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Revision of the Afrotropical land snail genus *Avakubia* Pilsbry, 1919, with description of *Pseudavakubia* gen. n. and eleven new species (Gastropoda: Pulmonata: Streptaxidae)

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ABSTRACT

A revision of the world-wide available material of the Afrotropical streptaxid subgenus *Avakubia* Pilsbry, 1919, prompted the change in status to independent genus and the detection of undescribed species. In addition to the two earlier described species, *A. avakubiensis* (Pilsbry, 1919) and *A. acuminata* (Thiele, 1933), the genus *Avakubia* is found to embrace at least seven new species, viz., *A. crystallum* de Winter, sp. n. from Gabon; *A. fruticicola* de Winter & Vastenhout, sp. n., *A. semenguei* de Winter & Vastenhout, sp. n. and *A. subacuminata* de Winter & Vastenhout, sp. n. from Cameroon; *A. ortizdezarateorum* de Winter & Vastenhout, sp. n. and *A. biokoensis* de Winter & Vastenhout, sp. n. from Bioko I., Equatorial Guinea, and *A. occidentalis* de Winter, sp. n. from Ghana. Of some other potentially new *Avakubia* species insufficient material is available to allow a formal description. For a West African radiation with remarkably similar shells, but differing from true *Avakubia* in protoconch and teleoconch characters, a new genus *Pseudavakubia* de Winter & Vastenhout, gen. n. is erected with four new species, viz., *P. atewaensis* de Winter, sp. n., *P. majus* de Winter & Vastenhout, sp. n. (type species), *P. ghanaensis* de Winter, sp. n., and *P. liberiana* de Winter, sp. n. *Avakubia avakubiensis* has been reported in the literature from Uganda to Liberia, a range of 4750 km. Study of this material restricts the range of this species to the eastern Democratic Republic of the Congo and Uganda, the remaining records were found to refer to five other species of *Avakubia* or *Pseudavakubia* described in this paper, each with a much more restricted range. The genital anatomy of both *Avakubia* and *Pseudavakubia* is found to deviate from most other members of the family Streptaxidae in the absence of chitinous spines in the penis. Both genera are ovoviviparous. In the penis of a specimen of *A. acuminata* a spermatophore-like structure was found. Some aspects of the ecology of these rainforest-dwelling snails are described. An identification key to the species of *Avakubia* and *Pseudavakubia* is provided.

KEY WORDS: Mollusca, Streptaxidae, *Avakubia*, *Pseudavakubia*, Equatorial Africa, systematics, biogeography, cryptic diversity, tropical rainforest, spermatophore, identification key.

INTRODUCTION

Avakubia is a rather poorly known taxon of the family Streptaxidae of small (*ca* 3–6 mm) and apparently uncommon land snails that inhabit the forests of equatorial Africa. *Avakubia* was introduced as a section of the genus *Gulella* Pfeiffer, 1856, by Pilsbry (1919) for a single shell of *Gulella (Avakubia) avakubiensis* Pilsbry, 1919 from the Ituri Forest in the eastern Democratic Republic of the Congo (formerly Belgian Congo, Zaïre). The only other formally named *Avakubia* species, *G. (A.) acuminata* Thiele, 1933, was described from a single specimen from Cameroon. The taxon was defined on the basis of a few shell characters, namely a spirally sculptured protoconch, a teleoconch with regularly spaced axial ribs and spiral lines in the interstices, a biconical shell shape, and a paucidentate aperture (Pilsbry 1919). Although all these characters individually occur in other streptaxid (sub)genera, *Avakubia* representatives were generally thought to be fairly typical (Degner 1934*b*). Schileyko's (2000) description of the genus is partly faulty, presenting the genital anatomy of *Gulella dautzenbergi* Connolly, 1928, copied from Degner (1934*a*), as representative for the (sub)genus. However, *G. dautzenbergi* clearly does not belong to *Avakubia*, lacking typical characters for the genus, such as

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the spiral sculpture on the apex (see Connolly 1928; Degner 1934*a*), and belongs to a rather different streptaxid radiation. Recent molecular work by Rowson *et al.* (2011) indicates that *A. avakubiensis* is not related to the genus *Gulella* and even occupies a basal position within the Streptaxidae. In the present study, *Avakubia* is for the first time treated as an independent genus.

Still, the delimitation of the genus *Avakubia* is rather unclear. Nothing has as yet been published on the anatomy. The two species described to date, *A. avakubiensis* and *A. acuminata*, are quite different in shell size and shape, and the erroneous assignment of *Gulella dautzenbergi* to *Avakubia* in an authoritative treatise (Schileyko 2000) underlines the need to critically define the boundaries of the genus.

The genus *Avakubia* appears to be confined to equatorial Africa, but available records are scarce. After the description of *A. avakubiensis* in 1919, a second specimen was recorded from Liberia (Degner 1934*b*). More than two decades later the species was reported from localities on the Isle of Fernando Poo, now Bioko Island, Equatorial Guinea (Ortiz de Zárate Lopez & Ortiz de Zárate Rocandio 1956). Verdcourt (1962) published a record from Uganda. Since the mid-1990's, additional records (albeit sometimes with tentative identifications) have been published from Gabon (de Winter 1995), Cameroon (de Winter & Gittenberger 1998), Democratic Republic of the Congo (van Bruggen & Van Goethem 1997) and Uganda (Wronski & Hausdorf 2010). Verdcourt (1984) mentioned *G. (A.) avakubiensis* as one of the few land snail species with a range extending all across the African equatorial forest belt ("the Fernando Poo – Cameroun – Zaire – western Kenya route"). This species has a published linear range of *ca* 4750 km across continental Africa. In contrast, *A. acuminata* has been recorded only once since its description, again from Cameroon (de Winter & Gittenberger 1998). Some studies have indicated the existence of additional *Avakubia* species (de Winter & Gittenberger 1998; Fontaine *et al.* 2007), but these have so far not been formally described.

The present paper offers a taxonomic revision of all available *Avakubia* specimens based on the morphology of the shell as well as, as far as available, of the soft parts. We address the question whether the material attributed to *Avakubia* in the literature and in unpublished collections constitutes a monophyletic grouping; this is not a phylogenetic study, however. The available material is too scanty, incomplete and partly too old to undertake a molecular study at this stage. In this paper we also addresses the biogeographically interesting question whether all records of *A. avakubiensis* in the literature indeed refer to a single, very widespread, species. The reported distribution seems at odds with Solem's (1984) assertion that most land snail species have a linear range of tens or perhaps hundreds of kilometres, but not one stretching over nearly 5000 km between the Liberian and Ugandan localities. Such a large range would be particularly surprising for a rainforest-dwelling species that is unlikely to have benefitted from human activities.

MATERIAL AND METHODS

The following collection acronyms have been used:

AMNH – American Museum of Natural History, New York, USA;
MCZ – Museum of Comparative Zoology Harvard University, Cambridge, Mass., USA;
MNHN – Muséum National d'Histoire Naturelle, Paris, France;

MNCN – Museo Nacional de Ciencias Naturales, Madrid, Spain;
NMW – National Museum of Wales, Cardiff, UK;
PT – collection of Peter Tattersfield, UK (to be deposited in NMW);
RBINS – Royal Belgian Institute of Natural Sciences, Brussels, Belgium;
RMNH – Naturalis Biodiversity Center, formerly Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands;
ZMB – Museum für Naturkunde, Humboldt University Berlin, Germany;
ZMH – Zoological Museum, University of Hamburg, Germany.

Other abbreviations used throughout the paper:

AA – apical angle;
ad. – adult;
BWH – height of body whorl;
D – shell diameter;
DRC – Democratic Republic of the Congo (Belgian Congo, Zaïre);
DW1 – diameter of first whorl;
DW2 – diameter of first two whorls;
H – shell height;
juv. – juvenile;
PH – peristome height;
PW – peristome width;
RD – width of five consecutive interstices (thus embracing six ribs) in the middle of the penultimate whorl;
SA – spire angle;
SEM – scanning electron microscopy;
sta. – station;
W – number of whorls.

We made an attempt to examine all *Avakubia* material reported in the literature, in addition to unpublished material attributed to *Avakubia* in museum collections and some recently collected material. In total, we have been able to examine some 151 specimens, of which 114 are adult shells. Apart from the holotype of *A. acuminata* (ZMB), previously published voucher material could be studied from Cameroon (RMNH), DRC (RBINS), Bioko I. (formerly Fernando Poo; MNCN, RBINS, RMNH), Gabon (MNHN, RMNH), Liberia (MCZ), and Uganda (ZMH). The holotype of *A. avakubiensis* could not be traced in AMNH (Dr Christine Johnson, pers. comm., Dec. 2011), but a photograph of the holotype shell in frontal view is available on http://research.amnh.org/iz/types_db/details.php?specimen_id=9951. Schileyko (2000) provided an accurate drawing of the holotype in frontal view. Specimens reported from the northern DRC (van Bruggen & Van Goethem 1997) were not available, as was the material published by Verdcourt (1962) from Entebbe, Uganda. Unpublished samples identified as *Avakubia* were studied from Uganda (PT), Cameroon (RMNH), Gabon (RMNH) and Ghana (RMNH, PT). The geographic distribution of the studied specimens is very uneven; a large proportion of the material (including 55 adult specimens) was collected within an area of *ca* 1500 km^2 in Southwest Cameroon by the senior author.

All shells were studied under a Leica M165c stereo microscope and sorted to tentative morphospecies taking qualitative characters like approximate size, shape and sculpture into account. Ten shell measurements (Fig. 1) were made on images of adult shells taken with a Leica DFC420 digital camera attached to the stereo microscope, using Leica LAS 2.8.1 software, and the number of whorls of each shell was counted according to Kerney and Cameron (1979) and rounded to the nearest quarter whorl. Each shell was mounted, photographed and measured twice in frontal and apical view, and the mean of both measurements was taken unless strongly deviating values could be attributed to measurement errors. Axial rib density on the teleoconch was measured as the distance

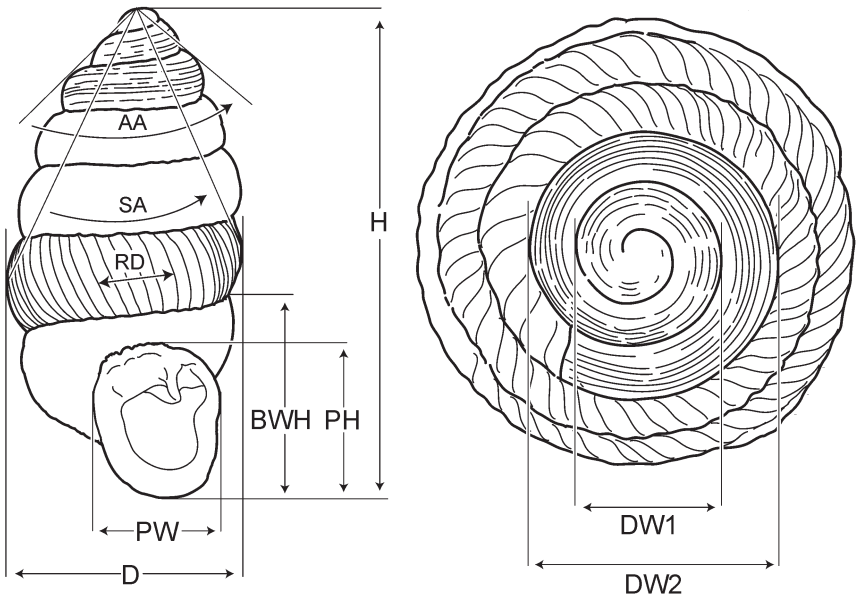


Fig. 1. Measurement taken from *Avakubia* shells in frontal and apical view. Abbreviations: AA – apical angle, BWH – height of body whorl, D – shell diameter, DW1 – diameter of first whorl, DW2 – diameter of first two whorls, H – shell height, PH – peristome height, PW – peristome width, RD – width of five consecutive interstices (thus embracing six ribs) in the middle of the penultimate whorl, SA – spire angle. Illustrated is *A. acuminata*.

of five interstices between six consecutive ribs, measured parallel to the sutures in the centre of the penultimate whorl. In species descriptions, shell measurements are often expressed as ratio's, like H:D, BWH:H, PH:H, PW:D, #ribs/mm and W:*ln*H (coiling tightness, Emberton 2001).

Measurement data were analysed by a principal component analysis (PCA) after log transformation to roughly equalize variances. The resulting grouping based on measurement data was compared with an initial tentative morphospecies assignment (which also took qualitative characters into account), and a preliminary classification of taxa was made. A MANOVA was done to test the significance of the overall difference between the pre-determined morphospecies. A canonical variate analysis (CVA) was done in order to maximize the difference between the groups in a multivariate space. Distinction between pairs of species was tested in a pairwise Hotelling's test. However, since the distribution of the measurements appeared not to be multivariately normal, this may not be a correct procedure. Equality of the means of sets of multivariate data of any combination of two morphospecies was therefore also tested by a non-parametric two-group permutation test using the Mahalanobis squared distance measure. Since the latter test resulted in higher significance levels of distinction between pairs of species than the pairwise Hotelling's test, the latter test was used to provide at least an indication of the degree of difference between pairs of species. All statistical analyses were performed using the free software program PAST (Hammer *et al.* 2001).

Qualitative characters used in species description include: colour of the soft parts (reddish or pale) based on field notes and/or from the colour of dried-in soft parts visible

through the shell, protoconch shape, protoconch sculpture, teleoconch sculpture (other than rib distance), umbilical development, peristome development, overall shell shape, whorl convexity, as well as the arrangement of barriers in the aperture and deeper within the body whorl (see below). The protoconch sculpture was studied by SEM, using a Jeol 6480LV, for which most examined shells were coated, others (especially type specimens) were studied uncoated in low-vacuum. The latter method resulted in less clear pictures. The alcohol-preserved material was mostly contracted and withdrawn in the upper whorls. In view of the scantiness of *Avakubia* specimens available, only few specimens were dissected since study of the soft parts inevitably involved destruction of the shell. We became particularly hesitant to sacrifice more alcohol-preserved specimens, after several animals of *A. acuminata* and *A. fruticicola* with fully developed shells were found to have rather juvenile genitalia still. Genitalia were studied in alcohol at up to 75× magnification, and partly sliced open to study internal structures. The preparations were extensively photographed using the microscope and camera described above. In one species focus stacking was used to obtain pictures with greater depth of field (Fig. 24), in the other dissected species the photographs served as a template to prepare drawings. Radulae were obtained by maceration of the buccal mass in 5 % KOH at 60 °C until the soft tissue appeared dissolved, after which the radula was rinsed with distilled water. Due to the long, narrow and transversely folded nature of these minute ribbons, most attempts to mount the radula on a SEM stub yielded unsatisfactory results.

After the presence of a deep-set palatal fold was observed in many but not in all shells (see below), special attention was paid to the presence/absence of this structure, which can be easily seen in fresh, translucent shells, or after moistening the shell surface. For those species where the available shells were too worn to ascertain the presence of this structure externally (as well as in *A. acuminata)*, a single intact adult shell was studied using a micro CT scanner (SkyScan 1172 X-ray Microtomograph, Kontich, Belgium). The morphology of the internal barriers was examined in more detail in shell fragments of three dissected species by SEM. We only scored presence/absence of the palatal fold for each species, and did not attempt to address (potentially species-specific) variability in the expression of the structure at this stage.

RESULTS

Based on careful comparison of the habitus of the available shells which conform to the description of the genus *Avakubia* (e.g. Pilsbry 1919; Thiele 1933), we hypothesized the existence of at least nine morphospecies. In the available shell material we found three (sets of) characters that were previously not or incompletely addressed in the descriptions of *Avakubia*: (1) Cryptic barriers: most shells were found to possess a deep-set fold on the palatal wall, which appears as a white line on the body whorl of fresh (translucent) or moistened shells, but may not be observed externally in worn shells. At least some shells possessing such a palatal fold were also found to possess a short lamella (tooth) on the columella of the body whorl (Fig. 5). These two structures are not discernable in the aperture in frontal view (or even when the shell is held obliquely, apart from one noticeable exception, Fig. 19F). However, in a number of shells the palatal fold (and the columellar lamella) were found to be genuinely absent. (2) Umbilical development: most specimens possess a narrow, crevice-like umbilicus, but in some shells the umbilicus is completely closed. (3) Protoconch: the apical whorls

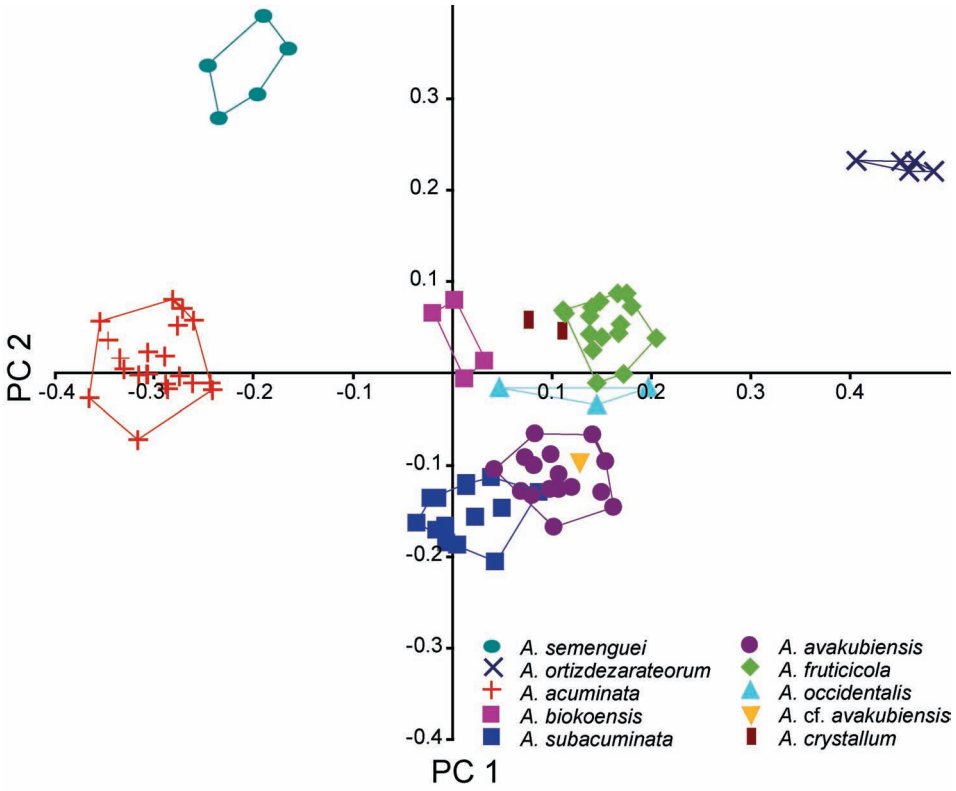


Fig. 2. Principal component ordination plot (PC1 and PC2) of conchometrical data (Fig. 1) of 87 adult *Avakubia* shells.

of most shells regularly increase in diameter with growth, but in some shells coiling of the protoconch is conspicuously irregular.

The three less commonly occurring character states (absent palatal fold, closed umbilicus, irregular coiled apical whorls) were found combined in specimens from Ghana and Liberia, and we concluded that these belong to a separate genus, described below. Additional shell characters, like details of the protoconch sculpture, support this conclusion, as did preliminary anatomical observations. A detailed study of the nine available adult shells attributable to the new genus prompted the recognition of four new species. Because of the irregularly coiled protoconch in the new genus, the width of the protoconch whorls, as well as the apical angle and spire angle could not be measured in the same way as in *Avakubia*. These specimens were therefore analysed separately from the remaining true *Avakubia* material, qualitatively rather than quantitatively because of the small number of available shells.

Of the nine initially recognised morphospecies, seven were assigned to true *Avakubia* and two to the new genus. More detailed study suggested the existence of at least four additional species, two of each genus.

Table 1 summarizes the measurements taken from adult true *Avakubia* shells. In a PCA involving 87 adult *Avakubia* shells, the first two principal components describe

TABLE 1

Conchometric data for 87 adult *Avakubia* shells. Measurements and abbreviations are explained in Fig. 1. Measurements of holotype of *A. avakubiensis* are taken from available illustrations (see species description), as far as possible (* – holotype excluded, ? – character not observable in available illustrations).

Shell heigth (mm)				
Species	**Holotype**	**mean**	**range**	**No.**
A. acuminata	5.4	5.4	5.1–5.8	21
A. avakubiensis	*ca* 3.2	3.3*	3.0–3.5*	16*
A. cf. *avakubiensis* [Gabon]			3.2	1
A. biokoensis	3.8	3.9	3.8–4.0	4
A. crystallum	3.6	3.7	3.6–3.8	2
A. fruticicola	3.1	3.3	3.1–3.5	16
A. occidentalis	3.6	3.3	3.2–3.6	3
A. ortizdezarateorum	3.0	3	2.9–3.1	5
A. semenguei	4.8	4.9	4.7–5.1	5
A. subacuminata	3.8	3.8	3.5–4.1	14
Shell diameter (mm)				
Species	**Holotype**	**mean**	**range**	**No.**
A. acuminata	2.7	2.7	2.7–2.8	21
A. avakubiensis	*ca* 1.9	1.9*	1.9–2.0*	16*
A. cf. *avakubiensis* [Gabon]			2.0	1
A. biokoensis	2.1	2.2	2.1–2.3	4
A. crystallum	2.0	2.0	2.0–2.1	2
A. fruticicola	1.9	1.9	1.8–2.0	16
A. occidentalis	2.0	2.0	1.9–2.0	3
A. ortizdezarateorum	1.8	1.7	1.7–1.8	5
A. semenguei	2.9	2.9	2.8–3.0	5
A. subacuminata	2.1	2.2	2.1–2.2	14
Number of whorls				
Species	**Holotype**	**mode**	**range**	**No.**
A. acuminata	6¾	6½	6¼–7	21
A. avakubiensis	?	5½	5–5¾	16*
A. cf. *avakubiensis* [Gabon]			5½	1
A. biokoensis	6	6	6	4
A. crystallum	5¼	5¼	5¼	2
A. fruticicola	5	5	5–5¼	16
A. occidentalis	5½	5¼	5–5½	3
A. ortizdezarateorum	5	5	5	5

TABLE 1 (*continued*)

Conchometric data for 87 adult *Avakubia* shells. Measurements and abbreviations are explained in Fig. 1. Measurements of holotype of *A. avakubiensis* are taken from available illustrations (see species description), as far as possible (* – holotype excluded, ? – character not observable in available illustrations).

Species	Holotype	mean	range	No.
A. semenguei	5	5	5–5¼	5
A. subacuminata	6¼	6½	6–7	14
Peristome height (mm)				
Species	**Holotype**	**mean**	**range**	**No.**
A. acuminata	1.64	1.76	1.56–1.93	21
A. avakubiensis	?	1.14	1.05–1.23	16*
A. cf. *avakubiensis* [Gabon]			1.04	1
A. biokoensis	1.38	1.42	1.38–1.45	4
A. crystallum	1.32	1.25	1.18–1.32	2
A. fruticicola	1.15	1.22	1.04–1.28	16
A. occidentalis	1.24	1.11	0.97–1.24	3
A. ortizdezarateorum	0.97	0.96	0.89–1.01	5
A. semenguei	1.93	1.90	1.86–1.94	5
A. subacuminata	1.20	1.17	1.04–1.22	14
Peristome width (mm)				
Species	**Holotype**	**mean**	**range**	**No.**
A. acuminata	1.49	1.50	1.30–1.66	21
A. avakubiensis	?	1.04*	0.97–1.14*	16*
A. cf. *avakubiensis* [Gabon]			1.09	1
A. biokoensis	1.23	1.24	1.20–1.29	4
A. crystallum	1.15	1.09	1.09–1.15	2
A. fruticicola	1.04	1.11	1.04–1.22	16
A. occidentalis	1.17	1.09	1.02–1.17	3
A. ortizdezarateorum	0.88	0.87	0.77–0.95	5
A. semenguei	1.67	1.64	1.60–1.72	5
A. subacuminata	1.10	1.10	1.0–1.23	14
Body whorl height (mm)				
Species	**Holotype**	**mean**	**range**	**No.**
A. acuminata	2.27	2.41	2.25–2.56	21
A. avakubiensis	?	1.59*	1.51–1.76*	16*
A. cf. *avakubiensis* [Gabon]			1.5	1
A. biokoensis	1.83	1.84	1.79–1.93	4
A. crystallum	1.78	1.77	1.77–1.78	2

TABLE 1 (*continued*)

Conchometric data for 87 adult *Avakubia* shells. Measurements and abbreviations are explained in Fig. 1. Measurements of holotype of *A. avakubiensis* are taken from available illustrations (see species description), as far as possible (* – holotype excluded, ? – character not observable in available illustrations).

Species	Holotype	mean	range	No.
A. fruticicola	1.75	1.71	1.63–1.86	16
A. occidentalis	1.75	1.64	1.51–1.64	3
A. ortizdezarateorum	1.40	1.38	1.34–1.46	5
A. semenguei	2.56	2.55	2.53–2.60	5
A. subacuminata	1.57	1.58	1.43–1.73	14
Apical angle (degrees)				
Species	**Holotype**	**mean**	**range**	**No.**
A. acuminata	90	95	89–97	21
A. avakubiensis	*ca* 122	120*	115–132*	16*
A. cf. *avakubiensis* [Gabon]			116	1
A. biokoensis	129	133	129–136	4
A. crystallum	125	123	120–125	2
A. fruticicola	140	136	128–144	16
A. occidentalis	126	127	126–129	3
A. ortizdezarateorum	133	132	124–140	5
A. semenguei	144	142	134–146	5
A. subacuminata	110	113	107–122	14
Diameter of 1st whorl (mm)				
Species	**Holotype**	**mean**	**range**	**No.**
A. acuminata	0.78	0.78	0.67–0.85	21
A. avakubiensis	?	0.75	0.68–0.83	16*
A. cf. *avakubiensis* [Gabon]			0.84	1
A. biokoensis	0.72	0.83	0.72–0.94	4
A. crystallum	0.9	0.9	0.9	2
A. fruticicola	0.83	0.82	0.71–0.95	16
A. occidentalis	0.86	0.84	0.82–0.86	3
A. ortizdezarateorum	0.86	0.87	0.84–0.91	5
A. semenguei	1.39	1.30	1.22–1.39	5
A. subacuminata	0.71	0.73	0.67–0.78	14
Diameter of 1st + 2nd whorl (mm)				
Species	**Holotype**	**mean**	**range**	**No.**
A. acuminata	1.44	1.45	1.32–1.69	21
A. avakubiensis	?	1.30	1.21–1.41	16*

TABLE 1 (*continued*)

Conchometric data for 87 adult *Avakubia* shells. Measurements and abbreviations are explained in Fig. 1. Measurements of holotype of *A. avakubiensis* are taken from available illustrations (see species description), as far as possible (* – holotype excluded, ? – character not observable in available illustrations).

