TAXONOMIC POSITION OF HELICELLA (JACOSTA) SYRENSIS CARINATOGLOBOSA HAAS, 1934

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Abstract The taxonomic position of the insufficiently known nominal taxon Helicella (Jacosta) syrensis carinatoglobosa Haas, 1934 is discussed on the basis of genital morphology. Our results show that the taxon is a separate species that ought to be classified in the genus Xerocrassa Monterosato, 1892 and not in the genus Trochoidea Brown, 1827 as proposed in several recent publications. Xerocrassa carinatoglobosa is a narrow-range endemic restricted to the Akrotiri Peninsula in southern Cyprus.

Key words Xerocrassa, Trochoidea, Cyprus, systematics, genital system.

INTRODUCTION

The as yet insufficiantly known nominal taxon Helicella (Jacosta) syrensis carinatoglobosa Haas, 1934 from Cyprus was originally described as a subspecies of the nominal taxon Helix syrensis Pfeiffer, 1846 and included in the subgenus Jacosta Gray, 1821 (supressed by ICZN Opinion 431 (1956)) of the genus Helicella Férussac, 1821 (type species by ICZN Opinion 431 (1956): Helix itala Linnaeus, 1758) on conchological grounds (Haas, 1934). Subsequently, Fuchs & Käufel (1936) regarded Helix syrensis (incl. Helix syrosina Bourguignat, 1876, Helix eugoniostoma Bourguignat, 1876, Helix eminens Westerlund, 1889, and Helix syrensis var. exserta Martens, 1889) from Syros Island (Cyclades, Greece) as the nominate subspecies of a 'Rassenkreis' widespread in the Eastern Mediterranean region (Euboea, Cyclades, Crete, Rhodes, Cyprus, Palestine). Based on genital characters of a single specimen of the nominal species Helix (Jacosta) siphnica Kobelt, 1883 from Sifnos Island (Cyclades), Fuchs & Käufel (1936) placed all taxa of the 'Rassenkreis' in Trochoidea Brown, 1827 (type species by monotypy: Trochus terrestris Pennant, 1777 (= Helix elegans Gmelin, 1791)) considered by these authors as a subgenus of Helicella. However, already Schuberth (1892) showed that Helix syrensis (sub Helix (Xerophila (Jacosta)) syrosina) has a dart apparatus consisting of a single dart sac and two bunches of mucus glands, a result confirmed by Mylonas et al. (1995). This configuration of the dart apparatus is shared by members of the genus Candidula Kobelt, 1871 (type species by absolute tautonymy: *Glischrus candidula* Studer, 1820 (= *Candidula uni-fasciata* Poiret, 1801)), in which the nominal taxon *Helix syrensis* is currently included (Triantis *et al.*, 2008; Cuttelod *et al.*, 2011).

Gittenberger (1991), in his revision of the Cyprian xerophilous hygromiids, showed that the "so-called" Cyprian subspecies of '*Helix'* syrensis can be divided into three groups, two of which were included in the genus *Helicopsis* Fitzinger, 1833 (type species by monotypy: *Helix striata* Müller, 1774) based partly on anatomical, but also on conchological and distributional data. The third group, including only the nominal taxon *Helicella (Jacosta) syrensis carinatoglobosa*, could not be classified with any genus by Gittenberger (1991) because preserved soft parts were unavailable to the author. Gittenberger (1991, p. 124) conjectured however that the taxon "most probably represents a separate species".

In the present study we propose that *Helicella* (*Jacosta*) *carinatoglobosa* should be placed in the genus *Xerocrassa* Monterosato, 1892 (type species by monotypy: *Helix seetzeni* Pfeiffer, 1847) and not in the genus *Trochoidea* as proposed in the recently published works by Cuttelod *et al.* (2011), Welter-Schultes (2012) and Vardinoyannis *et al.* (2012). Only Richardson (1980), without giving reasons or an explanation, previously affiliated the species with *Xerocrassa*, regarded by that author, however, as a subgenus of *Trochoidea*.

MATERIAL AND METHODS

This study is based on material kept in the following collections: FW, private collection of Frank Walther, Essen, Germany; MCZ, Museum

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of Comparative Zoology, Havard University, Cambridge, U.S.A.; MN, private collection of M.T. Neiber, Sehnde, Germany; SMF, Naturmuseum Senckenberg, Frankfurt a. M., Germany; ZMH, Zoological Museum, Universität Hamburg, Hamburg, Germany.

