Carination strikes the eye: extreme shell shapes and sibling species in three Andean genera of the Orthalicidae (Gastropoda, Stylommatophora)

A.S.H. Breure

Breure, A.S.H. Carination strikes the eye: extreme shell shapes and sibling species in three Andean genera of the Orthalicidae (Gastropoda, Stylommatophora).
Zool. Med. Leiden 82 (45), 31.xii.2008: 499-514, figs 1-15.— ISSN 0024-0672.
A.S.H. Breure, National Museum of Natural History, P.O. Box 9517, NL 2300 RA Leiden, The Netherlands (breure@naturalis.nnm.nl).

Key words: Gastropoda; Orthalicidae; *Bostryx*; *Neopetraeus*; *Scutalus*; Argentina; Chile; Peru; taxonomy; land snails.
Two new sibling species are described, *Bostryx multiconspectus* spec. nov and *B. primigenius* spec. nov., one of which is carinate. From the carinate taxa known in the Orthalicidae, 16 are occurring at localities in the Andes from northern Peru to northwestern Argentina. They belong to three genera, *Bostryx, Neopetraeus* and *Scutalus*. It is hypothesized that carination originated independently in these lineages.

Introduction

While working on a collection of *Bostryx* from Peru, collected by W.K. Weyrauch (probably during the 1950s) and myself (1976) near Lima, some remarkable sibling species were found. One of the species is carinate, which as an extraordinary phenomenon is known to occur within the Orthalicidae in some Andean *Bostryx*, *Scutalus* and *Neopetraeus* species (Pilsbry & Olsson, 1949) and in *Cochlorina*, *Oxychona* and *Pseudoxychona*. The latter three genera only occur in eastern Brazil and their shell shape readily distinguishes them from others (Breure, 1979; Simone, 2006). The three other genera occur in the central Andes, from northern Peru to northwestern Argentina. Their carinate species may be more enigmatic and are the subject of this paper.

Carinate or angular whorls as a terminology is sometimes confusing. In this paper I follow the definitions given by Burch (1962), who consideres a shell angular when "having an angle rather than a round contour" (fig. 472). A keel is "a sharp edge; carina" (fig. 494). From his figure it may here be further precised that a carina is a somewhat outward protruding ridge, which may or may not internally be thickened. When a carina occurs both at the periphery and around the umbilicus of a shell, it is defined as doubly carinate (Burch, loc.cit., fig. 12q). However, it remains a matter of subjectivity to make the distinction between obtusely keeled and angular sensu Burch. In some species a gradual transition between the two forms may be observed. In the context of this paper, obtusely keeled is defined as having the periphery strongly angled without becoming an outwardly protruding ridge.

As Pilsbry & Olsson (1949) noted, carination "is a character of little taxonomic significance, [but] it is a quality which strikes the eye". Besides being peculiar in shell morphology, the different species also elicit biologically interesting questions. E.g., is there any phylogenetic relationship? What is the underlying population genetical mechanism causing carination? And are there any ecological similarities which cause their occur-

rence at different localities? What is the evolutionary advantage of this shell form?

Part of the material described in this paper is evidently what Weyrauch referred to when he wrote (Weyrauch, 1956: 17): "As I will illustrate in a later paper [which was never published], the variation in a population of a new subspecies of *Bostryx eremothauma* (Pilsbry) comprises all forms hitherto placed in the polyphyletic 'shape-types' of *Peronaeus*, *Ataxus*, *Lissoacme*, *Platybostryx* and *Discobostryx* [at the time that Weyrauch wrote this, these were all considered as subgenera of *Bostryx*; now synonyms of *Bostryx* sensu lato (Breure, 1979)]. This great variation of shape, not observed in any other species of land shells, agrees with the still greater diversification of shapes in different species of the genus *Bostryx*. This is evidently due to the young age of this genus". It has been suggested that high-spired shells tend to be active on vertical surfaces, while low-spired species use horizontal substrates (Cain, 1977; Cain & Cowie, 1978; Cameron, 1978; Cook, 2008). Differences in shape are associated with microhabitats, which would suggest that

Table 1. Carinate species in *Bostryx, Scutalus* and *Neopetraeus*, their localities, ecology and forms of carination observed (a, angular; oc, obtusely carinate; cc, carinate; dc, doubly carinate).

	Taxon	Material	Ecology	Carination
1	*Bostryx c. carinatus* Breure, 1978	Peru, Dept. Ancash, 5 km SW Chavin de Huantar, 3300 m	at base of limestone ledges	cc
2	*Bostryx carinatus trochiformis* Breure, 1978	Peru, Dept. Ancash, Raracachaca	?	dc
3	*Bostryx cuyanus* (Pfeiffer, 1867)	Argentina, Prov. Mendoza, Villavicencio, 1900 m	?	cc
4	*Bostryx doelloi* Hylton Scott, 1954	Argentina, Prov. Mendoza, Cerro Pelado [2500 m]; Las Cuevas [2500 m]	?	cc
5	*Bostryx eremothauma* (Pilsbry, 1896)	Chile, Region Antofagasta, Cachinal [2575 m], Paposo [10 m]	under stones and at the root of cacti	dc
6	*Bostryx fisheri* Pilsbry, 1956	Peru, Dept. Junín, below [NE] Tarma	?	oc
7	*Bostryx lentiformis* Breure, 1978	Argentina, Prov. San Juan, Sierra de Tontal, 3500 m	?	cc
8	*Bostryx metagyra* (Pilsbry & Olsson, 1949)	Peru, Dept. Arequipa, Atiquipa	?	cc
9	*Bostryx multiconspectus* spec. nov.	Peru, Dept. Lima, Tambo de Viso, 2700 m	on shrubs on rather steep rock-face	oc-dc
10	*Bostryx planissimus* (Pilsbry & Olsson, 1949)	Peru, Dept. Ancash, 3 km S Macara	on face of limestone cliffs	dc
11	*Bostryx reentsi* (Philippi, 1851)	Peru, Dept. Arequipa, near Chala	? [subfossil]	oc-cc
12	*Bostryx solutus* (Troschel, 1847)	Peru, Dept. Lima, near San Mateo, 3300 m	in rock crevices	a-dc
13	*Bostryx weyrauchi* (Pilsbry, 1944)	Peru, Dept. Ayacucho, Ninabamba, 2000 m [13°27'00"S, 73°18'00"W]	?	oc-cc
14	*Scutalus baroni* (Fulton, 1896)	Peru, Dept. Cajamarca, near Tembladera, Yonan [7°15'10'' S, 79°6'7''W]	on rock-faces	dc
15	*Scutalus broggii* (Pilsbry & Olsson, 1949)	Peru, Dept. Lima, near Huacho, Cerro Colorado [11°8'00''S, 77°34'00''W]	? [fossil, probably Pleistocene]	dc
16	*Neopetraeus binneyanus* (Pfeiffer, 1857)	Peru, Dept. La Libertad, Chagual [07°50' 08"S 077° 38'03"W]	on rocks and trunks of trees; on trees and cacti	cc

the various forms of this species occupy different niches within the same locality. Unfortunately most museum labels do not provide details on the habitat, while Weyrauch's field notes have been destroyed after his death (Cuezzo, personal communication). It is, however, clear that regions like e.g. the area around Tambo de Viso – El Infernillo in the Río Rimac valley and near Tembladera in the Río Jequetepeque valley, are exceptionally interesting and certainly warrant further investigations to shed light on the questions mentioned above.