Species	Holotype	mean	range	No.
A. cf. *avakubiensis* [Gabon]			1.34	1
A. biokoensis	1.28	1.40	1.25–1.64	4
A. crystallum	1.47	1.49	1.47–1.50	2
A. fruticicola	1.46	1.44	1.29–1.64	16
A. occidentalis	1.44	1.44	1.36–1.51	3
A. ortizdezarateorum	1.39	1.43	1.34–1.48	5
A. semenguei	2.32	2.19	2.10–2.32	5
A. subacuminata	1.26	1.24	1.14–1.30	14
RD5 (mm)				
Species	**Holotype**	**mean**	**range**	**No.**
A. acuminata	0.75	0.77	0.65–0.94	21
A. avakubiensis	?	0.74*	0.67–0.83*	16*
A. cf. *avakubiensis* [Gabon]			0.7	1
A. biokoensis	0.55	0.59	0.55–0.61	4
A. crystallum	0.56	0.55	0.54–0.56	2
A. fruticicola	0.52	0.53	0.47–0.56	16
A. occidentalis	0.67	0.63	0.60–0.67	3
A. ortizdezarateorum			< 0.25	5
A. semenguei	0.52	0.58	0.52–0.69	5
A. subacuminata	0.87	0.79	0.64–0.91	14
Spire angle (degrees)				
Species	**Holotype**	**mean**	**range**	**No.**
A. acuminata	51	53	49–57	21
A. avakubiensis	*ca* 71	67*	61–75*	16*
A. cf. *avakubiensis* [Gabon]			65	1
A. biokoensis	65	64	61–66	4
A. crystallum	67	66	65–67	2
A. fruticicola	73	72	67–77	16
A. occidentalis	63	68	63–73	3
A. ortizdezarateorum	68	65	63–68	5
A. semenguei	75	73	71–76	5
A. subacuminata	59	58	51–62	14

TABLE 2
Loadings of 11 shell characters (Fig. 1) of 87 *Avakubia* shells on the first three principle component axes, and the percentage of the variation in the data explained by the axes.

	Axis 1	Axis 2	Axis 3
% variation accounted for	62.2	24.1	9.3
Character loadings:			
W	0.1765	-0.1684	-0.2918
H	0.4259	0.1128	-0.2401
D	0.3187	0.1204	-0.0299
AA	-0.2060	0.1645	0.3668
DW1	0.0147	0.3831	0.3455
DW2	0.0856	0.3607	0.3022
PH	0.4116	0.2448	0.0074
PW	0.4327	-0.6825	0.5732
SA	-0.1651	0.1285	0.4217
BWH	0.3694	0.2511	0.0096
RD	0.4327	-0.6825	0.5732

most (86%) of the variation in the data. Loadings of the characters on the first three principal component axes are given in Table 2. The PC1×PC2 plot produced fairly distinct groups (Fig. 2). PC1 largely relates to size (H, D, AH, AW, BWH), whilst PC2 relates to the apical parameters (AA, SA, DW1, DW2). Rib distance (RD) constitutes an important contribution to both PC1 and PC2. Three morphospecies are obviously distinctive in size, shape and sculpture (later identified as *A. acuminata*, *A. semenguei* and *A. ortizdezarateorum*, see below). The remaining material is more similar in shell morphology, but all morphospecies represented by four or more individuals form well separated groups. A MANOVA indicates significant differences among most morphospecies that were recognised on the basis of PCA (Wilks' Lambda = 3.0×10e-6, df 448.8, $P \ll 0.001$), which statistically may not be a robust conclusion, since the distribution of the data appears not to be multivariately normal.

Material from the eastern DRC and Uganda formed a single cluster in the first two principal components ordination plot (Fig. 2), differing highly significantly (all Hotelling's pairwise comparisons $P<0.001$) from other tentative morphospecies represented by four or more measured specimens. The DRC specimens did not differ from the Ugandan material in a pairwise comparison (Hotelling's $t^2=57.825$, $F=2.0652$, $P>0.2$). These shells resemble the available descriptions and illustrations of the holotype shell of *A. avakubiensis* (showing only characters measureable in frontal view), and were therefore classified with this species, the type locality of which is also geographically closest. A single, somewhat worn adult shell (Fig. 9K) from a central Gabonese locality (Reserve de la Lopé) was placed within the *A. avakubiensis* cluster in PCA. However, in view of subtle differences in shell characters (using also one juvenile shell and two shell fragments from this area) and for biogeographical reasons (distance to

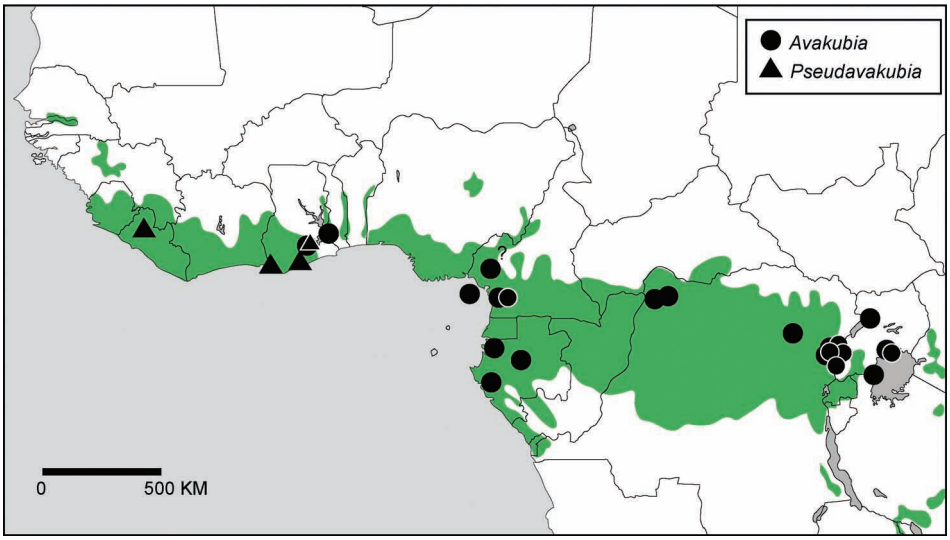


Fig. 3. Distribution records of the genera *Avakubia* (dots) and *Pseudavakubia* (triangles). Green colour indicates the approximate extent of the equatorial forest belt in Central Africa.

nearest locality of *A. avakubiensis* being 1750 km), the inclusion in *A. avakubiensis* seemed insecure. Fontaine *et al.* (2007) tentatively considered this a new species. For the time being we classify this material as *A.* cf. *avakubiensis.*

Material from Southwest Cameroon that in an earlier study (de Winter & Gittenberger 1998) had been addressed to as *Gulella (Avakubia)* cf. *avakubiensis*, formed a well separated group in the PCA ordination plot from true *avakubiensis* (Fig. 2), and the two morphospecies species differed highly significantly in a pairwise Hotelling's test ($P<<0.001$). Three specimens from Ghana were initially classified with this Cameroon material, but formed not clearly part of the Cameroon cluster in the PCA plot and proved significantly different in a in a pairwise Hotelling's test ($P<0.01$), in spite of the small sample size. The Ghanaian and Cameroonian specimens are described below as two distinct species (*A. occidentalis* and *A. fruticicola*, respectively), also on the basis of non-biometric characters.

Two specimens from western Gabon, which had been provisionally assigned to a morphospecies described below as *A. fruticicola*, were placed close to the cluster of this species in PCA (Fig. 2). Still, on account of the different shell shape and size, combined with noticeable differences in protoconch sculpture, the Gabonese material is considered a distinct species, *A. crystallum*.

A number of Southwest Cameroonian shells superficially resemble *A. acuminata* in shape, but are consistently smaller-sized, and were therefore tentatively recognised as a separate morphospecies. This was confirmed by their separation in PCA (Fig. 2), and in pairwise Hotelling's tests, in which the material differed highly significantly from all other morphospecies represented by more than four available specimens and just significantly ($P<0.05$) from the others. This Cameroonian material is described below as *A. subacuminata*.

The material from Bioko I. (Equatorial Guinea) that had been attributed to *A. avakubiensis* by Ortiz de Zárate Lopez and Ortiz de Zárate Rocandio (1956), clearly embraces two rather different species. The distinct nature of the shells from the high altitude sites was already acknowledged by these authors, but they refrained from formally naming the taxon. This species is described below as *A. ortizdezarateorum*, and can be easily distinguished from any other *Avakubia* species by its shell sculpture and arrangement of the apertural barriers, but also conchometrically (Fig. 2). Specimens of the second species from lower elevations superficially resemble *A. subacuminata*, *A. fruticicola*, *A. avakubiensis*, *A. occidentalis*, and *A. crystallum*, but can be distinguished from all these taxa by a combination of shell measurements and appear as a separate grouping in PCA (Fig. 2), which is (highly) significantly different from the former three species in pairwise Hotelling's tests, in spite of the small number of available shells. This species is described below as *A. biokoensis.*

TAXONOMY

Family Streptaxidae Gray, 1860
Genus *Avakubia* Pilsbry, 1919

Etymology: Pilsbry's name refers to the village of Avakubi in the DRC, where the type was found. Gender feminine.

Type species: *Gulella (Avakubia) avakubiensis* Pilsbry, 1919, by orig. des.

Description: Shell small, with 5–7 regularly coiled whorls, adult height 3.0–5.8 mm, ovate or elongate-ovate, diameter of the penultimate whorl always exceeds that of the body whorl. Apex rounded to strongly acuminate. Coiling tightness varies substantially between species (W:*ln*H=3.1–5.0). Body whorl height takes up 38–56 % of H, varying substantially between species. Peristome height 29–40 % of H. Peristome width 44–62 % of D. Aperture roundish or heart-shaped with a palatal tooth or swelling, which may be inconspicuous or virtually absent, and a protruding angular tooth that continues as an inrunning lamella for nearly a whorl. Body whorl with a deep-set palatal fold, which is generally not visible in the aperture, but appears in translucent specimens as a short white line, without a corresponding external depression. Columella with a tooth or lamella, which is externally (usually) not discernable. Umbilicus narrow, but always open. Umbilicus of juvenile specimens open and rounded, decreasing in diameter with increasing shell height. Aperture of juvenile shells edentate. Protoconch with 2–2½ whorls, sculptured by *ca* 9–16 spiral cords of roundish or rectangular particles on the second whorl; some species have fine spiral lines in between major ones. Transition of protoconch to teleoconch marked by a rather abrupt change in sculpture. Teleoconch with strong, more or less curved, axial ribs that run from suture to suture, the interstices with fine spiral lines that do not seem to cross the axial ribs. Teleoconch spirals are not a continuation of the spiral cords on the protoconch, being more close-set, more irregular and structurally different (solid, not made up of particles).

Anatomy (Figs 6, 15, 24; based on dissections of few specimens (singletons, except for *A. acuminata*) of three different species, supplemented with information from unpublished drawings of a dissected specimen of *A. avakubiensis* kindly supplied by B. Rowson (NMW)): Salivary gland single. Penis more or less elongate, the basal portion widest. Internal penial wall distally without obvious pilasters in some species (present in

A. avakubiensis, not studied in *A. fruticicola*), which exhibit instead irregularly shaped, larger (*A. subacuminata*) or smaller (*A. acuminata*), irregularly-shaped tissue pads. The convolute vas deferens widens more or less abruptly into a wider, rather muscular and shining terminal portion (epiphallus?). This terminal portion bends across the upper penis, and enters the penis somewhat laterally, cutting off a short apical caecum. The long penis retractor muscle originates from the columellar muscle and inserts on and/or laterally of the penial apex, extending under the terminal portion of the vas deferens close to its entrance. Penis of most species with a lateral diverticulum (rather indistinct or absent in *A. fruticicola*), which appears to consists of a fleshy structure within the penial envelope. In the penis of three species (not studied in *A. fruticicola*) no spines or denticles were observed. In the lower penis of a specimen of *A. acuminata*, an elongate spindle-shaped spermatophore-like structure was encountered. Female genital tract with a short but distinct vagina, followed by a narrow free oviduct. In two specimens of *A. acuminata*, the oviduct is inflated into a pouch-like uterus, containing a single shelled embryo, so at least this species is ovoviviparous. Bursa copulatrix (gametolytic gland) with a long narrow duct and an ovoid or round bursal sac, which reaches the albumen gland. Hermaphrodite duct with a long, convolute tube-like diverticulum (talon). Radula ribbon very long relative to its width; after maceration the radula ribbon appears transversely folded in two portions of unequal length. Radula typical carnivorous, with a small number (<20 teeth in half a row) of elongate, sharply pointed, curved lateral and marginal teeth. Rachis present in *A. acuminata*, noticeably smaller than other teeth, not observed in other species.

Species included: In addition to the type species, *A. acuminata* (Thiele, 1933); *A. biokoensis* de Winter & Vastenhout, sp. n.; *A. crystallum* de Winter, sp. n.; *A. fruticicola* de Winter & Vastenhout, sp. n.; *A. occidentalis* de Winter, sp. n.; *A. ortizdezarateorum* de Winter & Vastenhout, sp. n.; *A. semenguei* de Winter & Vastenhout, sp. n.; *A. subacuminata* de Winter & Vastenhout, sp. n.

Distribution (Fig. 3): Cameroon, DRC, Equatorial Guinea (Bioko I.), Gabon, Ghana, Uganda.

Avakubia acuminata (Thiele, 1933), **comb. n.**

Figs 4, 5A–F, 6, 7, 10A–D

Gulella (Avakubia) acuminata: Thiele 1933: 316, fig. 61; de Winter & Gittenberger 1998: 239.

Diagnosis: Differs from other *Avakubia* species by the comparatively large (>5 mm) shell with tapering spire and strongly acuminate apex.

Description:

Shell (Figs 4, 5A–F, 10A–D, Table 1): Large for the genus (mean H 5.4 mm), elongate (H:D 1.88–2.1, median 1.97, in holotype 2.01), biconical, spire tapering. Coiling tightness 3.7–4.1, median 3.9, in holotype 4.0. Whorls moderately convex. Apex strongly acuminate. Protoconch comparatively high-spired, consisting of 2¼–2.5 whorls. Protoconch sculpture (Figs 10A–D) consists of comparatively regularly spaced spiral cords, 10–12 on second whorl, each 6.6–8.5 µm wide. Cords composed of series of 13–22 µm long, elongate-rounded particles, that are individually just separated. Spiral sculpture starts *ca* ¼ whorl from nucleus. Teleoconch sculpture consists of slightly oblique, pro-

socline axial ribs, 6.4–9.2 ribs/mm on penultimate whorl, median 8 ribs/mm, in holotype 7.8 ribs/mm. Interstices with fine, solid, more or less irregular spiral lines. Body whorl proportionally small, BWH 41–47 % of H, median 44 %, in holotype 42 %. Peristome complete in most specimens; some otherwise fully developed specimens with

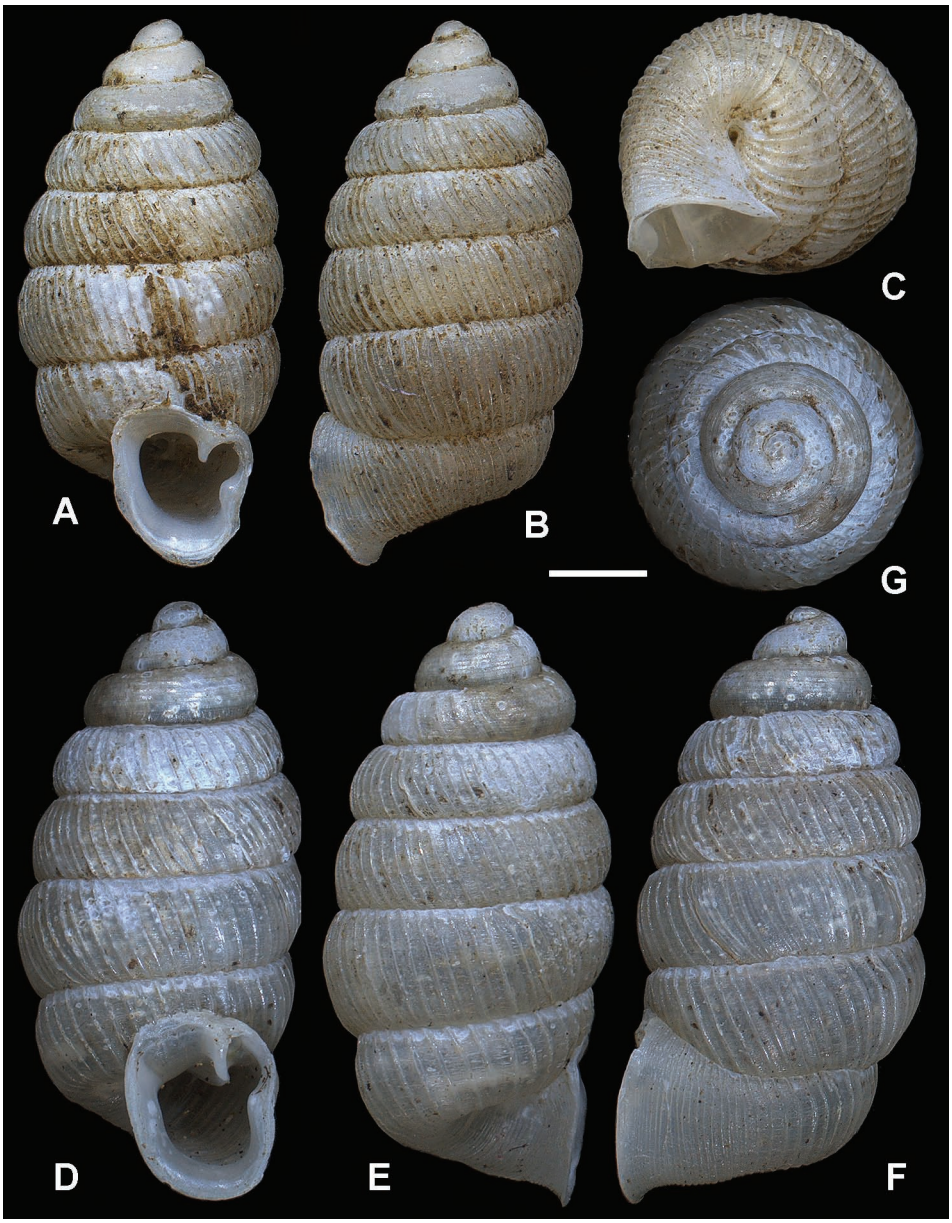


Fig. 4. *Avakubia acuminata* (Thiele, 1933): (A–C) holotype, ZMB 72855: apertural (A), lateral (B) and umbilical (C) views; (D–G) shell from S of Lolodorf, Cameroon, RMNH.MOL.42795: apertural (D), lateral (E, F), and apical (G) views. Scale bar = 1 mm.

incompletely developed parietal-angular margin are probably subadult. Peristome somewhat higher than wide, PH:PW 1.08–1.24, median 1.18, in holotype 1.19. PH 29–34% of H, median 33%, in holotype 31%. PW 49–60% of D, median 55%, in holotype 52%. Apertural lip expanded and flaring, not strongly incrassate. Two apertural barriers visible in frontal view: a more or less pointed, tooth-like, thickening on mid-palatal wall and a conspicuous, somewhat projecting angular tooth that extends inwards as a deeply entering lamella. Internal wall of body whorl with a deep-set palatal fold (Fig. 5), not visible in the aperture, but discernable in translucent specimens as short pale stripe (Figs 4D, E). Short, little conspicuous lamella present on columella (Fig. 5), but not visible in aperture. Umbilicus open but rather narrow.

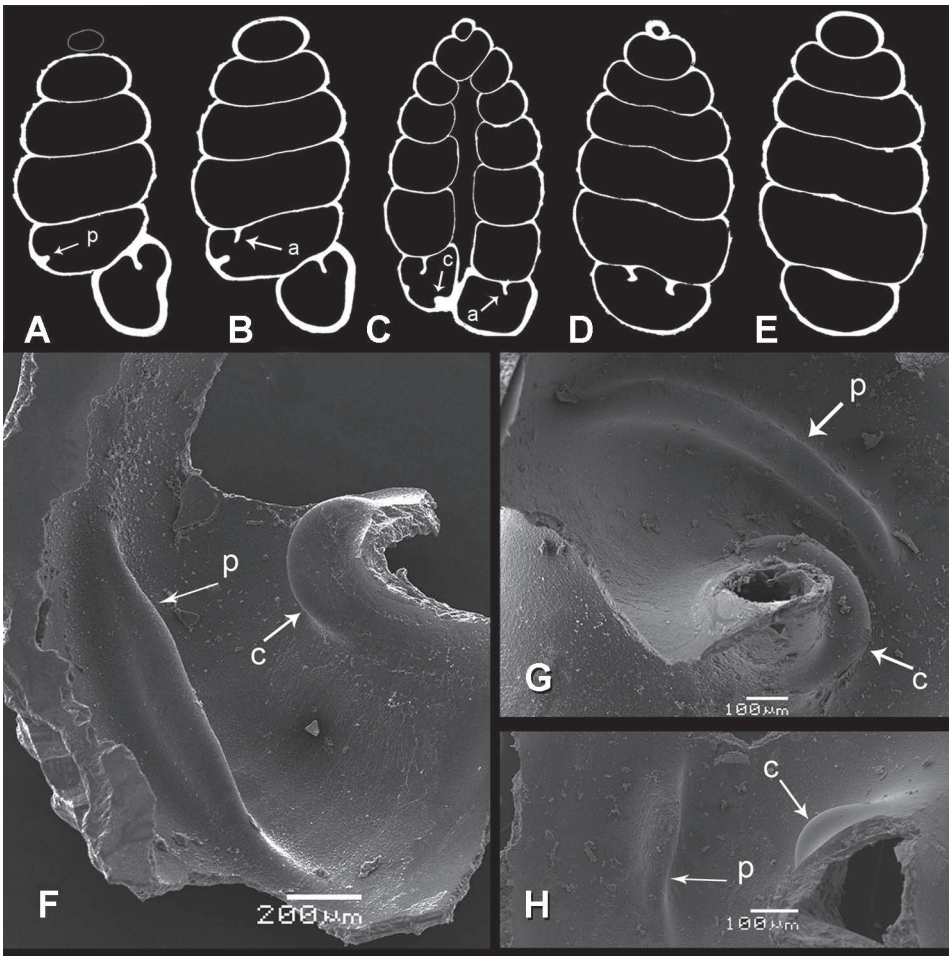


Fig. 5. Apertural dentition in *Avakubia* species: (A–E) *A. acuminata* (Thiele, 1933), series of longitudinal slice images acquired by a MicroCT scanner through a shell from S of Lolodorf, Cameroon, RMNH. MOL.42795, illustrating the arrangement of internal shell structures; (F–H) SEM photographs of body whorl fragments showing deep-set palatal fold and columellar lamella: (F) *A. acuminata*, (G) *A. subacuminata* sp. n., (H) *A. fruticicola* sp. n. Abbreviations: a – angular lamella, c – columellar lamella, p – palatal fold.

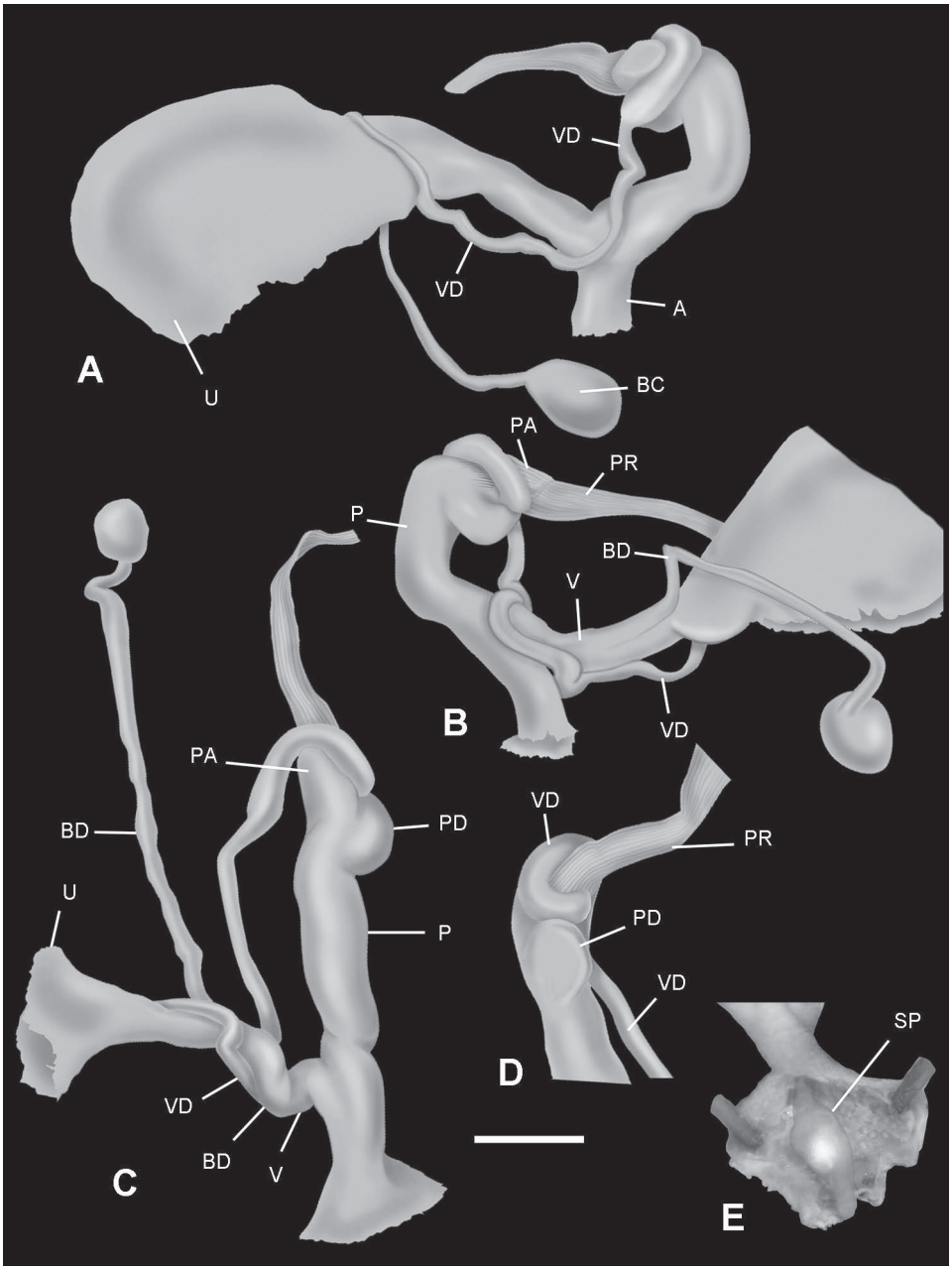


Fig. 6. *Avakubia acuminata* (Thiele, 1933), genital anatomy of specimens from S of Lolodorf, Cameroon: (A, B) RMNH.MOL.330317, (C–E) RMNH.MOL.330318, opened distal penis with spermatophore. Abbreviations: A – genital atrium, AG – albumen gland, BC – bursa copulatrix, BD – bursal duct, P – penis, PA – penial apex, PD – penial diverticulum, PR – penial retractor muscle, SOD – spermoviduct, SP – spermatophore, U – (remains of) dilated free oviduct (uterus – embryo removed), V – vagina, VD – vas deferens. Scale bar = 0.5 mm. (Drawn by Bas Blankenvoort from photographs of genitalia preparations)

Body colour: Live animal cream-whitish, without reddish pigment.