Living specimens were killed by immersing the crawling animals for 10–15 s in boiling water. Foot muscle tissue was conserved in 100% isopropanol and stored at -20 °C. The remaining soft parts were conserved in 70% ethanol. Shell measurements were taken using a digital calliper and measurements of the soft parts were taken with an ocular micrometre. The terminology of the individual parts of the genitalia follows Hausdorf & Sauer (2009). Shell whorls were counted according to the method described in Kerney *et al.* (1983).

SYSTEMATICS

The family level classification follows Razkin *et al.* (2015).

Geomitridae Boettger, 1909

Helicellinae Ihering, 1909

Trochoideini Nordsieck, 1987

Xerocrassa Monterosato, 1892

Type species by monotypy *Helix seetzeni* Pfeiffer, 1847

Xerocrassa carinatoglobosa (Haas, 1934)

Helicella (Jacosta) syrensis carinato-globosa Haas, 1934: 18–20, fig. 2–4

Helicella (*Trochoidea*) *syrensis carinato-globosa* Fuchs & Käufel, 1936: 632

Trochoidea (*Xerocrassa*) syrensis carinatoglobosa Richardson, 1980: 245

'Helicella' carinatoglobosa Gittenberger, 1991: 101, 123

Trochoidea carinatoglobosa Cuttelod *et al.*, 2011: 69 *Trochoidea carinatoglobosa* Welter-Schultes, 2012: 514, Q71

Trochoidea carinatoglobosa Vardinoyannis *et al.*, 2012: 32

Holotype "Zypern, Akrotiri-Wald" (= Cyprus, Akrotiri forest), leg. G.A. Mavromoustakis, 21.04.1933, SMF 6709/1.

Paratypes 4 sh, "Akrotiri-Wald", leg. G.A. Mavromoustakis, SMF 6710 (only the three adult shells were designated as paratypes by Haas (1934)); 6 sh, "Zypern, zw. Kap Gata u. Kap Zevgari" (= Cyprus, between Cape Gata and Cape Zevgari), leg. G.A. Mavromoustakis, 20.04.1933, SMF 6711/6.

Material examined 2 sh, "Zypern, Kap Gata" (= Cyprus, Cape Gata), leg. G.A. Mavromoustakis ex coll. A. Zilch, 1937, SMF 64372/2; 8 sh, "Zypern, Akrotiri Wald," leg. G.A. Mavromoustakis ex coll. K.L. Pfeiffer, 1938, SMF 97538/8; 3 sh, Cyprus, Akrotiri forest, leg. G.A. Mavromoustakis, Dec. 1935, leg. G.A. Mavromoustakis ex coll. T. van Benthem Jutting, MCZ 64467; 7 sp and 1 sh, Cyprus, Akrotiri, near the shore of the salt lake close to Agios Georgios (34°36'15" N, 32°56'25" E), leg. H.N. Büscher, 01.10.2011, ZMH 79331; 27 sp and 7 sh, Cyprus, Akrotiri, Agios Georgios (34°36'11" N, 32°56'23" E), leg. B. Hausdorf, 30.06.2012, ZMH 79636; 6 sp and 1 sh, Cyprus, Akrotiri, near the shore of the salt lake close to Agios Georgios (34°36'15" N, 32°56'25" E), leg. H.N. Büscher, 01.10.2011, MN GEO-58.

Shell (Figs 1–2, Tab. 1) Depressed-conical, conical to conical-globular, sometimes scalarid; with 4.25–5.75 convex whorls; protoconch smooth, 1–1.25 whorls, corneous; teleoconch irregularly ribbed, whitish to cream-coloured, usually with brown bands that may be fused and that are (if present) always interrupted by the whitish coarse radial ribs; body whorl with a crenulated



Figure 1 Holotype of *Xerocrassa carinatoglobosa* (Haas, 1934). "Zypern, Akrotiri-Wald" (= Cyprus, Akrotiri forest), leg. G.A. Mavromoustakis, 21.04.1933, SMF 6709/1.

