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STUDIES IN THE ACHATININAE, A GROUP  
OF AFRICAN LAND SNAILS

BY JOSEPH C. BEQUAERT

WITH EIGHTY-ONE PLATES

CAMBRIDGE, MASS., U. S. A.  
PRINTED FOR THE MUSEUM  
September, 1950

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No. 1. — *Studies in the Achatininae, a Group of African Land Snails*

By JOSEPH C. BEQUAERT

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CONTENTS

	PAGE
Introduction.....	4
Acknowledgments.....	6
Genus <i>Achatina</i> Lamarck.....	7
1. Subgenus <i>Achatina</i> , proper.....	9
West African Species of <i>Achatina</i> , proper.....	14
<i>Achatina (Achatina) achatina</i> (Linné).....	16
<i>Achatina (Achatina) balteata</i> Reeve.....	39
2. Subgenus <i>Pintoa</i> Bourguignat.....	47
3. Subgenus <i>Tripachatina</i> Bourguignat.....	48
4. Subgenus <i>Lissachatina</i> , new.....	49
East African Species of <i>Lissachatina</i> .....	50
<i>Achatina (Lissachatina) fulica</i> Bowdich.....	50
<i>Achatina (Lissachatina) lactea</i> Reeve.....	94
<i>Achatina (Lissachatina) panthera</i> (Férussac).....	98
<i>Achatina (Lissachatina) zanzibarica</i> Bourguignat.....	113
<i>Achatina (Lissachatina) allisa</i> Reeve.....	121
<i>Achatina (Lissachatina) delorioli</i> Bonnet.....	122
<i>Achatina (Lissachatina) iredalei</i> Preston.....	123
<i>Achatina (Lissachatina) albopicta</i> E. A. Smith.....	127
<i>Achatina (Lissachatina) reticulata</i> Pfeiffer.....	132
5. Subgenus <i>Euaethiopia</i> , new name.....	136
6. Subgenus <i>Leptocalina</i> Bequaert and Clench.....	136
7. Subgenus <i>Leptocallista</i> Pilsbry.....	137
8. Subgenus <i>Leptocala</i> Ancey.....	138
Genus <i>Archachatina</i> Albers.....	138
1. Subgenus <i>Archachatina</i> , proper.....	139
2. Subgenus <i>Calachatina</i> Pilsbry.....	140
<i>Archachatina (Calachatina) marginata</i> (Swainson).....	140
<i>Archachatina (Calachatina) ventricosa</i> (Gould).....	166
<i>Archachatina (Calachatina) degneri</i> Bequaert and Clench.....	172
<i>Archachatina (Calachatina) rhodostoma</i> (Philippi).....	176
3. Subgenus <i>Megachatinopsis</i> Bequaert and Clench.....	180
<i>Archachatina (Megachatinopsis) knorrii</i> (Jonas).....	180
<i>Archachatina (Megachatinopsis) siderata</i> (Reeve).....	185
<i>Archachatina (Megachatinopsis) papyracea</i> (Pfeiffer).....	186
<i>Archachatina (Megachatinopsis) purpurea</i> (Gmelin).....	193

4. Subgenus <i>Tholachatina</i> , new .....	200
<i>Archachatina (Tholachatina) sandgroundi</i> , new species .....	202
<i>Archachatina (Tholachatina) meadi</i> , new species .....	204
<i>Archachatina (Tholachatina) weberi</i> , new species .....	205
Index .....	209

## INTRODUCTION

Several years' acquaintance with the Achatinidae (or subfamily Achatininae, as some prefer), both in the laboratory and in their native African haunts, aroused the desire to write a Monograph that might do justice to these beautiful snails, which comprise the largest known living terrestrial mollusks. This project began to assume more concrete form about 1933, when I obtained a grant-in-aid from the Milton Research Fund of Harvard University. It enabled me to visit the more important European collections for the purpose of studying the type specimens of earlier malacologists. I have also had the opportunity of seeing most of the Achatinidae in the North American museums.

The writing and publication of a complete revision of all Achatininae, as a single work, is a task of such magnitude that I could hardly anticipate completing it at present with the limited time available for malacological studies. In order to ensure that at least part of my observations may be used by other students, it seems advisable to publish it by sections, as opportunity arises. In the present installment I shall deal primarily with certain species which were the object of recent anatomical studies by Dr. A. R. Mead or of ecological field work by Dr. F. X. Williams. In order to provide reliable names for these species it was necessary to revise their characters and synonymy and those of their close relatives. These investigations eventually led me to a comprehensive classification of the known species of *Achatina* and *Archachatina*.

I was fortunate to observe and collect several species during the past forty years on my journeys in Tropical Africa. It is my belief that field observations on any group of animals, not only furnish the basis for an understanding of their ecology, but also help considerably in tracing taxonomic relationships and in evaluating the extent of intra-specific variation. In addition I have had before me unusually large series collected by several of my colleagues, particularly by Dr. A. R. Mead in West Africa, and by Mr. A. Loveridge and Dr. F. X. Williams in East Africa. Material was studied from the following museums: Museum of Comparative Zoölogy (cited as M.C.Z.), United States National Museum (U.S.N.M.), Academy of Natural Sciences of

Philadelphia (Ac.N.S.Phila.), American Museum of Natural History, New York (A.M.N.H.), Carnegie Museum, Pittsburgh (Carn.M.), Chicago Natural History Museum (Chic.M.), Museum of Zoology of the University of Michigan (M.U.Mich.), Bernice P. Bishop Museum, Honolulu (Bish.M.), British Museum (Natural History) (Brit.M.), 's Rijksmuseum at Leiden (Leid.M.), Natura Artis Magistra in Amsterdam (Amst.M.), University Zoological Museum at Copenhagen (Copenh.M.), Naturhistoriska Riksmuseum at Stockholm (Stock.M.), Zoological Museum at Berlin (Berl.M.), the Hamburg Museum (Hamb.M.), Senckenberg Museum at Frankfurt (Frankf.M.), Royal Natural History Museum at Brussels (Brus.M.), Congo Museum at Tervuren (Terv.M.), and National Museum of Natural History at Paris (Par.M.). In addition I had the privilege of examining the private collections of S. Putzeys, P. Dautzenberg, and M. Connolly, all three since deceased.