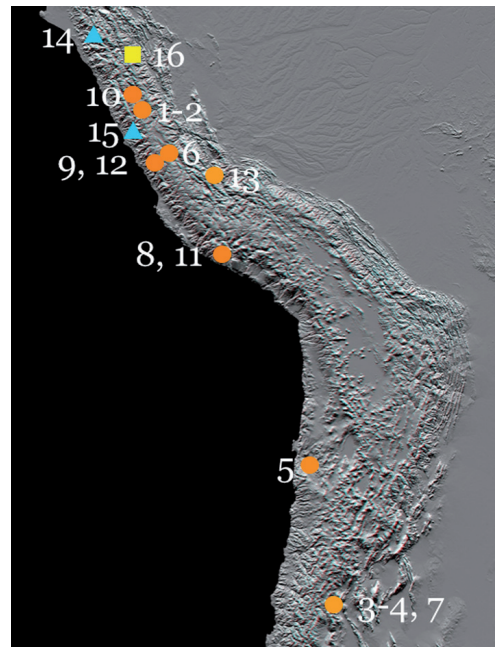

Fig. 1. Distribution of carinate species of *Bostryx*, *Scutalus* and *Neopetraeus* in the Central Andes. Numbers refer to Table 1.

Table 1 and fig. 1 summarize all known carinate species and their distribution within the three genera mentioned. From the data presented the following may be observed: (1) There is no clear connection between the group of species as a whole, although some might be closely related; (2) Although ecological data are limited, the available data show considerable variation; (3) The species are distributed over a vast area, both occurring in interandean valleys as well in the coastal plain; (4) Nearly all species are highly restricted in range, occurring at one or a few (nearby) localities.

It is now proposed that, as a null hypothesis, carination originated independently and is thus a striking case of convergence.

Material and methods

The following abbreviations are used to refer to the depositories of the material: ANSP – Academy of Natural Sciences, Philadelphia, USA; BMNH – The Natural History Museum, London, UK; DMNH – Delaware Museum of Natural History, Wilmington, USA; FLMNH – Florida Museum of Natural History, Gainesville, USA; FMNH – Field Museum of Natural History, Chicago, USA; MCZ – Museum of Comparative Zoology, Boston, USA; MNHN – Muséum Nationale d'Histoire Naturelle, Paris, France; RMNH – Nationaal Natuurhistorisch Museum / Naturalis, Leiden, the Netherlands; SBMNH – Santa Barbara Museum of Natural History, Santa Barbara, USA; SMF – Natur-Museum Senckenberg, Frankfurt am Main, Germany; ZMB – Zoologisches Museum der Humboldt-Universität, Berlin, Germany; ZMH – Zoologisches Museum der Universität, Hamburg, Germany.

Other abbreviations refer to the dimensions of the shells, measured with a digital sliding gauge and following the methods as in fig. 2: D, diameter of the shell; H, height of the shell; HA: height of aperture; LW, height of last whorl; W, number of whorls;

WA, width of aperture. All measurements in mm. Metrics are presented as the mean (M), together with standard deviation (s) for the number of specimens (n) measured per population. For the morphometrics all samples were treated as operational taxonomic units, despite the very close proximity of some of them in geographical sense (i.e. same population).

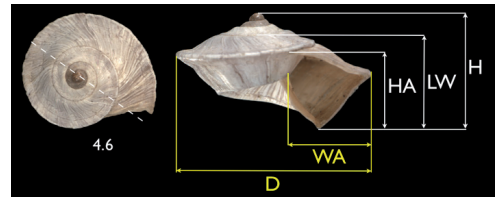

Fig. 2. Way in which (A) counts of whorls and (B) measurements were taken.

Where relevant, localities have been georeferenced as far as they could be traced, using the GEOnet Names Server (http://earth-info.nga.mil/gns/html/index.html). Altitudes have been derived from Google Earth when cited between square brackets, otherwise they are conform the original labels by their collectors.

Under type material in the systematic part, the manuscript names given by Weyrauch are mentioned for curational purposes. Further details on this collection are described elsewhere (Breure & Neubert, 2008; Breure & Neubert, in preparation). The specimens originally designated 'holotypes' by Weyrauch are marked with an asterisk (*). Unless mentioned otherwise all material has been collected by W.K. Weyrauch.

Systematic part

Class Gastropoda Cuvier, 1797
Clade Stylommatophora A. Schmidt, 1855
Family Orthalicidae Albers, 1860
Subfamily Bulimulinae Tryon, 1867

Bostryx Troschel, 1847

Bostryx Troschel, 1847: 49.

Bostryx multiconspectus spec. nov.
(figs 3-4)

Material.— Holotype: Peru, Dept. Lima, Río Rimac valley, Tambo de Viso [11° 48′ 39″ S 076° 20′ 48″ W], 2700 m (SMF 156286*). Paratypes: same data as holotype (ANSP 331844/1, DMNH 135140/2, FLMNH 109651/5, FMNH 53989/19, 193457/9, MCZ 202213/7, RMNH 109754/4, RMNH 109755/1, SBMNH 137895/5, SMF 156283/8, 156284/1, 156287/1, 155600/1, 208207/5, 284421/1, 284422/8, ZMB 101801/2) [all as *Bostryx bequaerti* Weyrauch MS. or *Bostryx eremothauma bequaerti* Weyrauch MS.]; opposite Tambo de Viso, 2650 m, A.S.H. Breure leg., 23.iv.1976 (RMNH 109756/6, RMNH 109757/1).

Diagnosis.— A carinate species up to 10.8 mm that can show multiple shell shapes, from discoidal to compressed-elongate; height/diamter ratio ranging from 0.45-1.00. Always widely umbilicate. Colour corneous-brown with the growth striae somewhat thickened, giving a whitish hue to the shell, usually with two or three small corneous spiral bands.

