NEW DATA ON SOUTHERN AFRICAN ACHATINIDAE (MOLLUSCA, GASTROPODA PULMONATA)

by

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With 18 text-figures and 1 plate

Increasing knowledge of the genital anatomy of the species of the African land snail family Achatinidae has greatly improved our understanding of the delimitation of the species and the intricate interrelationships of the various taxa (Mead, 1950). The genitalia of many achatinids are still unknown due to the absence of properly preserved animals. New data, mainly on the reproductive organs of recently collected material, are supplied here for two Southern African species, Archachatina sandgroundi Bequaert and A. dimidiata (Smith), which have now been dissected for the first time.

Acknowledgements are due to Mr. J. F. Peake and his staff at the British Museum (Natural History), London, Prof. K. J. Boss of the Museum of Comparative Zoology at Harvard University, Cambridge (Mass., U.S.A.), Dr. R. Kilias of the Zoologisches Museum der Humboldt-Universität, Berlin, Prof. A. R. Mead of the University of Arizona, Tucson (U.S.A.), and Dr. J. A. Pringle of the Natal Museum, Pietermaritzburg (South Africa), for assistance in various respects. The author repeatedly enjoyed the hospitality of the American Board Mission at Mount Selinda, Rhodesia, for which he is greatly indebted to the missionaries. Collecting trips to Rhodesia and the Transvaal from the author's then base at Pietermaritzburg were mainly financed through research grants received from the South African Council for Scientific and Industrial Research (C.S.I.R., Pretoria).

The following abbreviations have been used: alc. for alcohol, 1/d for the ratio length/major diameter of shells, which gives an indication of the shape of the specimen under discussion; BM for British Museum (Natural History), London; MRAC for Musée Royal de l'Afrique Centrale, Tervuren; NM for Natal Museum, Pietermaritzburg; RMNH for Rijksmuseum van Natuurlijke Historie, Leiden; ZMB for Zoologisches Museum der Humboldt-Universität, Berlin.

Archachatina (Tholachatina) sandgroundi Bequaert, 1950 (figs. 1-4)

Archachatina (Tholachatina) sandgroundi Bequaert, 1950, Bull. Mus. Comp. Zool. Harvard, 105: 202, pl. 2 fig. 3, pl. 6 fig. 4, pl. 20 fig. 4, pl. 57 fig. 3; Van Bruggen, 1965, Rev. Zool. Bot. Afr., 71: 80; Van Bruggen, 1970, S. Afr. Anim. Life, 14: 444 ¹).

The original description of *Archachatina sandgroundi* is adequate and matches all shells reported upon here. However, Bequaert obviously only had empty, probably somewhat weathered, shells at his disposal so that discrepancies may be noted when examining fresh material. Therefore an amended description is given below on the pattern of and using much of the original wording of Bequaert.

Adult shell small, slender, subulate or narrowly clavate, widest at lower third, the upper part of the body whorl and the spire forming a narrow cone with very blunt apex; imperforate, thin but fairly solid, translucent, showing the markings within the aperture, with a dull gleam when fresh. Whorls 6½-7¼, slightly convex, separated by narrow, weakly impressed sutures, apical whorls forming a broad, nearly hemispherical dome; the first flattened or even depressed, remainder gradually increasing in length and width. Body whorl long and narrow, under two thirds of the total length of the shell in front view, not more convex than penultimate whorl. Aperture long, but fairly wide, acuminate-ovate, about two fifths (always somewhat less than half) of the total length of the shell, with evenly curved, semi-elliptical outer margin. Inside bluish white. Outer lip thin and fragile, sharp. Parietal wall with a very thin, white to semitransparent, callus. Columella dark brown, yellowish brown or white, long and narrow, fairly strongly but evenly concave, obliquely truncate a short distance from the base. Apical whorls usually somewhat worn, but partly granulose, which sculpture rapidly changes into a distinct granulose decussation gradually turning into vertically elongate welts; from about the fifth whorl on the transverse engraved lines gradually weaken, being very superficial but still quite noticeable over the terminal half (above the periphery) of the body whorl; below the periphery the body whorl has only faint to very faint growth striae, but the transition at the periphery is very gradual; growth striae coarse below the finely and superficially crenulate sutures. Periostracum thin, dull, pale yellowish brown to light brown. Apical three whorls dull reddish yellow, sometimes even almost whitish in live specimens; remainder of shell straw-yellow to dark greenish yellow with reddish brown

¹⁾ The species is obviously inadvertently omitted by Knipper (1956: 342) in his list of species of the subgenus *Tholachatina* Bequaert, 1950.

or chestnut vertical streaks, straight, oblique or more or less wavy, usually narrowed toward the upper sutures, occasionally broken up, increasing in size towards the body whorl.