*Measurements.* I have followed with slight modifications the method of my earlier paper on the Strophocheilidae. All dimensions were measured to the half-millimeter only. Whenever sufficient material was available, I have attempted to show how extremes in size and shape are connected by intermediate sizes. It should be noted that, like all large snails, the Achatininae tend to produce occasional giants and dwarfs, which are invariably pounced upon to erect new "rare" species, the boon of dealers and the pride of collectors, but likely to confuse the student of variation and relationship for many years after. It is doubtful whether such specimens ever are of more taxonomic importance than sinistral, umbilicate and other abnormalities. The *length* (or height) is that of the longest vertical axis of the shell, from the tip of the spire to the basal edge of the outer lip. The *greatest width* is the largest diameter in front view, measured at right angles to the vertical axis, from the left margin of the body-whorl to the extreme outer edge of the outer lip. In the aperture, the *length* is the longest obtainable distance from the insertion of the outer lip on the parietal wall to the basal edge of the outer lip; the *width* is measured at right angles to the length as the greatest distance from the inner edge of the columella to the outer lip or to the outer margin of the rim, if the latter is expanded. This seems to be the only practical method of determining the width of the aperture in the Achatininae, which do not show any particular outer accretions on the lip after full adult size is reached. When the lip thickens in old age, it is by additions to the inner layer of the margin and does not change the total width of the aperture.

*Bibliography.* The bibliographies for the several species and subspecies are arranged chronologically. An attempt has been made to

make them as complete as possible. With very few exceptions the references have been verified with the original publications. Particular pains have been taken to determine the actual date of publication, which immediately follows the author's name in each citation. References listed in square brackets are to vernacular or nude names or to publications without standing in binomial nomenclature. Many of the references are no doubt of little or no importance; but in the process of collecting them, some interesting and valuable information was brought to light in obscure publications.

I have reproduced the original descriptions of all newly named forms, either as printed if they were in English or Latin, or in translation if they were in some other language. This seemed essential for an understanding of my interpretation of the several names. It will also allow future students to agree or disagree with my conclusions. For the same reason I have included in my illustrations copies of most of the original figures or, whenever possible, photographs of the older types. Words inserted in square brackets in the original descriptions or elsewhere, were added by myself for needed explanation. This includes the metric equivalents of other measures of length.

#### ACKNOWLEDGMENTS

The present study of *Achatina* and *Archachatina* is primarily intended to provide the necessary taxonomic basis for the anatomical researches of Dr. A. R. Mead and the ecological field observations of Dr. F. X. Williams. These are published as two separate articles in the same volume of the Museum Bulletin, following the present paper. Much of the East African material on which Dr. Mead's and my own work are based was obtained by Dr. F. X. Williams during investigations sponsored by the Insect Control Committee for Micronesia of the Pacific Science Board of the National Research Council. The United States Navy and particularly the Office of Naval Research not only provided the funds and transportation for Dr. Williams' field work but were also most efficient and helpful in delivering live material for dissection. The same Government agencies made it possible, through appropriate grants, to illustrate and publish in their present form the three papers, covering the taxonomy, anatomy, and ecology of *Achatina*. These advantages were obtained chiefly through the steady interest shown in the *Achatina* work by Mr. Harold J. Coolidge, to whom the authors are under great obligations.

I am particularly indebted for information, photographs and other assistance to my friends and colleagues here and abroad, the late



Major M. Connolly, Mr. T. Pain (in London), Dr. Harald Rehder and Mr. R. Tucker Abbott (at the U. S. National Museum), Dr. H. A. Pilsbry and Mr. C. W. Wurtz (at the Philadelphia Academy of Natural Sciences), Mr. John Armstrong and Mr. F. Weir (at the American Museum of Natural History), Dr. E. Fischer-Piette (at the Paris Museum), and Dr. H. Mermod (at the Geneva Museum). As usual, my colleagues at the Museum, Mr. W. J. Clench and Miss Ruth Turner, have helped me in every possible way with routine matters and with critical advice. Unless otherwise indicated, photographs were made by Mr. F. P. Orchard. I owe to the great kindness of Dr. E. Fischer-Piette photographs of Petit's, Bourguignat's, Révoil's, Crosse's and Germain's types, several of which had not been figured before. Some of these types are part of the collections of the Paris National Museum; others are in the collection of the "Journal de Conchyliologie," at present in the custody of Dr. Fischer. I acknowledge my indebtedness also to the Trustees and Authorities of the British Museum (Natural History) for contributing the photographs of types reproduced in Pl. 81, and to Dr. W. J. Rees, Assistant Keeper of Mollusca, for kindly supervising the making of these photographs.

### Genus ACHATINA Lamarck

The genus *Achatina* comprises in the present paper all Achatininae with the base of the columella more or less truncate (as a rule distinctly, rarely rather weakly), a conical, pointed spire with a narrow apex, and a simple outer lip, usually sharp and thin, more rarely thickened, never reflexed, although in some species slightly expanded or flaring at the base. The nepionic (or embryonic) whorls, formed in a small egg (9 mm. or less in length), are comparatively narrow, either mostly granulose or smooth. All species are normally dextral.

*Achatina* is endemic throughout continental Africa south of the Sahara. As known at present, its northern limits are Gambia (14° N.) in the West, the region of Lake Chad (about 14° N.) and the southern Anglo-Egyptian Sudan (about 8° N.) in the center, and southern Abyssinia (about 7° 30' N.) and Somaliland (about 5° N.) in the East. These limits are as yet approximate, as some of the published records from the Sudan are open to question, being possibly based on dead shells carried beyond the true range by man or even on shells bearing erroneous localities. In South Africa the genus extends to the Orange River on the West Coast and to the District of George on the South Coast of Cape Province. One species has been found occasionally introduced near Cape Town, but has not become established. *Achatina*

does not occur with certainty in any of the islands of the Gulf of Guinea. It appears to be indigenous in the smaller islands close to the East African coast, including the Island of Zanzibar. Its presence in Madagascar may be due to relatively recent introduction by man, as both species of the genus now found there live also on the East African mainland. The genus was certainly carried by man to Mauritius, Comoros, Réunion and Seychelles. Its recent further spread by man to India, the East Indies, the Orient and the Pacific Islands is more fully considered in the discussion of *A. fulica*.