Anatomy (Fig. 6; five specimens dissected, including two with fully grown shells but still poorly developed genitalia): Atrium mostly longer than wide, thin-walled. Penis more or less elongate, with a short apical caecum as well as a more conspicuous lateral diverticulum. In some (juvenile or contracted?) specimens diverticulum appears sub-apically, nearby apical caecum, giving penis a bifid appearance. Vas deferens in some specimens coiled around vagina. Vas deferens abruptly widens close to upper penis into a muscular terminal portion that enters upper penis laterally, cutting off a short apical caecum. Penis retractor muscle long and twisted, originating from columella muscle and inserting on penial caecum, extending under widened terminal vas deferens. Interior of penis distally without strong pilasters, internal wall with small irregular tissue pads. No chitinous spines were found inside penis. A pale, elongate spindle-shaped spermatophore-like structure (Fig. 6E) with yellow content was encountered inside lower penis of one specimen. Bursa copulatrix arises from oviduct, cutting off short but distinct vagina, consisting of long narrow bursal duct with roundish oval sac. Free oviduct narrow, in two specimens strongly inflated to form a pouch-like uterus containing single, shelled, embryo. Hermaphrodite duct with long, tube-like, convolute talon.

Radula (Fig. 7): Ribbon very long and narrow. Row formula 16-C-16, number of rows not counted (n=2). Central tooth distinctly smaller than laterals. Distinction between

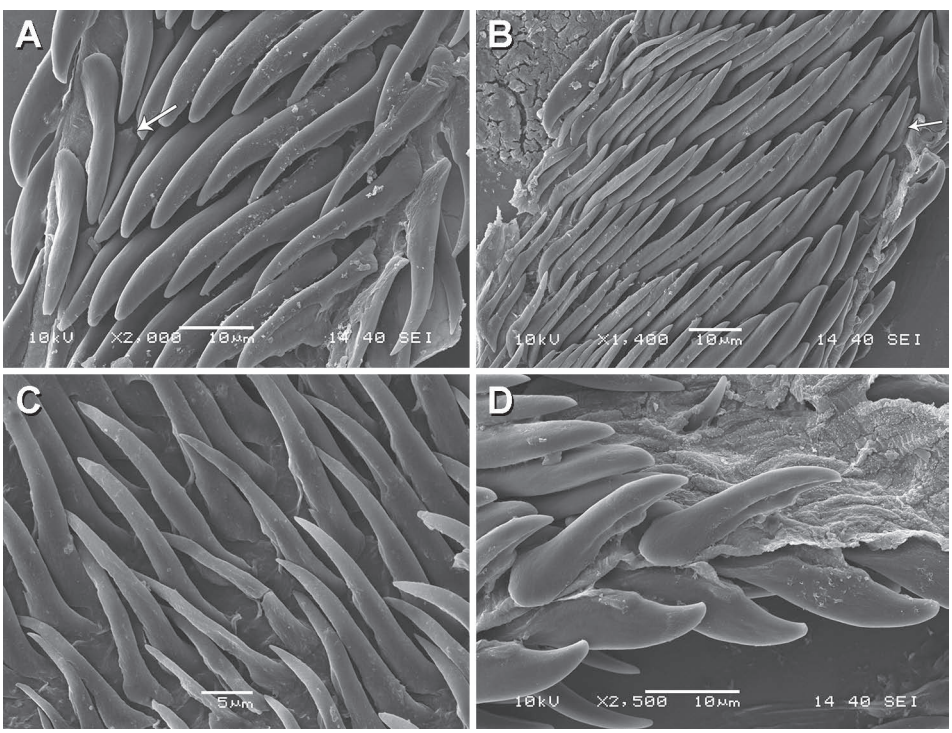


Fig. 7. *Avakubia acuminata* (Thiele, 1933), radula of specimen from S of Lolodorf, Cameroon: (A) central tooth and marginals; (B) entire half row; (C) marginal teeth; (D) lateral teeth. Arrows indicate central tooth.

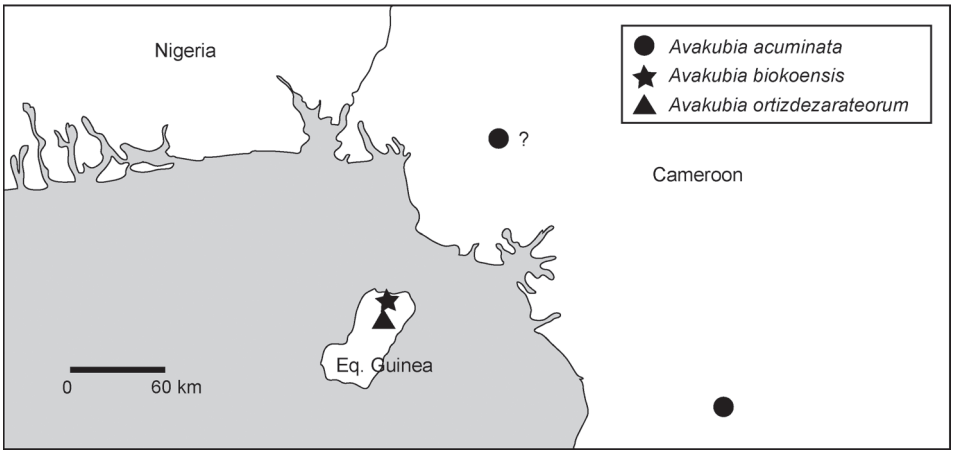


Fig. 8. Distribution records of *Avakubia acuminata* (Thiele, 1933) (dot with question mark indicates the uncertain type locality), *A. biokoensis* sp. n. and *A. ortizdezarateorum* sp. n.

laterals and marginals gradual, latter appearing more slender. Viewed from above, mesocone of lateral and marginal teeth appear as elongate, sharply pointed, curved blades; in other views, endocone becomes visible as a lateral dilatation.

Holotype (examined): CAMEROON: "Kamerun, wahrscheinlich [probably] Johann Albrechtshöhe", Conradt (ZMB 72855).

Other material examined: CAMEROON: *Sud Prov.*: Minwo area *ca* 6 km NE Ebom, 15 km S Lolodorf, 3.10°N 10.73°E, 400–500 m, all collected within a single square kilometre of near-primary evergreen forest, from 1–3 m high understorey vegetation, except for three rather eroded empty shells (2 juv. and 1 ad.), viii–x.1995 and iii–iv.1996, A.J. de Winter & E.J. Semengue (16 samples containing 20 ad. & 6 juv. dry and 17 ad. in alcohol, of which 5 were dissected; RMNH).

Distribution (Fig. 8): For a long time *A. acuminata* was only known by the holotype shell, until the species was rediscovered near Lolodorf in Southwest Cameroon (de Winter & Gittenberger 1998). The type locality is uncertain ["Wahrscheinlich (probably) Johann Albrechtshöhe" (Thiele 1933), presently Kumba, 4.63°N 9.45°E], which actually lies more than 200 km NW of Lolodorf. Although the occurrence of the species near the surmised type locality cannot be disproved, it may well be that the holotype was actually found closer to the second locality. Thiele (1933) mentioned Conradt as collector. It appears that Leopold Conradt, who collected especially insects, not only visited the surmised type locality, but also the Lolodorf area where he might have collected the type specimen while capturing, for example, stingless bees using a sweep net (as indicated in Eardley 2004).

Habitat: Found in a near-primary rainforest at 400–500 m elevation. Specimens were collected alive from 1–3 m high understorey vegetation, except for three rather eroded empty shells. The species lives syntopically with *A. semenguei* and *A. fruticicola*.

Remarks: *A. acuminata* is the largest species of *Avakubia*, and is readily recognizable by its characteristic elongate shell with tapering spire and acuminate apex. Its attribution to *Avakubia* is supported by a number of shell characters shared with *A. avakubiensis*, some of which may be synapomorphies, notably the beaded spiral sculpture on the protoconch, and the deep-set palatal lamella.

Avakubia avakubiensis (Pilsbry, 1919), **comb. n.**

Figs 9A–J, 10E–H

Gulella (Avakubia) avakubiensis: Pilsbry 1919: 234, fig. 102; Verdcourt 1962: 8; van Bruggen & Van Goethem 1997: 9, fig. 5; Schileyko 2000: 817, fig. 1069A; Wronski & Hausdorf 2010: 92; Rowson *et al.* 2011: 89, 91, 92.

not *Gulella (Avakubia) avakubiensis* of Degner 1934, nor of Ortiz de Zárate Lopez & Ortiz de Zárate Rocandio 1956.

Diagnosis: Shell differs from other *Avakubia* species by a combination of characters, like small size, subacute apex, and distant axial teleoconch ribs. *Avakubia subacuminata* generally has a larger, more elongate shell with a more sharply pointed apex and less convex protoconch whorls.

Description:

Shell (Figs 9A–J, 10E–H, Table 1; characters of the holotype are taken from the available illustrations of this shell (see Remarks)): Small (mean H 3.3 mm), ovate-biconical, largest width at penultimate whorl. H:D 1.57–1.84 in available specimens, median 1.72, in holotype *ca* 1.62. Coiling tightness holotype unknown, 4.3–4.6 in available specimens, median 4.5. Whorls rather convex, including protoconch whorls. Apex subacute. Protoconch consisting of *ca* 2.0 whorls. Pilsbry's (1919) description of the holotype protoconch sculpture broadly agrees with our observations. On last protoconch whorl, specimens from Kibale (Uganda), and Virunga National Park (DRC) have 14 irregularly-spaced spiral cords of strongly varying width, at most *ca* 9.5 µm wide but mainly (considerably) less. Spiral cords composed of rectangular particles of variable length, individually separated by a narrow cleft. Much finer lines are distinguishable between major spiral cords (Fig. 10H). Teleoconch sculpture consists of distantly spaced, curved axial ribs, 7.2–9.4 ribs/mm on penultimate whorl, median 8.3, with fine spirals in interstices. Body whorl height generally less than half of shell height, BWH 45–53 % of H in available specimens, median 47 %, in holotype 49 %. Peristome complete, mostly somewhat higher than wide, PH:PW 0.96–1.16 in available specimens, median 1.11, in holotype 1.05. PH 31–37 % of H in available specimens, median 34 %, in holotype 35 %. PW 50–60 % of D in available specimens, median 53 %, in holotype 55 %. Apertural lip expanded and flaring, slightly reflected and not strongly incrassate. Two barriers visible in aperture: a weak, sometimes almost wanting, tooth-like thickening on mid-palatal wall and a projecting angular tooth that extends inwards as deeply entering lamella. Internal wall of body whorl with deep-set palatal fold, a short pale stripe is externally visible in translucent specimens. Presence of columella fold not discernible in aperture. Umbilicus narrow but open, widest in comparatively low-spired shells (e.g. Fig. 9J).

Body colour: Not recorded.

Anatomy (a specimen from Uganda was dissected by B. Rowson, who kindly allowed us to study his unpublished drawings): Vas deferens enters penis subapically. Penis with distinct lateral diverticulum and short apical caecum, on which the penial retractor muscle is attached. Overall penial morphology similar to *A. acuminata* (Fig. 6), but penis seems less elongate. Interior of penis with two strong and one minor pilasters, without any hooks or spines.

Holotype: DRC: Ituri, Avakubi, *ca* 1.318°N 27.544°E, J. Bequaert (shell could not be traced in AMNH, Christine Johnson, pers. comm., Dec. 2011). A photograph of the holotype shell in frontal view is available on http://research.amnh.org/iz/types_db/details.php?specimen_id=9951.

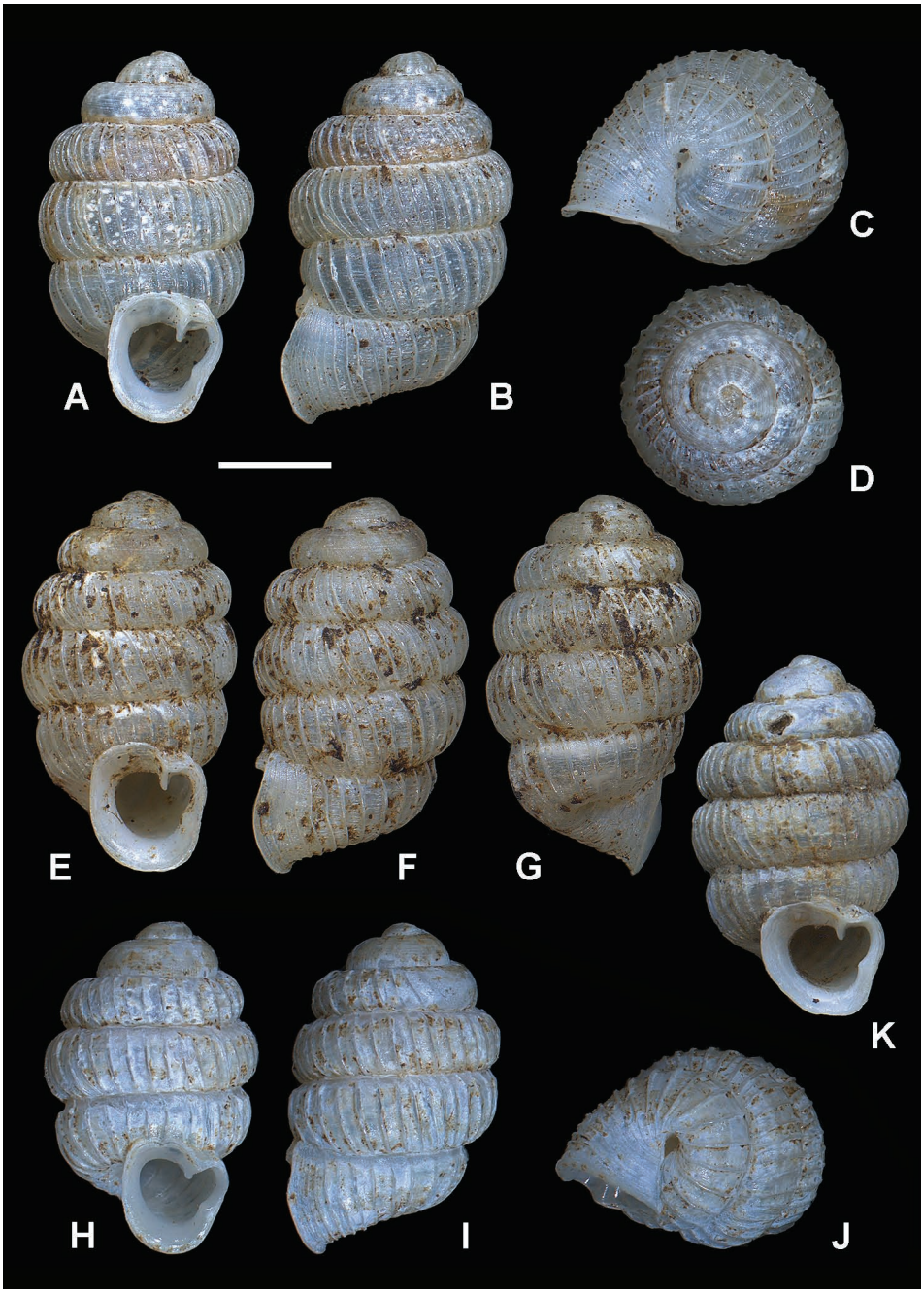


Fig. 9. *Avakubia avakubiensis* (Pilsbry, 1919): (A–D) shell from Kasyoha-Kitumi, Uganda, ZMH 52796: apertural (A), lateral (B), umbilical (C) and apical (D) views; (E–G) shell from Virunga National Park, DRC, IRSNB, sta. A476: apertural (E) and lateral (F, G) views; (H–J) shell from Abyalose, Virunga National Park, DRC, IRSNB, sta. A511: apertural (H), lateral (I) and umbilical (J) views; (K) *A.* cf. *avakubiensis*, shell from Réserve de la Lopé, Gabon, MNHN, apertural view. Scale bar = 1 mm.

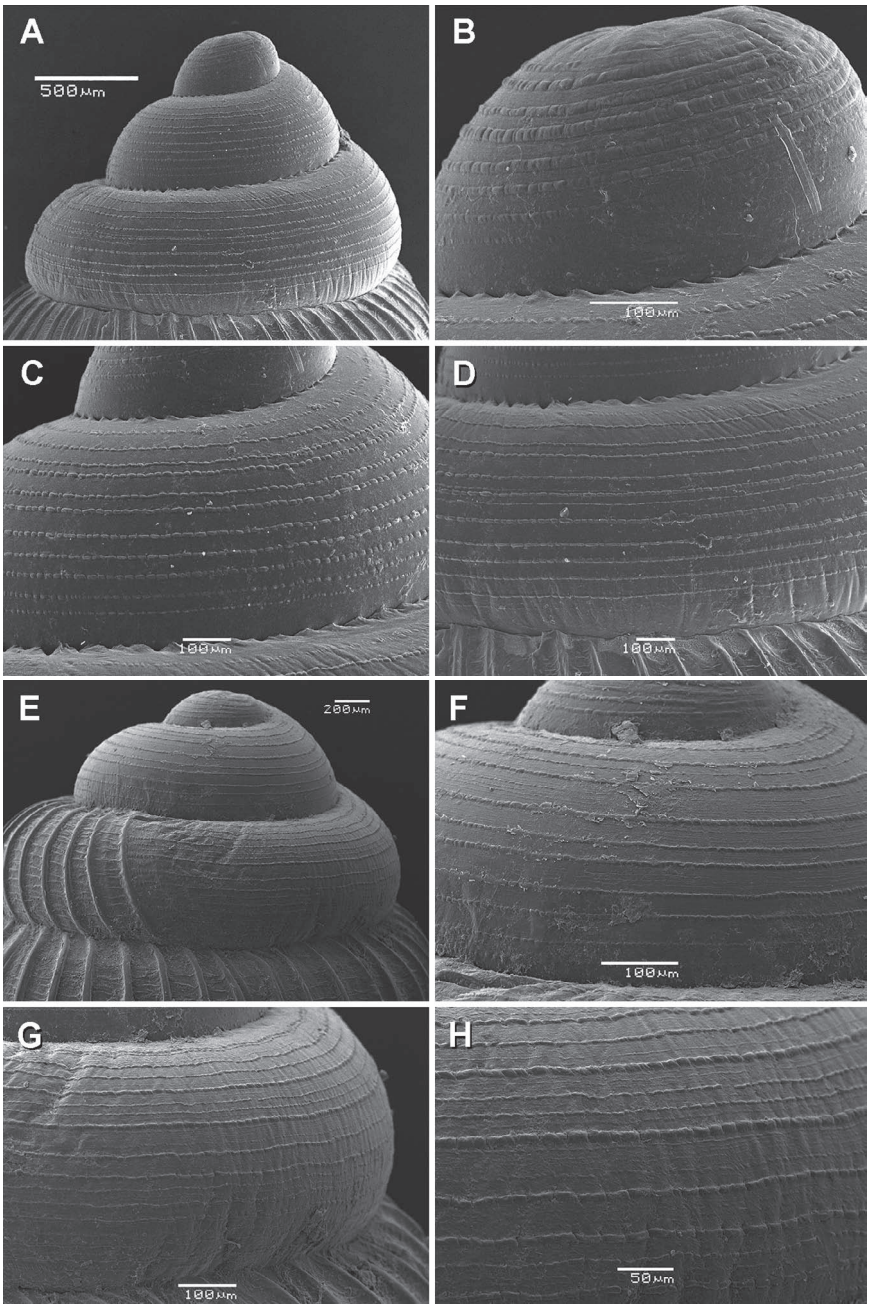


Fig. 10. SEM photographs of shell sculpture of *Avakubia* species: (A–D) *A. acuminata* (Thiele, 1933) from S of Lolodorf, Cameroon, RMNH.MOL.330324: (A) entire protoconch, (B) tip of apex, (C) sculpture on first protoconch whorl, (D) sculpture on second protoconch whorl; (E–H) *A. avakubiensis* (Pilsbry, 1919), juvenile specimen from Kibale forest, Uganda (ZMH 52709): (E) protoconch and transition to teleoconch, (F) first protoconch whorl, (G) second protoconch whorl, (H) detail of second protoconch whorl sculpture.

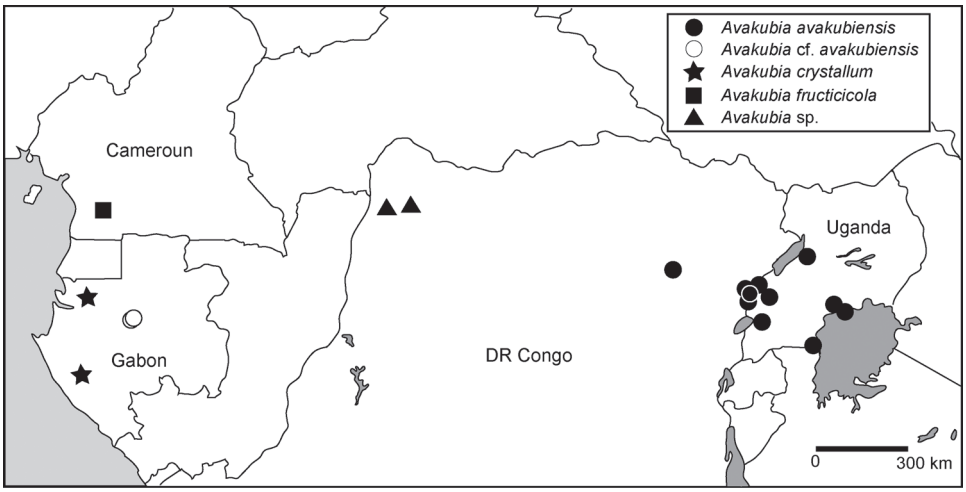


Fig. 11. Distribution records of *Avakubia avakubiensis* (Pilsbry, 1919), *A.* cf. *avakubiensis*, *A. crystallum* sp. n. and *A. fruticicola* sp. n. Material of *Avakubia* sp. (identified as *A. avakubiensis* by van Bruggen and Van Goethem (2007)) was not examined.

Other material examined: DRC: various sites within Virunga National Park [formerly Parc National d'Albert (PNA)]: 2 ad. dry shells, Abyalose, affl. Djuma, PNA, sta. A511, 800 m, 12.vi.1953, G.F. de Witte (RBINS); 2 ad., 1 juv. dry shells, Kabalwa, affl. dr. Talya, PNA, sta. A476, 1130 m, 21.v.1953, P. Vanschuytbroeck & J. Kekenbosch (RBINS); 1 ad. dry shell, Tungula, PNA, sta. A1223, 16.xii.1959, H. Synave (RBINS); 2 ad. in alcohol, Makano-Kisisile River, PNA, sta. B432, 1150 m, 27.v.1957, G.F.de Witte (RBINS); 1 ad. dry shell, PNA, sta. A877, no further data (RBINS). UGANDA: 5 ad., 2 juv. dry shells, Bushenyi, Kasyoha-Kitumi Central Forest Reserve, Kamuzuku, *ca.* 0°15'S 30°09'E, 1250 m, 11–12.iv.2006, T. Wronski (ZMH 52796, 52819, 53543, 53478); 1 ad., 1 juv. dry shell, Kamwenge, Kibale Forest National Park, Fort Portal towards Ibanda at bridge crossing Dura River, 0°27'26"N 30°22'51"E, 1390 m, 13.iv.2006, T. Wronski (ZMH 52709); 1 ad., 1 juv. dry shell, Kibale Forest National Park, Kanyanchu, Elephant wallow, 0°26'25"N 30°23'42"E, 1250 m, 14.iv.2006, T. Wronski (ZMH 52637); 1 dry shell, Kibale Forest National Park, Kanyanchu, 0°26'13"N 30°23'42"E, 1230 m, 14.iv.2006, T. Wronski (ZMH 52744); 1 ad. dry shell, Masindi, Budongo Central, Forest Reserve: Masindi-Butiaba road between Karongo and Busingiro, 1°42'26"N 31°28'57"E, 1080 m, 17.iv.2006, T. Wronski (ZMH 52425); 1 juv. dry shell, Mpigi, Mpanga Central Forest Reserve, Kafumo, 0°13'15"N 32°17'03"E, 1190 m, 24.iii.2006, T. Wronski (ZMH 53293); 1 ad. dry shell, Bundibugyo District, Bwamba County, Semuliki National Park, *ca* 0.82°N 30.16°E, 720 m, 16.vii.1996, P. Tattersfield & J.A. Allen (NMW.Z.1997.009); 1 ad. dry shell, 1 ad. in alcohol, Malabigambo Forest, *ca* 0°57'N 13°38'E, 1150 m, 4.ii.2007, P. Tattersfield & B. Rowson (PT).

Distribution (Fig. 11): Specimens attributed here to *A. avakubiensis* originate from a large area extending from Avakubi in the eastern DRC to Kampala, Uganda, a linear distance of *ca* 500 km. This species has the easternmost distribution of the genus and by far the largest known range. Material from the north-western DRC (Bozene, Gemena) attributed by van Bruggen and Van Goethem (1997) to this species would, if correct, increase the range considerably. Unfortunately these specimens were not available. Material from central Gabon is attributed to *A. avakubiensis* with doubt (see Remarks).

Habitat: The species appears to have been collected in leaf litter on the forest floor in mid-altitude moist evergreen forest between 720 and 1390 m.

Remarks: Shells from the eastern DRC and Uganda agree rather well with the original description (Pilsbry 1919) and available illustrations of the holotype of *A. avakubiensis* in (proportional) shell dimensions, rib distance, apical angle, and in whorl convexity.

We therefore confidently attribute these specimens to *A. avakubiensis*, although the holotype shell could not be studied. Still we stress the need to examine the holotype in order to confirm generic characters like an open umbilicus and the presence of a deep-set palatal fold; the latter character may have been addressed by Pilsbry (1919) as "a low transverse fold … within the basal margin", but this may also refer to what we here term the columellar lamella.

Material from two nearby localities in central Gabon (Reserve de la Lopé, Ogooué-Ivindo) is considered too poor (one worn adult and one juvenile shell plus two fragments) to confidently attribute this material to *A. avakubiensis*. In the PCA, the only adult shell was placed well within the *A. avakubiensis* cluster (Fig. 2), indicating a strong resemblance in shell proportions. Fontaine *et al.* (2007) tentatively considered this a new species. In view of the large distance between the Gabonese records and the nearest locality of *A. avakubiensis* (nearly 1800 km), their view could well be correct. For the time being we classify these Gabonese specimens as *A.* cf. *avakubiensis.*

Avakubia biokoensis de Winter & Vastenhout, sp. n.

Figs 12, 18E, F

Gulella (Avakubia) avakubiensis: Ortiz de Zárate Lopez & Ortiz de Zárate Rocandio 1956: 118, fig. 22; van Bruggen & Van Goethem 1997: 9.

Etymology: The species name refers to the Bioko I., where the species is likely to be endemic.