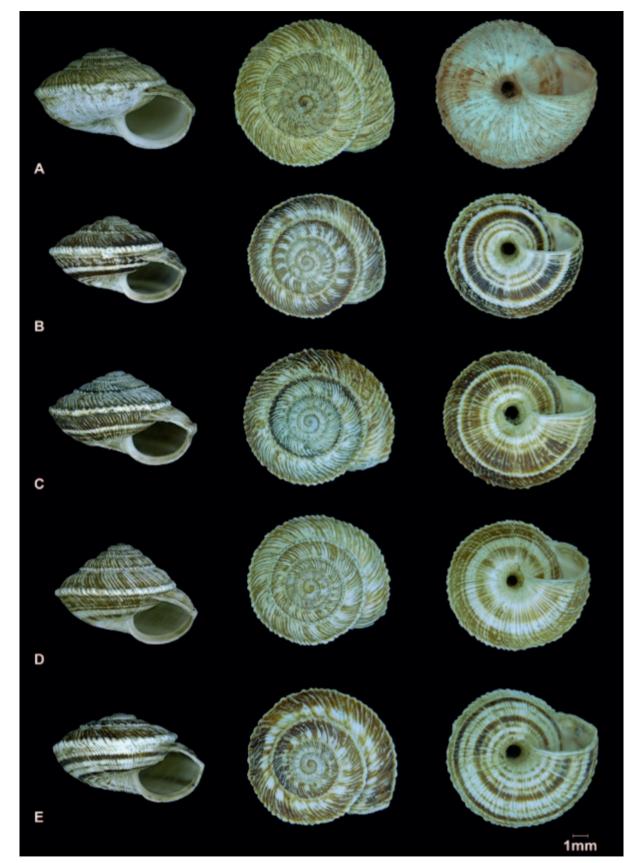


Figure 2 A–E Shell variability of *Xerocrassa carinatoglobosa* (Haas, 1934). All specimens from Cyprus, Akrotiri, near the shore of the salt lake close to Agios Georgios (34°36'15'' N, 32°56'25'' E), leg. H.N. Büscher, 01.10.2011, MN GEO-58.

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Table 1	Shell measurement	(in mm)) and	proportions	of Xerocrassa	carinatoglobos	a (Haas,	, 1934).
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Voucher	D		Н		DU		D/H		DU/D	
	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean
SMF 6709/1	14.28	_	9.88	_	1.58	_	1.45	_	0.11	_
(Holotype)										
SMF 6711b	10.51	_	7.71	_	1.25	_	1.36	_	0.12	_
(Paratype)										
SMF 6711c	10.75	-	7.16	_	1.42	_	1.50	_	0.13	-
(Paratype)					1.00		4.05		0.4.0	
SMF 6711d	10.56	_	5.71	—	1.33	_	1.85	_	0.13	—
(Paratype)	0.00				1 1 🗖		1 (0		0.10	
SMF 6711e	8.92	—	5.57	_	1.17	—	1.60	—	0.13	—
(Paratype) SMF 6711f	8.97		5.90		1.17		1.52		0.13	
(Paratype)	0.97	_	5.90	_	1.17	—	1.32	_	0.15	_
SMF 6711h	8.48	_	5.32	_	1.00	_	1.59	_	0.12	_
(Paratype)	0.10		0.02		1.00		1.07		0.12	
SMF 64372	12.22-12.94	12.58	9.47-10.45	9.96	1.58–1.17	1.38	1.24-1.29	1.27	0.09-0.13	0.11
(n=2)	12.22 12.71	12.00	,		1.00 1.17	1.00	1.21 1.2/	1.2/	0.07 0.10	0.11
SMF 79636	7.37-13.12	10.16	4.36-9.72	6.72	0.67-1.58	1.14	1.34-1.72	1.52	0.08-0.15	0.11
(n=34)										
MN GEO-58	9.35-11.07	10.03	5.59-7.17	6.47	0.75 - 1.42	1.08	1.38-1.72	1.56	0.08 - 0.14	0.11
(n=7)										

Abbreviations: D, maximum shell diameter; DU, diameter of umbilicus; H, shell height, n, number of specimens.

keel that sometimes almost disappears towards the aperture; aperture elliptical (slightly notched if keel reaches the aperture); upper insertion of the peristome slightly to distinctly descending; peristome sharp, upper margin not, basal and columellar margins slightly expanded, internally with a whitish rib; umbilicus moderately narrow (8%–15% of maximum shell diameter), hardly obscured by columellar margin.