*Subgenera of Achatina.* Numerous trivial names have been proposed in combination with the generic term *Achatina*. Many of these should be referred to other genera, some of them not now included in the family Achatinidae. Others should be relegated to the synonymy or reduced to less than specific rank. Such reevaluation leaves nevertheless a fairly large number of valid species in *Achatina*, even as here restricted, with the definition given above. While their total number is difficult to determine at present, I surmise that it will be somewhere between 65 and 80.

It is both desirable and practical to subdivide this rather large aggregate into natural groups, which may be conveniently treated as subgenera. I propose to accept eight of these, based on characters seemingly of more than specific value, and possibly indicating main trends of evolution within the genus. I stress in the first place the presence or absence of granulose sculpture on the nepionic shell or protoconch, formed within the egg. I also use to some extent the sculpture of the post-nepionic whorls, the structure of the columella, the shape of the aperture and the general outline of the shell. Whether or not the anatomy of the soft parts will support this classification must be left an open question for the present. Only a few species, belonging to three subgenera, have been examined in this respect and some of them very superficially.

In view of the importance which I attach to the sculpture of the nepionic whorls, it should be emphasized that, unless the earliest whorls are clearly granulose in the adult, this character must be studied in very young, preferably newly hatched shells. Where such early stages are not available or have never been examined, the species must sometimes be placed provisionally with what appear to be its closest relatives, particularly if the earliest whorls are smooth or lacking. Robson's statement (1921, Proc. Zool. Soc. London, p. 264) that "examination of a number of examples in the British Museum Collection has made it clear that the sculpture of the embryonic whorls of these forms [the Achatininae] differs in individuals of the same species," is no doubt correct for *adult* shells. Yet it does not

impair the value of this character for purposes of classification. A similar difficulty is encountered in the families Strophocheilidae and Bulimulidae, where the type of sculpture of the nepionic whorls is now generally accepted as a valuable character, even though it is often partly or wholly lost in adult shells. It should also be noted that in certain species of Achatininae with a granulose nepionic shell, part of the very first whorl may lack the characteristic sculpture even in newly hatched snails. Moreover, the number of nepionic whorls is not necessarily the same for all subgenera or species, so that one should not merely compare the same number of whorls of different species. It is usually possible to trace the extent of the embryonic shell on immature or adult specimens, the limit being as a rule indicated by a superficial vertical break in the texture of the shell, frequently by the first color markings, or, in the case of species with smooth nepionic whorls, by the appearance of granulation on the post-nepionic whorls.

*Cochlitoma*, the oldest name proposed for a segregate of *Achatina*, is here regarded as not separable from the subgenus *Achatina*, proper, since the type of the latter, *A. achatina*, does not differ in the sculpture of the nepionic whorls of young shells from the type of the former. In both cases the earliest whorls are granulose, but they are worn smooth in older shells in *A. achatina*. There are, however, several species of *Achatina* with a smooth shell even in the newly hatched young, while some at least of the succeeding whorls are decussate or granulose. These species are here grouped in a distinct subgenus *Lissachatina*. Bourguignat (1889) made the first formal attempt at subdividing *Achatina*; but only two of the four groups for which he proposed names are here accepted with subgeneric status. *Leptocala*, originally introduced as a genus under the name *Petitia* by Jousseau (1884), is here given subgeneric rank, following Pilsbry's example; while *Euaethiops* Clench and Archer (1930) is similarly degraded. It should also be pointed out that some of the South and East African species placed by Pilsbry (1904, *Man. of Conch.*, (2), **17**, pp. 66-104) in *Cochlitoma*, are in the present paper removed to *Archachatina*, where they form a new subgenus.

### 1. Subgenus ACHATINA, proper

*Achatina* Lamarek, 1799 (*An VII*), *Mém. Soc. Hist. Nat. Paris*, p. 75. Monotypic for *Bulla achatina* Linné, 1758.

*Achathina* Latreille, 1804, *Nouv. Diet. Hist. Nat.*, **24**, *Tabl. Méthod.*, p. 113 (misspelling of *Achatina*; same type; with description, but without species).

*Achatium* Link, 1807, *Beschr. Naturh.-Samml. Rostock*, **3**, p. 137 (for several

- species). Type by designation of Pilsbry, 1919, *The Nautilus*, **32**, p. 98: *Achatium elegans* Link, 1807 [= *Achatina achatina elegans*], one of the species originally included.
- Helix* subg. *Agathina* Férussac, 1807, *Essai Méthod. Conchyl.*, p. 49 (probably an emendation of *Achatina*). Type by present designation: *Bulla achatina* Linné, 1758, one of three species originally included.
- Achatinus* Denys de Montfort, 1810, *Conch. Syst.*, **2**, p. 418 (here based on an unlabelled figure possibly of *Achatina panthera* Férussac) and 419 (type here said to be *Achatinus zebra* = *Bulimus zebra* Bruguière, 1792). According to Opinion 120 of the International Commission of Nomenclature (1931, *Smithson. Misc. Coll.*, **73**, No. 7, p. 29), *Achatinus* was an emendation of *Achatina*, hence an objective synonym of the latter.
- Aghatina* "Lamarck" Deshayes, 1831 (Plate dated May 1830), *Mag. de Zool.*, **1**, Part 1, Class 5, Moll., p. 3 of letterpress to Plate 3, where the name is printed *Achatina* (misspelling of *Achatina*, with same type).
- Achantina* "Sw. et Grun." Deshayes, 1842, *Dict. Univ. Hist. Nat.*, **1**, p. 69 (without definition or species; misspelling of *Achatina*; same type).
- Achatinum* "Mus. Berl." J. E. Gray, 1859, in *Mrs. M. E. Gray, Figures Moll. Anim.*, **4**, p. 116 (as a synonym of *Achatina*; same type).
- Chersina* [Humphrey, 1797, *Museum Calonnianum*, p. 62; ruled to be not available for purposes of nomenclature] Férussac, 1821 (May 26), *Tabl. Syst. Moll.*, *Tabl. Limaçons*, pp. 49-50 (or 53-54) (in the synonymy of four species). Type by designation of Kennard, 1942, *Proc. Mal. Soc. London*, **25**, pt. 3, p. 113: *Bulimus zebra* Bruguière, 1792, one of the species mentioned by Férussac in combination with the name *Chersina*.<sup>1</sup>
- Helix* subg. *Cochlitoma* Férussac, 1821, *Tabl. Syst. Moll.*, *Tabl. Limaçons*, p. 48 (or 52) (for several species). Type by designation of Pilsbry, 1904, *Man. of Conch.*, (2), **17**, p. 77: *Bulimus zebra* Bruguière, 1792, one of the species originally included, herewith restricted to Férussac's *Helix* (*Cochlitoma*) *zebra* "Chemnitz" (with reference to Chemnitz, **9**, Pl. 118, fig. 1014).<sup>2</sup>
- Oncaea* Gistel (or Gistl), 1847, *Handbuch Naturgeschichte Drei Reiche*, (1850), p. 550 (without description or species; a substitute name for *Achatina*); 1848, *Naturgeschichte d. Thierreichs*, p. 168 (with brief description;