Table I
Measurements of shells of Archachatina sandgroundi Bequaert

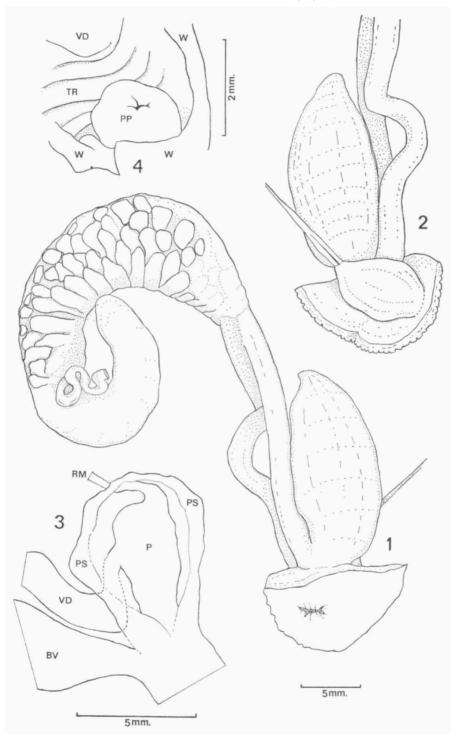
aperture									
length x	maj.	diam.	1/d 1	ength	x	maj.	diam.	whor1s	particulars
59.6 x	23.0	mm	2.59	24.0	x	14.1	nm	71	1959, RMNH
58.7 x	23.5	mm	2.49	24.0	x	14.1	mm	7	1959, RMNH
58.5 x	23 7	num	2.47	24.4	x	14.4	mm	7	1959, RMNH, empty shell
58.5 x	23.0	mm	2.54	24.5	x	13.0	mm	7	paratype ex literature
57.8 x	22.3	mm	2.59	23.3	x	14.0	mm	7	1965, RMNH
57.5 x	22.5	mm	2.55	24.0	x	11.5	mm	7	holotype ex literature
57.0 x	23.5	nm	2.43	25.5	x	11.5	mm	7	paratype ex literature
56.8 x	22.6	mmı	2.51	23.5	x	14.0	mm	63	1963, NM
56.6 x	22.0	mm	2.57	23.3	x	13.5	mm	61/2	1963, NM
56.5 x	24.0	mm	2.35	26.0	x	13.0	mm	7	paratype ex literature
55.5 x	22.0	nım.	2.52	24.0	x	11.5	mm	6 ½	paratype ex literature
55.4 x	21.1	mm	2.63	23.0	x	13.5	mm	61/2	1963, NM
55.0 x	22.5	mm	2.44	23.3	x	14.3	mm	6}	1965, RMNH
54.7 x	20.7	mm	2.64	21.5	x	12.7	mm	6 <u>1</u>	1963, NM
<u>+</u> 54 x 2	21.8	mm	-	23.0	x	12.7	mm	-	1965, RMNH, damaged empty shell
53.6 x	21.6	mm	2.48	23.0	x	13.0		6 ½	1959, RMNH

The measurements are shown in table 1, and may be summarized as follows: $53.6-59.6 \times 20.7-24.0$ mm, 1/d 2.35-2.64 (mean 2.49, average 2.52), $6\frac{1}{2}-7\frac{1}{4}$ whorls (16 adult shells). Specimens with shells of 52 mm and less are very probably juveniles. The last whorl of the largest shell (length 59.6 mm) measures 37.0 mm.

The living animal has a very characteristic colour pattern, which type of pattern however is known to occur throughout the genus and family (see e.g., the pattern of the other species discussed below). The body is very dark grey, almost black, with two lateral white (or at least a colour very much paler than the ground colour) longitudinal bands from the base of the small tentacles upwards to the large tentacles and alongside the foot; the posterior part of the foot is dark grey.

Three specimens were dissected (one of each of the three samples) in order to study seasonal and individual variation while at the same time trying to exclude differences caused by distortion during fixation and preservation. However, the genitalia of all three specimens are reasonably uniform.

At first sight the most striking feature of the reproductive organs, best



shown in the 1965 specimen (fig. 1), is the comparatively very large spermatheca 1) almost without a proper duct and inserted at a very low point on to the basal vagina. This has caused the basal complex to be quadripartite (fig. 2), consisting of penis, vas deferens, basal yagina, and spermatheca. The penis is completely ensheathed. The penial complex is short, thick and bulbous with an apically inserted penial retractor muscle, which is attached to the floor of the diaphragm. The very thick vas deferens, which always has one noticeable twist or loop not necessarily at the same place, reaches the peniovaginal angle and enters the penial sheath at about the middle, but this also varies in the three specimens studied. In longitudinal section (fig. 3) the penis sheath is shown to have a very thick wall; this also shows that the vas deferens enters the sheath at a point below that where it enters the penis itself. Upon opening the very thick and muscular penis a number of coarse muscular transverse ridges may be seen, probably enabling the penis to be contracted transversely in order to eject the sperm. The fairly spaceous lumen inside the penis is connected with the genital atrium by means of a distinct penis papilla or verge (terminology of Mead, 1950: 251) and a very limited prepuce that is hardly separated from the genital atrium (fig. 4). The surface of the penis papilla is distinctly warty or coarsely granulose. The basal vagina is about as thick as the vas deferens, while attention has already been drawn to the basally inserted, thus almost ductless spermatheca.