Genitalia (Fig. 3, Tab. 2) Right ommatophoral retractor passing outside penioviducal angle. Penis innervated from the right cerebral ganglion. Dart apparatus symmetrical, consisting of two small accessory sacs (slightly shifted to one side of vagina) inserting just distal of the four mucus glands (each with 2–4 terminal branches), which are about twice as long as the accessory sac. Internal wall of vagina with several irregular longitudinal folds. Free Oviduct 0.23–0.34 times the length of vagina; vagina 1.12–1.43 times the length of penis; stalk of bursa copulatrix adhering to spermoviduct in situ, 0.57–0.64 times the length of flagellum and epiphallus together; bursa copulatrix ovoid-spherical, reaching albumen gland.

Vas deferens (in situ) loosely attached by connective tissue to angle between female and male parts of genitalia. Flagellum somewhat shorter to about as long as epiphallus, penis retractor muscle inserting in the distal fifth to fourth of its total length. Penis/epiphallus boundary well-visible from the outside, marked by a slight constriction; penis translucent, wider than epiphallus, about 0.3 times the length of epiphallus. Penial papilla elongate-ovoid, with a subapical pore, towards its base with rugose annular streaks, circular in crossection, lumen between outer wall and wall of seminal duct filled with rather loose connective tissue, inner wall of seminal channel with longitudinal folds. Genital atrium short, sometimes laterally with an indistinct, small bulge-like dilatation with a single fold inside, inner wall with irregular folds, some of which running along the wall into the penis, some finer and a prominent fold into the vagina.

Habitat Reported from open forests and Mediterranean (xerophilous) shrub land. The specimens for this study were collected close to Agios Georgios church, aestivating on low sclerophylous/halophilous shrubs growing on sandy soils (Fig. 4).

Geographic range Only known from the Akrotiri Peninsula, Sovereign Base Area Akrotiri (British Overseas Territory), Cyprus. *Remarks and comparisons* According to Hausdorf & Sauer (2009), the genus *Xerocrassa* is characterised by possessing a symmetric dart apparatus consisting of two small accessory sacs (possibly homologous to the accessory sacs of other Hygromiidae) and usually four branched

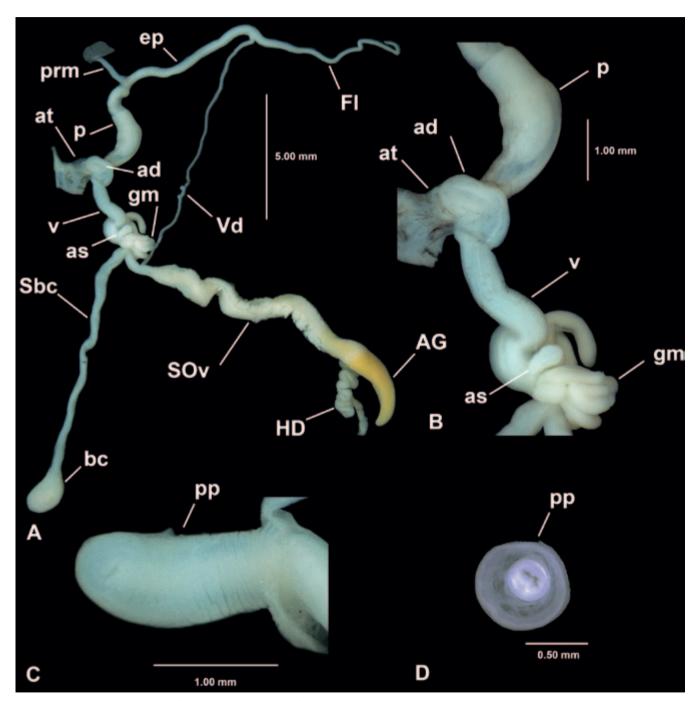


Figure 3 Genital system of *Xerocrassa carinatoglobosa* (Haas, 1934). Cyprus, Akrotiri, Agios Georgios (34°36'11" N, 32°56'23" E), leg. B. Hausdorf, 30.06.2012, ZMH 79636. **A–B** distal parts of male and female sections of genitalia. **C** penial papilla. **D** cross section through penial papilla. Abbreviations: ad, dilatation of genital atrium; AG, albumen gland; as, accessory sac; at, genital atrium; bc, bursa copulatrix, ep, epiphallus; Fl, flagellum; gm, mucus glands; HD, hermaphroditic duct; p, penis; pp, penial papilla; prm, penis retractor muscle; Sbc, stalk of bursa copulatrix; SOv, spermoviduct; v, vagina; Vd, vas deferens.