<sup>1</sup> As *Bulimus zebra* Bruguière, 1792, was a composite species, which included both the South African *Achatina zebra* of modern authors and *Achatina fulica* Bowdich, it may be worthwhile to designate herewith more definitely as type of *Chersina* Férussac, *Helix* (*Cochlitoma*) *zebra* "Chemnitz" Férussac (1821, with reference to Chemnitz, **9**, Pl. 118, fig. 1014), which is the South African species. If *Chersina* Férussac were rejected for some technicality, the name would have to be dated from Beck (1837, *Index Moll.*, pt. 1, p. 74; as *Achatina* subg. *Chersina*). The type of this was designated by Clench (1946, *Oec. Papers Moll. Dept. M.C.Z.*, **1**, No. 10, p. 121) as *Bulla virginea* Linné, not one of the Achatininae. Moreover, *Chersina* Beck, 1837, would be a homonym of *Chersina* Gray, 1831, in *Reptiles*. Pilsbry's earlier designation (1919, *The Nautilus*, **32**, p. 98) of *Bulla achatina* Linné was for *Chersina* Humphrey, which has no standing in nomenclature.

<sup>2</sup> Kennard (1942, *Proc. Mal. Soc. London*, **25**, pt. 3, p. 113) claims that, because Férussac first introduced the name *Cochlitoma* in the "Tableau Synoptique" of his "Tableau des Limaçons" (p. 24 or 28), with a definition but without mentioning a species, it was stillborn and automatically a synonym of the older name *Achatina*, with the same genotype. I am unable to follow this line of reasoning, since Férussac not only defined the subgenus, but later in the same work included also several described species. See also H. B. Baker, 1946, *The Nautilus*, **59**, p. 118. The matter is fortunately of little practical importance, since I do not regard the South African *A. zebra* as generically or subgenerically separable from *Achatina achatina* (Linné).

- several described species included). Type by designation of Pilsbry, 1919, *The Nautilus*, **32**, p. 99: *Achatina perdix* Lamarck, 1822 = *Bulla achatina* Linné, 1758, one of the species originally included. Not *Oncaea* Philippi, 1843.
- Geodes* Gistel (or Gistl), 1848, *Naturgeschichte d. Thierreichs*, p. viii (without description or species; a substitute name for *Achatina*). Type by designation of Pilsbry, 1919, *The Nautilus*, **32**, p. 99: *Bulla achatina* Linné, 1758.
- Euachatina* Shuttleworth, 1856, *Notitiae Malacologicae*, **1**, p. 33 (without description; intended to cover the true *Achatinae*, as distinguished from the *Limicolariae*, *Achatina perdix* and *A. marginata* being cited). Type by present designation: *Achatina perdix* Lamarck, 1822 = *Bulla achatina* Linné, 1758.
- Achatina* subg. *Urceus* Mörch, 1857, *Cat. Conch. Suenson*, p. 6 (without description; for 4 species: *A. variegata* de Roissy, *A. purpurea* Lamarck, *A. knorrii* Jonas, and *A. fulminea* Lamarck). Type by present designation: *Achatina variegata* Lamarck, 1801 (de Roissy, 1805) = *Bulla achatina* Linné, 1758.
- Urceus* "Klein" H. and A. Adams, 1858, *Gen. Rec. Moll.*, **2**, p. 658 (as a possible substitute for *Achatina* Lamarck). Type by designation of Pilsbry, 1919, *The Nautilus*, **32**, p. 99, and by present designation: *Bulla achatina* Linné, 1758. [*Urceus* Klein, 1753, *Tentamen Ostracologicae*, p. 46, is pre-Linnean and without standing in nomenclature].
- Parachatina* Bourguignat, 1889, *Moll. Afr. Equat.*, p. 73 (for *Achatina thomsoni* Smith, *A. dohrniana* Pfeiffer, and *A. welwitschi* Morelet). Type by designation of Pilsbry, 1904, *Man. of Conch.*, (2), **17**, p. 17: *Achatina dohrniana* Pfeiffer, 1870.
- Serpaea* Bourguignat, 1889, *Moll. Afr. Equat.*, pp. 74 and 85 (for *Achatina hortensiae* Morelet, *A. dammarensis* Pfeiffer, *A. knorrii* Jonas [misspelled *knori*], *A. varicosa* Pfeiffer, *A. obesa* Pfeiffer, and *A. pintoii* Bourguignat). Type by designation of Pilsbry, 1904, *Man. of Conch.*, (2), **17**, p. 24: *Achatina hortensiae* Morelet, 1866.

