜTZ A., N. REISCHÜTZ & P. L. REISCHÜTZ (2010a): Beiträge zur Kenntnis der Molluskenfauna Albaniens.- Nachrichtenblatt der Ersten Vorarlberger Malakologischen Gesellschaft 17:29-31, Rankweil.
- REISCHÜTZ A., N. REISCHÜTZ & P. L. REISCHÜTZ (2010b): Helleniká pantoía, 29: Neue Fundorte von Serrulininae (Clausiliidae: Gastropoda) in Griechenland und Albanien.- Nachrichtenblatt der Ersten Vorarlberger Malakologischen Gesellschaft 17:37-39, Rankweil.
- REISCHÜTZ A., N. REISCHÜTZ & P. L. REISCHÜTZ (2012): Helleniká pantoía, 33: *Tsoukatosia evauemgei* nov. spec. (Clausiliidae: Pulmonata).- Nachrichtenblatt der Ersten Vorarlberger Malakologischen Gesellschaft 19:19-20, Rankweil.
- REISCHÜTZ A. & P. L. REISCHÜTZ (2014a): Helleniká pantoía, 35: Ein Beitrag zur Kenntnis der Molluskenfauna des Agion Oros (Chalkidike, Griechenland).- Nachrichtenblatt der Ersten Vorarlberger Malakologischen Gesellschaft 21:67-76, Rankweil.
- REISCHÜTZ A., N. REISCHÜTZ & P. L. REISCHÜTZ (2014b): Ein Beitrag zur Kenntnis der Verbreitung von der Gattung *Sciocochlea* C. R. BOETTGER 1935 (Gastropoda: Clausiliidae).- Nachrichtenblatt der Ersten Vorarlberger Malakologischen Gesellschaft 21:81-82, Rankweil.
- RETOWSKI O. (1887): Am Strande der Krim gefundene angeschwemmte Binnenconchylien.- Malakozoologische Blätter, Neue Folge 9:22-43, Kassel.
- STURANY R. (1904): Ueber einige von Herrn G. PAGANETTI-HUMMLER entdeckte Höhlenschnecken.- Nachrichtenblatt der Deutschen Malakozoologischen Gesellschaft 36:103-107, Frankfurt am Main.
- SUBAI P. (1993): Neue Arten seltener Landschnecken aus Griechenland und aus der Türkei (Gastropoda: Prosobranchia: Cyclophoridae; Pulmonata: Pupillidae, Clausiliidae).- Archiv für Molluskenkunde 122:63-69, Frankfurt am Main.
- SUBAI P. & M. SZEKERES (1999): *Sciocochlea cryptica* n. sp., a new representative of the Serrulina group (Gastropoda: Clausiliidae) from Epirus.- Schriften zur Malakozoologie 13:9-12, Cismar, Ostholstein.
- SYSOEV A. & A. SCHILEYKO (2009): Land snails and slugs of Russia and adjacent countries.- pp. 312, Pensoft, Sofia, Moskva.
- UIT DE WEERD D.R. & E. GITTEBERGER (2013): Phylogeny of the land snail family Clausiliidae (Gastropoda, Pulmonata).- Molecular Phylogenetics and Evolution 67: 201-216.
- URBAŃSKI J. (1960): Bemerkenswerte Clausiliiden (Moll., Pulm.) aus Bulgarien.- Bulletin de la Société des Amis de Sciences et de Lettres de Poznań, Ser. D, 1:113-147, Poznań.
- URBAŃSKI J. (1978): Bemerkenswerte Clausiliiden (Moll., Pulm.) der nördlichen Balkan-Halbinsel.- Bulletin de la Société des Amis de Sciences et de Lettres de Poznań, Ser. D, 17:235-252, Poznań.

- WAGNER A. J. (1914): Höhlenschnecken aus Süddalmatien und der Herzegovina.- Sitzungsberichte, Kaiserliche Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse, Abteilung I, 123:33-48, Wien.
- WELTER-SCHULTES F. W. (2012): European non-marine molluscs, a guide for species identification.- pp. 760, Planetposter, Göttingen.
- WENZ W. & A. ZILCH (1959): Gastropoda. Teil 2. Euthyneura.- pp. 400, Borntraeger, Berlin.

Addresses of the authors

Alexander and Peter L. Reischütz, Puechhaimgasse 52, A-3580 Horn, Austria.

Miklós Szekeres, Institute of Plant Biology, Biological Research Centre HAS, Temesvári krt. 62, H-6726 Szeged, Hungary.



Fig.7: Left – Locus typicus of *Sciocochlea llogaraensis* in July 2008; right in May 2015.