Voucher	р	ep _d	ep _p	Fl	V _{ap}	V _{gm}	Vt	Sbc	fOv
ZMH 79636/1	2.8	2.1	7.2	7.1	4.0	4.2	4.5	10.5	1.1
ZMH 79636/2	2.6	1.8	6.6	8.3	3.7	4.0	4.9	10.1	1.1
ZMH 79636/3	2.5	2.0	6.4	6.0	3.2	3.8	4.2	8.2	1.4
ZMH 79636/4	2.6	2.0	6.6	6.4	2.9	3.2	3.9	9.3	1.1

Table 2 Measurements of some parts of the genital system (in mm) of Xerocrassa carinatoglobosa (Haas, 1934).

Abbreviations: ep_d , epiphallus distal of the insertion of the penis retractor muscle; ep_p , epiphallus proximal of the insertion of the penis retractor muscle; Fl, flagellum; fOv, free Oviduct; p, penis; Sbc, stalk of bursa copulatrix; v_{av} , vagina up to the base of vaginal appendiculae; v_{gm} , vagina up to the mucous gland; v_t , total length of vagina.



Figure 4 A Habitat of *Xerocrassa carinatoglobosa* (Haas, 1934) near the church Agios Georgios (34°36'15" N, 32°56'25" E), Akrotiri Peninsula, Cyprus.

B Aestivating specimens on sclerophilous/halophilus shrubs (Chenopodiaceae) (B). Photographs by H. N. Büscher (Belgium).

mucus glands inserting into the lumen of the vagina. An appendix on the genital atrium is missing or weakly developed, and the internal wall of the vagina is equipped with irregularly arranged folds. The genus Trochoidea differs from Xerocrassa by the presence of a well-developed appendix on the genital atrium, and four strong longitudinal folds on the internal wall of the vagina, two of which each surround the opening of an accessory sac, and fuse at their proximal and distal ends, respectively (Hausdorf & Sauer, 2009). The anatomical findings presented in this study (i.e. the structure of the dart apparatus, the absence of an atrial appendix and the arrangement of folds in the vagina) clearly indicate a placement of the nominal taxon Helicella (Jacosta) syrensis carinatoglobosa Haas, 1934 in the genus Xerocrassa.

Table 3 Ratios of some parts of the genitalia of*X. carinatoglobosa* (Haas, 1934) (n=4 individuals). For
abbreviations see Table 2.

ep _p :p	ep _p :ep _d	ep _p :Fl	$ep_p:v_t$	$v_t:p$	$v_t : v_{ap}$	$v_t : v_{gm}$
2.5–2.6	3.2–3.7	0.8–1.1	1.3–1.7	1.6–1.9	1.1–1.3	1.1–1.2

Two other congeneric species, X. cretica (Férussac, 1821) and X. nicosiana (Gittenberger, 1991), also occur in Cyprus. Both are easily distinguished from X. carinatoglobosa by their rather finely striated to smooth shells, usually with a rounded distal half of the body whorl. Furthermore, X. nicosiana differs from X. carinatoglobosa according to Gittenberger (1991) and Fuchs & Käufel (1936) (mentioned as a transitional form between X. cretica and X. seetzeni) by possessing a vagina that is twice as long or more than twice as long as the penis, whereas this ratio does not exceed a value of 1.9 in X. carinatoglobosa (Tab. 3). Trochoidea liebetruti (Albers, 1852) and T. pyramidata (Draparnaud, 1805), the only other Trochoideini reported from Cyprus do not resemble X. carinatoglobosa conchologically and can easily be saparated from it by the presence of a well-developed atrial appendage (Hesse, 1934; Giusti et al., 1995). Some forms of Xeropicta ledereri are conchologically similar to X. carinatoglobosa, anatomically Xeropicta differs by the presence of two symmetrically arranged dart-bearing sacs with accessory sacs on the vagina and a large atrial appendage (Gittenberger, 1991).