Bequaert (1950: 203) has compared the shell of Archachatina sandgroundi

I) The rigid spermatheca of the 1965 specimen was found to contain an amorphous yellowish white mass, presumably consisting of spermatozoa, and also about fifteen irregular little pellets of a pinkish brown colour and with a diameter of approximately 1 mm. A close scrutiny of these bodies, partly together with Prof. Mead, has led to the conclusion that these have to be considered artefacts. The inner lining of the spermatheca very probably secretes a substance which may "sustain the life and viability of the otherwise short-lived spermatozoa" (Mead, 1950: 279). This viscous substance was repeatedly found by Prof. Mead in the spermatheca of freshly killed achatinids. After the joint examination of the above pellets during the Geneva malacological congress, he wrote to me (8 October 1971): "... most likely could be this viscous substance which had suffered dehydration and hence coagulation in the preserving process. But this is only the most likely guess." The specimen in question was fixed and preserved in alcohol 70%, which in the field was subsequently also injected by means of a syringe.

Figs. 1-4. Archachatina sandgroundi Bequaert, Chirinda Forest (RMNH), genitalia. I, genitalia of 1965 specimen in ventral aspect. 2, basal genital structures of do. in dorsal aspect, same scale. 3, basal genital structures of 1959 specimen, longitudinal section through penis sheath, half-schematic. 4, bottom of opened penis to show prepuce, 1965 specimen. Abbreviations: BV = basal vagina, P = penis, PP = penis papilla with opening leading to genital atrium, PS = penis sheath, RM = penial retractor muscle, TR = transverse ridges inside the penis, VD = vas deferens (in fig. 4: point of entry of VD), W = wall of the penis.

with that of A. (T.) ustulata (Lamarck, 1821) and A. (T.) pentheri (Sturany, 1898). A. ustulata sometimes grows to a much larger size (shell length up to but usually much less than 88.0 mm, fide Van Bruggen, 1967: 23), and is geographically widely separated, occurring in the southeastern Cape Province. Moreover, the genitalia of A. ustulata (cf. Van Bruggen, 1967: 23 and fig. 10) are entirely different from those of A. sandgroundi, e.g., in having a bulbous spermatheca with a proper duct inserted much higher than is the case in A. sandgroundi. A. pentheri is a poorly understood species from Natal of which little material is available; the genital anatomy is as yet unknown, but differences in the shell seem to separate it from the Rhodesian species.

The genitalia of A. sandgroundi superficially resemble those of A. (T.) saskai Knipper (1956: 348 and figs. 3a-c). However, apart from a host of minor differences, A. saskai has no penis papilla. Its shell is easily distinguished from that of A. sandgroundi.

According to Mead (1950: 251-258, 268, 276, 283-285) a (long) prepuce combined with a penis papilla in the Achatinidae only occur in the genera Limicolaria Schumacher, 1817, and Limicolariopsis d'Ailly, 1910; the shells and genitalia of these genera are otherwise very different from those of A. sandgroundi. The prepuce of this species is very short or indeed almost non-existent; the penis papilla is quite different from those as yet known in both Limicolaria and Limicolariopsis. On the other hand A. sandgroundi may well share its penis papilla pattern with other species in the subgenus Tholachatina; of the few species dissected data on the inside of the penis are not always available. In view of our as yet limited knowledge of the relationships of the species in the genus Archachatina it seems futile to further dwell upon the relative position of A. sandgroundi.

Archachatina sandgroundi was described from the Chirinda Forest, Mount Selinda, on the Rhodesian Eastern Escarpment. For the time being it is considered endemic to the Chirinda Forest. This forest enjoys a geographically somewhat isolated position and has a number of endemic elements among its fauna (Van Bruggen, 1961). Some of these so-called endemics have subsequently been shown to be more widely distributed in the forests of the Eastern Escarpment, both in Rhodesia and Mozambique. However, so far malacological explorations in this area in 1959, 1963, and 1965 by the present author and his wife have failed to produce A. sandgroundi anywhere else but at Mount Selinda. The Chirinda Forest has an average elevation of 3600 ft. which equals about 1100 m.