Diagnosis: *Avakubia biokoensis* differs from *A. subacuminata* in having closer-set axial ribs on the teleoconch, a less acuminate apex, less tightly coiled whorls, and a proportionally larger peristome. *A. avakubiensis* can be readily distinguished from *A. crystallum* in having a smaller shell, more pointed apex and more widely spaced teleoconch ribs. *Avakubia biokoensis* differs from both *A. occidentalis* and *A. fruticicola* in having larger shell with less dense teleoconch ribs.

Description:

Shell (Figs 12, 18E, F, Table 1): Medium-sized (mean H 3.9 mm), elongate ovoid-biconical, largest width at penultimate whorl. H:D 1.68–1.91, median 1.81, in holotype 1.81. All specimens with 6 moderately convex whorls. Coiling tightness 4.33–4.47, median 4.45, in holotype 4.46. Protoconch raised but not acuminate, consisting of *ca* 2.0 whorls. Protoconch sculpture of holotype consists of 9–10 major spiral cords on second whorl, each 12–20 μm wide, built of poorly individualized squarish particles of very unequal length. Major cords are irregularly interspaced by thinner lines. Cords tend to be wider towards lower suture. In the RBINS paratype the spiral cords are more numerous (*ca* 13), and less wide, at most 8 μm. Teleoconch sculpture with relative dense, regularly spaced, curved axial ribs, about 9.8–10.8 ribs/mm on penultimate whorl, median 10.0 ribs/mm, in holotype 10.8 ribs/mm, with fine, irregular spirals in interstices. Last whorl not exceeding half the shell height, BWH 47–48 % of H, in holotype 47 %. Peristome complete, higher than wide; PH:PW 1.12–1.18, median 1.14, in holotype 1.13. PH 36–37 % of H, median 36 %, in holotype 36 %. PW 53–62 % of H, median 58 %, in holotype 58 %. Apertural lip wide and flaring, but hardly incrassate. Two apertural barriers visible in frontal view: a weak, blunt thickening on mid-palatal wall and a projecting angular tooth that extends inwards as deeply entering lamella. Internal wall body whorl

with short, deep-set palatal fold, externally visible as pale stripe in holotype (Figs 12C, D). Columellar lamella externally not discernable in the available specimens. Umbilicus narrow but open.

Body colour: Dried tissue in holotype shell pale orange-red.

Anatomy: Unknown.

Holotype: EQUATORIAL GUINEA: *Bioko I.*: Basilé Bubi, *ca* 3.7°N 8.8°E, *ca* 400 m, ix.1946, Antonio Ortiz de Zárate, ex colln Altimira (see van Bruggen (1973)) (RMNH.MOL.327295).

Paratypes (localities verbatim from label in italics): 1 ad. dry shell *Basilé Bubi* [*Rio Bireborico* (=Bericorico?], ix.1946, Antonio Ortiz de Zárate (RBINS 21612); 1 ad. dry shell *Basilé Bubi*, *En Rio Borabecho*, 4.iv.1954, Antonio Ortiz de Zárate (MNCN 15.05/26565); 1 ad. dry shell *Basilé*, *Bericorico y Borabecho* (orig. hand-written lable, printed museum label reads: *Rios Ericorico y Borabecho*, *Basilé*), ix.1947, Adolfo Ortiz de Zárate (MNCN 15.05/26569).

Distribution (Fig. 8): Only known from a few localities near Basilé. The species is likely to be endemic to Bioko I.

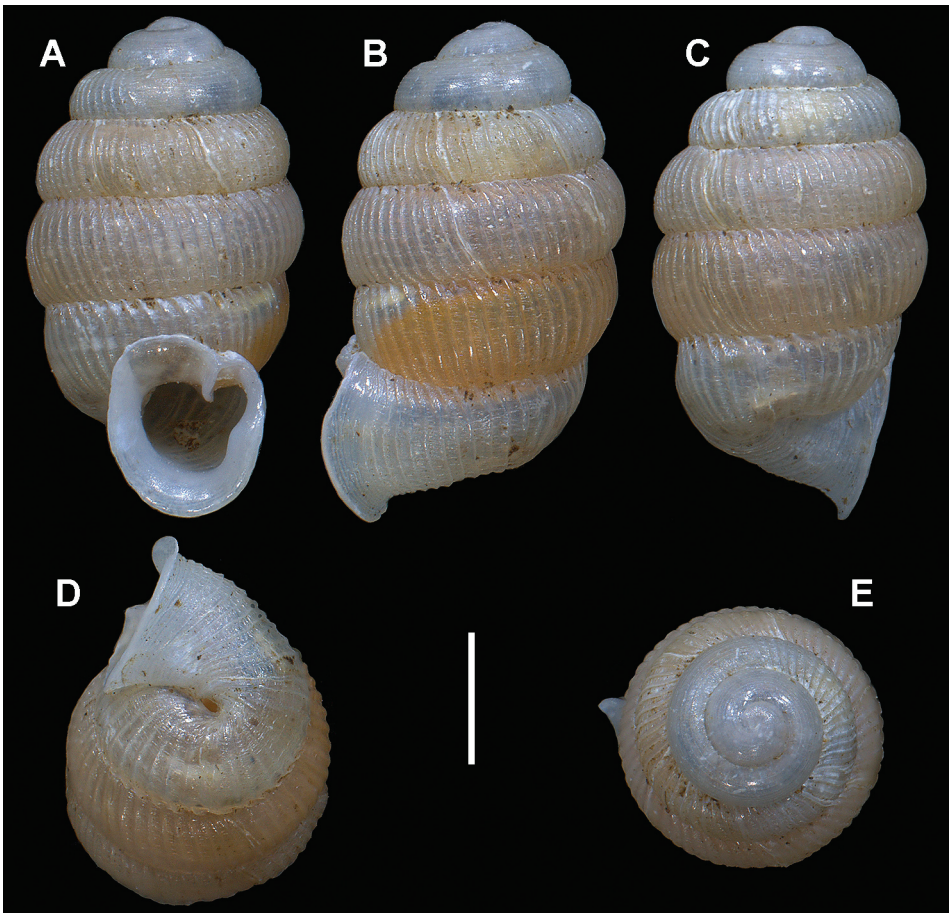


Fig. 12. *Avakubia biokoensis* sp. n., holotype, RMNH.MOL.327295, apertural (A), lateral (B, C), umbilical (D) and apical (E) views. Scale bar = 1 mm.

Habitat: Unknown except for a few notes by Ortiz de Zárate Lopez and Ortiz de Zárate Rocandio (1956: 118): lives in forest along a stream; a specimen from Bonyoma (see Remarks) was found in secondary forest. *A. biokoensis* is probably a lowland species (in contrast to *A. ortizdezarateorum*), the area around Basilé lying at around 400 m.

Remarks: The apical sculpture of two specimens, the holotype and the RBINS paratype, differs in number and width of the spiral cords (studied by SEM). The sculpture of the third available specimen (studied under a stereomicroscope, 60× magnification) resembles that of the holotype, the fourth shell that of the Brussels paratype. We provisionally consider this a case of intraspecific variation.

All material of this species was originally in the collection of Adolfo Ortiz de Zárate Lopez, who exchanged Fernando Poo land snails with various professional and amateur malacologists. Only four specimens of *A. biokoensis* could be located for this study. Ortiz de Zárate Lopez's collection with two specimens arrived in MNCN Madrid after his death. The best preserved, evidently live-collected, shell studied by us was originally in the collection of C. Altimira, now in RMNH. Another specimen was exchanged with the late W. Adam and is now in RBINS. Ortiz de Zárate Lopez and Ortiz de Zárate Rocandio (1956) list seven specimens from Basilé Bubi, but the collection dates differ from those on the labels of the material studied here. This suggests that the number of shells of *A. biokoensis* in the Ortiz de Zárate Lopez's collection originally has been larger, the whereabouts of missing material being unclear. In RMNH, there is a copy of an unpublished list (dated March 1958, probably compiled by A. Ortiz de Zárate Lopez) of terrestrial Mollusca from Fernando Poo sent to the "Direccion General de Provincias y Plazas Africanas", mentioning material of "*G. (A.) avakuviensis*" (sic) from Basilé Bubi. The fate of this institute's collection appears to be unknown (Villena *et al.* 1997).

Ortiz de Zárate Lopez and Ortiz de Zárate Rocandio (1956) mention a single specimen from Bonyoma that is said to differ by a smaller shell, proportionally less elongate aperture, straight outer lip and a not ascending last whorl. The whereabouts of this specimen, which might constitute still another *Avakubia* species on Bioko, is presently unknown. Material from the Pico de Isabel listed by these authors belongs to *A. ortizdezarateorum*.

Avakubia crystallum de Winter, sp. n.

Figs 13, 18G, H

Gulella (Avakubia) cf. *avakubiensis*: de Winter 1995: 225.

Etymology: The species name is a noun in apposition and refers to the type locality (Monts de Cristal), as well as to the glassy, gem-like appearance of the fresh shell (especially with the red softparts inside), which, however, is not unique for this species.

Diagnosis: Resembles *A. fruticicola*, especially by its (slightly less) close-set teleoconch ribs, but this species has a smaller, less elongate shell with less rapidly expanding whorls, less sharp apical angle and spire angle, proportionally larger body whorl, and differs in protoconch sculpture. The shell of *A. biokoensis* is larger and more oval, with a smaller number of spiral cords on the protoconch; the shell of *A. occidentalis* is similarly shaped, but has a less densely ribbed teleoconch, tighter coiled whorls and different protoconch sculpture; *A. crystallum* resembles *A. avakubiensis* only superficially, differing by a

larger shell with much less widely spaced ribs, as well as in details of the protoconch sculpture.

Description:

Shell (Figs 13, 18G, H, Table 1): Medium-sized (mean H 3.7 mm), ovate-biconical, largest width at penultimate whorl. H:D in holotype 1.79, in other specimen 1.79. Whorls expanding rather fast: coiling tightness in holotype 4.1, in other specimen *ca* 4.0. Whorls moderately convex. Apex slightly pointed. Protoconch consisting of *ca* 2.0 whorls, second protoconch whorl convex, contour resembling that of *A. avakubiensis*. Protoconch sculpture of holotype consists of 15 regularly spaced spiral cords on last protoconch whorl, each 6.2–8.5 µm wide, without noticeably thinner lines between them. Spiral cords made up of adjoining but distinct particles of variable length, but generally longer than wide. Teleoconch sculpture of rather close-set, curved, slightly oblique axial ribs, *ca* 10.7 ribs/mm on penultimate whorl in holotype, 11.1 ribs/mm in other specimen, with fine spirals in interstices. Last whorl takes up half the shell height or less, in holotype BWH 50% of H, in other specimen 47%. Peristome complete in holotype (not in other specimen, measurements are estimates), somewhat higher than

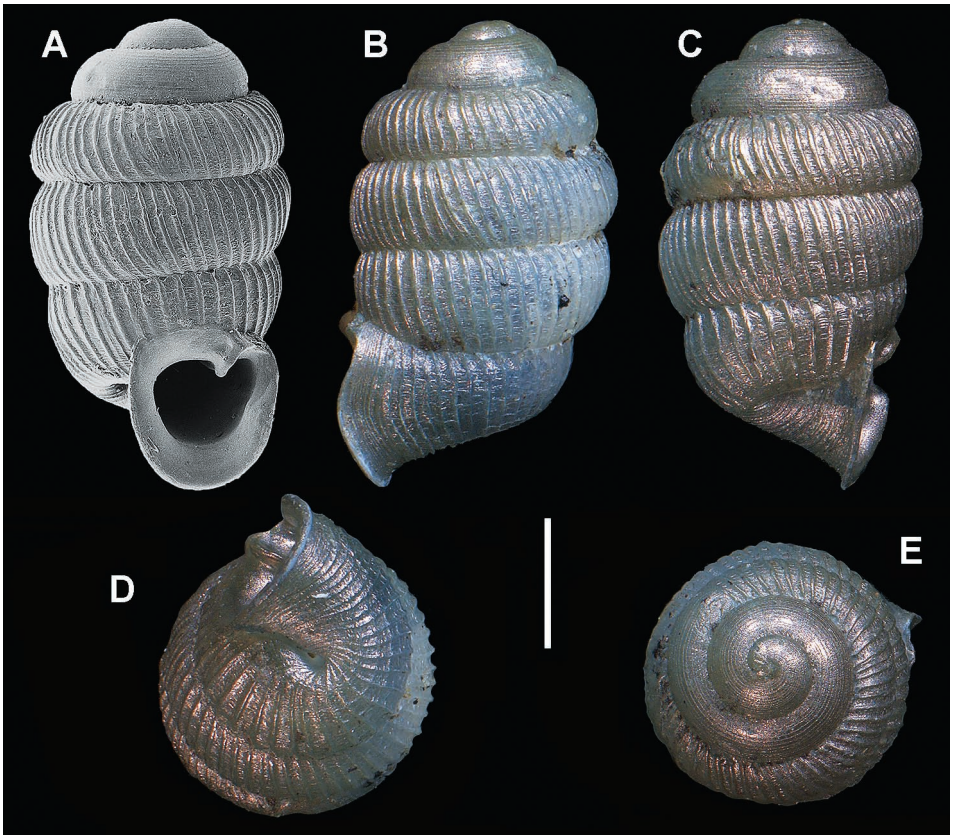


Fig. 13. *Avakubia crystallum* sp. n., holotype, RMNH.MOL.330185, apertural (A), lateral (B, C), umbilical (D) and apical (E) views. Scale bar = 1 mm.

wide, PH:PW in holotype 1.15, in other specimen 1.08. PH 37% of H in holotype, in other specimen 29%. PW 58% of D in holotype, in other specimen 49%. Apertural lip holotype expanded and flaring, slightly reflected and somewhat incrassate. Two apertural barriers visible in aperture: a weak, thickening on mid-palatal wall and a slightly projecting angular tooth that extends inwards as deeply entering lamella. Internal palatal wall of body whorl with a deep-set palatal fold (no longer visible in coated holotype, nor in other specimen which is worn). Columellar lamella not visible in aperture. Umbilicus narrow but open.

Body colour: Holotype with conspicuously pinkish red coloured soft parts (collector's observation).

Anatomy: Unknown.

Holotype: GABON: *Région Estuaire*: Monts de Cristal, *ca* 5 km N of Kinguélé, 0.5°N 10.3°E, 400 m, 26.xii.1989 J.J. Wieringa, wet rocky slope in rainforest (RMNH.MOL.330185).

Other material examined: GABON: *Région Ngounié*: 1 ad. dry shell, Ofoubou area, *ca* 30 km W of Mandji, 1.75°S 10.10°E, *ca* 50 m, vii.1991, J. Reitsma, rainforest (RMNH.MOL.330186).

Distribution (Fig. 11): Western Gabon.

Habitat: The holotype was collected from a *Begonia* plant (*B. letouzeyi* Sosef) growing on a wet rock along a stream in undisturbed rainforest at 400 m. The other specimen, an eroded empty shell, was found in a leaf-litter sample in undisturbed lowland rainforest.

Remarks: This species is somewhat intermediate between *A. fruticicola* and *A. biokoensis* in shell size and rib sculpture. In shell shape it best resembles *A. occidentalis*. Still, the two western Gabonese shells appear to be recognisable by a number of characters, and we prefer to treat these specimens as a new species, also in view of the considerable (300 to 1200 km) geographic separation between the known localities of these species and those of *A. crystallum*. Specimens reported from Central Gabon by Fontaine *et al.* (2007) are clearly not conspecific with *A. crystallum*, and more closely resemble *A. avakubiensis* (as discussed there).

Avakubia fruticicola de Winter & Vastenhout, sp. n.

Figs 5H, 14, 15, 18A–D

Gulella (Avakubia) cf. *avakubiensis*: de Winter & Gittenberger 1998: 239.

Etymology: From Latin *frutex* (shrub, bush) and *colere* (to inhabit), in reference to the understorey-dwelling habit of this species.

Diagnosis: *Avakubia fruticicola* differs from other *Avakubia* species by the combination of its small sized shell with proportionally large body whorl, rounded apex, and close-set teleoconch ribs.

Description:

Shell (Figs 14, 18A–D, Table 1): Small (mean H 3.3 mm), ovate-biconical, largest width at penultimate whorl. H:D 1.62–1.79, median 1.68, in holotype 1.67. Whorls expanding comparatively fast, coiling tightness 4.0–4.4, median 4.2, in holotype 4.2. Whorls convex. Apex raised, but more flattened than most similarly-sized species. Protoconch consisting of *ca* 2 whorls. Protoconch sculpture (on second whorl) composed of *ca* 13 spiral cords, more or less regularly spaced, each 3.5–7.6 µm wide, without thinner lines

between them. Spirals cords are made up of series of adjoining, but distinct, particles of variable length. Teleoconch sculpture with comparatively close-set, regularly spaced, curved axial ribs, 10.7–12.8 ribs/mm on penultimate whorl, median 11.3, in holotype 11.5, interstices with fine spiral lines. Body whorl proportionally large, BWH 49–55 % of shell height, median 53 %, in holotype 53 %. Peristome complete, roundish to (mostly) somewhat higher than wide; PH : PW 0.92–1.15, median 1.11, in holotype 1.10. PH 35–39 % of H, median 37 %, in holotype 37 %. PW 53–61 % of D, median 57 %, in holotype 56 %. Apertural lip expanded and flaring, slightly reflected, not strongly incrassate. Two barriers visible in aperture: a rather weak, often nearly absent, thickening on mid-palatal wall and a projecting angular tooth that extends inwards as deeply entering lamella. Internal wall of body whorl with deep-set palatal fold, externally visible as pale stripe in fresh specimens (Figs 18C, D). Columellar lamella not visible in aperture, facing palatal fold, little pronounced (Fig. 5H). Umbilicus punctiform but open.

Body colour: Live animal reddish, dried-in tissue often retains red pigments.

Anatomy (Fig. 15; one paratype dissected): Genitalia overall similar to those in *A. acuminata* and *A. subacuminata*, but smaller. Upper penis appreciably narrower and more muscular than distal portion. Lateral diverticulum of penis, if present, rather poorly

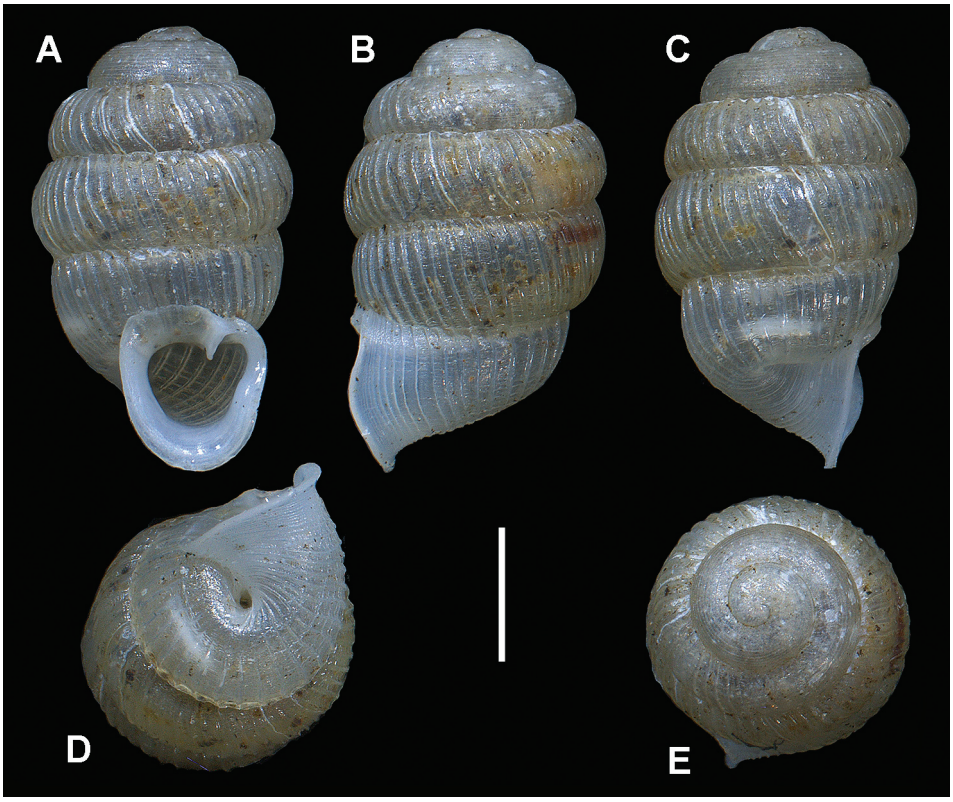


Fig. 14. *Avakubia fruticicola* sp. n., holotype, RMNH.MOL.42806, apertural (A), lateral (B, C), umbilical (D) and apical (E) views. Scale bar = 1 mm.

developed, merely an inconspicuous dilatation at the transition of two penial portions. Internal penis not examined.

Radula: No complete row could be studied, but individual lateral/marginal teeth similar in shape to those in *A. acuminata*.

Holotype: CAMEROON: *Sud Prov.*: 14 km S Lolodorf, plot I2 (de Winter & Gittenberger 1998, sta. CAM.22a), 3.10°N 10.73°E, 470 m, 21.ix.1995, A.J. de Winter & E.J. Semenguei (RMNH.MOL.42806).

Paratypes: CAMEROON: same locality and collectors as for holotype but 460–530 m: 1 juv. dry shell, 1 ad. in alcohol, sta. CAM.010, 30.viii.1995 (RMNH.MOL.42802, RMNH.MOL.254634); 1 ad. dry shell, sta. CAM.011a, 30.viii.1995 (RMNH.MOL.42803); 1 juv. dry shell, sta. CAM.012a, 31.viii.1995 (RMNH.MOL.42804); 2 ad. dry shells, sta. CAM.018a, 19.ix.1995 (RMNH.MOL.42805); 3 ad. dry shells, sta. CAM.038, 6.x.1995 (RMNH.MOL.42807); 1 ad. dry shell, sta. CAM.039a, 6.x.1995 (RMNH.MOL.42808); 1 ad., 1 juv. dry shell, sta. CAM.068a, 1.iv.1996 (RMNH.MOL.254637); 1 ad., 1 juv. dry shell, 1 juv. in alcohol, sta. CAM.075a, 10.iv.1996 (RMNH.MOL.254635; RMNH.MOL.254640); 1 ad. in alcohol, sta. CAM.076a, 9.iv.1996 (RMNH.MOL.330189); 1 ad. in alcohol, sta. CAM.077a, 10.iv.1996 (RMNH.MOL.254638); 1 ad., 1 juv. dry shell, sta. CAM.078a, 10.iv.1996 (RMNH.MOL.254641); 1 juv. dry shell, sta. CAM.081a, 11.iv.1996 (RMNH.MOL.254642).

Other material examined: CAMEROON: *Sud Prov.*: 1 specimen in alcohol, sta. CAM. 34a, *ca* 250 m SW of Ebom II, 19 km S of Lolodorf, 3.05°N 10.70°E, 400 m, 5.ix.1995 (RMNH.MOL.330325); 1 ad., 2 juv. dry shells, sta. CAM.86a, Nyangong, 30 km S of Lolodorf, 2.966667°N 10.73333°E, 650 m, swamp forest, 24.iv.1996 (RMNH.MOL.330326); 1 ad. dry shell, sta. CAM.101a, Nyangong, 2.95°N 10.73°E, 700 m, undisturbed forest on steep, N-facing slope, 9.v.1996 (RMNH.MOL.330327); 1 juv. dry shell, sta. CAM.111a, Meka'a-II, W of Nyangong, 2.966°N 10.733°E, 690 m, 18.v.1996 (RMNH.MOL.330328).

Distribution (Fig. 11): Only known from two areas in Southwest Cameroon, *ca* 25 km distant and differing somewhat in altitude (400–500 vs 600–700 m).

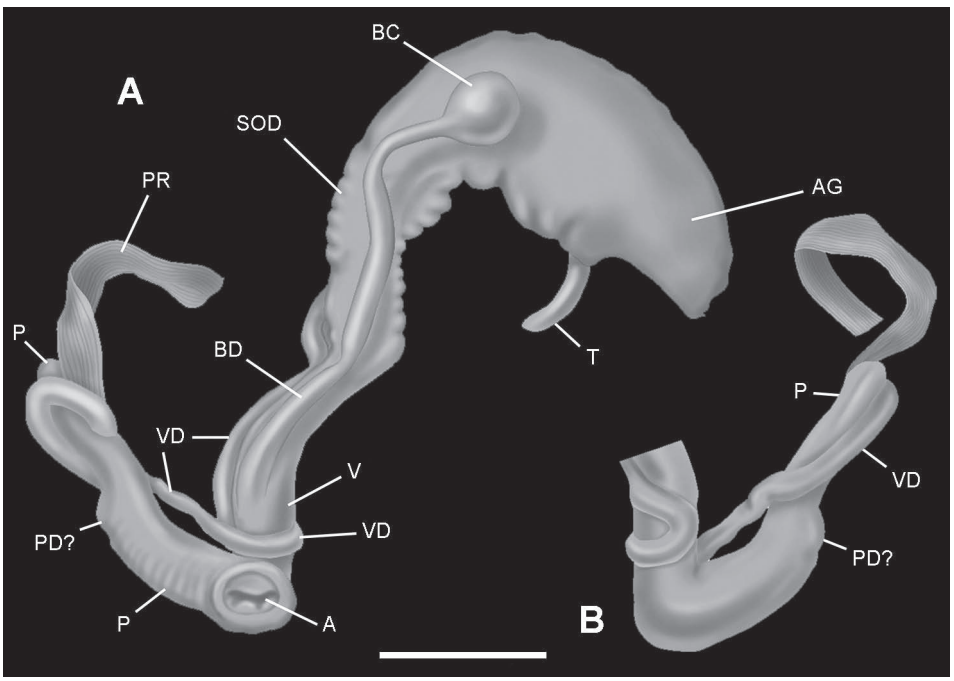


Fig. 15. *Avakubia fruticicola* sp. n.: (A, B) genital anatomy of paratype from S of Lolodorf, Cameroon, RMNH.MOL.330189. Abbreviations: T – talon, otherwise as in Fig. 6. (Drawn by Bas Blankenvoort from photographs of mounted genitalia preparations)

Habitat: Live specimens and empty shells were collected from the understorey vegetation up to three metres above the forest floor in little disturbed rainforest between 400 and 700 m. At the type locality *A. fruticicola* lives syntopically with *A. semenguei* and *A. acuminata*. In the Nyangong area *A. fruticicola* occurs sympatrically with *A. subacuminata*, but the latter species was more often found on the forest floor.

Remarks: *Avakubia fruticicola* is quite distinct from *A. avakubiensis*, to which species the material had earlier been tentatively attributed (de Winter & Gittenberger 1998). The two species differ in teleoconch rib spacing, coiling tightness, width of the apical whorls, apical angle, proportional aperture and body whorl size, and whorl convexity. *A. occidentalis* has a proportionally smaller aperture and body whorl, and slightly wider spaced (but still comparatively close-set) ribs. *A. fruticicola* resembles *A. crystallum* in axial ribbing, but has a smaller and less cylindrical shell with more convex whorls, a less pointed apex, and a proportionally larger body whorl. *A. biokoensis* differs by the larger, more cylindrical shell and proportionally smaller body whorl.