Several *Xerocrassa* species from the eastern Mediterranea region possess a keeled shell (Brandt, 1959; Forcart, 1976; Mylonas *et al.*, 1995; Welther-Schultes, 1998, 2012; Hausdorf & Sauer, 2009; Heller, 2009; De Mattia & Páll-Gergely, 2014). *Xerocrassa picardi* (Haas, 1933) from Israel is easily distinguishable from *X. carinatoglobosa* by its pagoda-shaped shell and X. tuberculosa (Conrad, 1852) from Israel and Sinai differs from X. carinatoglobosa e.g. by its conical shell and much narrower umbilicus. Xerocrassa pseudojacosta (Forcart, 1976) has a wider umbilicus, a flatter lenticular shell and a less coarse radial sculpture, while X. davidiana (Bourguignat, 1863) has a hardly elevated spire, which is conical or sometimes step-like to slightly scalariform in *X*. carinatoglobosa. Among the keeled species from Crete, X. franciscoi Hausdorf & Sauer, 2009 differs by its much flatter shell, a finer radial sculpture and a much wider umbilicus. Anatomically X. franciscoi differs by the lower length ratios of proximal epiphallus/penis (epp/p), proximal epiphallus/distal epiphallus (ep_p/ep_d) and proximal epiphallus/flagellum (ep_p:Fl) (Tab. 3 and Hausdorf & Sauer, 2009). The shell of Xerocrassa siderensis (Maltzan, 1883) usually is rather blutly angled than keeled or rounded at the periphery, and the radial sculpture is much less prominent. Anatomically this species is easily distinguished by the significantly greater ep_p:Fl ratio (Tab. 3) and Hausdorf & Sauer, 2009). Xerocrassa amphiconus (Maltzan, 1883) differs from X. carinatoglobosa by the more depressed shell, finer radial sculpture and the very narrow, prick-like umbilicus and the greater ep_n:Fl ratio (Tab. 3 and Hausdorf & Sauer, 2009). The very variable X. mesostena (Westerlund, 1879) cannot be distinguished from X. carinatoglobosa on the basis of genital ratios, however in keeled populations of this species the radial sculpture is much finer in this species. Xerocrassa lasithiensis Hausdorf & Sauer, 2009, X. subvariegata (Maltzan, 1883) and X. heraklea Hausdorf & Sauer, 2009 from Crete may have an angulated body whorl, but the narrow umbilicus and the much more weakly developped radial sculpture readyly distinguish these species from X. carinatoglobosa. Xerocrassa heraklea differs anatomically in the lower ep_p/p ratio, X. subvariegata in the greater ep_p/ep_d ratio and X. lasithiensis in the greater ep_p/v_t ratio from X. carinatoglobosa (Tab. 3 and Hausdorf & Sauer, 2009). Xerocrassa claudiconus Hausdorf & Welter-Schultes, 1998 from Gávdos island has a flatter shell and finer radial sculpture, and a distinct widening of the flagellum towards its insertion point into the epiphallus (Welter-Schultes, 1998) is not observed in X. carinatoglobosa. Keeled forms of X. siphnica, endemic to Siphnos Island, have a flatter shell with a less coarse radial sculpture (Mylonas et al.

1995) and a comparatively well-developed atrial appendage, which is at most rudimentary in *X. carinatoglobosa*.

Most of the numerous species and subspecies of the tribe Trochoideini reported by Brandt (1959) from Libya are in need of revision. The taxa assigned to the subgenera Xeroregima Brandt, 1959, Ereminella Pallary, 1919, Xeroptyca Monterosato, 1892 and Xeroamanda sensu Brandt, 1959 not Monterosato, 1892 differ from X. carinatoglobosa anatomically in the markedly shorter flagellum (except for the nominal taxon T. (Xeroregima) liebetruti klemmi Brandt, 1959 which has a high, conical shell). In Xerobarcana Brandt, 1959 the flagellum is even rudimentary. All of the taxa from Libya assigned to Xerocrassa by Brandt (1959) have a rounded or at most slightly angled and finely striated body whorl, characteristics distinguishing all these forms readily from X. carinatoglobosa.

Although the endemic Xerocrassa radiation on Crete (Hausdorf & Sauer, 2009; Sauer & Hausdorf, 2009, 2010a, b, 2012; Sauer et al., 2013) and the phylogeography of X. geyeri (Soós, 1926) (Pfenninger et al., 1996; Pfenninger et al., 2003b) have been intensively studied and individual species have been included in various molecular studies (Pfenninger & Magnin, 2001; Pfenninger et al. 2003a; Steinke et al. 2004; Manganelli et al. 2005; Groenenberg et al., 2011; Razkin et al., 2015), the phylogenetic relationships within Trochoideini are, at present, not well understood. Brandt (1959) separates several groups as subgenera of Trochoidea including Xerocrassa mainly on the basis of differences in the length of the flagellum in relation to the epiphallus and shell ornamentation. Hausdorf & Sauer (2009), Sauer & Hausdorf (2009, 2010a, b, 2012) and Sauer et al. (2013) have shown that these characters are widely variable among species of the Cretan Xerocrassa radiation. Even a rudimentary flagellum, which is an autapomorphy of Xerobarcana, may be variable among species in the same genus (Gittenberger & Ripken, 1987). The anatomical characters of X. meda (Porro, 1840) and X. gharlapsi (Beckmann, 1987), the only two species widely accepted to belong to the subgenus Xeroclausa Monterosato, 1892 (type species: Helix meda Porro, 1840), fall into the limits of the generic concept of Xerocrassa as presented by Hausdorf & Sauer (2009). Aside from the separation of Trochoidea and Xerocrassa, which can be founded