Three samples have been studied: 14 to 26 January and 6 to 8 February 1959, A. C. van Bruggen (RMNH, alc. and dry); 7 to 13 February 1963,

A. C. and W. H. van Bruggen (NM, alc. and dry); 9 November 1965, A. C. and W. H. van Bruggen (RMNH, alc. and dry).

Within the Chirinda Forest A. sandgroundi is not altogether rare, although by no means common. In 1959 (wet season) five specimens were collected in 14 days, in 1963 (wet season) six specimens in seven days by two persons and in 1965 (dry season) three specimens by two persons in the course of one day. Its cryptic colour on the forest floor contributes to its protection. According to the present author's field notes it was found along the Gungunyana trail, a forest track leading to the remains of Swynnerton's house, and along the path to the Big Tree. This snail is usually found on the ground, on leaves of low shrubs or low on tree trunks. At least nine of the 14 shells examined and at least two (if not three) of the four shells figured by Bequaert (1950) exhibit repairs which may have been necessitated by damages sustained by falling from trees. The nature of these damages confirms that the species does probably not climb beyond a few feet onto the boles of forest trees.

Apart from the type lot in the Museum of Comparative Zoology at Harvard University, Cambridge (Mass., U.S.A.) and the present material, there are some specimens in the National (formerly Coryndon) Museum, Nairobi (Kenya) (Verdcourt in litt., 1961) and in the Transvaal Museum, Pretoria (South Africa). The Chirinda Forest enjoys quite a reputation among Southern African zoologists and the existence of more material in Rhodesian and South African museums is to be expected. The American Board Mission, established at Mount Selinda since 1893 and with strong New England ties, has indirectly caused the species to be discovered at Harvard. The collector, Dr. Jack Sandground, who visited Mount Selinda mission station in 1930 in connection with a medical research project, sent the first specimens in the same year to Dr. W. J. Clench at the Cambridge museum. Thanks to the various mission people there may thus be odd specimens of A. sandgroundi also in other American collections. There are no specimens in the British Museum (Natural History), which is surprising in view of the local collecting activities of Sir Guy Marshall and C. F. M. Swynnerton (cf. Van Bruggen, 1961: 65).

To sum up: A. sandgroundi is easily recognized because of its shell and genitalia. On account of its geographically isolated position it may for the time being be considered endemic to the Chirinda Forest.

Archachatina (Tholachatina) dimidiata (E. A. Smith, 1878) (figs. 5-18, pl. 1)

Achatina dimidiata Smith, 1878, Quart. J. Conch., 1: 348; Craven, 1880, Proc. Zool. Soc. Lond.: 616; Paetel, 1889, Cat. Conch.-Samml., 2: 239; Smith, 1890, Ann. Mag. Nat.

Hist. (6), 6: 392; Melvill & Ponsonby, 1898, Proc. Malac. Soc. Lond., 3: 178; Sturany, 1898, Denkschr. Kais. Akad. Wiss. Math.-Naturw. Cl., 67: 591 (55); Connolly, 1912, Ann. S. Afr. Mus., 11: 193; Connolly, 1922, Proc. Malac. Soc. Lond., 15: 70, 76; Connolly, 1939, Ann. S. Afr. Mus., 33: 3061).

Cochlitoma dimidiata; Pilsbry, 1904, Man. Conch. (2), 17: 95, pl. 32 fig. 6 (col., 1905); Kobelt, 1909, Abh. Senckenb. Naturf. Ges., 32: 66.

Archachatina (Tholachatina) dimidiata; Bequaert, 1950, Bull. Mus. Comp. Zool. Harvard, 105: 201; Van Bruggen, 1965, Rev. Zool. Bot. Afr., 71: 80.

Archachatina (Tholachatina) d. dimidiata; Knipper, 1956, Veröff. Ueberseemus. Bremen (A), 2: 342.

Achatina Schencki Von Martens, 1889, Sitz.-ber. Ges. Naturf. Fr. Berlin: 164; Von Martens, 1894, Conch. Mitt., 3 (3): 8, pl. 43 fig. 3 (erroneously cited as pl. 45) (col.).

Achatina schencki; Sturany, 1898, Denkschr. Kais. Akad. Wiss. Math.-Naturw. Cl., 67: 593 (57); Connolly, 1912, Ann. S. Afr. Mus., 11: 200.

Achatina schrencki (sic!); Gude, 1899, J. Malac., 7: 90.

Cochlitoma schencki; Pilsbry, 1904, Man. Conch. (2), 17:96, pl. 5 fig. 1 (col.); Kobelt, 1909, Abh. Senckenb. Naturf. Ges., 32:66.

Achatina dimidiata var. schencki; Connolly, 1939, Ann. S. Afr. Mus., 33: 306.

Archachatina (Tholachatina) dimidiata schencki; Bequaert, 1950, Bull. Mus. Comp.

Zool. Harvard, 105: 201; Knipper, 1956, Veröff. Ueberseemus. Bremen (A), 2: 342.