*Ampulla* "Bolten" Röding, 1798, is not listed in the foregoing synonymy of *Achatina*, although it originally included, among other species, *Bulla achatina* Linné. Pilsbry (1908, *The Nautilus*, **22**, p. 83), however, designated *Achatina priamus* "Bolten" (a species of *Halia*) as the type, it would seem validly. This designation was evidently overlooked by Winckworth (1945, *Proc. Mal. Soc. London*, **26**, pts. 4-5, p. 137) when he proposed selecting *Ampulla zebra* Röding as the type of *Ampulla*.<sup>1</sup>

*Acathina* Say, 1817, *Achatinia* Swainson, 1821, and *Agatina* (or *Agathina*) Rafinesque, 1831, although possibly misspellings or emendations of *Achatina*, did not as originally proposed or used include

<sup>1</sup> *Ampulla zebra* Röding, 1798, was based only on Chemnitz, 1786, *Syst. Conch.-Cab.*, **9**, pt. 2, Pl. 118, fig. 1014, which represents the South African *Achatina zebra* (Bruguère, 1792). It is not a synonym of *Buccinum zebra* Müller, 1774, as Winckworth implies.

any species now placed in Achatinidae. For this reason I do not list these variants among the synonyms of *Achatina*.

Most of the names listed above in the synonymy of *Achatina* were proposed without descriptions, hence call for no further discussion. *Parachatina*, however, was introduced by Bourguignat for species previously placed in *Achatina*, "characterized by the lack of columellar truncation, the truncation being replaced by a tubercular protuberance." This character does not have the importance attributed to it by the author. In *A. dohrniana*, later selected as the type, the columella does not have a "tubercular protuberance", but is merely more twisted and somewhat less and more obliquely truncate than in the closely related *A. iostoma* Pfeiffer, *A. bandeirana* Morelet, *A. balteata* Reeve, and *A. stuhlmanni* v. Martens (= *rugosa* Putzeys). Of the other species mentioned by Bourguignat, *A. welwitschi* Morelet is extremely close to *A. dohrniana*, if at all distinct. Both *A. dohrniana* and *A. welwitschi* have granulose nepionic whorls, like the other species of the subgenus *Achatina*, proper. *A. thomsoni*, however, belongs in a different subgenus with smooth nepionic whorls, being closely related to *A. allisa* Reeve. Neither *A. welwitschi* nor *A. thomsoni* show any trace of a "tubercular protuberance" on the columella, which is moreover obliquely truncate.

Bourguignat's genus *Serpæa* was intended "for the small globose species," and was later (p. 85) defined "by the shortened shape, ovoid-ventricose or almost spherical, with the shell thin and transparent." The species he included were a heterogeneous lot, *A. knorrii* being an *Archachatina*, while *A. obesa* is a subspecies of *A. zebra*, which Bourguignat left in *Achatina*, proper. *A. hortensiae*, later selected as the type of *Serpæa*, although smaller, more obese and lighter than most *Achatinae*, agrees with *A. achatina* in all essential characters, including the shape of the apex and the granulose nepionic whorls. There is so much variation in the general outline of the shell among the large and medium-sized East and South African *Achatinae*, even sometimes within specific limits, that I have been unable to use this character for a natural or practical grouping of the species. It should also be pointed out that if the need were ever felt to segregate subgenerically these South and East African species, the generic name *Cochlitoma* Férussac (1821) might be available for at least some of them.

*Achatina*, proper, as here restricted, comprises large to medium-sized species, with a broadly ovate, elongate ovate or subglobular shell, and a regular conical spire, the summit a bluntly angular cone, not narrowly drawn out at the tip. The nepionic whorls, when intact, as in newly hatched shells, are almost entirely covered with granulations in closely set, regular, spiral and vertical rows. Later whorls

have either granulose, decussate, wavy or striate sculpture, or are almost smooth.

Of the species of which I was able to study specimens, the following belong in this subgenus. In most cases the granulation of the nepionic shell was determined either on very young shells or on adults with unworn apex. A few species, mentioned in each case, were included in the list on the basis of obvious relationship with others. They should be studied again on better material.

1. *A. achatina* (Linné, 1758). See below.
2. *A. balteata* Reeve, 1849. See below.
3. *A. bandeirana* Morelet, 1866.
4. *A. bisculpta* E. A. Smith, 1878. Position doubtful.
5. *A. dammarensis* Pfeiffer, 1870 (Synonym: *A. schinziana* var. *degenerata* O. Boettger, 1910).
6. *A. dohrniana* Pfeiffer, 1870.
7. *A. hortensiae* Morelet, 1866.
8. *A. iostoma* Pfeiffer, 8154.
9. *A. natalensis* Pfeiffer, 1855 (Synonym: *A. occidentalis* Pilsbry, 1904).
10. *A. paivaiana* Morelet, 1866. Position doubtful.
11. *A. schinziana* Mousson, 1887; with subsp. *passargei* v. Martens, 1900.
12. *A. schweinfurthi* v. Martens, 1873; with subsp. *buchneri* v. Martens, 1882 (Synonyms: *A. schweinfurthi* subsp. *rhodacme* Pilsbry, 1919; *A. s. r.* "mut." *rhodostemma* Pilsbry, 1919; and *A. s. r.* "mut." *levior* Pilsbry, 1919); subsp. *okapia* C. R. Boettger, 1927; and subsp. *semifusca* Spence, 1923.
13. *A. smithii* Craven, 1881 (Synonym: *A. scaevola* Melvill and Ponsonby, 1893, a sinistral specimen). Position doubtful.
14. *A. stuhlmanni* v. Martens, 1892.
15. *A. tavaresiana* Morelet, 1866 (Synonyms: *A. studleyi* Melvill and Ponsonby, 1897; *A. greyi* da Costa, 1907).
16. *A. tincta* Reeve, 1842; with subsp. *oblitterata* Dautzenberg, 1891.
17. *A. tracheia* Connolly, 1929. Position doubtful.
18. *A. varicosa* Pfeiffer, 1861.
19. *A. welwitschi* Morelet, 1866.
20. *A. weynsi* Dautzenberg, 1900; with "mut." *rosaxis* Pilsbry, 1919.
21. *A. zebra* (Bruguière, 1792); with subsp. *fulgurata* Pfeiffer, 1853; subsp. *kraussii* Reeve, 1842; subsp. *linterae* G. B. Sowerby, 1890; subsp. *obesa* Pfeiffer, 1854; subsp. *tigrina* Beck, 1837 (Synonym: *A. indotata* Reeve, 1849); and subsp. *zebroides* E. A. Smith, 1878.