Avakubia occidentalis de Winter, sp. n.

Figs 16, 21C, D

Etymology: From Latin *occidentalis* (western), in reference to the westernmost distribution of this species among any known *Avakubia* species.

Diagnosis: A small species of *Avakubia*, differing from similar-sized congenerics by a combination of conchometrical characters, as well as by the large number of spiral cords on the protoconch.

Description:

Shell (Figs 16, 21C, D, Table 1): Small to medium-sized (mean H 3.3 mm), subcylindrical, largest width at penultimate whorl. H:D 1.59–1.84, in holotype 1.84. Number of whorls 5–5.5. Coiling tightness 4.45–4.65, in holotype 4.45. Whorls moderately convex. Protoconch slightly acuminate, consisting of *ca* 2 whorls. Protoconch on second whorl with >16, more or less regularly spaced cords, 6.3–8.6 µm wide, without finer spiral lines between them. Spiral cords made up of series of adjoining, poorly differentiated rectangular particles of variable length (*ca* 8–19 µm). Teleoconch sculpture of regularly spaced, curved axial ribs, 9.0–10.0 ribs/mm on penultimate whorl, median 9.9 ribs/mm, in holotype 9.0, with fine spirals in interstices. BWH 48–49 % of H, in holotype 48 %. Peristome holotype entire (peristome of other shells damaged, PW measurements not accurate). PH:PW 0.88–1.10, in holotype 1.06. PH 32–34 % of H, median 34 %, in holotype 34 %. PW 52–59 % of D, median 56 %, in holotype 59 %. Apertural lip expanded and flaring, reflected and incrassate in holotype. Two barriers visible in aperture: a blunt, tooth-like thickening on mid-palatal wall and a conspicuous angular tooth that extends inwards as deeply entering lamella. Internal wall of body whorl with deeply-set palatal fold, externally barely visible in opaque shells. Columellar lamella not visible in aperture, but probably present. Umbilicus punctiform but open, slightly wider than in *A. fruticicola*.

Body colour: Soft parts at least partly reddish (dried-in tissue paratype).

Anatomy: Unknown.

Holotype: GHANA: *Volta Region*: Logba Tota, 6.88363°N 0.46804°E, 470 m, 30.i.2010, P. Tattersfield, M.E. Nutsuakor & A.J. de Winter, semi-deciduous forest on steep slope near waterfall (NMW.Z. 2013.055.00001).

Paratype: 1 dry shell, same data as holotype (RMNH.Mol.254654).

Other material examined: GHANA: *Eastern Region*: 1 dry shell, Atewa Range Forest Reserve, 6.12368°N 0.60445°W, 655 m, 23.i.2010, P. Tattersfield, M.E. Nutsuakor & A.J. de Winter, in litter of recently logged high forest (RMNH.MOL.330190).

Distribution (Fig. 17): Known from two localities in eastern Ghana.

Habitat: Found in semi-deciduous forest near waterfall at 470 m, as well as in upland evergreen forest at 650 m. All specimens were collected from the forest floor.

Remarks: This species superficially resembles *A. fruticicola* in size, teleoconch sculpture and colour of the soft parts. However, the Ghanaian shells differ in a number of characters, such as a more cylindrical shell, tighter coiled whorls (about half a whorl more at the same size), proportionally smaller body whorl, more pointed apex, and slightly wider umbilicus and wider spaced axial ribs, in addition to details of the protoconch sculpture. Two *A. occidentalis* specimens were found alive on the forest floor, whilst specimens of

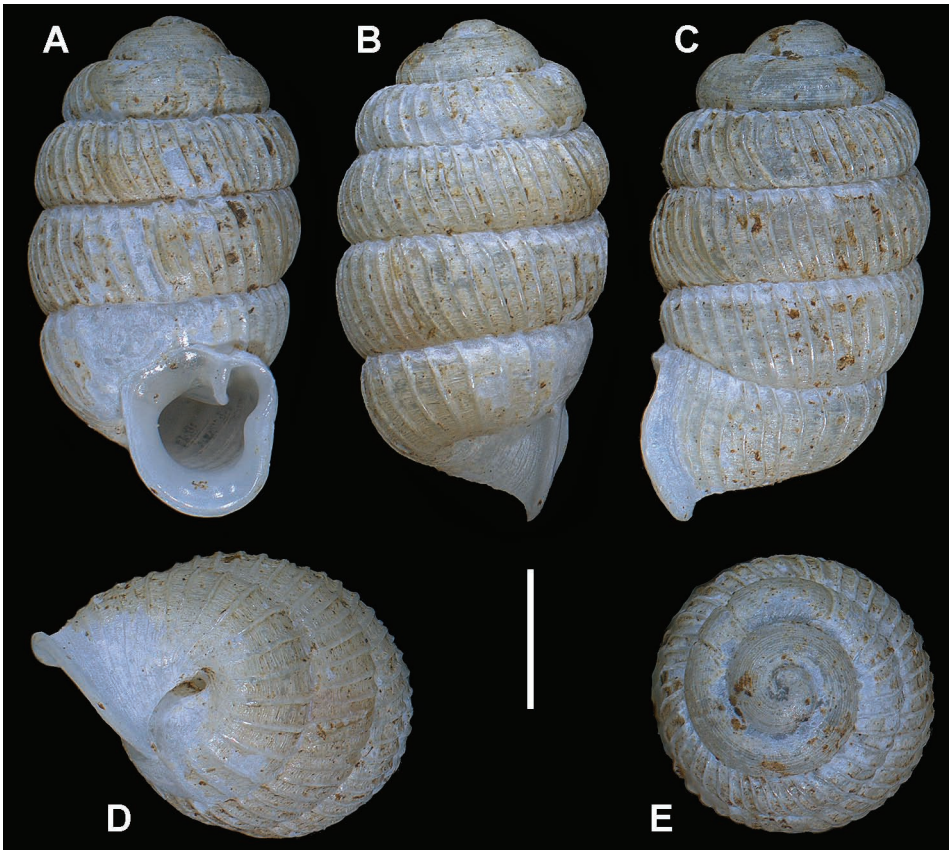


Fig. 16. *Avakubia occidentalis* sp. n., holotype, NMW.Z.2013.055.00001, apertural (A), lateral (B, C), umbilical (D) and apical (E) views. Scale bar = 1 mm.

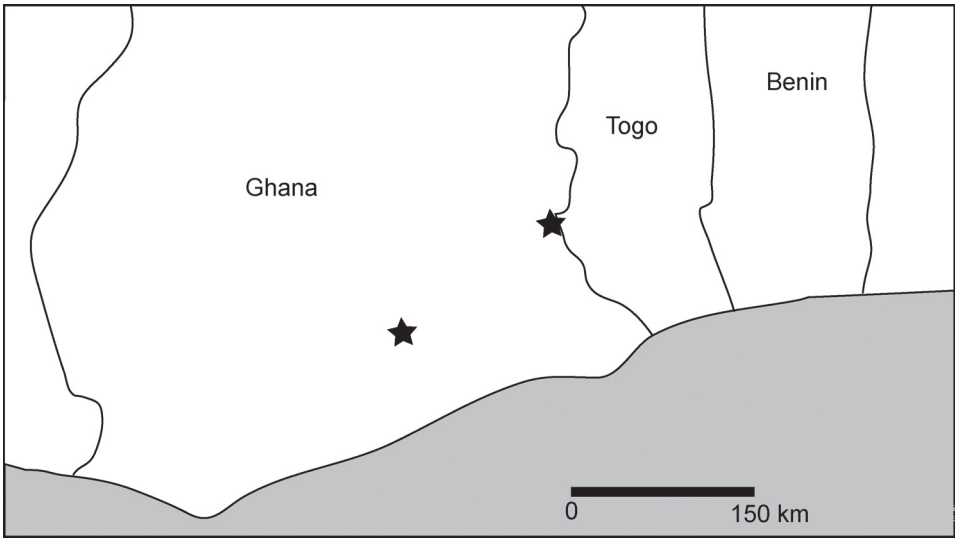


Fig. 17. Distribution records of *Avakubia occidentalis* sp. n.

A. fruticicola were exclusively collected from the understorey vegetation. The Ghanaian localities are situated some 1200 km from those of *A. fruticicola* in Cameroon.

Avakubia occidentalis is the only *Avakubia* species known in the Upper Guinea forest block. Traditionally postulated biogeographic barriers like the Dahomey Gap and Cross River have apparently not restricted the distribution of the genus, which might suggest a considerable age for the taxon. On molecular grounds Rowson *et al*. (2011) suggested *Avakubia* to be an ancient taxon that possibly survived the Mesozoic/Cainozoic mass extinctions, whilst the streptaxid diversity is otherwise known from the Cainozoic only.

Avakubia ortizdezarateorum de Winter & Vastenhout, sp. n.

Figs 19, 21A, B

Gulella (Avakubia) avakubiensis: Ortiz de Zárate Lopez & Ortiz de Zárate Rocandio 1956: 118 (in part).

Etymology: The species is named after Adolfo Ortiz de Zárate Lopez and his son Antonio Ortiz de Zárate Rocandio, who collected and described this peculiar form without formally naming it.

Diagnosis: Shell easily distinguished by the very fine, close-set axial ribs, and narrow apertural lip. In contrast to all other congenerics, the palatal fold and columellar lamella whorl can be seen in the aperture in oblique view. Spiral sculpture on protoconch little conspicuous.

Description:

Shell (Figs 19, 21A, B, Table 1; all shells except holotype are in poor condition): Small (mean H 3 mm), fragile, ovate-biconical, largest width at penultimate whorl. H:D 1.69–1.78, median 1.75, in holotype 1.69. Coiling tightness 4.4–4.6, median 4.6, in holotype 4.6. Whorls little convex. Protoconch raised, but not acuminate, consisting of

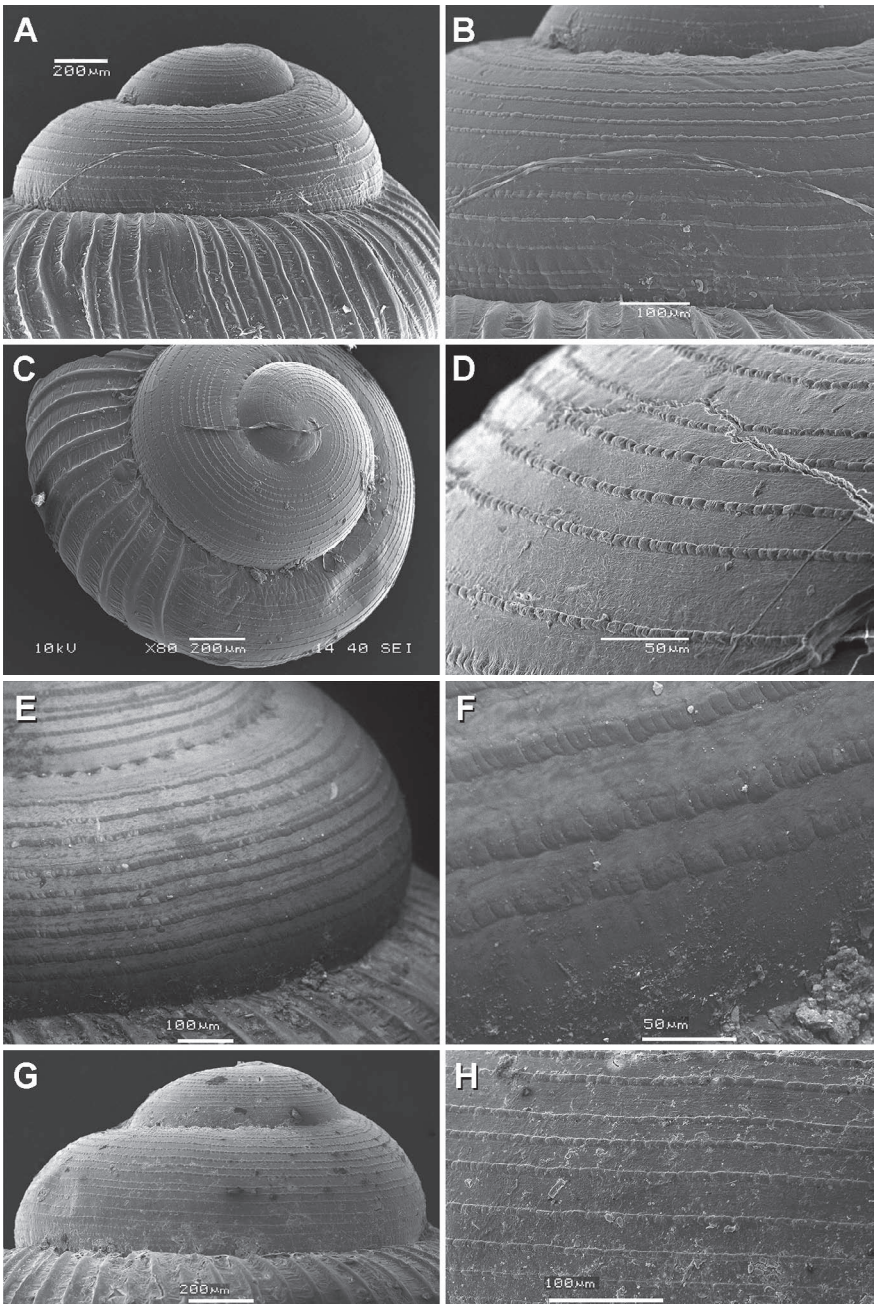


Fig. 18. SEM photographs of shell sculpture of *Avakubia* species: (A–D) *A. fruticicola* sp. n., paratype, RMNH.MOL.254642: (A) apex, (B) enlarged view of second protoconch whorl, (C) apical view of protoconch; (D) detail of sculpture on second protoconch whorl; (E, F) *A. biokoensis* sp. n., low vacuum SEM of holotype, RMNH.MOL.327295: (E) second protoconch whorl, (F) detail of sculpture of second protoconch whorl; (G, H) *A. crystallum* sp. n., holotype, RMNH.MOL.330185: (G) apex, (H) detail of sculpture on second protoconch whorl.

ca 2.0 whorls. Protoconch sculpture consists of low and little conspicuous spiral cords, *ca* 15–20 on second whorl, each <10 µm wide. Distinction between major cords and thinner, irregularly spaced lines is gradual. Cords composed of low, barely separated, elongate-oval or rectangular-squarish particles (*ca* 6–12 µm long). Teleoconch whorls somewhat smooth with patches of very fine, more or less regular, close-set ribs, about 20 ribs/mm on penultimate whorl, giving the shell a silky lustre. Spiral sculpture on teleoconch present but little prominent; very fine spiral lines in interstices appear continuous where ribs are low. Body whorl proportionally small, BWH 44–47% of H, median 46%, in holotype 47%. Peristome complete, slightly higher than wide; PH:PW 1.06–1.15, median 1.09, in holotype 1.1. PH 29–33% of H, median 32%, in holotype 33%. PW 44–54% of D, median 52%, in holotypee 50%. Apertural lip little expanded, thin, hardly reflected. Slightly projecting angular tooth extends inwards as high, deeply entering lamella. Mid-palatal wall slightly indented, palatal tooth or labial thickening is virtually wanting. Wall of body whorl with deep-set, short palatal fold, together with columellar lamella discernable in aperture in oblique view (Fig. 19F). Umbilicus extremely narrow, but open.

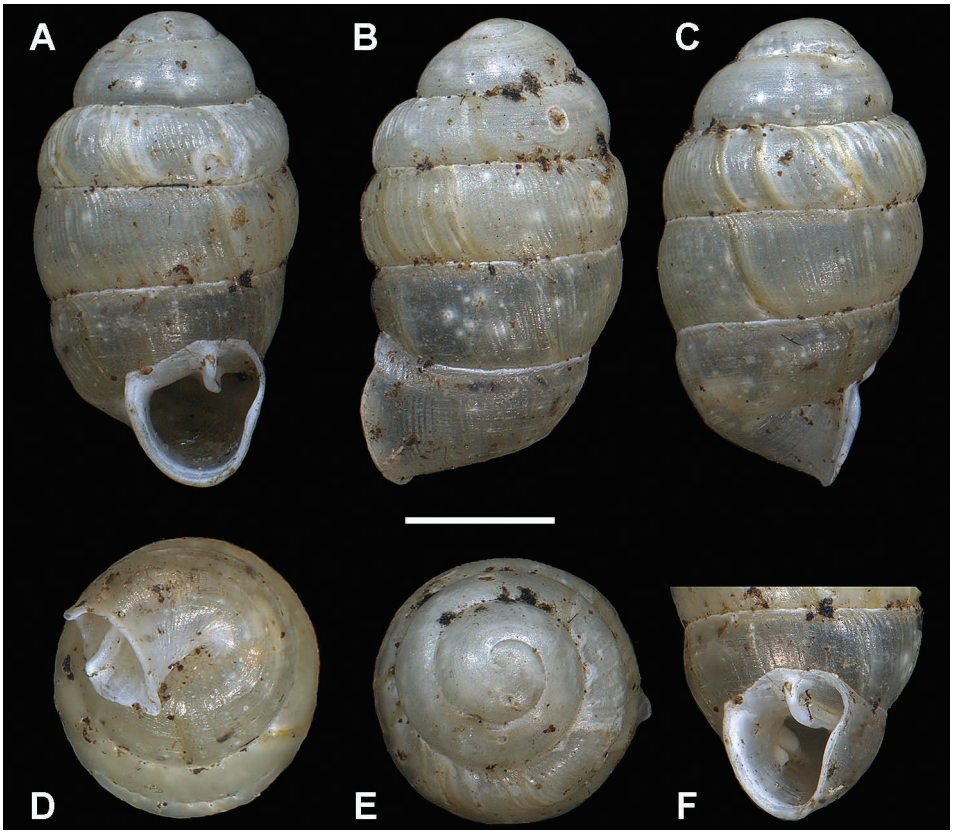


Fig. 19. *Avakubia ortizdezarateorum* sp. n., holotype, MNCN 15.05/26566: apertural (A), lateral (B, C), umbilical (D) and apical (E) views, (F) oblique view of aperture showing deep-set barriers. Scale bar = 1 mm.

Body colour: Unknown.

Anatomy: Unknown.

Holotype: ECUATORIAL GUINEA: *Bioko I.*: Refugio del Pico Basilé (formerly Pico de Sta Isabel), *ca* 3.6116°N 8.7783°W, up till ("hasta") 2350 m, 1.i.1946 (MNCN 15.05/26566).

Paratypes: ECUATORIAL GUINEA: *Bioko I.*: 5 damaged dry shells, Pico Basilé, 2000 m, Antonio Ortiz de Zárate (MNCN 15/05/26567).

Distribution (Fig. 8): Only known from the type locality and probably endemic to the Island of Bioko.

Habitat: This species has been found at around 2000 m, the highest known altitude for any *Avakubia* species.

Remarks: Ortiz de Zárate Lopez and Ortiz de Zárate Rocandio (1956) already recognised substantial differences in shell morphology between this high altitude form and the lowland type of "*Gulella (Avakubia) avakubiensis*" on Bioko I. (here treated as a separate species *A. biokoensis*, sp. n.), which they attributed to different climatic conditions. However, *A. ortizdezarateorum* is very distinct conchologically. It differs not only considerably in size, but also in the rather different arrangement of apertural barriers and in sculpture of both the protoconch and teleoconch, which characters also separate it from all other *Avakubia* species. These peculiarities may well be grounds to assign it to a different (sub)genus, but this should be based on more, preferably alcohol preserved, specimens.

Avakubia semenguei de Winter & Vastenhout, sp. n.

Figs 20, 21E–G

Gulella (Avakubia) n. sp.: de Winter & Gittenberger 1998: 240.

Etymology: The species is named after Eric-Joël Semengue, in recognition of the importance of his guiding and collection assistance in the field.

Diagnosis: *A. semenguei* is easily recognised from other *Avakubia* species by its large ovate shell (only the shell of *A. acuminata* is larger) with rapidly increasing whorls, flattened apex and very wide protoconch.

Description:

Shell (Figs 20, 21E–G, Table 1): Large (mean H 4.9 mm), largest width at penultimate whorl. H:D 1.66–1.77, median 1.70, in holotype 1.66. Whorls expanding rapidly, coiling tightness 3.1–3.3, median 3.2, in holotype 3.2. Whorls moderately convex. Protoconch little elevated, consisting of *ca* 2.0–2.25 whorls. Apex comparatively flat. Protoconch sculpture consists of *ca* 11 distinct, comparatively conspicuous spiral cords, each 9–14 µm wide, consisting of poorly individualized, irregular-rectangular or quadrangular particles, on average 9 particles per 100 µm. In many spots the coarse spirals resemble wrinkled continuous cords, rather than series of beads. One or two spirals of intermediate coarseness, as well as very thin lines, occur occasionally between major cords. Teleoconch sculpture consists of obliquely curved axial ribs, with rather irregularly spaced spiral lines in interstices, 8.7–11.5 ribs/mm on penultimate whorl, median 10.5 ribs/mm, in holotype 11.5 ribs/mm. Last whorl proportionally large, BWH 51–54% of H, median 53%, in holotype 53%. Peristome complete, higher than wide; PH:PW 1.08–1.29, median 1.16, in holotype 1.15. Peristome proportionally large: PH

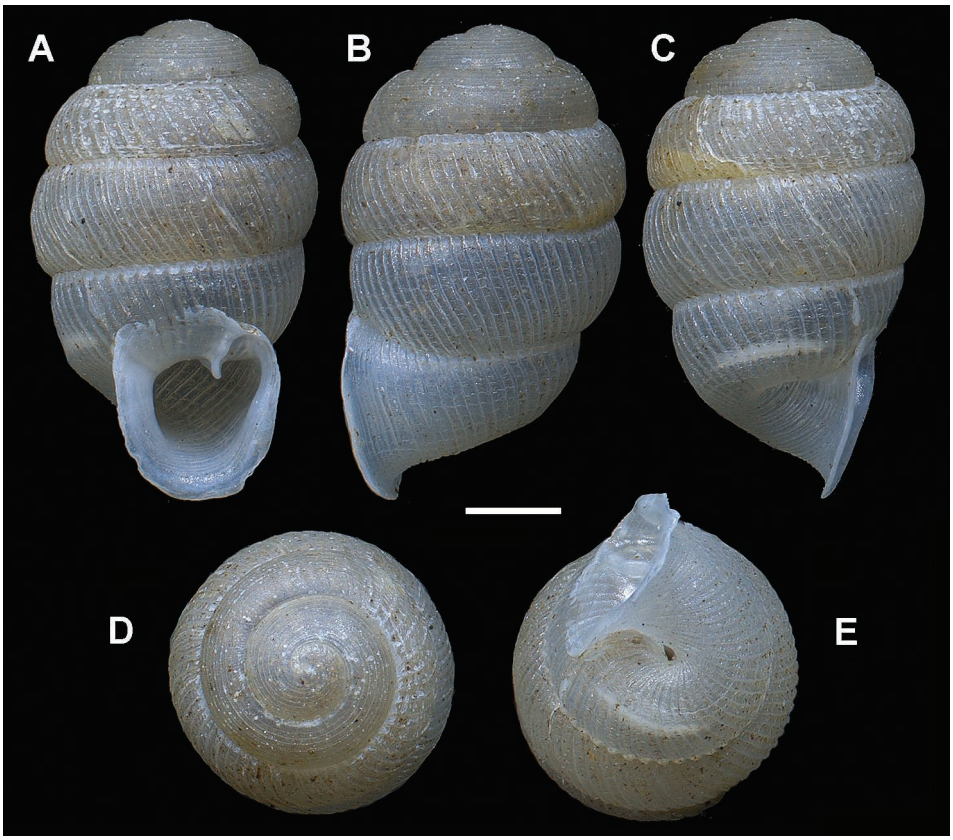


Fig. 20. *Avakubia semenguei* sp. n., holotype, RMNH.MOL.330191, apertural (A), lateral (B, C), apical (D) and umbilical (E) views. Scale bar = 1 mm.

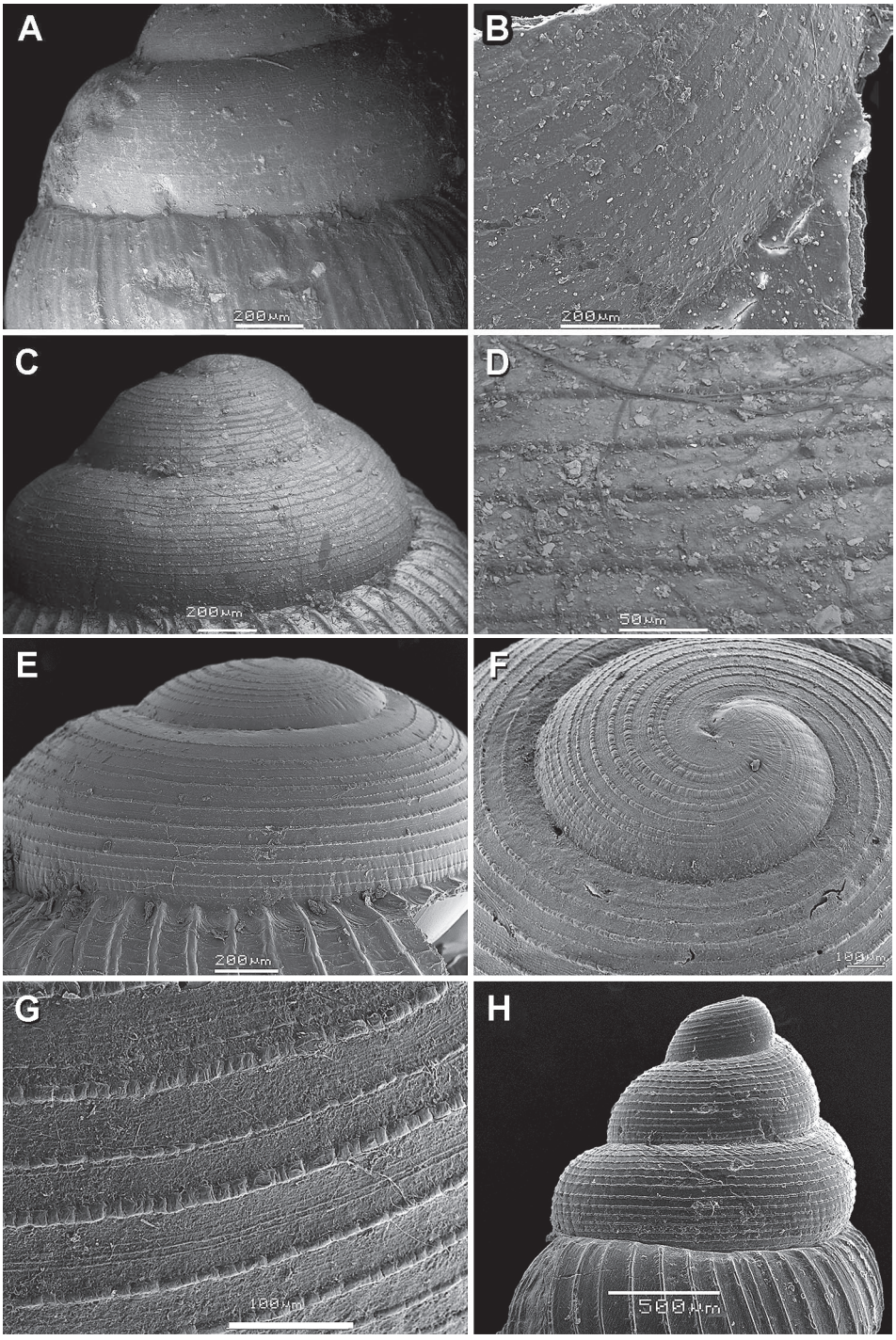
36–40% of shell height, median 39%, in holotype 40%. PW 54–59% of shell width, median 57%, in holotype 58%. Apertural lip expanded and flaring, slightly reflected, not strongly incrassate. Two barriers visible in aperture: a weak (or almost wanting) thickening on mid-palatal wall and not (or barely) projecting angular tooth that extends inwards as deeply entering lamella. Internal wall body whorl with comparatively long, deep-set palatal fold, externally visible in fresh specimens as a pale stripe (Figs 20C, E). Columellar lamella not visible in aperture. Umbilicus rather narrow but open.