Description.— Shell up to 10.8 mm, 0.59 times as long as wide, the last whorl angled

at the periphery, carinate, a second keel around the widely and deep umbilicus; quite variable in shell shape but mostly rather compressed in height, rather thin. Colour corneous-brown, the growth striae thickened, giving the shell a whitish appearance. In most specimens with small, corneous spiral bands, two or three on the last whorl. Protoconch smooth, projecting, convex and nipple-like, apruptly changing into the remaining whorls, in total 4.5 (mean). Suture hardly impressed, but projecting when the next whorl is attached (slightly) below the carinated periphery. Aperture subtriangular, variable in form, mostly oblique to outwardly projecting, angular or rounded above, hardly descending in front, 0.96 times as long as wide, 0.69 times the total length. Peristome simple and acute, columellar margin concave, arcuate, parietal callus transparent.

Dimensions of holotype: H 8.1, D 14.5, HA 5.7, WA 6.0, LW 7.0, W 4.6. See also table 2.

Comparisons.— This species may be compared to *Bostryx fisheri* Pilsbry, 1956, which occurs in an interandean valley ca. 100 km NE Tambo de Viso. It differs from that species in (1) being larger, while having more or less the same number of whorls (4.6); (2) upper whorls, except the protoconch, flat, the suture hardly impressed. This new species may also be compared to *Bostryx eremothauma* (Pilsbry, 1896), from which it differs in (1) the less descending aperture in front; (2) growth striae less thickened, resulting in a smoother appearance.

Remarks.— The variation in shell shape is shown in fig. 4.

Etymology.— The epithet refers to the variation in shell shape of this conspicuous species; Latin *multus*, multitude and *conspectus*, catching the eye.

Fig. 3. *Bostryx multiconspectus* spec. nov. A-C, different views of holotype (SMF). Actual shell diameter 14.5 mm.

Table 2. Dimensions in *Bostryx multiconspectus* spec. nov.

	H	D	HA	WA	LW	H/D	HA/WA	HA/H	LW/H
Tambo de Viso (n = 16)									
M	7.5	12.9	5.1	5.3	6.3	0.59	0.96	0.69	0.84
s	1.37	1.13	0.63	0.60	1.14	0.15	0.17	0.09	0.03
max	10.8	14.5	6.3	6.4	9.0	1.00	1.36	0.85	0.90
min	5.5	10.8	4.0	4.5	4.7	0.45	0.70	0.51	0.78

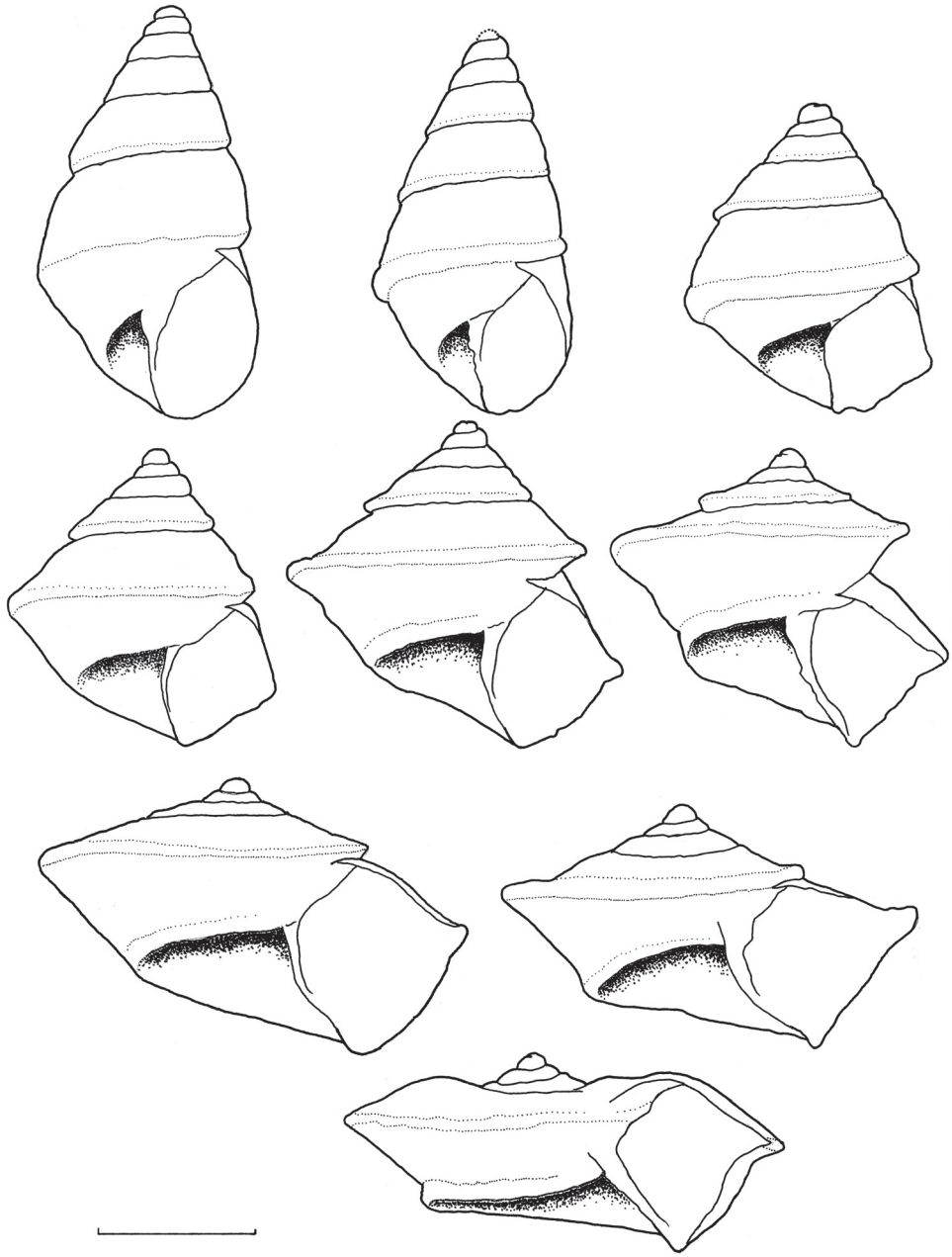

Fig. 4. *Bostryx multiconspectus* spec. nov. Variation in shell shape (RMNH, SMF). Scale line: 5 mm.