anatomically as discussed above, we regard any further subdivision into genera or subgenera as premature until a detailed revision or molecular genetic analysis becomes available that ought to include the North African taxa along with the groups from the Near East, the Mediterranean region and Central to Western Europe.

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References

- BRANDT RA 1959 Die Helicellinae der Cyrenaika. Archiv für Molluskenkunde 88: 81–150.
- CUTTELOD A, SEDDON M & NEUBERT E 2011 European Red List of Non-marine Molluscs. Luxembourg, Publications Office of the European Union, 10+97 pp.
- DE MATTIA W & PALL-GERGELY B 2014 Records of *Xerocrassa muehlfeldtiana* (Rossmässler 1837) refer to *X. rhabdota* (Sturany 1901): redescription of the species and detailed anatomical description of other Balkan *Xerocrassa* species (Gastropoda: Pulmonata: Hygromiidae). *Journal of Conchology* **41**: 1–12.
- FORCART L 1976 Die Cochlicellinae und Helicellinae von Palästina und Sinai. *Archiv für Molluskenkunde* **106**: 123–189.
- FUCHS A & KÄUFEL F 1936 Anatomische und systematische Untersuchungen an Land- und Süßwasserschnecken aus Griechenland und von den Inseln des Ägäischen Meeres. *Archiv für Naturgeschichte (Neue Folge)* **5**: 541–662.
- GITTENBERGER E 1991 Ön Cyprian Helicellinae (Mollusca: Gastropoda: Pulmonata: Helicidae), making a new start. *Zoologische Mededelingen* 65: 99–128.
- GITTENBERGER E & RIPKEN TEJ 1987 The genus *Theba* (Mollusca: Gastropoda: Helicidae), systematics and distribution. *Zoologische Verhandelingen* **241**: 3–59.
- GIUSTI F, MANGANELLI G & SCHEMBRI PJ 1995 The non-marine molluscs of the Maltese Islands. *Museo Regionale di Scienze Naturali, Torino, Monografie* **15**: 1–608.
- GROENENBERG DSJ, NEUBERT E & GITTENBERGER E 2011 Reappraisal of the "Molecular phylogeny of western Palaearctic Helicidae s. l. (Gastropoda: Stylommatophoa)": when poor science meets Genbank. *Molecular Phylogenetics and Evolution* **61**: 914–923.
- HAAS F 1934 Über einige Landschnecken von Zypern. *Senckenbergiana* **16**: 16–21.