Body colour: Soft parts of live animal pale, without reddish pigment.

Anatomy: Unknown.

Holotype: CAMEROON: *Sud Prov.*: Minwo area, 6 km NE of Ebom, 15 km S of Lolodorf, plot I2 (de Winter & Gittenberger 1998), sta. CAM.055a, 3.10°N 10.73°E, 520 m, 21.iii.1996, A.J. de Winter & E.-J. Semengue, undisturbed high forest on hilly terrain (RMNH.MOL.330191).

Paratypes: CAMEROON: all from same square km as holotype, same collectors: 2 ad., 1 juv. dry shell, sta. CAM.022a, 470 m, 21.ix.1995 (RMNH.MOL.42809); 1 ad. dry shell, sta. CAM.028a, 400 m, 27.ix.1995 (RMNH.MOL.330192); 1 ad. dry shell, sta. CAM.039a, 470 m, 6.x.1995 (RMNH.MOL.42810); 1 juv. dry shell, sta. CAM.065, 470 m, 2.iv.1996 (RMNH.MOL.330193); 1 juv. in alcohol, sta. CAM.070a, 590 m, 2.iv.1996 (RMNH.MOL.330194); 1 juv. dry shell, sta. CAM.076a, 480 m, 9.iv.1996 (RMNH.MOL.330195); 4 juv. in alcohol, sta. CAM.082a, 470 m, 12.iv.1996 (RMNH.MOL.330196).



Distribution (Fig. 25): Only known from a single square km in Southwest Cameroon, 90 km east of Kribi. The collecting technique of beating the vegetation over an umbrella was used extensively in other areas in Southwest Cameroon, but yielded only other *Avakubia* species. The species might be a narrow range endemic.

Habitat: Collected from understorey vegetation up to 3 m above the forest floor in relatively undisturbed rainforest between 400 and 500 m. The species lives syntopically with *A. acuminata* and *A. fruticicola*, which are also arboreal.

Avakubia subacuminata de Winter & Vastenhout, sp. n.

Figs 5G, 22–24

Etymology: Refers to the superficial resemblance to the larger and more strongly acuminate *A. acuminata.*

Diagnosis: Superficially resembles *A. acuminata* by the acuminate apex and tapering spire, but has a much smaller, shorter-spired shell with tighter coiled whorls and a less sharp apical angle. The shell of *A. avakubiensis* is generally smaller with less tightly coiled whorls, proportionally larger body whorl, more convex protoconch whorls, and less acute apex. It is easily distinguished from other *Avakubia* species by the acuminate apex, proportionally small body whorl and slowly increasing whorls, among other characters.

Description:

Shell (Figs 22, 23, Table 1): Small to medium-sized (mean H 3.8 mm), ovate-biconical, largest width at penultimate whorl, occasionally preceding whorl equally wide. H:D 1.65–1.93, median 1.75, in holotype 1.76. Whorls expanding rather slowly, coiling tightness 4.5–5.0, median 4.8, in holotype 4.8. Whorls moderately convex. Apex acuminate. Protoconch with *ca* 2.0–2 ¼ whorls. Protoconch of specimens from the Ebimimbang area with 10–11 major spiral cords on second whorl, each at most 6.5 µm wide, usually somewhat less, made up of rectangular particles of rather unequal size (each *ca* 5–17 µm long, on average 9 particles per 100 µm), which become individually less distinct towards teleoconch. Major cords irregularly interspaced by thinner, seemingly solid, lines. Material from the Nyangong area has a larger number of somewhat wider (up to 8 µm) major cords (12–15) on second whorl; distinction between major and minor cords much less clear than in the Ebimimbang material, and individual particles appear to be shorter, but they are individually less clearly recognisable than in the Ebimimbang material. Teleoconch with sculpture of slightly oblique, regularly spaced axial ribs, *ca* 6.6–9.4 ribs/mm on penultimate whorl, median 7.6 ribs/mm, in holotype 6.9 ribs/mm, interstices with fine, comparatively regularly spaced spiral lines. Last whorl proportionally small, BWH 38–45% H, median 41%, in holotype 42%. Peristome

Fig. 21. SEM photographs of shell sculpture of *Avakubia* species: (A, B) *A. ortizdezarateorum* sp. n.: (A) low vacuum SEM of sculpture on second protoconch whorl of holotype, MNCN 15.05/26566, (B) detail of sculpture on second protoconch whorl; (C, D) *A. occidentalis* sp. n., low vacuum SEM of holotype, NMW.Z.2013.055.00001: (C) protoconch, (D) detail of sculpture on second protoconch whorl; (E–G) *A. semenguei* sp. n., paratype, RMNH.MOL.330195: (E) protoconch, (F) apical view of first protoconch whorl, (G) detail of sculpture on second protoconch whorl; (H) juvenile shell of unknown ?*Avakubia* species from Ebimimbang, Cameroon, RMNH.

entire, proportionally small, generally slightly higher than wide; PH:PW 0.97–1.15, median 1.07, in holotype 1.09. PH 29–32% of H, median 31%, in holotype 32%. PW 48–56% of D, median 51%, in holotype 51%. Apertural lip expanded and flaring,

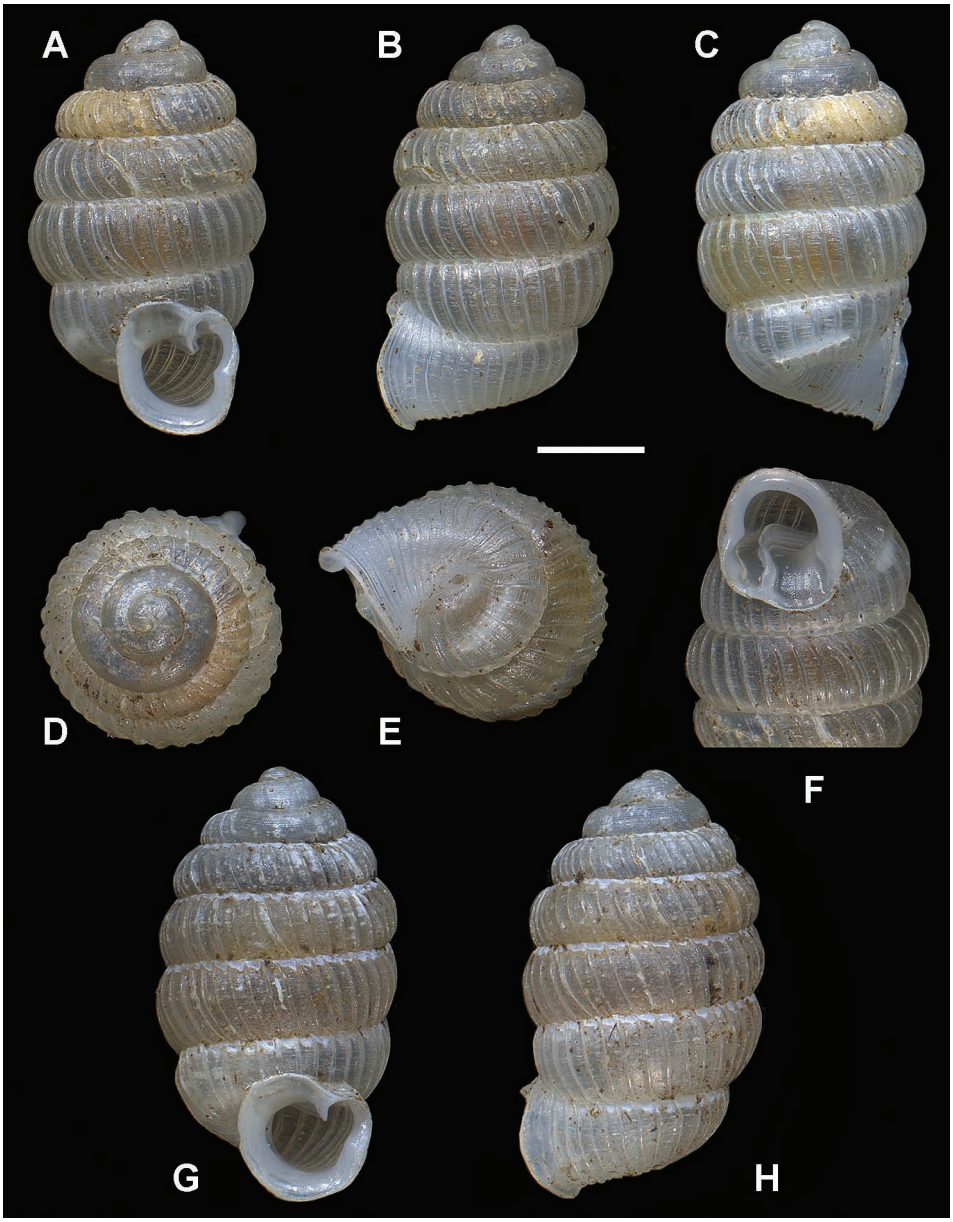


Fig. 22. *Avakubia subacuminata* sp. n.: (A–F) holotype, RMNH.MOL.330197: apertural (A), lateral (B, C), apical (D), umbilical (E) views, and apertural view showing entering angular lamella (F); (G, H) paratype from type locality, RMNH.MOL.330203, apertural (G) and lateral (H) views. Scale bar = 1 mm.

slightly reflected, not strongly incrassate. Two barriers visible in aperture: a weak or almost wanting, tooth-like thickening on mid-palatal wall and a projecting angular tooth that extends inwards as deeply entering lamella. Wall of body whorl with deep-set palatal fold (Fig. 5G), externally visible in fresh specimens as a pale stripe (Figs 22C, E). Columellar lamella rather small (Fig. 5G), not visible externally. Umbilicus narrow, slightly more open than in most other *Avakubia* species.

Body colour: Live animal with orange-reddish soft parts.

Anatomy (Fig. 24; one specimen dissected): Atrium about as wide as long, thin-walled. Penis subcylindrical, elongate, with short apical caecum as well as lateral diverticulum that is longer than wide. Vas deferens convolute along female genital tract, becoming more straight, wider and muscular upon reaching penis; it enters penis subapically cutting off a short caecum. Penis retractor muscle convolute, originating from columella muscle and inserting on penial apex, extending under terminal portion of vas deferens. Interior of distal penis without obvious pilasters but with irregularly-shaped tissue pads. Vagina short but distinct. Bursa copulatrix with *ca* 2.5 mm long narrow duct and elongate terminal sac close to albumen gland. Free oviduct short. Hermaphrodite duct with long, tube-like, convolute talon. No chitinous spines found inside penis.

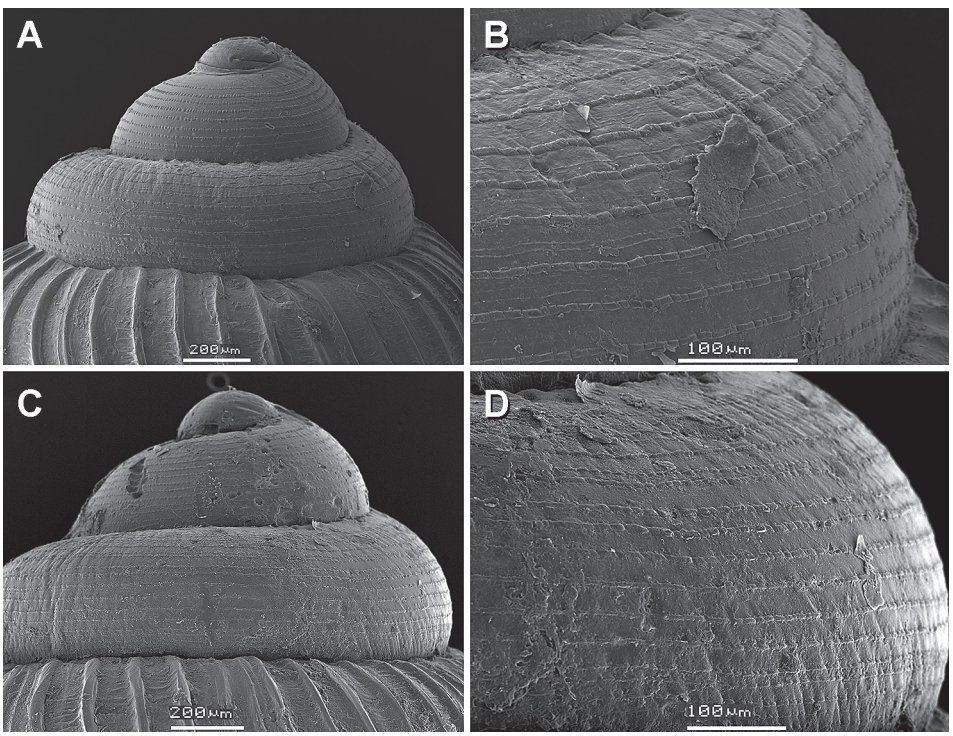


Fig. 23. SEM photographs of shell sculpture of *Avakubia subacuminata* sp. n.: (A, B) paratype, RMNH. MOL.330204: (A) apical whorls, (B) sculpture on second protoconch whorl; (C, D) specimen from Nyangong, Cameroon, RMNH.MOL.330210: (C) apical whorls, (D) sculpture on second protoconch whorl.

Radula: No complete row could be studied, but individual lateral/marginal teeth are similar in shape to those in *A. acuminata*.

Holotype: CAMEROON: *Sud Prov.*: Ebimimbang, *ca* 3 km SW of Saa, sta. CAM.124, 3.033°N 10.443°E, 150 m, 28.v.1996, A.J. de Winter & E.J. Semengue, high forest on slope (RMNH.MOL.330197).

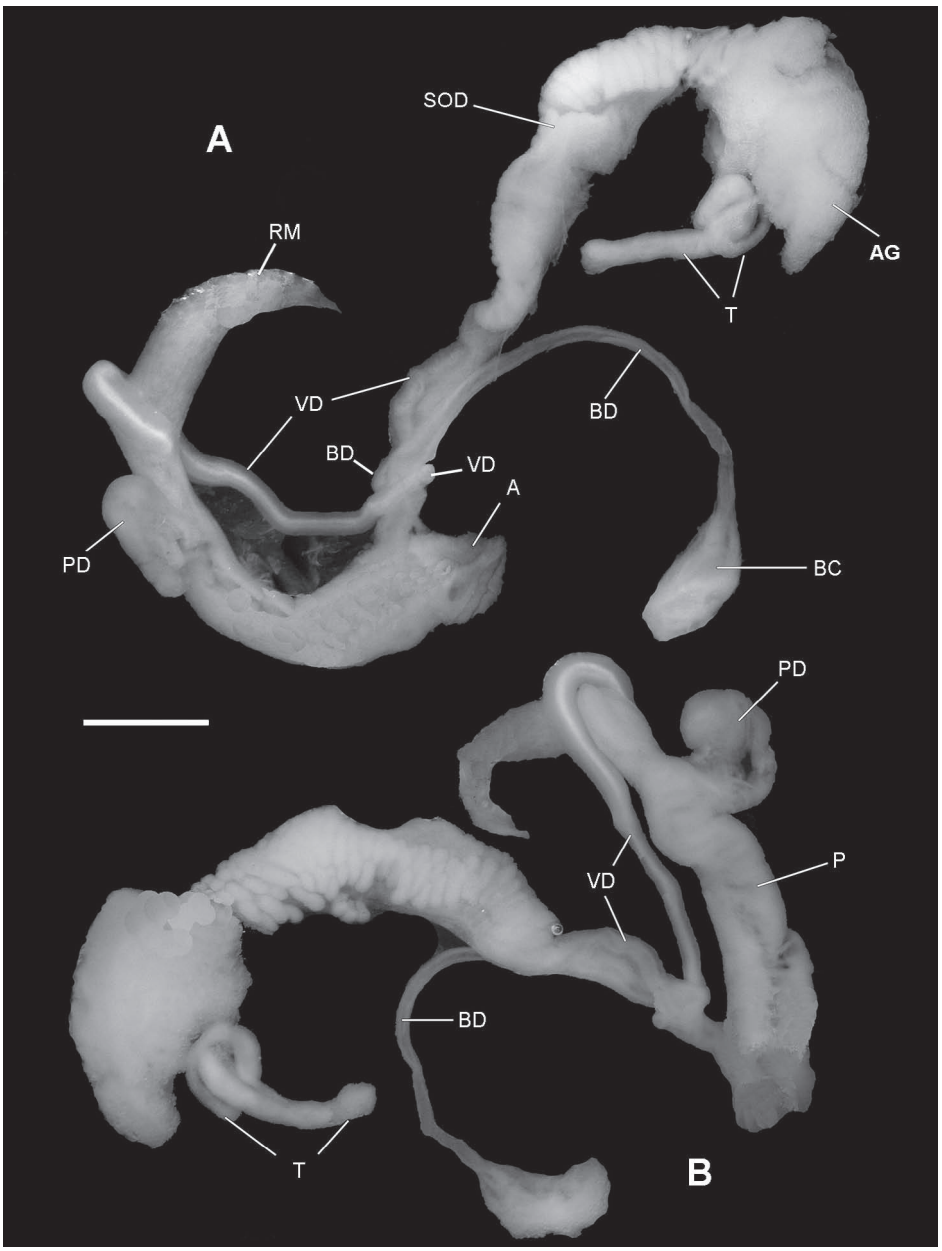


Fig. 24. *Avakubia subacuminata* sp. n.: (A, B) photographs of genital anatomy of paratype, RMNH. MOL.330202. Abbreviations as in Figs 6, 15. Scale bar = 0.5 mm.

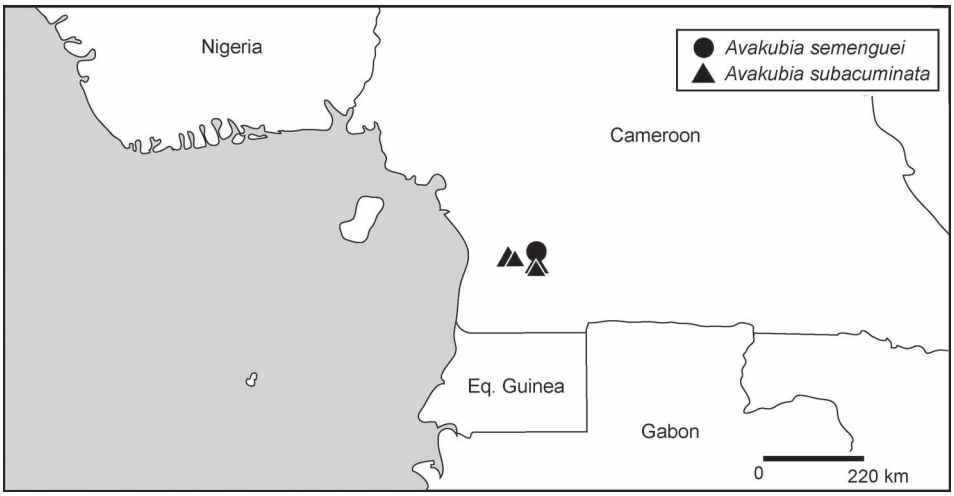


Fig. 25. Distribution records of *Avakubia semenguei* sp. n. and *A. subacuminata* sp. n.

Paratypes: CAMEROON: *Sud Prov.*: all within 5 km from Ebimimbang-Saa, S of the Bikoui River (= R. Lokoundjé), same collectors as holotype: 1 ad. dry shell Ebimimbang, *ca* 2 km WSW of Saa, sta. CAM.042, 3.038°N 10.456°E, 120 m, 10.x.1995, swamp forest (RMNH.MOL.330198); 1 ad. dry shell, Ebimimbang, 1 km SW of Saa, sta. CAM.043, 3.041°N 10.457°E, 110 m, 11.x.1995, high forest on flat terrain (RMNH. MOL.330199); 2 ad. dry shells, 1 ad. in alcohol Ebimimbang, sta. CAM.051, 3.038°N 10.477°E, 120 m, 12–18.x.1995, 25-year-old cocoa plantation with scattered large forest trees (RMNH.MOL.330200–330201); 1 ad., dissected soft parts in alcohol, Ebimimbang, 1 km S of Saa, secondary forest on an abandoned field along River Bikoui (= R. Lokoundjé), sta. CAM.052, 3.042°N 10.467°E, 110 m, 19.x.1995, floor litter (RMNH.MOL.330202); 1 ad. dry shell, sta. CAM.052, 23.v.1996 (RMNH.MOL.330203); 1 juv. dry shell, Ebimimbang, 4 km WSW of Saa, high forest, sta. CAM.117, 3.050°N 10.433°E, 150 m, 25.v.1996 (RMNH.MOL.330204); 2 ad. dry shells, Ebimimbang, 4 km W of Saa, swamp forest, sta. CAM.120, 3.050°N 10.433°E, 120 m, 27.v.1996 (RMNH.MOL.330205); 1 ad. in alcohol, Ebimimbang, 4 km W of Saa, swamp forest, sta. CAM.129, 3.050°N 10.433°E, 120 m, 29.v.1996 (RMNH.MOL.330206); 1 ad. dry shell Ebimimbang, 3 km WSW of Saa, young secondary forest, sta. CAM.133, 3.046°N 10.435°E, 110 m, 30.v.1996 (RMNH.MOL.330207).

Other material examined: CAMEROON: *Sud Prov.*: 1 juv. dry shell, Nyangong, 30 km S of Lolodorf, undisturbed rainforest, sta. CAM.100, 2.943°N 10.736°E, 700 m, 7.v.1996 (RMNH.MOL.330208); 1 ad., 4 juv. dry shells, Meka'a II, W of Nyangong, undisturbed rainforest, sta. CAM.106, 107, 110, 111, 2.967°N 10.733°E, 690–1000 m, 17–18.v.1996 (RMNH.MOL.330209–330212).

Distribution (Fig. 25): Known from two areas in Southwest Cameroon, which are some 35 km apart and differ substantially in altitude (100–150 m in Ebimimbang vs 690–1000 m in Nyangong).

Habitat: Collected from leaf-litter on the forest floor, except for a single specimen in a vegetation beating sample. The species was taken at *ca* 100–150 m in a variety of habitats: little disturbed high forest, more or less undisturbed swamp forest, a 25-year-old cocoa plantation with some remaining forest trees as well as in young secondary forest. A few specimens were collected in floor litter in undisturbed forest at 690–1000 m altitude (see below). In the Ebimimbang area *A. subacuminata* appears to be the only *Avakubia* species present (but see Remarks); in the Nyangong area it occurs sympatrically with *A. fruticicola*, which inhabits the understorey vegetation, however.

Remarks: *A. subacuminata* superficially resembles *A. acuminata* in shape, but is not a small geographic form of this species. Apart from clear conchological differences,

the animal is differently coloured (reddish orange instead of colourless/whitish), the genital anatomy differs in various details, and the species has ground-dwelling rather than arboreal habits. *A. subacuminata* does not seem to occur in an intensively sampled square km of forest in between both localities at an intermediate altitude (400–500 m), where three other *Avakubia* species were observed. The attribution of the Nyangong material to *A. subacuminata* is somewhat doubtful, because of small differences in protoconch sculpture details. The only adult shell from the Nyangong area could not be separated from the lowland specimens by shell proportions, however. Confirmation of the tentative identification requires collection of fresh material for anatomical and molecular studies.

Two juvenile shells with *Avakubia*-like sculpture were collected in leaf-litter in the Ebimimbang area. The protoconchs are very small and possess a more acuminate apex than any of the recognised *Avakubia* species, as well as distinctive coarse spiral sculpture (Figs 23E, F). These potentially represent still another unknown *Avakubia* species, but adult shells are necessary to confirm the tentative generic attribution.

Genus **Pseudavakubia** de Winter & Vastenhout, gen. n.

Etymology: The name refers to the strong resemblance of the shells to those of the genus *Avakubia.* Gender feminine.

Type species: *P. majus* de Winter & Vastenhout, sp. n.

Description: Shell small, H 2.9–4.3 mm, elongate ovate or cylindrical, penultimate whorl always wider than body whorl, with 6–7¼ whorls that generally expand slower than in *Avakubia* species, hence coiling tightness is higher (4.9–5.8). Last whorl proportionally smaller than in most *Avakubia* species, taking up 38–44 % of H. Peristome proportionally small, PH 29–35 % of H, PW 50–57 % of D. Aperture in most species (*P. liberiana* excepted) with a conspicuous, pointed palatal tooth, and a protruding angular tooth that continues as a deeply inrunning angular lamella. Palatal fold and columellar lamella absent. Umbilicus closed, umbilical depression with radiating ribs. Protoconch with *ca* 2¼ whorls not regularly increasing in width, but appearing more or less laterally compressed. Protoconch consists of two distinct portions: the first *ca* 1½ whorls appear rather smooth and shining at lower magnification, but at high magnification fine spiral sculpture can be distinguished (Fig. 29B); the sculpture changes abruptly to sharp, distant spiral cords on the last *ca* ¾ whorl. These spiral cords are solid, not composed of series of particles as in *Avakubia* (Fig. 29C). Teleoconch sculpture consists of sharp, regular ribs, with fine spiral lines in the interstices.

Anatomy (Fig. 27; based on a single dissection of *P. majus*): Penis twice as long as wide, muscular, robust, with a strong retractor muscle inserting subapically, next to the entrance site of the vas deferens, cutting off a short, spherical apical caecum. Vas deferens proximally rather straight, becoming convolute between the vagina and penial apex; the terminal portion somewhat rounded, swollen and muscular, narrowing just before entering the penis. Penis internally with two bulky, longitudinal pilasters. No chitinous spines were found inside the penis. Vagina short but distinct, rather wide close to the penis. Free oviduct abruptly widening into a pouch-like uterus containing a single, shelled embryo. Duct of bursa copulatrix rather long, distally widest, tapering towards the small bursal sac, which is situated close to the albumen gland. Talon a long, stiff,

exposed, tube at the base of the (remains of) the albumen gland. Spermoviduct with large, elongate acini. Radula typical carnivorous; a complete row no could be studied; individual lateral/marginal teeth elongate, curved and sharply pointed, similar in shape to those in *A. acuminata*.