Bostryx primigenius spec. nov.
(figs 5-7)

Material.— Holotype: Peru, Dept. Lima, right bank Rio Rimac, El Infernillo [11°44'16"S 076°16'34"W], 3360 m. (SMF 155706*). Paratypes: same locality as holotype (ANSP 204511/5, DMNH 49744/5, RMNH 55428/4, SBMNH 137885/5, SMF 155707/1, 156282/8, 208038/6); Idem, 3340-3360 m (SMF 162094/10); Idem, left bank Rio Rimac, 3320-3340 m (SMF 162093/10); Idem, right bank Rio Rimac, opposite "San Mateo" water company [11°45'46"S 076°18'22"W], 3280-3300 m (SMF 162095/20); Idem, near "San Mateo", 3150 m, A.S.H. Breure leg., 23.iv.1976 (RMNH 109753/3); Idem, left bank Rio Rimac, between Matucana and Tambo de Viso [11°48'39"S 076°21'14"W], 2600 m (SMF 162091/10) [all as *Bostryx primigenius* Weyrauch MS.]; right bank of Rio Rimac, near Tambo de Viso, 2700 m (SMF 162090/3) [as *Bostryx primigenius* >< *pilsbryi* Weyrauch MS.]; Tambo de Viso, 2700-2750 m (SMF 156285/1*); Idem, 2700 m (SMF 156279/1)[as *Bostryx pilsbryi* Weyrauch MS.]; Idem (SMF 155597/1, 155598/3, 155599/1, 162089/1) [as *Bostryx pilsbryi* >< *bequaerti* Weyrauch MS.].

Diagnosis.— A small, relatively stout species of *Bostryx* with variable colouration of axial corneous streaks or spiral bands.

Description.— Shell up to 14.2 mm, 1.83 times as long as wide, narrowly but distinct perforated, with straight sides, elongate, rather thin. Colour whitish with axial corneous streaks and/or small spiral bands; in the latter case at least two on the last whorl, one at the periphery and one halfway between the periphery and the suture above, lighter spiral bands in between. Upper whorls corneous. Surface rather shining, with incrassate growth striae. Protoconch smooth, corneous or bluish. Whorls 5.8, nearly flat; suture hardly impressed. Aperture subovate, the margins converging, 1.46 times as long as wide, 0.40 times the total length. Peristome

Table 3. Dimensions in *Bostryx primigenius* spec. nov.

	H	D	HA	WA	LW	H/D	HA/WA	HA/H	LW/H
El Infernillo, right margin (n = 19)									
M	11.8	6.6	4.9	3.4	7.6	1.79	1.42	0.41	0.65
s	1.19	0.49	0.51	0.23	0.72	0.16	0.09	0.02	0.03
max	13.3	7.5	5.7	3.8	8.7	2.08	1.58	0.45	0.70
min	10.0	5.8	3.8	3.1	6.5	1.43	1.21	0.37	0.57
El Infernillo, left side (n = 10)									
M	11.3	6.1	4.6	3.1	7.3	1.84	1.49	0.41	0.65
s	1.13	0.48	0.54	0.29	0.67	0.18	0.07	0.04	0.03
max	13.3	7.2	5.8	3.7	8.3	2.13	1.61	0.47	0.71
min	9.6	5.7	4.2	2.8	6.6	1.57	1.35	0.36	0.60
San Mateo (n = 9)									
M	11.3	6.3	4.6	3.2	7.4	1.81	1.45	0.41	0.65
s	0.82	0.43	0.31	0.26	0.34	1.39	0.09	0.02	0.03
max	12.5	7.0	5.2	3.7	8.0	2.06	1.61	0.45	0.70
min	10.0	5.8	4.2	3.0	7.0	1.54	1.35	0.37	0.61
Between Matucana and Tambo de Viso (n = 4)									
M	12.5	6.4	4.7	3.2	7.6	1.97	1.47	0.37	0.61
s	0.91	0.64	0.45	0.24	0.37	0.19	0.05	0.04	0.04
max	13.5	7.0	5.0	3.3	8.0	2.24	1.53	0.43	0.66
min	11.3	5.5	4.0	2.8	7.2	1.79	1.41	0.32	0.58
Tambo de Viso (n = 10)									
M	12.1	6.8	4.6	3.0	7.3	1.86	1.54	0.38	0.61
s	1.37	1.50	0.53	0.48	0.76	0.42	0.15	0.06	0.08
max	14.2	10.3	5.3	4.0	8.5	2.21	1.75	0.50	0.76
min	9.7	5.2	3.7	2.5	6.2	1.00	1.29	0.33	0.53

Fig. 5. *Bostryx primigenius* spec. nov., holotype (SMF). Actual shell height 13.0 mm.
Fig. 6. *Bostryx primigenius* spec. nov., paratype (SMF 156285). Actual shell height 13.5 mm.

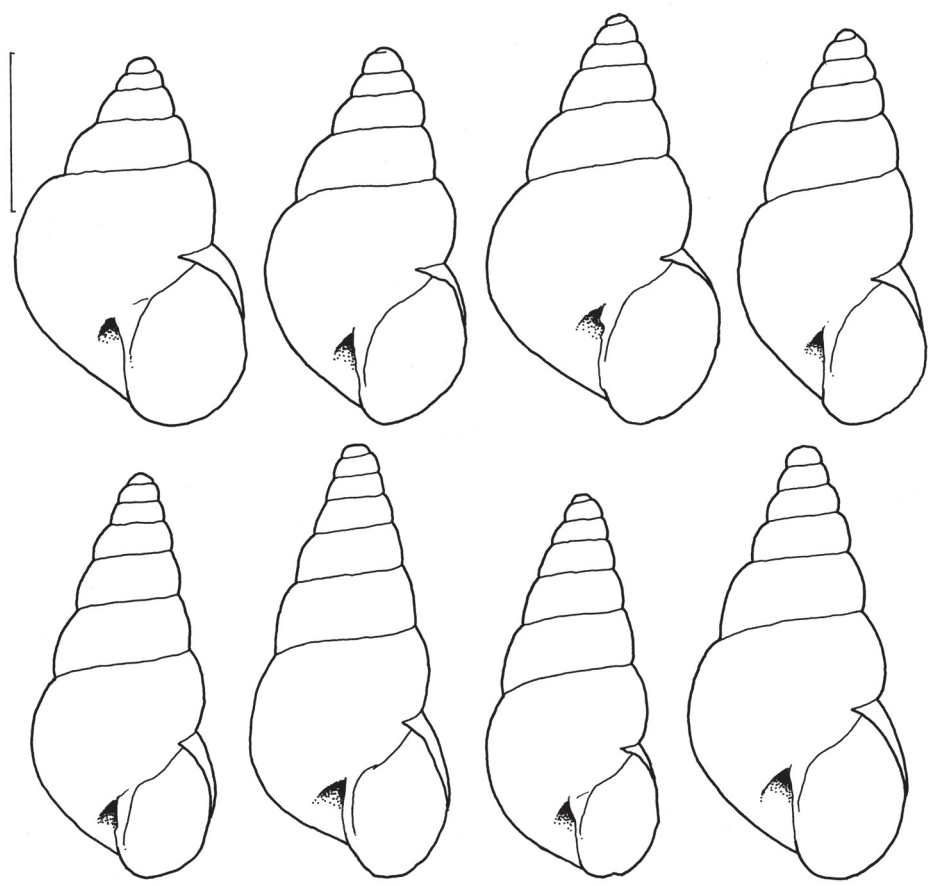

Fig. 7. *Bostryx primigenius* spec. nov. Variation in shell shape along an altitudinal transect (SMF). Scale line: 5 mm.

thin and simple. Columellar margin straight, narrowly dilated above.