Originally Achatina dimidiata and A. schencki were described as separate species. Connolly (1939: 306) was the first to officially connect the two forms: he considered A. schencki to be a variety of A. dimidiata. From 1950 (Bequaert, 1950: 201) both have been interpreted as subspecies of a polytypic species. Bequaert was the first to correctly classify it under the genus Archachatina Albers, 1850, in the new subgenus Tholachatina Bequaert, 1950. Old labels accompanying the type of Achatina schencki show that various malacologists already had their doubts about keeping it separate from A. dimidiata. In 1933 Bequaert labelled the specimen under discussion as being A. dimidiata. but there was already a much older label to that effect. However, he subsequently changed his mind as witnessed by his monograph (1950: 201). Renewed studies of the two type specimens and abundant new material have convinced the present author that both names are indeed synonymous. A redescription follows below.

Adult shell moderately large, fairly slender, elongate-ovate, widest below mid-length, the upper part of the body whorl and the spire forming a slender cone with very blunt apex; imperforate, thin but fairly solid, translucent, with a noticeable gleam when fresh. Whorls 6½-7¼, slightly convex, separated by narrow, deeply impressed sutures, apical whorls forming a broad, nearly hemispherical dome; the first flattened or almost depressed, remainder gradually increasing in length and width. Body whorl

¹⁾ Nec Achatina dimidiata Von Martens, 1889; this author proposed a new name for his species, A. infrafusca Von Martens, 1897, now considered to be a form of A. balteata Reeve, 1849 (fide Bequaert, 1950).

long and moderately narrow, more than two thirds of the total length of the shell in front view, not more convex than penultimate whor! Aperture long, but wide, acuminate-ovate, always (slightly) more than half the total length of the shell, with evenly curved, semi-elliptical outer margin. Inside yellowish or brownish white. Outer lip thin and fragile, sharp. Parietal wall with a very thin, white to semitransparent callus. Columella dark brown, yellowish brown or white, long and narrow, fairly strongly but evenly concave, obliquely truncate a short distance from the base. Apical whorls usually somewhat worn, but partly granulose, which sculpture rapidly changes into a distinct granulose decussation gradually turning into vertically elongate welts; from about the fifth whorl on the transverse engraved lines gradually weaken, being almost absent over the terminal half of the body whorl; there is hardly any transition in sculpture at the periphery of the body whorl; growth striae coarse below the finely and superficially crenulate sutures.

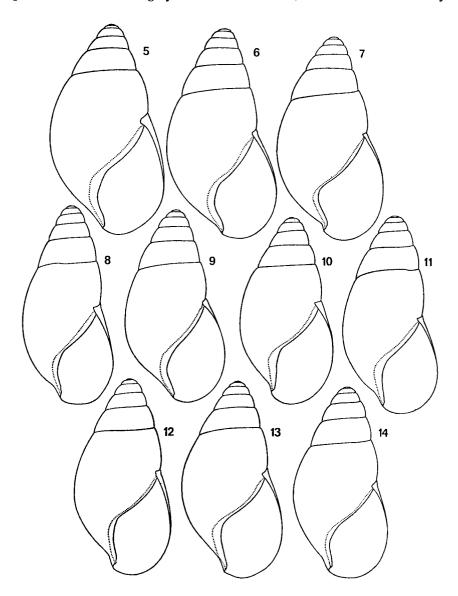
TABLE 2

Measurements of shells of Archachatina dimidiata (Smith); ex alc. = shell from which the body was removed for anatomical examination, MFR = Mariepskop Forest Reserve. See also figs. 5-14.

		aperture		
length x maj. diam.	1/d	length x maj. diam.	whorls	particulars
79.0 x 44.0 mm	1.79	47.6 x 25.0 mm	-	Connolly, 1939: 306
78.5 x 43.5 mm	1.80	-	-	holotype shell, BM, pl. 1
73.2 x 34.2 mm	2.14	37.6 x 25.1 mm	7 ₺	MFR,NM, empty shell, fig. 6
72.9 x 34.3 mm	2.12	-	-	MFR,NM, alc.
71.3 x 36.6 mm	1.95	36.0 x 24.5 mm	7	holotype shell A. schencki, ZMB, fig.5
71.2 x 33.9 mma	2.10	-	-	MFR,NM, alc.
71.0 x 34.6 mm	2.05	-	7	MFR,NM, ex alc., fig.7
71.0 x 32.5 mm	2.18	-	-	MFR,NM, alc.
71.0 x 31.8 mm	2.25	-	-	MFR,NM, alc.
70.1 x 34.8 mm	2.01	-	-	MFR,NM, alc.
70.0 x 35.6 mm	1.97	38.0 x 20.5 mm	6	Connolly, 1939: 307
70.0 x 31.2 mm	2.24	-	7	MFR,NM, empty shell, fig.11
69.8 x 30.8 mm	2.27	-	71	MFR,NM, ex alc., fig.8
69.5 x 40.4 mm	1.72	40.0 x 23.0 mm	-	Connolly, 1939: 306
69.0 x 32.7 mm	2.11	-	6	MFR,NM, ex alc., fig.13
68.6 x 33.3 mm	2.06	-	6}	MFR,NM, ex alc., fig.12
68.3 x 33.3 mm	2.05	-	-	MFR,NM, alc.
67.9 x 31.3 mm	2.17	-	-	MFR,NM, alc.
67.7 x 31.4 mm	2.16 [.]	•	6}	MFR,NM, empty shell, fig.14
67.1 x 32.6 mm	2.06	34.5 x 22.5 mm	6}	MFR,NM,empty shell, fig.9
66.3 x ± 35 mm	<u>+</u> 1.87	-	61	MFR,NM, ex alc., base damaged, fig.10