Species included: In addition to the type species, *P. atewaensis* de Winter, sp. n.; *P. ghanaensis* de Winter, sp. n.; *P. liberiana* de Winter, sp. n.

Distribution: Ghana, Liberia.

Pseudavakubia majus de Winter & Vastenhout, sp. n.

Figs 26, 27

Etymology: From Latin *majus* (larger), in reference to the comparatively large shell of this species.

Diagnosis: A comparatively large, cylindrical species of *Pseudavakubia*.

Description:

Shell (Fig. 26): Large, H 4.3 (holotype) – 4.4 mm, cylindrical-biconical, largest width at penultimate whorl, high-spired, H:D 1.94–1.95. Whorls 7¼, little convex, whorl increase fast, coiling tightness 4.9–5 (holotype). Protoconch diameter 1.4 (holotype) – 1.6 mm. Protoconch irregularly coiled, whorl diameter increase of first whorls uneven. First 1½ protoconch whorl almost smooth (not studied with SEM), shining. Remaining ¾ protoconch whorl with 5–6 low, irregularly spaced cords. Boundary between smooth and spirally sculptured portion of protoconch sharp; transition from protoconch to teleoconch more gradual with a short zone of reticulate sculpture of axial ribs crossed by spirals. Body whorl proportionally large, BWH 42–44% of H, in holotype 42%. Periphery of last whorl rounded. Peristome entire, not strongly incrassate, higher than wide, PH:PW 1.06–1.14, in holotype 1.14. PH 33–34% of H, in holotype 33%, PW 57–62% of D, in holotype 57%. Palatal-basal lip in lateral view curved and arching forward. Tooth on mid-palatal wall blunt. Angular tooth protrudes, proceeding inwards as low, deeply entering lamella. Umbilicus closed, umbilical depression with radiating ribs. Teleoconch sculptured by slightly oblique, regularly spaced axial ribs, 9.2–10.7 ribs/mm, in holotype 9.2, with fine spirals in interstices.

Body colour: Ommatophores of preserved specimen bright orange, other soft parts without obvious colouration.

Anatomy (Fig. 27): See genus diagnosis.

Holotype: GHANA: *Eastern Region*: Atewa Range Forest Reserve, 6.24558°N 0.54654°W, 660 m, steep, East-facing slope in upland evergreen forest, 22.i.2010, M.E. Nutsuakor, P. Tattersfield & A.J. de Winter (RMNH.MOL.123136).

Paratype: 1 specimen, shell fragments, soft parts dissected, same data as holotype (RMNH.MOL.123323).

Other material examined: GHANA: *Eastern Region*: 1 ad. dry shell, Atewa Range Forest Reserve, plateau in upland evergreen forest, 6.23204°N 0.57471°W, 735 m, 22.i.2010, M.E. Nutsuakor, P. Tattersfield & A.J. de Winter (RMNH.MOL.125937).

Distribution (Fig. 31): Only known from the Atewa Range Forest Reserve in Ghana.

Habitat: Two live specimens were collected from the understorey vegetation in upland evergreen forest at 660–735 m. Found sympatrically with *P. atewaensis*.

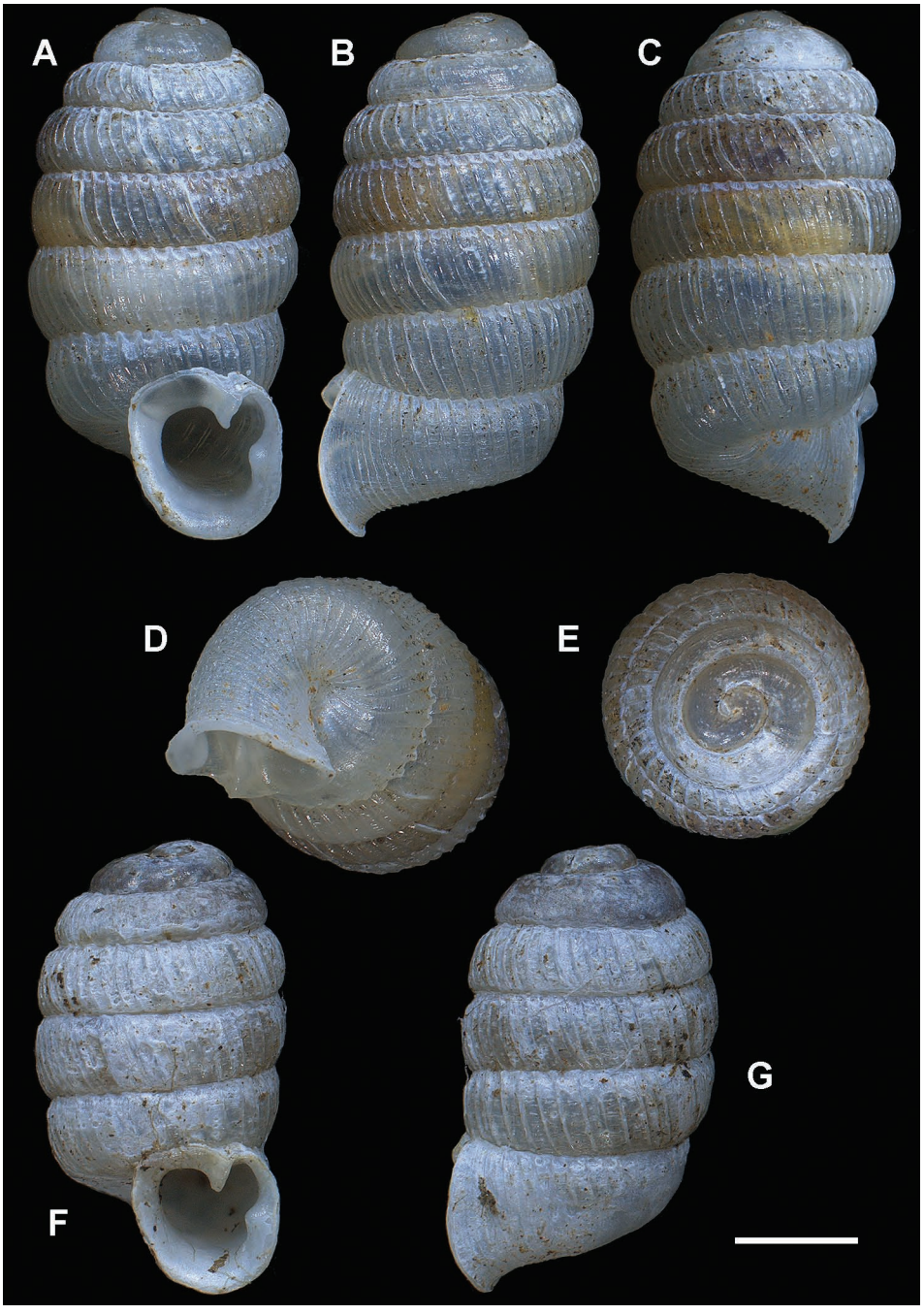


Fig. 26. *Pseudavakubia majus* sp. n.: (A–E) holotype, RMNH.MOL.123136: apertural (A), lateral (B, C), umbilical (D) and apical (E) views; (F, G) small-sized specimen from Ghana, Atewa Range Forest Reserve, RMNH.MOL.125937, apertural (F) and lateral (G) views. Scale bar = 1 mm.

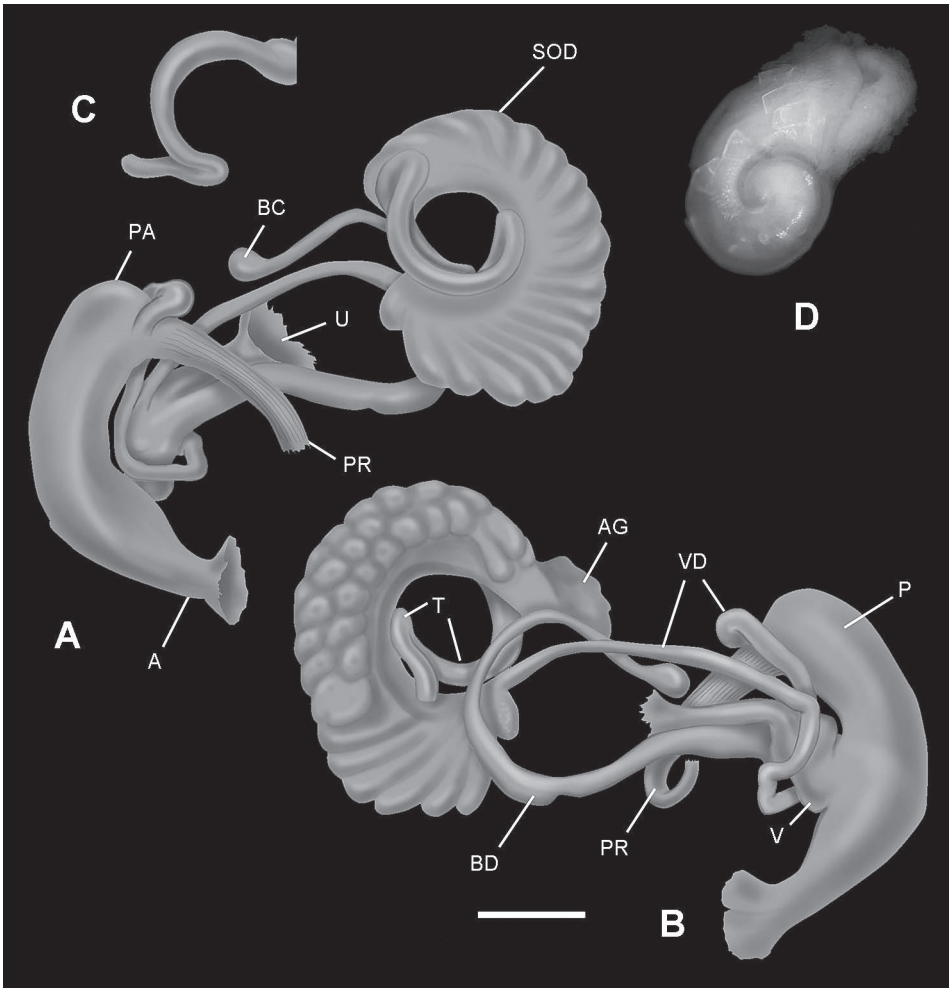


Fig. 27. *Pseudavakubia majus* sp. n., paratype from type locality, RMNH.MOL.123323: (A, B) genital anatomy; (C) talon; (D) embryo from uterus. Abbreviations as in Figs 6, 15. Scale bar = 0.5 mm. (Figs 27A–C drawn by Bas Blankenvoort from photographs of mounted genitalia preparations)

Remarks: One adult shell with a clearly shorter spire (Figs 26F, G) may have prematurely reached adulthood (shell with developed aperture with barriers and reflected lip), as is suggested by the smaller shell height, smaller number of whorls and less tightly closed umbilicus. Measurements of this specimen are not included in the above description as the specimen may be atypical for the species.

Pseudavakubia atewaensis de Winter, sp. n.

Figs 28A–I, 29

Etymology: Name refers to the type locality, the Atewa Range Forest Reserve, one of very few mid-altitude forest areas in Ghana, which is severely threatened by illegal

logging and plans for bauxite exploitation (McCullough *et al.* 2007). The area has a very high land snail diversity, with various land snail taxa not found elsewhere in Ghana so far (de Winter, Tattersfield & Nutsuakor, unpubl. data).

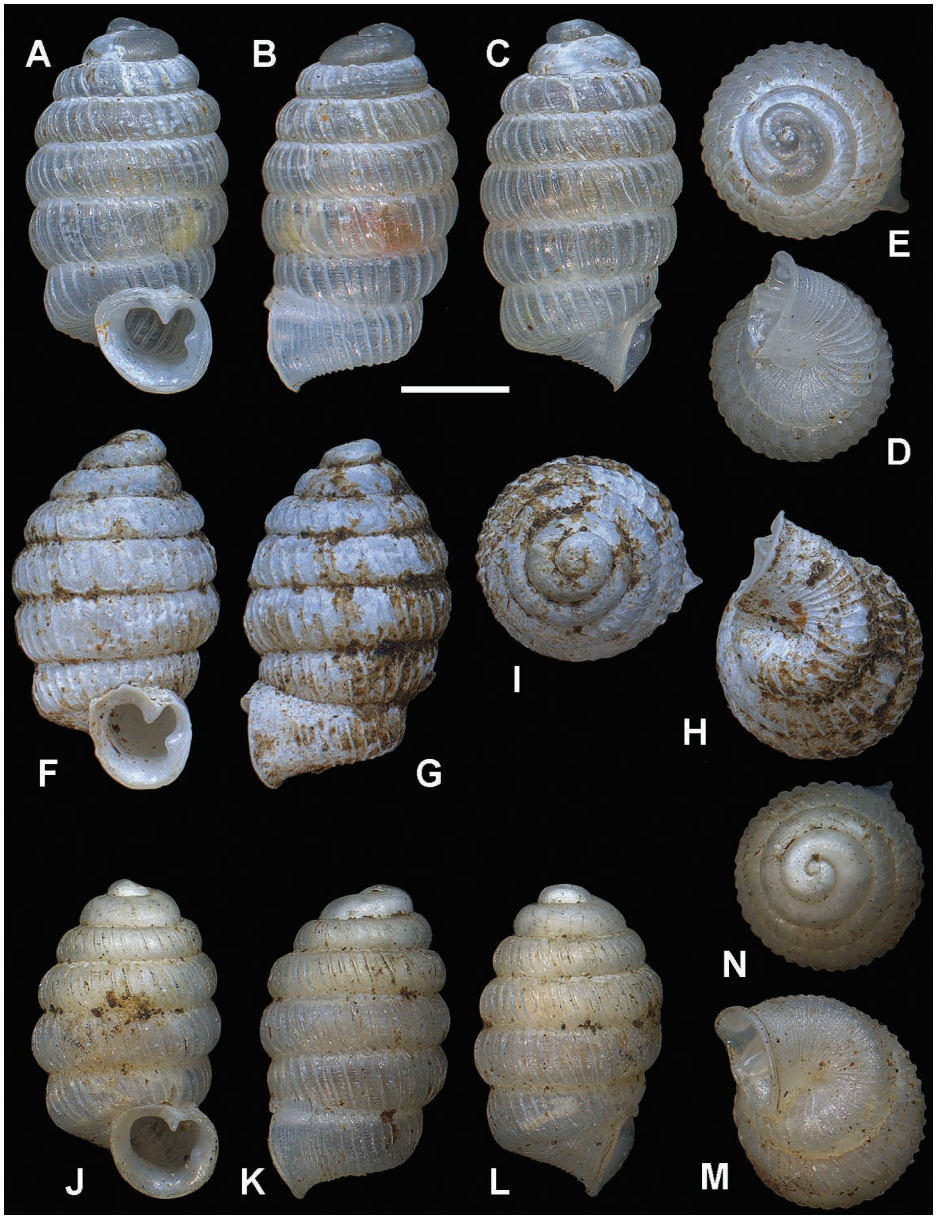


Fig. 28. Shells of *Pseudavakubia* species: (A–E) *P. atewaensis* sp. n., holotype, RMNH.MOL.122875: apertural (A), lateral (B, C), umbilical (D) and apical (E) views; (F–I) *P. atewaensis* sp. n., paratype from type locality, NMW.Z.2013.055.00002: apertural (F), lateral (G), umbilical (H) and apical (I) views; (J–N) *P. liberiana* sp. n., holotype, MCZ 77342, apertural (J), lateral (K, L), umbilical (M) and apical (N) views. Scale bar = 1 mm.

Diagnosis: *P. atewaensis* differs from *P. ghanaensis* by having less depressed apical whorls, a straight palatal lip (not arching forward in lateral view), a more rounded peristome, and a more angulate and proportionally smaller body whorl. The holotype shell of *P. liberiana* is smaller and less slender with a proportionally larger body whorl and a weaker palatal tooth. *P. majus* has a distinctly larger and more cylindrical shell with less tightly coiled whorls.

Description:

Shell (Figs 28A–H, 29): Small (H 3.3–3.4 mm), subcylindrical to strongly biconical, high-spired (H:D 1.75–1.85), greatest diameter at penultimate whorl. Whorls above widest portion of shell moderately to strongly tapering towards apex. Whorls 6¾, moderately convex, whorl increase comparatively slow (coiling tightness *ca* 5.7). Protoconch diameter 1.0–1.1 mm. Protoconch irregularly coiled, which is noticeable in lateral views of the shell. First 1¼ whorls distinctly raised above nucleus, providing apex with strongly distorted-acuminate appearance, with very fine spiral sculpture crossed by low growth lines (Fig. 29B), appearing smooth and shining at lower magnification. Later protoconch (*ca* ¾ whorl) with six distant spiral ridges. Transition of 'smooth' to spirally sculptured portion of protoconch abrupt, transition from protoconch to teleoconch more gradual, first 5 axial ribs of the teleoconch being crossed by spiral cords. Body whorl proportionally small, BWH 38–39 % of H. Periphery of body whorl somewhat angular.

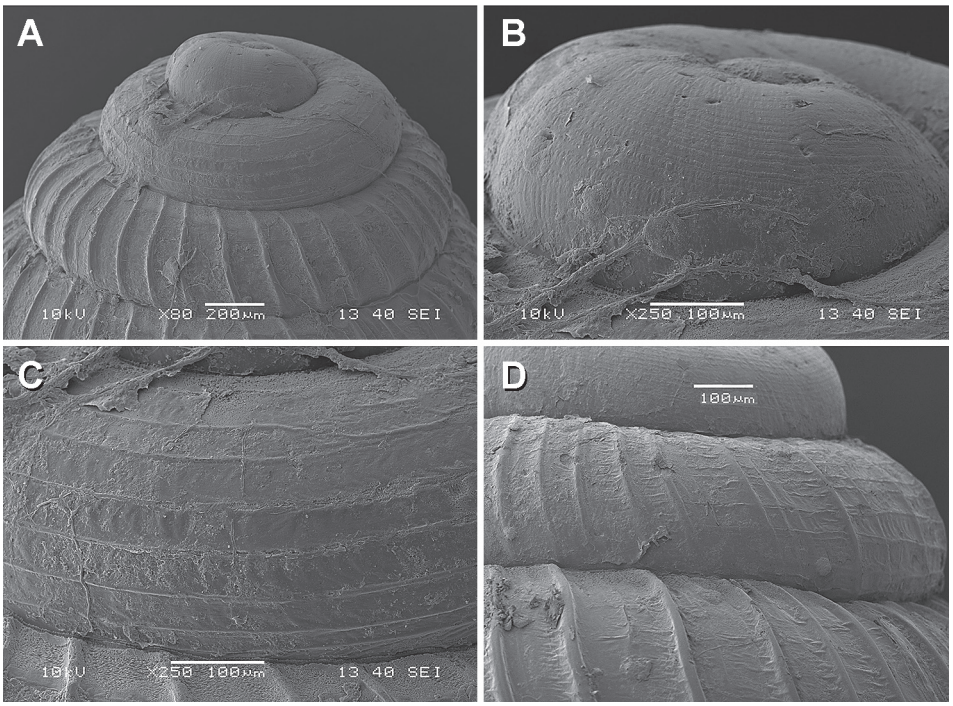


Fig. 29. SEM photographs of shell sculpture of *Pseudavakubia atewaensis* sp. n., RMNH.MOL.330214: (A) apex; (B) sculpture on first protoconch whorl; (C) sculpture on second protoconch whorl; (D) transition of protoconch to teleoconch.

Peristome entire, incrassate, proportionally small, roundish in outline, about as high as wide or wider than high, PH : PW 0.93–1.03, PH 29 % of H, PW 0.5–0.56 % of D. Palatal margin of peristome in lateral view comparatively straight, not arching forward. Angular tooth somewhat protruding, continuing as deeply entering lamella. Tooth on midpalatal wall strong and pointed. Umbilicus closed, umbilical chink with radiating ribs. Teleoconch sculpture consists of slightly oblique, curved axial ribs, 8.7–8.8 ribs/mm, with fine spirals in interstices.

Body colour: Dried-in soft parts of holotype reddish.

Anatomy: Unknown.

Holotype: GHANA: *Eastern Region*: Atewa Range Forest Reserve, 6.24558°N 0.54654°W, 660 m, 22.i.2010, M.E. Nutsuakor, P. Tattersfield & A.J. de Winter, steep E-facing slope in upland evergreen forest (RMNH. MOL.123111).

Paratype: 1 ad. shell in alcohol, same data as holotype (NMW.Z.2013.055.00002).

Other material examined: GHANA: *Eastern Region*: 1 juv. dry shell Atewa Range Forest Reserve, 6.12368°N 0.60445°W, 655 m, 23.i.2010, M.E. Nutsuakor, P. Tattersfield & A.J. de Winter, SE-facing slope in recently logged upland evergreen forest (RMNH.MOL.330214).

Distribution (Fig. 31): Only known from the Atewa Range Forest Reserve in Ghana.

Habitat: Both adult specimens were obtained from floor litter samples in upland evergreen forest at about 650 m. A juvenile was collected from the understorey vegetation. Found sympatrically with *P. majus*.

Remarks: *P. atewaensis* resembles *P. liberiana*, sharing a strait palatal lip, a proportionally small, rounded peristome and close-set axial ribs on the teleoconch. The holotype shell of *P. liberiana* is smaller and less slender with a proportionally larger body whorl and a weaker palatal tooth.

Pseudavakubia ghanaensis de Winter, sp. n.

Fig. 30

Etymology: The species name refers to the country of origin.

Diagnosis: Differs from the similarly sized *P. atewanensis* by the less elongate shell with lower protoconch; peristome proportionally larger and less rounded, with the palatal lip curved in lateral view. The shell of *P. liberiana* is smaller and has less strong apertural dentition. *P. majus* has a much larger shell.

Description:

Shell (Fig. 30): Small (H 3.3–3.4 mm, holotype 3.3 mm), ovoid-subcylindrical, moderately high-spired, H : D 1.62–1.75, in holotype 1.74, greatest diameter at penultimate whorl. Whorls above widest portion of shell moderately tapering. Whorls 6½–7, moderately convex, whorl increase slow, coiling tightness *ca* 5.4–5.8, in holotype 5.8. Protoconch diameter 1.04–1.15 mm, of holotype 1.12 mm. Protoconch irregularly coiled with greatly varying whorl width, apex appearing less acuminate than in *P. atewanensis*. Protoconchs of all shells more or less eroded, obscuring fine details. First 1¼ whorl without prominent sculpture, later protoconch (*ca* ¾ whorl) with five distant spiral ridges. Transition of smooth to spirally sculptured portion of protoconch abrupt, transition from protoconch to axially ribbed teleoconch somewhat gradual, first 3–4 axial ribs of teleoconch being crossed by spiral cords of protoconch. BWH 41–44 % of

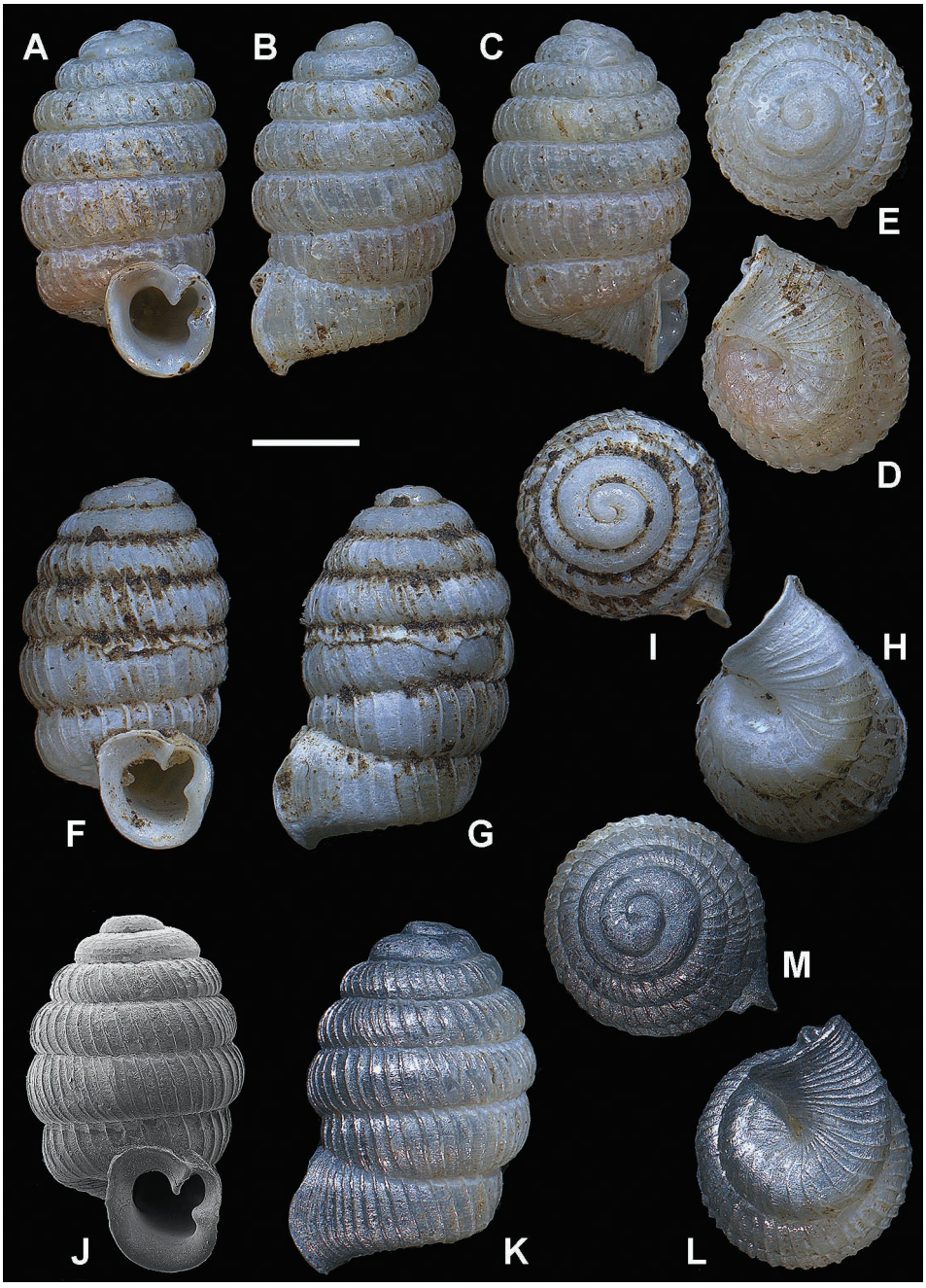


Fig. 30. *Pseudavakubia ghanaensis* sp. n.: (A–E) holotype, RMNH.MOL.122857: apertural (A), lateral (B, C), umbilical (D) and apical (E) views; (F–I) shell from Kakum National Park, Ghana, RMNH.MOL.330217: apertural (F), lateral (G), umbilical (H) and apical (I) views; (J–M) shell from Pra Suhien Forest Reserve, Ghana, RMNH.MOL.330215: apertural (J), lateral (K), umbilical (L) and apical (M) views. Scale bar = 1 mm.