Dimensions of holotype: H 13.0, D 7.3, HA 5.1, WA 3.5, LW 8.6, W 5.7. See also table 3.

Comparisons.— This new species differs from *Bostryx pauli* Breure, 1978 in (1) being slenderer; (2) having a more subovate aperture; (3) the less impressed suture. It differs from *B. ploegerorum* Breure, 1978 in (1) being stouter (height/diamter 1.83 vs. 2.83); (2) having the aperture more subovate (height/width 1.46 vs. 1.74). *Bostryx primigenius* may also be compared to *B. aileenae* Breure, 1978, from which it differs in (1) being somewhat smaller; (2) the surface without spiral lines; (3) being somewhat stouter (height/diameter 1.83 vs. 2.07). Finally, this species may be compared to *B. circuliportus rimacensis* Breure, 1978, from which it differs in (1) being smaller; (2) being less slender; (3) the presence of (traces of) spiral bands, most noticable on the last whorl.

Remarks.— As may be seen from fig. 8 some specimens from Tambo de Viso are transitional to *Bostryx multiconspectus* spec. nov., the sibling species living in the same area.

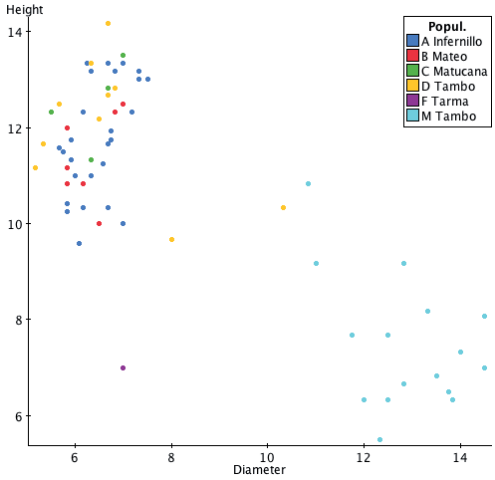

Fig. 8. Diagram showing the variation in shell height and diameter in *Bostryx fisheri* Pilsbry, 1856, *B. multiconspectus* spec. nov. and *B. primigenius* spec. nov., respectively population F, M, and A-D.

Fig. 9. *Bostryx solutus* (Troschel, 1847) (SMF 155601). Actual shell height 9.9 mm.

Etymology.— For practical reasons the original manuscript name given by Weyrauch has been retained; Latin *primigenius*, first and foremost. The epithet is used as a noun in apposition.

Bostryx solutus (Troschel, 1847)
(fig. 9)

Bulimus (Bostryx) solutus Troschel, 1847: 49. Peru. Lectotype ZMB 10252.
Bostryx solutus, Richardson, 1995: 44 (references).

Material.— Peru, Dept. Lima, opposite San Mateo, 3300-3350 m (SMF 155601); San Mateo, 3400 m, J. Hemmen leg., 29.ix.2005 (ZMH 36466/18).

Remarks.— In the same area as the previous species, a population of *Bostryx solutus* was found which shows both carination and detached whorls. The shells are thus corkscrew curled. This was most notable around San Mateo, in the Río Rimac valley. More details on the variation in this species will be given elsewhere (Breure & Neubert, in preparation).