Last whorl: 65.0 mm (length shell 79.0 mm), 53.0 mm (73.2 mm), 50.4 mm (71.3 mm), 56.5 mm (70.0 mm), 54.0 mm (69.5 mm), 48.0 mm (67.1 mm).

Consequently on the whole the shell does not exhibit any well-marked sculpture. Periostracum thin, dull, pale yellowish brown to dark brown. Apical three whorls dull greyish or reddish brown; remainder of shell fairly



Figs. 5-14. Archachatina dimidiata (Smith), outline of shell to show individual variation. 5, holotype shell of Achatina schencki Von Martens (cf. table 2). 6-14, Mariepskop Forest Reserve, refer to table 2 for measurements and particulars. H. Heijn del.

uniform, yellowish or greenish brown or olive, sometimes almost dark chestnut without any trace of streaks. Many specimens have the body whorl distinctly bicoloured, the upper half of the whorl being noticeably darker than the lower half, but without a well-marked demarcation line.

The measurements are shown in table 2, and may be summarized as follows: $66.3-79.0 \times 30.8-44.0$ mm, 1/d 1.72-2.27 (mean 1.99, average 2.06), $6\frac{1}{2}-7\frac{1}{4}$ whorls (21 adult shells).

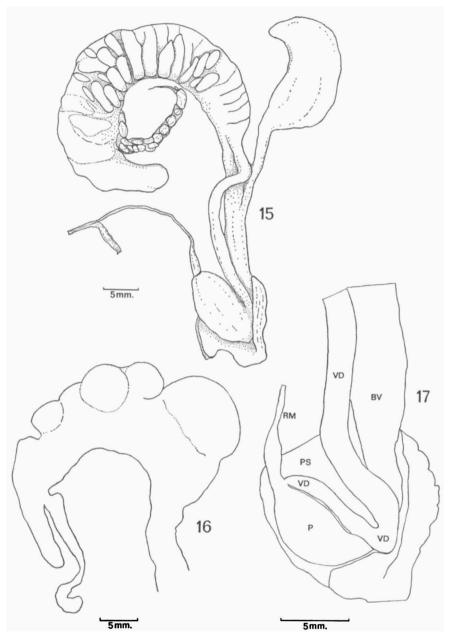
The type shell of Achatina schencki was figured in colour by Von Martens in 1894. The figure available to the present author (copy in 'Artis' library, Amsterdam) is good and accurate, but the actual specimen is now (1971) much darker and the two colour zones on the body whorl are much less evident. It is possible that the shell has darkened in the course of the many decades since it was collected. The type of A. dimidiata still shows quite noticeable bands of different colour intensity. The Mariepskop series shows that there exist all kinds of intermediates and that contrasting colours of the upper and lower portions of the body whorl in itself have no diagnostic value.

A. dimidiata and A. schencki were kept apart by Connolly only by their different contours, A. schencki having a "more slender contour" (Connolly, 1939: 307). Figs. 5-14, pl. 1 and table 2 show that all intermediates are present and that anyhow the differences between the respective type specimens are really not all that significant.

The living animal has a dark grey body with two much paler lateral longitudinal bands from the base of the small tentacles upwards to the large tentacles and alongside the foot (cf. Archachatina sandgroundi, see above).

Five specimens from the Mariepskop population with shell lengths of 71.0, 69.8, 69.0, 68.6, and 66.3 mm, respectively, (cf. table 2, "ex alc.") were dissected in order to obtain the reproductive organs.