- HAUSDORF B & SAUER J 2009 Revision of the Helicellinae of Crete (Gastropoda: Hygromiidae). Zoological Journal of the Linnean Society **157**: 373–419.
- HELLER J 2009 Land Snails of the land of Israel. Pensoft, Sofia and Moscow, 360 pp.
- HESSE P 1934 Zur Anatomie und Systematik palaearktischer Stylommatophora. Zweiter Teil. *Zoologica* 85: 1–59, pls 1–9.
- INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE (ICZN) 1956 Opinion 431, 1956, Use of the plenary powers to secure that the generic name *Helicella* Férussac, 1821 (Class Gastropoda) shall be available for use in its accustomed sense. *Opinions and Declarations rendered by the ICZN* **14**: 347–372.
- KERNEY MP, CAMERON RAD & JUNGBLUTH JH 1983 Die Landschnecken Nord- und Mitteleuropas. P. Parey, Hamburg and Berlin, 1+386+1 pp.
- MANGANELLI G, SALOMONE N & GIUSTI F 2005 A molecular approach to the phylogenetic relationships of the western Palaearctic Helicoidea (Gastropoda: Stylommatophora). *Biological Journal of the Linnean Society* **85**: 501–512.
- MYLONAS M, BOTSARIS J, SOURDIS J & VALAKOS E 1995 On the development, habitat selection and taxonomy of *Helix (Jacosta) siphnica* Kobelt (Gastropoda, Helicellinae). *Zoological Journal of the Linnean Society* **115**: 347–357.
- PFENNINGER M, BAHL A & STREIT B 1996 Isolation by distance in a population of a small land snail *Trochoidea geyeri*: evidence from direct and indirect methods. *Proceedings of the Royal Society of London B* **263**: 1211–1217.
- PFENNINGER M & MAGNIN F 2001 Phenotypic evolution and hidden speciation in *Candidula unifasciata* ssp. (Helicellinae, Gastropoda) inferred by 16S variation and quantitative shell traits. *Molecular Ecology* **10**: 2541–2554.
- PFENNINGER M, EPPENSTEIN A & MAGNIN F 2003a Evidence for ecological speciation in the sister species *Candidula unifasciata* (Poiret, 1801) and *C. Rugosiuscula* (Michaud, 1831) (Helicellinae, Gastropoda). *Biological Journal of the Linnean Society* **79**: 611–628.
- PFENNINGER M, POSADA D & MAGNIN F 2003b Evidence for survival of Pleistocene climatic changes in northern refugia by the land snail *Trochoidea geyeri* (Soós 1926) (Helicellinae, Stylommatophora). *BMC Evolutionary Biology* **3**: 8.
- RAZKIN O, GÓMEZ-MOLINER BJ, PRIETO CE, MARTÍNEZ-ORTÍ A, ARRÉBOLA JR, MUÑOZ B, CHUECA LJ & MADEIRA MJ 2015 Molecular phylogeny of the western Palaearctic Helicoidea (Gastropoda, Stylommatophora). *Molecular Phylogenetics and Evolution* 83: 99–117.
- RICHARDSON L 1980 Helicidae: Catalog of species. *Tryonia* **3**: 1–697.
- SAUER J & HAUSDORF B 2009 Sexual selection is involved in speciation in a land snail radiation on Crete. *Evolution* **63**: 2535–2546.

- SAUER J & HAUSDORF B 2010a Palaeogeography or sexual selection: Which factors promoted Cretan land snail radiations? *In* M. Glaubrecht (ed) *Evolution in Action* 437–450 Springer, Berlin.
- SAUER J & HAUSDORF B 2010b Reconstructing the evolutionary history of the radiation of the land snail genus *Xerocrassa* on Crete based on mitochondrial sequences and AFLP markers. *BMC Evolutionary Biology* **10**: 299.
- SAUER J & HAUSDORF B 2012 A comparison of DNAbased methods for delimiting species in a Cretan land snail radiation reveals shortcomings of exclusively molecular taxonomy. *Cladistics* **28**: 300–316.
- SAUER J, OLDELAND J & HAUSDORF B 2013 Continuing fragmentation of a widespread species by geographical barriers as initial step in a land snail radiation on Crete. *Plos One* **8**: e62569.
- SCHUBERTH O 1892 Beiträge zur vergleichenden Anatomie des Genitalapparates von *Helix* mit besonderer Berücksichtigung der Systematik. *Archiv für Naturgeschichte* **58**: 1–66, pls I–VI.

- STEINKE D, ALBRECHT C & PFENNINGER M 2004 Molecular phylogeny and character evolution in the western Palaearctic Helicidae s. L. (Gastropoda: Stylommatophora). *Molecular Phylogenetics and Evolution* **32**: 724–734.
- TRIANTIS KA, VARDINOYANNIS K & MYLONAS M 2008 Biogeography, land snails and incomplete data sets: the case of three island groups in the Aegean Sea. *Journal of Natural History* **42**: 467–490.
- VARDINOYANNIS K, DIMITROPOULOS S & MYLONAS M 2012 Atlandas ton salingarión tis Kíprou Cyprus Wildlife Society, Natural History Museum of Crete, University of Crete, Lefkosía, 48 pp.
- WELTER-SCHULTES F 1998 Die Landschnecken der griechischen Insel Gávdos, der südlichsten Insel Europas. Schriften zur Malakozoologie aus dem Haus der Natur–Cismar **12**: 1–120.
- WELTER-SCHULTES F 2012 European non-marine molluscs, a guide for species identification. Planet Poster Editions, Göttingen, 3+679+78 pp.