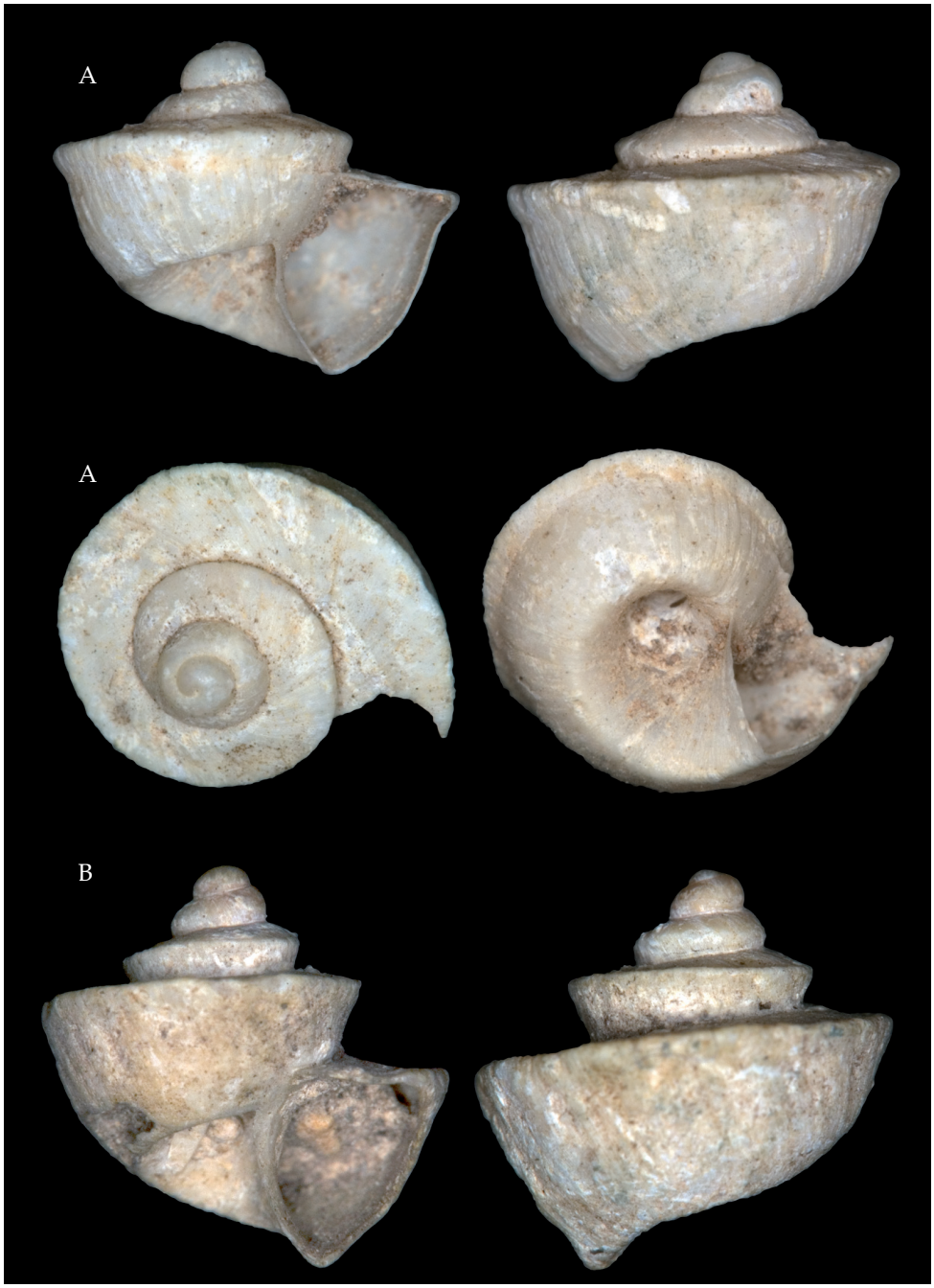

Fig. 10. *Bostryx fisheri* Pilsbry, 1956. A-B, different view of (A) paratype and (B) holotype (ANSP 196550). Actual shell height 7.0 mm.

Bostryx fisheri Pilsbry, 1956
(fig. 10)

Bostryx (Platybostryx) fisheri Pilsbry, 1956: 92, pl. 5 figs 4-5. Peru, Dept. Junín, below Tarma on the Tarma-Chanchamayo road. Holotype ANSP 196550.
Bostryx fisheri, Richardson, 1995: 25 (references).

Remarks.— In the original publication, the type material was poorly illustrated. *Bostryx fisheri* was described from (slightly) immature specimens and is refigured here. The measurements of the holotype are: H 7.0 D 7.0 HA 3.1 WA 2.9 LW 5.0 W 4.2.

Bostryx metagyra Pilsbry & Olsson, 1949
(fig. 11)

Bostryx metagyra Pilsbry & Olsson, 1949: 9, fig. 12. Peru. Holotype ANSP 184899.
Bostryx metagyra, Richardson, 1995: 33 (references).

Remarks.— This species was described without a specific locality. Specimens have been found in several museums which reveal the first precise localities: Dept. Lima, lomas near Huacho (DMNH 49752/5); Dept. Arequipa, Atiquipa, near Chala, W.K. Weyrauch leg. (FLMNH 109663, collection date unknown).

It is remarkable that this species has been found at two locations that are more than 600 km apart; the other species are very range-restricted.

Bostryx planissimus Pilsbry & Olsson, 1949
(fig. 12)

Bostryx (Discobostryx) planissimus Pilsbry & Olsson, 1949: 12, fig. 13. Peru (?). Holotype ANSP 184269.
Bostryx planissimus, Richardson, 1995: 38 (references).

Remarks.— The two specimens on which the description was based, were purchased in a shop in Lima mixed with marine shells and *Bostryx*, *Drymaeus* and *Epiphragmophora* species that are known to occur in different regions in Peru. Pilsbry & Olsson (1949: 13) suggested that *B. planissimus* occurred "somewhere in the 'lomas' of coastal

Fig. 11. *Bostryx metagyra* Pilsbry & Olsson, 1949, A-C, different views (FLMNH 109663). Actual shell diameter 8.7 mm.

Fig. 12. *Bostryx planissimus* Pilsbry & Olsson, 1949, A-C, different views (FLMNH 156792). Actual shell diameter 19.9 mm.

southern Peru, or possibly Chile". Fred G. Thompson collected, however, this species in Dept. Ancash, 3 km S Macará, 2700 m, 4.iv. and 9.iv.1972 (FLMNH 156792-4, 249235, 257891), to which the type locality is now restricted. Details on the anatomy can be found in Breure, 1978: 112, figs 155-162.

Bostryx reentsi (Philippi, 1851)
(fig. 13)

Bulimus reentsi Philippi, 1851: 30. Peru, near Chala.
Bostryx reentsi, Richardson, 1995: 40 (references).

Material.— Peru, Dept. Arequipa, above Chala, 100 m (RMNH 55436, topotypes); sandy hill near Chala, 150 m (RMNH 55437, topotypes).

Remarks.— A subfossil specimen of this species has been found amidst a series of large Nazca Culture shell middens at loma Ullujaya near Ica, Dept. Ica (O. Whalley leg., ix.2007, RMNH). Also J. & C. Hemmen (personal communication) collected *Bostryx reentsi* (Philippi, 1851) as subfossil specimens at Dept. Arequipa, 11 km from Chala on the road to Atico, in a desert-like area with only a few cacti-remains.

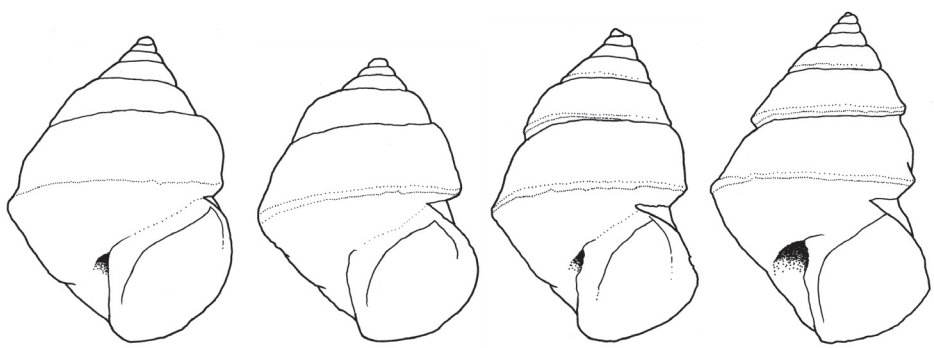

Fig. 13. *Bostryx reentsi* (Philippi, 1851). Variation in shell shape (RMNH 55436). Scale line: 5 mm.

Bostryx weyrauchi Pilsbry, 1944
(fig. 14)

Bostryx weyrauchi Pilsbry, 1944: 87, pl. 9 fig. 5. Peru, near Ayacucho, Ninabamba, 2000 m. Holotype ANSP 179979a.
Bostryx weyrauchi, Richardson, 1995: 50 (references).