The genitalia (fig. 15) are comparatively large, which may have been caused by the fact that all were collected in the reproductive season. The specimens with shells of 69.8 and 66.3 mm have large oblong-ovate eggs of varying size in the uterus and visible from the outside, viz., five (from 13.7 × 9.6 to 7.2 × 7.0 mm) and one, respectively; all have well calcified shells (fig. 16). The largest egg and a smaller one were broken open, but were only found to contain a firm, coagulated albuminous mass; in the former the egg shell is 0.18 mm thick. The penis is completely ensheathed, the complex being thick and bulbous, with a (sub)apically inserted retractor muscle, which in all specimens dissected is attached to the columellar muscle together with the right tentacular retractor. Shortly after leaving the penis sheath the retractor muscle is kept down over a short distance by a strong



Figs. 15-17. Archachatina dimidiata (Smith), Mariepskop Forest Reserve. 15, genitalia of specimen with shell length of 69.0 mm, cf. fig. 13. 16, genitalia of specimen with five eggs in the uterus, shell length 69.8 mm, cf. fig. 8. 17, basal genitalia of specimen of fig. 15, with the penis sheath cut to expose penis and vas deferens. Abbreviations: BV = basal vagina, P = penis, PS = penis sheath (opened and partly removed), RM = penial retractor muscle, VD = vas deferens.

transverse ligament (not shown in the figures, but quite obvious when dissecting). The vas deferens is thick and does not exhibit any noticeable twisting; it reaches the peniovaginal angle and enters the penis sheath at its very bottom. The large spermatheca enters the vagina at about or below the middle of the distance between the genital atrium or peniovaginal angle and the point where male and female conduits become firmly attached to each other. The spermatheca has a fairly long duct and varies from bulbous to clavate; its wall is thin. Upon opening the very thick and muscular penis sheath the vas deferens is found to double up onto itself by entering at the bottom of the sheath and entering the penis itself at its apex, running parallel to the penis almost over its entire length (fig. 17). Inside the penis sheath penis and vas deferens are kept together by numerous tough strands of tissue and ligaments. The large penis is bulbous and flattened at its backside where the vas deferens lies close to it. Upon opening the penis the lumen was found to be fairly spacious while the thick muscular wall shows a pattern of coarse vertical ridges. The penis of Archachatina (Tholachatina) simplex crawfordi (Morelet, 1889) as described by Mead (1950: 247) is even "concave and infolded" where the vas deferens runs parallel and is attached to it. The penis of A. dimidiata is only slightly concave at that point, which is also clearly shown inside the longitudinally opened penis.

At first sight the shell of A. dimidiata somewhat resembles that of A. montistempli Van Bruggen, 1965, particularly as far as the colour is concerned. However, the latter species, apart from being larger, much more slender, and having from ½ to 1½ more whorls, belongs to another group of species characterized by a very marked sculpture on the whorls. Connolly (1939: 305) classifies A. dimidiata together with A. (T.) burnupi (Smith, 1890) in group (iii) of Southern African Achatina, which group he describes as "Usually large shells with unusually broad apex; last whorl smooth and glossy." Archachatina burnupi is somewhat smaller than the other species and a bit more squat, also having a comparatively larger body whorl and narrower aperture; its colour is pale, i.e. tawny or olive yellow. This poorly known species is confined to montane forests over 5000 ft. (= about 1500 m) in the Natal Drakensberg range to the south of where A. dimidiata occurs. Probably both species are closely allied and A. burnupi may be a southern subspecies of the latter if indeed quite allopatric. So far the genital anatomy of A. burnupi has not been studied so that further discussion about possible relationships is as yet entirely premature.

The genitalia of A. dimidiata are fairly typical for the genus: the penis is enlarged though still completely confined to the sheath. The main features are the peculiar penis and the part of the vas deferens contained inside the

penial sheath. This so far is only known to occur in A. simplex crawfordi (see above). In this widely distributed (Natal and eastern Cape Province) species this is the only form that has been studied as regards its reproductive organs. However, the shell of A. simplex (Smith, 1878) is utterly different from that of A. dimidiata. Conclusions concerning relationships are very probably only to be drawn from similarities in both the genitalia and the shell, so that much of the present work has not yet reached a stage where definite conclusions may be drawn.

Archachatina dimidiata is distributed over the forests on the eastern slopes (approximately between 4000 and 6000 ft. = about 1200 and 1800 m) of the

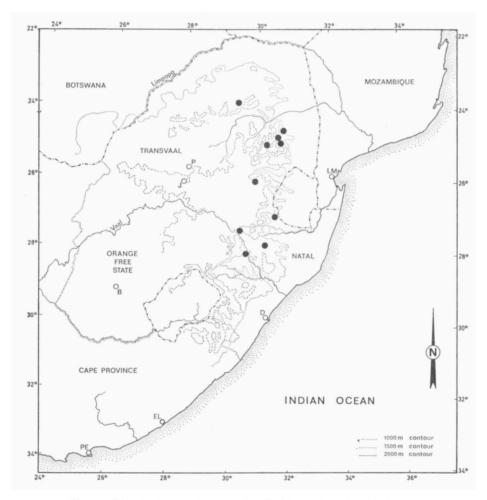


Fig. 18. Distribution of Archachatina dimidiata (Smith). H. Heijn del.

Drakensberg range in Natal and the Transvaal between Ladysmith and Pietersburg. It may have disappeared over much of its range in the wake of the destruction of much of the indigenous forest, particularly in Natal and southeastern Transvaal, although it may locally still occur in scattered remnants of forest. At least at Mariepskop it is still quite common. The following locality records are available (fig. 18) in which the altitudes of the towns are given, although it is obvious that the species occurs only in the surrounding forest, while at the same time the relief of the country is subject to a great deal of variation.