West African Species of *Achatina*, Proper

In West Africa proper or Upper Guinea, that is in the more or less forested area extending some distance from the Coast between the Senegal and Mt. Cameroon, the genus *Achatina* is seemingly represented by only two species, *A. achatina* (Linné) and *A. balteata* Reeve. Of the other species described or reported from this area from time to time, some are synonyms or intraspecific variants of *A. achatina* or *A. balteata* and will be discussed as such in the sequel. The remainder are either misidentifications or erroneous locality records, as shown presently.

*Achatina acuta* Lamarck (1822; supposedly from "Sierra Leone"). The type, in Lamarck's Collection at the Geneva Museum, is a specimen of typical *A. fulica* Bowdich, as shown in the discussion of that species.

*Achatina albicans* Pfeiffer (1853; from "West Africa"). According to the holotype, seen at the British Museum in 1933, this is a species of Angola.

*Achatina allisa* Reeve (1849; supposedly from "Cape Palmas"). The figured holotype and one paratype were seen at the British Museum in 1933, and are of an East African species discussed in the sequel.

*Achatina fulgurata* Pfeiffer (1853; supposedly from "West Africa"). The figured holotype and one paratype, seen at the British Museum in 1933, belong to a race of the South African *A. zebra* (Bruguère).

*Achatina glutinosa* Pfeiffer (1854; supposedly from "West Africa"). According to the holotype, seen at the British Museum in 1933, this is a fairly common East African species, later redescribed as *Achatina petersi* v. Martens (1860). I saw the type of the latter at the Berlin Museum in 1933.

*Achatina hamillei* Petit (1859; supposedly from the "West Coast of Africa, probably the region of Gambia"). This is in my opinion the common continental East African form of *A. fulica* Bowdich, to be discussed at length in the sequel.

*Achatina immaculata* Lamarck (1822; without locality). Mörch (1852, Cat. Conch. Yoldi, 1, p. 21) listed it from "Senegal", where no species of *Achatina* is now known to occur. One of Lamarck's types, now at the Geneva Museum, is shown on Férussac's Plate 127 (Atlas to Hist. Nat. Moll. Terr. Fluv.; Plate published in 1823 in Livr. 20, with name "*Helix (Cochlitoma) immaculata*" in an accompanying printed explanatory sheet). According to information supplied by Dr. G. Mermod, this appears to be the East African species later described by Ancey (1894) as *Achatina mariei*.



*Achatina indotata* Reeve (1849; supposedly from "West Africa"). The type, from the Cuming Collection, examined by me at the British Museum in 1933, is a race of the South African *Achatina zebra* (Bruguière), identical with subsp. *tigrina* Beck.

*Achatina obesa* Pfeiffer (1854; supposedly from "West Africa"). This is evidently a race of the South African *A. zebra* (Bruguière). Pfeiffer noted that the smaller middle figure of Férussac's Pl. 133 (published by Férussac in 1832 in Livr. 28 of his Hist. Nat. Moll. Terr. Fluv., with the name "*Helix (Cochlitoma) zebra*" engraved on it) seemed to represent his *obesa*.

*Achatina studleyi* Melvill and Ponsonby (1897; supposedly from "Old Calabar, Southern Nigeria"). The locality was no doubt erroneous and the specimen came most probably from Angola. A study of the holotype at the British Museum in 1933 failed to disclose characters to differentiate it from *Achatina tavaresiana* Morelet (1866) and *Achatina greyi* Da Costa (1907), with the types of which it was compared. I regard both *studleyi* and *greyi* as synonyms of *A. tavaresiana*, a species found in Angola and adjoining sections of the southern Belgian Congo.

*Achatina tinctoria* Reeve, a species from the Portuguese and Belgian Congo and northern Angola, is said by Gruvel (1912, Ann. Inst. Océanogr. Monaco, 5, pt. 3, p. 143) to occur in Lower French Guinea at Konakry and particularly in the Los Archipelago (at Tamara), and to be used there as food by the natives. The snail is described as being almost the size of *A. achatina*. No doubt the name *tinctoria* was misapplied through some oversight to a form of *A. achatina*, most probably the subsp. *elegans* (Link), which Germain (1912) records (as *A. achatina* var. *minima*) from Konakry after specimens collected by Gruvel.

*Achatina occidentalis* Pilsbry (1904; from "West Africa: Corisco Island", Spanish Guinea). This species is not likely to occur in the section of West Africa considered in the present paper. It presents a baffling problem which I am unable to solve now to my own satisfaction. It was described from a single specimen, which I have examined most carefully at Ac.N.S.Phila. I reached the conclusion that it could not be separated from *Achatina natalensis* Pfeiffer (1855), described supposedly from Natal. While I feel certain that both names refer to the same species, this does not settle the true country of origin. The type of *natalensis*, from the Cuming Collection and presumably collected by Plant in Natal, is at the British Museum, where I saw it in 1933. The M.C.Z. has several examples which agree well with this type, but they are from old collections and without reliable localities. The species has sometimes been misidentified. Connolly, who figured

the type for the first time (1939, Ann. South Afr. Mus., 33, pt. 1, p. 308; Pl. 11, fig. 3), stated that the only authentic examples he knew were three at the British Museum (including the type), all collected by Plant supposedly at Port Natal and Delagoa Bay; but he added that the correctness of Plant's localities is open to question. It seems strange indeed that this fairly large species was not collected for nearly a century in Natal or elsewhere in South Africa. *A. natalensis* appears to be most closely related to *A. welwitschi* Morelet, from Angola. Both species have the nepionic whorls granulose when unworn, hence belong in subgenus *Achatina*, *sensu stricto*, of my classification. In all probability *A. natalensis* is a West African species and will eventually be rediscovered somewhere in Lower Guinea, that is in the region from Cameroon to the Orange River.