Material.— Dept. Ayacucho, Ninabamba, Cerro Huachulla, 2300 m, leg. 31.i.1969 (RMNH 55438, topotypes).

Remarks.— Specimens collected by Weyrauch and labelled by him as topotypes, show some variation in carination. Those with a carina have a split at the intersection of the carina and the peristome. Inside the aperture the carina is visible as a shallow gutter.

Neopetraeus binneyanus (Pfeiffer, 1857)
(fig. 15)

Bulimus binneyanus Pfeiffer, 1857: 229. Peru, [Dept. La Libertad] Prov. Pataz. Lectotype BMNH 1975426.
Neopetraeus binneyanus, Richardson, 1995: 239 (references).

Remarks.— The first precise locality for this species is Dept. La Libertad, Chagual, F. Gutierrez leg., vi.2000, on trees and cactus (ZMA/1). In this specimen the carina is also visible inside the aperture as a shallow gutter and the peristome is split at the place where the carina ends.

Ecology

For part of the species it has been possible to obtain information on the habitats. In northern Peru *Scutalus baroni* (Fulton, 1896) occurs near Tembladera in the Río Jequetepeque valley (Pilsbry & Olsson, 1949; Breure, 1978). Near that village this carinate species has been found on mountains with limestone soils, very rocky with sparse grasses (small and desiccated half of the year or more). Cerro Sapo, type locality of its synonym *S. nobilis* Pilsbry & Olsson, 1949 (see Breure, 1978), has some bushes and cactus near the top (upper third) and some bigger grasses (until 0.8 meters high). Tembladera has a

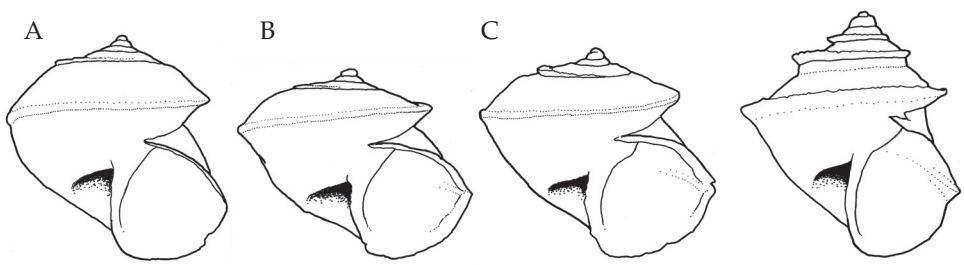

Fig. 14. *Bostryx weyrauchi* Pilsbry, 1944. A-C: Variation in shell shape (RMNH 55438). Scale line: 5 mm.
Fig. 15. *Neopetraeus binneyanus* (Pfeiffer, 1857) (ZMA). Scale line: 5 mm.

four month rainy season, four months when the rains are scarce and four months with a very dry climate (Gutierrez, personal communication). Breure (unpublshed field notes) collected *S. baroni* alive 1 km E Tembladera, aestivating on boulders on the upper part of the hill.

To the east, in the Río Marañon valley, *Neopetraues binneyanus* was found alive on rocks, together with *N. arboriferus paucistriagatus* Weyrauch, 1967 (Hemmen, unpublished field notes).

In Dept. Ancash *B. planissimus* Pilsbry & Olsson, 1949 was collected along the base of limestone ledges on hills on the east side of Rio Santos opposite Huaraz airport. The hillside has a dense growth of thorn scrubs and branching cacti, and cliffs with clusters of bromeliads and *Agave*. It was found only under *Agave* and bromeliads on the face of cliffs, together with other Bulimulidae (*Drymaeus, Thaumastus* and *Bostryx*). Further south in Ancash *B. c. carinatus* Breure, 1978 was collected at the base of limestone ledges on the north side of the Rio Mosna. The area is submesic with shrubs, grasses and *Agave* as dominant vegetation, and extensively cultivated for potatoes. The species was rare; two live specimens were found aestivating on limestone and one live specimen in sedges. The species lives together with other *Bostryx*, *Scutalus*, *Epiphragmophora*, Clausiliidae and Systrophiidae (Thompson, unpublished field notes).

In Dept. Lima *Bostryx multiconspectus* spec. nov. was found alive at Tambo de Viso on shrubs on a steep rock-face. The species was, however, not abundant and few dead specimens were collected at the base of the rock-face under stones ('pedregal') (Breure, unpublished field notes). In the same area *Bostryx solutus* (Troschel, 1847) was found alive in crevices of rocks (Hemmen, unpublished field notes).

Discussion

Just as *Bostryx multiconspectus* spec. nov. and *B. primigenius* spec. nov. are sibling species, the same has been shown for *Scutalus baroni* (Fulton, 1896) and *S. cretaceus* (Pfeiffer, 1855) (Breure, 1978). It is now hypothesized that a similar situation may be found in other carinate species. *Bostryx weyrauchi* Pilsbry, 1944 may be a sibling of *B. rhodolarynx* (Reeve, 1849), occurring in the same area. Also the *Bostryx cuyanus*-group, occurring in a mountain range that runs through two provinces of northwestern Argentina, may prove to be an example of this phenomenon. Additonal collecting in their respective areas may reveal either transitions or shed light on the barriers that separate populations. Further morphometric and phylogenetic studies may clarify the relationship between such sibling species (Chiba, 2005; Elejalde et al., 2005; Teshima et al., 2003).

Goodfriend (1986) mentions several examples of keeled shells as intraspecific variation from different families and continents. Cain & Cowie (1978) suggested that flat shells are an adaptation to horizontal surfaces. Keeled shells are regarded as an adaptation to limestone substrates (Gould, 1971; Alonso et al., 1985) or supposed to be more resistant to crushing (Cook & Pettitt, 1979). Teshima et al. (2003), studying an example of intraspecific variation, conclude that no phylogeny-controlled studies have tested the assumption of a relationship between limestone and a keeled shell. From the notes above on the ecology (see also table 1) a relationship could also be postulated between a keeled shell form and rock surfaces. It has been suggested before (Goodfriend, 1986)

that selection for flatter shells in populations that use rock crevices as resting sites might produce keeled shells.

In some of the species, apart from the carination, the last whorl descends in front and the aperture is oblique with the length axis of the shell (e.g. *Bostryx eremothauma, B. reentsi, B. weyrauchi; Scutalus baroni*). A similar phenomenon may be observed in several other families, e.g. the Camaenidae (*Letitia* and *Rhynchotrochus* species; Parkinson et al., 1987: pl. 54, 59, 73), Polygyridae (*Euchemotrema*; Anderson & Smith, 2005) and Oreohelicidae (*Oreohelix*; Hendricks, 1998). Further research has to show if there is any common mechanism involved.