Natal: Dundee (4098 ft. = about 1250 m); Vryheid (3867 ft. = about 1200 m); Majuba (approximately 5000 ft. = about 1500 m) (all fide Connolly, 1939). Transvaal: Carolina (5610 ft. = about 1700 m); Piet Retief (4171 ft. = about 1300 m) (both fide Connolly, 1939); "Eastern slope of the Drakensberg Mts, at Lydenburg Gold-fields", A. E. Craven (BM 1877.12.17.6, holotype and juv. paratype) (Lydenburg, 4820 ft. = about 1500 m); Mac Mac (4241 ft. = about 1300 m), between Sabie and Graskop, 20 July 1886, A. Schenck (ZMB, holotype of Achatina schencki); Pilgrim's Rest (approximately 5000 ft. = about 1500 m; fide Connolly, 1939); Mariepskop Forest Reserve, 24°33′S 30°51′E, NE. area (Nature Reserve), 4500 ft. = about 1400 m, 28-29 January 1966, A. C. and W. H. van Bruggen (NM, alc. and dry; alc. duplicates in BM, MRAC, RMNH); Shiluwane (Pietersburg District; Pietersburg, 4269 ft. = about 1300 m; fide Connolly, 1939).

According to field notes the species is common at Mariepskop. All specimens were taken on the forest floor among grass and herbs along the track except for a single snail which was found on the bole of a tree at about 5 ft. from the ground. The snails were very active after heavy summer rains; various smaller species of terrestrial molluscs were also collected but no other achatinids. The chestnut to olive shells and dark grey bodies of A. dimidiata afford it a seemingly satisfactory camouflage against visually inclined predators.

In Acocks's classification (1950: 43) the forest at Mariepskop belongs to the "Inland tropical forest types. 8. North-eastern mountain sourveld". Acocks writes: "Extensive patches of it survive on the mountain range between Nongoma and Vryheid (Ceza, Ngome and other forests); northwards it occurs on the Louwsburg heights, the mountains of Swaziland, the mountains south and west of Barberton, there passing on to the Drakensberg and continuing northwards to the Zoutpansberg, with outliers on the higher, wetter parts of the mountains westwards to the Waterberg. The rainfall is high, ranging on the average from 35 to over 75 inches per

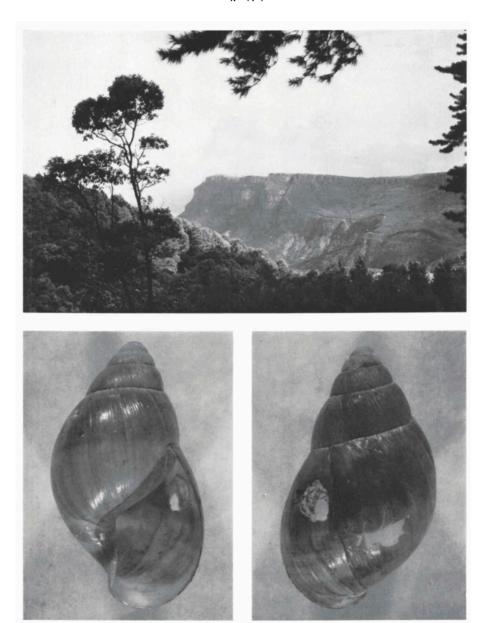
annum, but it has been declining steadily for about 15 years." "The climax all through will have been high forest, and although miles of this forest survive, especially north of the Crocodile River along the Drakensberg escarpment, most of it has been replaced by sour grassveld,..." Van der Schijff (1964) has published some very interesting notes on the Mariepskop complex. Part of his summary reads: "Evergreen montane forest with strong tropical affinities occurs in deep kloofs and in slopes facing south and south-east and is the most conspicuous component of the vegetation of this area." He also mentions that the mean annual rainfall over a period of 25 years at Mariepskop Forest Station is 53.78 inches or 1366.89 mm. Van der Schijff's photograph of the forest (fig. 5 on p. 49) gives a good impression of the type of vegetation where A. dimidiata was obtained. Large tracts of indigenous forest are surrounded by plantations; few flowers were seen in the forest. There are large, partly or wholly overgrown, rocks scattered throughout the part of the forest visited by the present author in 1966.

One may conclude that A. dimidiata is a well-defined species by virtue of its shell and genitalia, and its somewhat limited distribution.

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Top: Mariepskop Mountain seen from an adjoining ridge, January 1966. Photograph Mrs. W. H. van Bruggen-Gorter. Bottom: holotype shell of *Achatina dimidiata* Smith, BM 1877.12.17.6. Photographs courtesy British Museum (Natural History).