*Achatina inaequalis* Pfeiffer (1855; supposedly from Fernando Po) is an unfigured species, which has not been recognized since it was first described. The type, from the Cuming Collection, now at the British Museum, is shown in my Pl. 81, fig. 4, and I have examined it in 1933. I am unable to separate it from specimens of *Achatina zebra tigrina* Beck. There is no form even remotely like it in West Africa. The locality "Fernando Po" may safely be regarded as one more of Cuming's errors. It may be noted that the type of *indotata*, likewise from the Cuming Collection, was also stated wrongly to be West African.

#### ACHATINA (ACHATINA) ACHATINA (Linné)

The full-grown shell of the nominate race of *A. achatina* has from seven to eight whorls and is very broadly ovate, with a long and greatly swollen body-whorl comprising most of the bulky shell. The regularly conical, relatively short spire, occupying only about one-fourth of the total length, is considerably narrower than the base and its whorls are only slightly convex. As a result immature shells are relatively more slender than adults. In the smaller races, the full-grown shell is narrower, more elongate-oval, with the body-whorl moderately inflated, while by contrast the spire appears longer and wider. This is true even in subsp. *elegans*, which is merely based on dwarf specimens of typical *achatina*, usually occurring in the same locality with the normal, larger ones. A study of subsp. *elegans* is instructive as showing the connection with typical *achatina* of the more distinctive subspecies *monochromatica*, *togoënsis*, and *bayoli*. The little-known subsp. *bayoli* is the most aberrant of all and may possibly represent a distinct species: it is fusiform or spindle-shaped rather than oval in outline, while the summit of the spire is unusually blunt for an *Achatina*.

Nevertheless, the summit is too narrow to be called dome-shaped, while the sculpture is similar to that of the other forms of *A. achatina*, which has led me to include it in the "form group" ("Rassenkreis") of this species, thus removing it from the genus *Archachatina* where it had been placed thus far.

The sutures are shallow, the upper part of each whorl being flattened against the periphery of the preceding whorl. This subsutural area is covered with coarse vertical folds and as a rule set off by a strong impressed line on the penultimate and body-whorl. The suture itself is finely and irregularly crenulate. On full-grown shells the first two to three whorls are either worn smooth or corroded or show traces only of the granulation which originally covered them (as described below). The succeeding whorls show typically a decussate sculpture of elongate welts, best developed on the penultimate whorl and gradually weaker on the body-whorl, particularly below the periphery; a few traces only of the sculpture remain on the last portion of the body-whorl, behind the outer lip. The welts are produced by the decussation of moderately strong vertical growth-striae by weak or superficial spiral engraved lines, placed rather far apart and at irregular intervals. In some specimens the decussate sculpture is barely indicated. The glazing of the parietal wall is slight, the outer lip sharp and thin and the columella strongly concave, slightly curved upward at the base, which is almost squarely truncate some distance above the lower margin of the aperture.

On newly hatched and very young snails, only the very first whorl is superficially wrinkled or almost smooth; the other nepionic whorls are uniformly and finely decussate-granulose (Pl. 14, fig. 4). The granules are evenly rounded and placed in regular vertical and spiral rows. At this stage the granulose sculpture of the earliest whorls differs in no respect from that of the South African *Achatina zebra* (Bruguère), so that it is not possible to use this character to separate *A. zebra* generically or subgenerically from *A. achatina*. For this reason *Cochlitoma* Férussac (1821), as redefined by Pilsbry (1904), with *Bulimus zebra* Bruguère as the type, cannot for the present be considered as distinct from *Achatina*. The difference in the sculpture of the apex only appears later, after the early whorls are worn smooth or corroded in *A. achatina*; while they usually retain the granulations in full-grown *A. zebra*. The nepionic sculpture of *A. achatina* is frequently well preserved in shells up to 40 or 45 mm. long.

The first post-nepionic whorls are more coarsely granulose than those of the nepionic shell, numerous spiral incised lines cutting the strong vertical wrinkles at regular intervals. The granules do not extend below the periphery, the lower part of the whorls being nearly

smooth with only light growth-striae and a microscopic sculpture like the weave of a fine cloth. From the fifth whorl on the granules gradually change into low, vertical welts, the spiral incised lines being wider, shallower and farther apart. This eventually leads to the sculpture of the penultimate and body-whorl of full-grown shells, described before. In very young shells the periphery is obtusely carinate, but this feature disappears from the fifth whorl on. At first the columella is perfectly straight and merges fairly evenly with the base of the outer lip, with scarcely a trace of truncation, and, as first pointed out by Shuttleworth (1856), with an open, though narrow umbilical slit partly covered by the reflexed outer margin of the columella. When the shell reaches 20 to 25 mm. in length, the columella begins to show a slight curve, as well as a fairly distinct truncation, and both features become more marked as growth goes on. The umbilicus closes much later, traces of the slit persisting in some shells 45 to 50 mm. long.

*A. achatina* occurs with certainty only in Upper Guinea, that is the northern section of West Africa. Here it has been definitely observed from French Guinea (Konakry), through Sierra Leone, Liberia, the Ivory Coast, the Gold Coast, Togo, and Dahomey, to Southern Nigeria (Nun River). All records in the older literature of its supposed occurrence in Senegambia, Cameroon, San Thomé, Gaboon, and Angola have not been reliably confirmed, and I regard them as erroneous. These territories have all been well explored malacologically in recent years, but have never yielded an authentic locality for living *A. achatina*. Inland it extends farthest in Liberia (to some 180 miles from the Coast) and in the Gold Coast (to some 100 miles).