Carination is a relatively rare phenomenon in land snails and its occurrence in different families may be considered as just another case of convergence. The questions posed in the introduction of this paper remain open until further field work may yield additional material. But obviously, we are still far from understanding more generally the evolution of this shell form.

Acknowledgements

Valentín Mogollón and Federico Gutierrez (Lima), as well as Jens Hemmen (Wiesbaden) have been kind enough to supply information on several localities and habitats. I am most grateful to Fred G. Thompson (Gainesville) for providing me with his field notes, which are invaluable for our understanding of the ecology of the species. Gabriela Cuezzo (Tucumán) kindly provided some information on the legacy of Weyrauch. Many thanks are due to Paul Callomon (Philadelphia), Eike Neubert (Frankfurt am Main) and John Slapcinsky (Gainesville) for photographs of specimens in their museum collections. I am indebted to Ronald Janssen (Frankfurt am Main), who let me study material from SMF collected by Weyrauch and to B. Verdcourt (Kew), who sent material found at archeological sites in southern Peru for identification. Finally, I like to thank Francisco Borrero (Cincinnati) for sharing his data from American museums and his stimulating discussions and Dolf van Bruggen (Leiden) for his constructive suggestions which improved the manuscript.

References

Alonso, M.R., López Alcántara, A., Rivas, P. & Ibañez, M., 1985. A biogeographic study of *Iberus gualterianus* (L.) (Pulmonata: Helicidae).— Soosiana 13: 1-10, figs 1-15.

Anderson, F.E. & Smith, D.A., 2005. Redescription of the carinate pillsnail, *Euchemotrema hubrichti* (Pilsbry, 1940) (Pulmonata: Polygyridae), with notes on habitat and genetics.— Zootaxa 807: 1-11, figs 1-5.

Breure, A.S.H., 1978. Notes on and descriptions of Bulimulidae (Mollusca, Gastropoda).— Zoologische Verhandelingen Leiden 164: 1-255, figs 1-421, pls 1-22.

Breure, A.S.H., 1979. Systematics, phylogeny and zoogeography of Bulimulinae (Mollusca).— Zoologische Verhandelingen Leiden 168: 1-215, figs 1-182, pls 1-3.

Breure, A.S.H. & Neubert, E., 2008. A preliminary revision of Weyrauch's unpublished names: taxa of the genus *Bostryx* Troschel, 1847 (Gastropoda, Pulmonata, Orthalicidae).— Basteria 72: 319-330, figs 1-29.

Burch, J.B., 1962. How to know the eastern land snails. Pictured-keys for determining the land snails of the United States occurring east of the Rocky Mountain Divide: 214 pp., figs 1-519.— Wm. C. Brown, Dubuque.

Cain, A. J., 1977. Variation in the spire index of some coiled gastropod shells, and its evolutionary significance.— Philosophical Transactions of the Royal Society London B 277: 377-428, figs 1-37.
Cain, A.J. & Cowie, R.H., 1978. Activity of different species of land-snail on surfaces of different inclinations.— Journal of Conchology 29: 267-272, figs 1-3.
Cameron, R. A. D., 1978. Differences in the sites of activity of coexisting species of land mollusc.— Journal of Conchology 29: 273-278.
Chiba, S., 2005. Appearance of morphological novelty in a hybrid zone between two species of land snail.— Evolution 59: 1712-1720.
Cook, L. M., 2008. Species richness in Madeiran land snails, and its causes.— Journal of Biogeography 35: 647-653, figs 1-3.
Cook, L.M. & Pettitt, C.W.A., 1979. Shell form in *Discula polymorpha*.— Journal of Molluscan Studies 45: 45-51, figs 1-4.
Elegalde, M.A., Muñoz, B., Arrébola, J.R. & Gómez-Moliner, B.J., 2005. Phylogenetic relationships of *Iberus gualtieranus* and *I. alonensis* (Gastropoda: Helicidae) based on partial mithochondrial 16S rRNA and CO1 gene sequences.— Journal of Molluscan Studies 71: 349-355, figs 1-2.
Goodfriend, G. A., 1986. Variation in land-snail shell form and size and its causes: a review.— Systematic Zoology 35: 204-223.
Gould, S.J., 1971. Precise but fortuitous convergence in Pleistocene land snails from Bermuda.— Journal of Paleontology 45: 409-418, figs 1-4.
Hendricks, P., 1998. Rediscovery of *Discus brunsoni* Berry, 1955 and *Oreohelix alpina* (Elrod, 1901) in the Mission Mountains, Montana, with comments on *Oreohelix elrodi* (Pilsbry, 1901).— Nautilus 112: 58-62.
Hylton Scott, M.I., 1954. Una neuva especie de *Bostryx* (Bulimulidae).— Physis 20: 409-413, figs 1-6.
Parkinson, B., Hemmen, J. & Groh, K., 1987. Tropical landshells of the world: 1-279.— Verlag Christa Hemmen, Wiesbaden.
Pfeiffer, L., 1857. Diagnosen neuer Heliceen.— Malakozoologische Blätter 4: 229-232.
Philippi, R.A., 1851. Centuria quarta testaceorum novorum.— Zeitschrift für Malakozoologie 8: 29-32.
Pilsbry, H.A., 1956. A new *Bostryx* from Peru.— Nautilus 69: 92-93, pl. 5.
Pilsbry, H.A. & Olsson, A.A., 1949. The landsnail genus *Xenothauma* and other carinate Bulimulidae of Peru.— Notulae Naturae 215: 1-14, figs 1-19.
Richardson, C.L., 1995. Bulimulidae: catalog of species.— Tryonia, 28: 1-458.
Simone, L.R.L., 2006. Land and freshwater molluscs of Brazil: 390 pp., figs 1-1074, 1-33.— EGB, Fapesp, São Paulo.
Teshima, H., Davison, A., Kuwahara, Y., Yokoyama, J., Chiba, S., Fukuda, T., Ogimura, H. & Kawata, M., 2003. The evolution of extreme shell shape variation in the land snail *Ainohelix editha*: a phylogeny and hybrid zone analysis.— Molecular Ecology 12: 1869-1878, figs 1-10.
Troschel, F.H., 1847. Zwei neue Peruanische Schnecken.— Zeitschrift Malakozoologie 4: 49-52.
Weyrauch, W.K., 1956. The genus *Naesiotus*, with descriptions of new species and notes on other Peruvian Bulimulidae.— Proceedings of the Academy of Natural Sciences, Philadelphia 108: 1-17, pl. 1.

Received: 28.vii.2008
Accepted: 3.ix.2008
Edited: A.C. van Bruggen