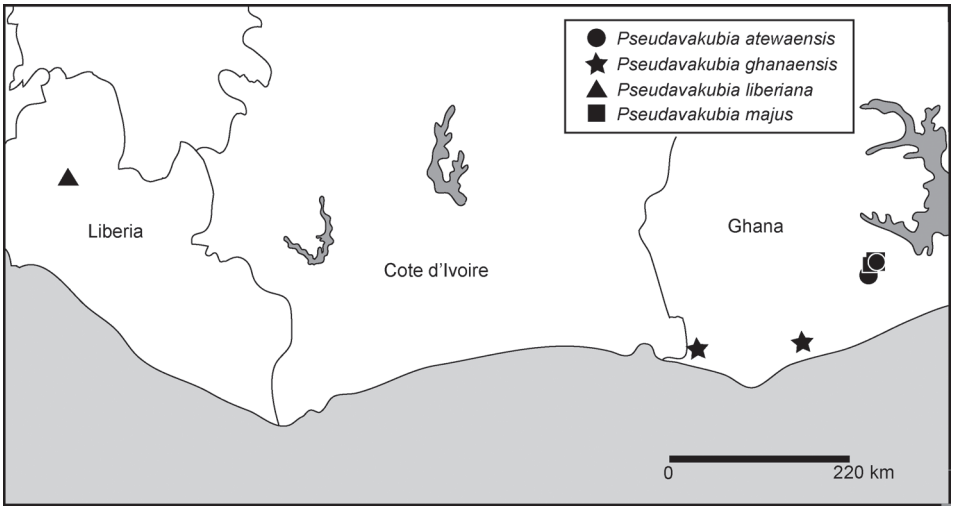


Fig. 31. Distribution records of *Pseudavakubia* species.

shell height, in holotype 41 %. Periphery of body whorl more or less rounded. Peristome entire, not strongly incrassate, squarish in outline, higher than wide; PH:PW 1.03–1.12, in holotype 1.07, PH 32–36 % of H, in holotype 33 %, PW 52–55 % of D, in holotype 54 %. Apertural lip rather wide and flaring. Palatal-basal lip in lateral view curved, arching forward. Angular tooth somewhat protruding, continuing as deeply entering lamella. Tooth on mid-palatal wall strong and pointed. Umbilicus fully closed, umbilical depression with radiating ribs. Teleoconch sculpture consists of slightly oblique, somewhat curved axial ribs, 6.5–9.4 ribs/mm, with fine spirals in interstices.

Body colour: Dried-in soft parts of holotype at least partly red.

Anatomy: Unknown.

Holotype: GHANA: *Western Region*: Ankasa Conservation area, 5.25411°N 2.64037°W, 60 m, 15.i.2010, M.E. Nutsuakor, P. Tattersfield & A.J. de Winter, wet evergreen forest (RMNH.MOL.122857).

Other material examined: GHANA: *Central Region*: 2 ad. dry shells, Pra Suhien Forest Reserve, 5.34807°N 1.39002°W, 230 m, 10.vi.2008, M.E. Nutsuakor & A.J. de Winter, moist evergreen forest (RMNH.MOL. 330215–330216); 1 ad. dry shell, Kakum National Park, 5.3558°N 1.3925°W, 220 m, moist evergreen forest along stream, 6.vi.2008, M.E. Nutsuakor & A.J. de Winter (RMNH.MOL.330217).

Distribution (Fig. 31): So far known from south-central and south-western Ghana.

Habitat: All material was collected from leaf-litter on the floor of old secondary lowland (wet and moist) evergreen forest.

Remarks: In *P. ghanaensis* we provisionally lodge the scanty material (four adult shells, one of which severely damaged) from three localities in central and western Ghana. These shells differ from those of *P. atewanensis* and *P. liberiana* by a comparatively less irregularly coiled protoconch (resulting in a flatter apex which seems less conspicuous distorted in lateral views), a higher than wide peristome, and by a distinctly curved, forward arching palatal lip (in lateral view). In view of the variation in these shells it seems possible that more than one species is involved, and additional material from more localities is needed to assess the variability.

Pseudavakubia liberiana de Winter, sp. n.

Figs 28J–N

Gulella (Avakubia) avakubiensis: Degner 1934*b*: 377.

Description:

Shell (Figs 28J–N): Rather small (H 2.9 mm), ovoid-biconical, H:D 1.68, greatest diameter at penultimate whorl. Whorls above widest portion of shell moderately tapering towards apex. Whorls 6, strongly convex, whorl increase slow (coiling tightness 5.6). Protoconch diameter 1.15 mm. Protoconch irregularly coiled, which is noticeable in lateral views of the shell. First *ca* 1¼ whorls distinctly raised above nucleus, giving apex a distorted, acuminate appearance, with extremely fine spiral sculpture, appearing smooth and shining at lower magnification. Transition to spirally sculptured portion of the protoconch marked by axial thickening and slight change in colour. Spirals on later protoconch portion (*ca* ¾ whorl) initially extremely weak and confined to lower quarter of whorl. Sculpture becomes more prominent (but still comparatively weak), towards teleoconch, where six or seven fine spiral cords discernable. Body whorl 44% of H. Periphery of last whorl slightly angular. Peristome entire, incrassate, roundish in outline, wider than high, PH:PW 0.89, PH 30% of SH, PW 57% of D. Palatal-basal lip in lateral view comparatively straight, not arching forward. Angularis is a somewhat protruding tooth, continuing inwards as low lamella for at least half a whorl. Tooth on mid-palatal wall rather weak. Umbilicus fully closed, umbilical depression with radiating ribs. Teleoconch sculpture consists of slightly oblique, axial ribs, about 9.1 ribs/mm, with fine spirals in interstices.

Body colour: Unknown.

Anatomy: Unknown.

Holotype: LIBERIA: Banga, *ca* 7.28°N 10.06°W, *ca* 200 m, 1926–1927, J. Bequaert, Harvard African Expedition (MCZ 77342).

Distribution (Fig. 31): Only known from the type locality.

Remarks: This species is represented by a single fresh shell only, which was originally identified as a specimen of *A. avakubiensis* (Degner 1934*b*). It best resembles *P. atewaensis*, of which it eventually may turn out to be a geographical form. However, the Liberian shell was collected at some considerable distance (almost 1000 km) from the Atewa Range, and differs by a smaller shell with more convex whorls, larger protoconch with more and finer spiral cords, a proportionally larger body whorl, and a much weaker tooth on the palatal lip. We prefer to describe this shell as specifically distinct. More material is required to test this taxonomic decision.

The holotype shell exhibits a pale marking on the body whorl which might be incorrectly interpreted as the palatal fold characteristic of the genus *Avakubia.* By means of a CT-scan the absence of internal barriers could be confirmed.

Key to the species of *Avakubia* and *Pseudavakubia*

1 Apical whorls regularly increasing in diameter. Internal palatal wall of body whorl with shorter or longer fold (externally visible by transparency as a pale stripe). Umbilicus open but narrow. Whorl increase fast (coiling tightness usually <4.8, rarely 5) .....(**Avakubia**) 2

– Apical whorls not regularly increasing in diameter, providing protoconch with a distorted appearance. Internal palatal wall of body whorl without fold. Umbilicus closed. Whorl increase slow (coiling tightness usually >5, but at least 4.9) .... (**Pseudavakubia**) 10

2 Shell with distinctly acuminate apex and tapering spire (apical angle generally <120°, spire angle <60°) 3
– Shell apex more rounded, spire aspect less tapering (apical angle at least 120°, spire angle >62°) 4

3 Adult shell >5 mm, elongate, apex strongly acuminate, spire appearance less tapering; apical angle <100°. (SW Cameroon) ..... **A. acuminata**
– Adult shell height at most 4.1 mm, apex less strongly acuminate; apical angle >100°. (SW Cameroon) ..... **A. subacuminata**

4 Adult shell >4.7 mm, protoconch very wide and flattened, diameter of first two whorls >2.2 mm. (SW Cameroon) ..... **A. semenguei**
– Adult shell <4.3 mm, diameter of first two whorls <1.7 mm 5

5 Columellar lamella and palatal fold visible in aperture in oblique view. Shell appearing smooth or with little pronounced and very close-set ribs. Spirals on protoconch not prominent. (Bioko I.) ..... **A. ortizdezarateorum**
– Columellar lamella and palatal fold not visible in aperture; ribs strong and more distant, spirals on protoconch prominent 6

6 Protoconch whorls strongly convex; axial ribs distant (*ca* 8 ribs/mm on penultimate whorl); shell height <3.5 mm; apical angle about 120°. (Eastern DRC & Uganda) ..... **A. avakubiensis**
– Protoconch whorls less convex; axial ribs closer 7

7 Shell ribbing dense (*ca* 11–13 ribs/mm on penultimate whorl) 8
– Ribs less close-set (*ca* 9–10 ribs/mm on penultimate whorl) 9

8 Shell small (shell height <3.5 mm); body whorl >50 % of shell height. (SW Cameroon) ..... **A. fruticicola**
– Shell larger (shell height >3.6 mm), body whorl <50 % of shell height. (NW Gabon) ..... **A. crystallum**

9 Shell height 3.8–4.0 mm, shell width 2.1–2.3 mm, about 10 ribs/mm on penultimate whorl. (Bioko I.) ..... **A. biokoensis**
– Shell height 3.2–3.6 mm, shell width 1.9–2.0 mm, about 9 ribs/mm on penultimate whorl. (Ghana) ..... **A. occidentalis**

10 Shell comparatively large and cylindrical, shell height generally >4 mm. Protoconch width 1.4–1.6 mm. Coiling tightness *ca* 5 ..... **P. majus**
– Shell height 2.9–3.4 mm. Protoconch width not exceeding 1.3 mm. Coiling tightness >5.4 11

11 Apertural lip in lateral view strongly curved and arching forward. Peristome higher than wide. (Ghana) ..... **P. ghanaensis**
– Apertural lip in lateral view comparatively straight, not arching forward. Peristome as wide as high or wider than high 12

12 Shell height <3 mm. Palatal tooth very weak. Last whorl 45 % of shell height. (Liberia)..... **P. liberiana**
– Shell height >3.3 mm. Palatal tooth prominent, pointed. Last whorl <40 % of shell height. (Ghana)..... **P. atewana**

DISCUSSION

Diversity and systematics

The present study has revealed the genus *Avakubia* to be considerably more speciose than previously known, with at least nine species instead of two. The resulting classification is largely based on shell characters of a limited number of specimens per species. Nevertheless, we think the recognised species are not geographic variants of a small number of widespread species. The sympatric occurrence of four *Avakubia* taxa within a 1500 km^2 area in Southwest Cameroon (see de Winter & Gittenberger 1998: fig. 1), one of the few malacologically better sampled areas in western Africa, supported the evaluation of species limits in this area, and assisted in the interpretation of conchological differences in other populations, in addition to multivariate statistical analysis of shell measurements. Alcohol-preserved material needed to confirm the taxonomic conclusions of this study by molecular data is either not available at this stage, or too scarce and probably too old. Molecular data should be used to test the species hypotheses once sufficient fresh material has been collected. The nine *Avakubia* species recognised, represented by only 105 adult specimens, come from a tiny portion of the potential range of the genus; from huge areas in tropical Africa no *Avakubia* material has as yet been reported (Fig. 3). The presence of still more undescribed species seems therefore likely. Future use of molecular data may reveal additional cryptic species, the existence of which has been suspected in this study in a few instances (e.g. in *A. subacuminata*).

At the first glance, *Avakubia* (and *Pseudavakubia*) species share surprisingly characteristic shells that readily separate them from other *Gulella*-like streptaxids, resembling more or less closely the description and illustration of the type species *A. avakubiensis* by Pilsbry (1919). Later records in the literature of the type species from a huge part of Equatorial Africa are found to actually embrace five additional morphospecies, which are all described in this paper as new species with much more restricted distributions; one of these actually belongs to *Pseudavakubia*. In addition, three *Avakubia* species (*A. acuminata*, *A. semenguei* and *A. ortizdezarateorum*) with more distinctive shells are recognised. The first two occur sympatrically with *A. fruticicola* in the same microhabitat, leaving open the possibility of character displacement as a cause of their deviating shell morphology. The atypical shell sculpture and apertural dentition of *A. ortizdezarateorum* may suggest a different generic position. However, in the absence of information on the soft parts, this species is provisionally retained in *Avakubia*.

The type species of *Avakubia* was described on the basis of a limited set of shell characters, like the beaded spiral sculpture on the protoconch, the teleoconch sculpture of axial ribs with spiral lines in the interstices, the presence of only a few barriers in the aperture and the biconical shell shape with the greatest width above the body whorl (Pilsbry 1919). In the present study we have found that the available material is not homogenous and cannot be attributed to a single genus, although all shells conform to the description of *Avakubia* provided by authorities like Thiele (1933), Degner (1934*b*) and Schileyko (2000). These authors did not explicitly refer to the granular nature of the apical

spirals, although this character was mentioned in the original description. Likewise, the presence of a deep-set palatal fold was not indicated. Pilsbry (1919) mentioned the presence of "a low, transverse fold [is] visible some distance within the basal margin", an unclear and easily misinterpreted description, and the character is not visible in the original shell drawing. In later treatments the palatal fold was only mentioned by Ortiz de Zárate and Ortiz de Zárate Rocandio (1956).

The discovery of four species with non-granular apical spirals and lacking the palatal fold (and other features) prompted the erection of the new genus *Pseudavakubia*. Many shell characters typical of *Avakubia* are shared by members of *Pseudavakubia*. It is therefore not surprising that Degner (1934*b*: 377), a sharp observer and competent malacologist, was quite certain about the correct identification of his Liberian specimen of "*Gulella* (*Avakubia) avakubiensis"* (described in the present paper as *Pseudavakubia liberiana*): "Die Art ist so trefflich gekennzeichnet dass Verwechselungen unmöglich erscheinen" [the species is so characteristic that mistakes seem to be impossible]. The identity of Degner's unfigured shell only became clear after study of the unique specimen.

The cryptic palatal fold is potentially a synapomorphy supporting the monophyly of the genus *Avakubia*. In this position the structure is not known in other Streptaxidae (exclusive of streptaxomorph taxa), where palatal folds, if present, are readily visible in the aperture and generally have corresponding external depressions on the back of the shell. The beaded spiral sculpture on the protoconch appears to be unknown among other Streptaxidae. Various streptaxid species have spiral sculpture on the protoconch, but of most species this has not been studied in sufficient detail. Unique characters for *Pseudavakubia* may be the irregularly coiled protoconch consisting of two sharply demarcated and differently sculptured portions, followed by a regularly coiled teleoconch. The genital anatomy of both *Avakubia* and *Pseudavakubia* are superficially not dissimilar. The systematic importance of the observed differences could not be assessed due to small number of dissected specimens and species. The most conspicuous difference is that in *Pseudavakubia* no trace of a lateral penial caecum has been observed. *Pseudavakubia* may be related to one of the West African streptaxid radiations that have been assigned to either *Gulella s.l.* or *Ptychotrema* L. Pfeiffer, 1853 *s.l.*, the soft parts morphology of which are largely unknown. Whilst speculating about phylogenetic affinities, it should be kept in mind that the knowledge of the land snails, including Streptaxidae, of West and Central Africa is rather imperfect. Additional, especially live collected, streptaxid material is needed to address these questions.

Although we are convinced that *Avakubia* and *Pseudavakubia* represent separate taxa, each with a number of species sharing a distinctive set of characters, it remains unclear whether they are related, or even part of a monophyletic clade, as would be suggested by the remarkable similarities in shell size, shape and teleoconch sculpture. The fact that representatives of both genera share the absence of chitinous hooks and spines in the penis provides the strongest support for a close relationship. This is an uncommon character within the Streptaxidae, but not a unique one, however (Schileyko 2000; Sutcharit *et al.* 2010). According to Sutcharit *et al.* (2010) chitinized penial structures are fully absent in *Careoradula* Gerlach & van Bruggen, 1999, *Impertubaria constans* (von Martens & Wiegman, 1898), *Diaphera* Albers, 1850 and *Discartemon* L. Pfeiffer, 1856 (actually, only the genital anatomy of *D. stenostomus* van Benthem Jutting, 1954,

appears to be known, not that of the type species *D. discus* (L. Pfeiffer, 1851), see Berry (1965)). Sutcharit *et al.* (2010) separated Diapheridae as an independent early offshoot from the Streptaxidae on the basis of molecular characters of *Diaphera prima* Panha, 2010, a species from Thailand attributed to the genus (the type species of *Diaphera*, *D. cumingiana* (L. Pfeiffer, 1845) from the Philippines is only known by its shell). These authors considered the absence of penial armature in *D. prima* a plesiomorphic condition. Rowson *et al*. (2011) retained *A. avakubiensis* as a basal taxon within the Streptaxidae on the basis of molecular data, so the penial armature may have evolved in the Streptaxidae *s.l.* after the origin of a clade including both *Avakubia* and *Pseudavakubia*, but may also have been lost independently in these taxa. Too few Streptaxidae taxa are anatomically and molecularly known to infer phylogenetic conclusions from this character.

In a specimen of *A. acuminata* a spermatophore-like structure was found inside the lower penis. This appears to be the third record of a spermatophore in a species of Streptaxidae, after reports in *Sinistrexcisa* de Winter, Gomez & Prieto, 1999, and *Dadagulella* Rowson & Tattersfield, 2013 (de Winter *et al.* 1999; Rowson & Tattersfield 2013). As was recently discussed by Rowson and Tattersfield (2013), it remains to be proven that such structures are true spermatophores. The location in the male genitalia of *Avakubia* where a spermatophore could be produced is unclear; a possibility may be the dilated, muscular portion of the vas deferens shortly before it enters the penis, which may then be termed epiphallus.

Ecology and conservation

Only some 150 *Avakubia* specimens, juvenile shells included, were worldwide available for this study. Various factors possibly contribute to this apparent scarcity, alone or in combination, as discussed below.

Insufficient collecting in Central Africa is no doubt a major cause of the paucity of material. Most recent *Avakubia* material was obtained by litter sieving methods (de Winter 1995 and unpubl. data; Fontaine *et al.* 2007; Wronski & Hausdorf 2010; Tattersfield, pers. comm.), or by beating the understorey vegetation over an umbrella (de Winter & Gittenberger 1998). Large areas of tropical Africa have not been surveyed at all as regards molluscs, let alone by these labour-intensive methods; especially the latter method is not commonly employed by malacologists. Three out of four *Avakubia* species found in Southwest Cameroon were exclusively collected from the understorey vegetation; a fourth species was mostly found on the forest floor. Neglect of the arboreal habitat might explain, for example, the marginal occurrence of *Avakubia* in Lopé National Park in Gabon (Fontaine *et al.* 2007), where in total only three shells were obtained from two litter samples out of 100 systematically litter-sampled forest plots.

Avakubia species appear to be largely confined to rainforests. In Africa such forests usually grow mostly on nutrient-poor, acidic soils (e.g. Showers 2006 and references therein) where snail abundance is low. In addition, land snails in tropical forests tend to have quite small ranges or at least very patchy distributions (Solem 1984; Schilthuizen 2011).

Most specimens for which habitat data are available, were collected from little disturbed forest sites. One species (*A. subacuminata*) was observed in both undisturbed forest and anthropogenic habitat (cocoa plantation and young secondary forest on abandoned field), but lack of records from disturbed habitat may be due to sampling bias.

Undisturbed rainforests in Africa are rapidly disappearing. The arboreal species may depend on a stratified vegetation, as present in such forests. Also in view of the apparently small ranges of various *Avakubia* species, at least some species are likely to be threatened, together with many other African rainforest-dwelling land snail species. One example is *A. acuminata*. An intensively studied 1 km^2 area in Southwest Cameroon yielded 34 specimens, i.e. 1.3% of all land snail specimens found there (de Winter & Gittenberger 1998). This species was not encountered in some plots a few kilometres away from this km area, nor in two areas 20–30 km away with similar forest habitat, which were studied using the same collection effort and techniques, yielding only other *Avakubia* species. The *Pseudavakubia* species may be even more vulnerable, given the rapid deforestation of the upper Guinea forest area, but as yet very little is known of their distribution. Especially *P. atewana* and *P. majus* inhabiting the threatened Atewa Range in Ghana (McCullough *et al*. 2007) may be endangered.

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REFERENCES

Berry, A.J. 1965. The genital systems of *Discartemon stenostomus* van Benthem Jutting and *Huttonella bicolor* (Hutton) (Pulmonata: Streptaxidae) from Malaya. *Proceedings of the Malacological Society of London* **36**: 221–228.

Bruggen, A.C., van. 1973. Papers on African non-marine molluscs by Ortiz de Zárate. *Achatina* **4**: 83–84.

Bruggen, A.C., van & Van Goethem, J.L. 1997. Dr. William Adam's iconography of Central and West African *Gulella* species (Gastropoda Pulmonata: Streptaxidae). Part 1: nominal taxa. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie* **67**: 5–30.

Connolly, M. 1928. The non-marine Mollusca of Sierra Leone. *Annals and Magazine of Natural History, including Zoology, Botany, and Geology, Ser. 10* **1**: 529–551, pl. 18.

Degner, E. 1934*a*. Westafrikanische Landschnecken. I. Streptaxiden, Helicarioniden, Vaginuliden. *Zoologische Jahrbücher (Systematik)* **65**: 209–308.

————1934*b*. Streptaxiden aus Liberia. *Revue de Zoologie et de Botanique Africaines* **24**: 369–379.

Eardley, C.D. 2004. Taxonomic revision of the African stingless bees (Apoidea: Apidae: Apinae: Meliponini). *African Plant Protection* **10**: 63–96.

Emberton, K.C. 2001. Dentate *Gulella* of Madagascar (Pulmonata: Streptaxidae). *American Malacological Bulletin* **16**: 71–129.

Fontaine, B., Gargominy, O. & Neubert, E. 2007. Land snail diversity of the savanna/forest mosaic in Lopé National Park, Gabon. *Malacologia* **49**: 313–338.

Hammer, Ø., Harper, D.A.T. & Ryan, P.D. 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontologia electronica* **4**: 1–9. (http://folk.uio.no/ohammer/past)

KERNEY, M.P. & CAMERON, R.A.D. 1979. *A field guide to the land snails of Britain and north-west Europe*. London: Collins.

MCCULLOUGH, J., ALONSO, L., NASKRECKI, P. & OSEI-OWUSU, Y., eds. 2007. A rapid biodiversity assessment of the Atewa Range Forest Reserve, Ghana. *RAP Bulletin of Biological Assessment* **47**: 1–193.

ORTIZ DE ZÁRATE LOPEZ, A. & ORTIZ DE ZÁRATE ROCANDIO, A. 1956. Contribuciones al conocimiento de la fauna malacológica terrestre de la isla de Fernando Poo. II. Familia Streptaxidae. *Boletin de Real Sociedad Espanola de Historia Natural* **53**: 75–140.

PILSBRY, H.A. 1919. A review of the land Mollusks of the Belgian Congo chiefly based on the collections of the American Museum Congo Expedition, 1900–1915. *Bulletin of the American Museum of Natural History* **40**: 1–370.

ROWSON, B. & TATTERSFIELD, P. 2013. Revision of *Dadagulella* gen. n., the "*Gulella radius*" group (Gastropoda: Streptaxidae) of the eastern Afrotropics, including six new species and three new subgenera. *European Journal of Taxonomy* **37**: 1–46.

ROWSON, B., TATTERSFIELD, P. & SYMONDSON, W.O.C. 2011. Phylogeny and biogeography of tropical carnivorous land-snails (Pulmonata: Streptaxoidea) with particular reference to East Africa and the Indian Ocean. *Zoologica Scripta* **40**: 85–98.

SCHILEYKO, A.A. 2000. Treatise on Recent terrestrial pulmonate molluscs. Part 6: Rhytididae, Chlamydephoridae, Systrophiidae, Haplotrematidae, Streptaxidae, Spiraxidae, Olecinidae, Testacellidae. *Ruthenica Supplement* **2**: 731–880.

SCHILTHUIZEN, M. 2011. Community ecology of tropical forest snails: 30 years after Solem. *Contributions to Zoology* **80**: 1–15.

SHOWERS, K.B. 2006. A history of African soil: Perceptions, use and abuse. *In*: McNeill, J.R. & Winiwarter, V., eds, *Soils and societies. Perspectives from environmental history*. Isle of Harris, UK: The White Horse Press, pp. 118–176.

SOLEM, A. 1984. A world model of land snail diversity and abundance. *In*: Solem, A. & van Bruggen, A.C., eds, *Word-wide snails. Biogeographical studies on non-marine Mollusca*. Leiden, The Netherlands: Brill, pp. 6–22.

SUTCHARIT, C., NAGGS, F., WADE, C.M., FONTANILLA, I. & PANHA, S. 2010. The new family Diapheridae, a new species of *Diaphera* Albers from Thailand, and the position of the Diapheridae within a molecular phylogeny of the Streptaxoidea (Pulmonata: Stylommatophora). *Zoological Journal of the Linnean Society* **160**: 1–16.

THIELE, J. 1933. Die von Oskar Neumann in Abessinien gesammelten und einige andere afrikanische Landschnecken. *Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin* **1933**: 280–323.

VERDCOURT, B. 1962. Preliminary keys for the identification of the species of the genus *Gulella* Pfr. occuring in East Africa. *Annales Musee Royal de l'Afrique Centrale* **8**: 1–39.

————1984. Discontinuities in the distribution of some East African land snails. *In*: Solem, A. & van Bruggen, A.C., eds, *Word-wide snails. Biogeographical studies on non-marine Mollusca*. Leiden, The Netherlands: Brill, pp. 134–155.

VILLENA, M., APARICIO, M.T., BARATECH, L. & TEMPLADO, J. 1997. Los "ejemplaros typo" de las colecciones malacológicas del Museo Nacional de Ciencias Naturales. Volúmen II. *Monografías del Museo Nacional de Ciencias Naturales* **11**: 1–170, pls 1–3.

WINTER, A.J. DE. 1995. Gastropod diversity in a rain forest in Gabon, West Africa. *In*: van Bruggen, A.C., Wells, S.M. & Kemperman, Th.C.M., eds, *Biodiversity and conservation of the Mollusca*. Oegstgeest-Leiden, The Netherlands: Backhuys, pp. 223–228.

WINTER, A.J. DE & GITTENBERGER, E. 1998. The land snail fauna of a square kilometer patch of rainforest in southwestern Cameroon: high species richness, low abundance, and seasonal fluctuations. *Malacologia* **40**: 231–250.

WINTER, A.J. DE, GOMEZ, B.J. & PRIETO, C.E. 1999. *Sinistrexcisa*, a new genus of land snail from Central West Africa with four new species (Gastropoda: Pulmonata: Streptaxidae). *Journal of Molluscan Studies* **65**: 209–221.

WRONSKI, T. & HAUSDORF, T. 2010. Diversity and body-size patterns of land snails in rain forests in Uganda. *Journal of Molluscan Studies* **76**: 87–100.