It is a strictly terrestrial snail, so far as my own observations go, most active at night, and exclusively vegetarian. It inhabits densely forested areas, where it prefers primary rain forest and moist second-growth "bush," being found occasionally also in native plantations. I found it commonly in the large cemetery outside the town of Monrovia. Even in the rain forest of Liberia, which is one of the most humid sections of West Africa, the snail buries for estivation during the drier months (from December to March) in the superficial loose soil and litter. It then closes the aperture temporarily with a white, brittle, calcareous epiphragm, provided with a longitudinal slit and similar in appearance to that made by other estivating Achatininae. It is not considered to be a pest in West Africa, being scarcely abundant enough to damage crops. It shows a predilection for decaying vegetable matter and is often even coprophagous. The natives consider it rather an economic asset, as it is a favorite article of the diet of many of the aboriginal tribes, particularly in Sierra Leone, Liberia and the Ivory Coast. As a result, freshly discarded empty shells may be collected

without much trouble in or near most villages. The snails are usually found crawling on the trails in the early morning. In order to carry the large and cumbersome snail without risk of slipping, a hole is cut in the last whorl some distance from the mouth, so that the shell can be tied onto a rope or creeper. Dead shells picked up in villages often bear this tell-tale mark. The snail is either boiled, after which the animal is readily removed, or sometimes roasted directly in the shell. Empty shells of this species being light, thin and rather fragile, are seldom used for domestic purposes, the heavier and more solid *Archachatina ventricosa*, *A. degneri* and *A. marginata* being much preferred as containers or utensils.

Mating apparently occurs chiefly at night and starts long before the snails reach their maximum size. Two shells found mated in the very early morning, after a heavy rain, on a trail through dense primary rain forest between Nyandamolahun and Vasala, Liberia, February 25, 1944, were 160 and 164 mm. long, of 7 whorls, and apparently not quite full-grown. The eggs are surprisingly small for the size of the snail, broadly oval, dirty yellowish, 8 to 8.7 mm. long and 6.5 to 7 mm. wide in the nominate race, slightly smaller (7 by 5.5 to 6 mm.) in subsp. *elegans*.<sup>1</sup> They are deposited many at a time, in clusters in loose soil.

Wingless physogastric females of a phorid fly, *Wandolleckia achatinae* O. F. Cook, are commonly seen in Liberia running over the foot of *A. achatina*. They feed on the slimy excretion of the snail's skin. The males and early stages of the fly are as yet unknown.

Although *A. achatina* was known at least since the beginning of the Seventeenth Century by naturalists and collectors of curios, its true habitat remained a mystery for a long time. Even Linné shared the belief of his predecessors that it was a marine snail, an error which persisted until Favanne (1780), Bruguière (1792) and Férussac (1821). The correct locality was first given by Chemnitz (1786) as the Gold Coast. Yet Lamarck (1822) thought that it might have come from South America, while Férussac (1821) surmised that it was from Madagascar. Rang (1831) first observed the snail alive in West Africa and gave a description of the animal and the egg.

*Synopsis of Subspecies.* On size, shape, and color I recognize seven forms of *A. achatina* by names, all being given here subspecific status for nomenclatorial reasons. I found the very large, boldly marked typical form by far the most abundant in Liberia and the Gold Coast. Among several hundred Liberian specimens studied, only one belonged

<sup>1</sup>The egg of *A. achatina* was correctly described by Rang (1831), Standen (1917) and Lamy (1929), for the typical form of the species. The large egg, 25 mm. by 17 mm., claimed by v. Martens (1891, Sitzungsber. Ges. Naturf. Fr. Berlin, p. 33) to be that of *A. achatina*, was obviously that of a species of *Archachatina*.

to subsp. *depravata*, five to subsp. *roseolabiata*, and about a dozen to subsp. *elegans*. I have not collected subsp. *monochromatica*, *togoënsis* and *bayoli* myself and little is known as yet of their true habitat. In some respects these three forms are better defined than the others and it would be of interest to investigate the environmental conditions they prefer, as well as their internal anatomy.

A. Shell large and bulky when full-grown, 150 to 200 mm. long and up to 100 mm. wide. Columella and parietal wall vinaceous-red.

a. Boldly marked with dark chestnut-brown zigzag streaks. Outer lip bluish-white. Typical *A. achatina*.

b. Chestnut-brown zigzag markings as in the foregoing. Outer lip with a broad violaceous-red inner margin. Subsp. *roseolabiata*.

c. Uniformly fulvous-yellow, without darker streaks. Outer lip bluish-white. Subsp. *depravata*.

B. Shell much smaller and relatively narrower when full-grown, 150 mm. or less in length and 85 mm. or less in greatest width.

d. Markings of shell and color of columella, parietal wall and outer lip as in typical form. Ovate in outline, the spire much narrower than the base. Subsp. *elegans*.

e. Uniformly fulvous-yellow, without darker streaks. Columella and parietal wall vinaceous-red. Outer lip bluish-white. Subsp. *monochromatica*.

f. Boldly marked with chestnut-brown zigzag streaks. Columella, parietal wall and outer lip bluish-white. Subsp. *togoënsis*.

g. Boldly marked with rather narrow, widely spaced, straight, vertical dark brown streaks, which are sometimes incomplete or broken up into spots. Outline more fusiform than in the other races, the spire scarcely narrower than the base. Subsp. *bayoli*.

#### a. Typical *A. ACHATINA*

Pl. 3, fig. 1; Pl. 4, fig. 3; Pl. 8, fig. 4; Pl. 11, fig. 2;

Pl. 13, fig. 4; Pl. 14, fig. 4; Pl. 16, fig. 4; Pl. 39, fig. 3

[*Buccinum exoticum variegatum laevius* Fabius Columna (or Fabio Colonna), 1616, *Aquat. et Terr. Animal. Observ.*, p. xviii, Cap. VIII; Pl. on p. xvi, lower right hand figure (type figure for *Bulla achatina* Linné, 1758). Dollfus and Dautzenberg, 1932, *Jl. de Conchyl.*, 76, p. 308, fig. on Plate (copy of Columna's figure; refer it to *Bulla achatina* Linné)].

[Bonanno (or Buonanno), 1684, *Recreatio Mentis et Oculi*, p. 137, No. 192; Pl. of Classis 3, fig. 192 (included by Linné among the original references for *Bulla achatina*); 1709, *Museum Kircherianum*, p. 460, No. 190; Plates of Mollusks, Classis 3, fig. 190 (copy of his 1684 fig.)].

- [*Buccinum parvum, integrum*, etc. Gualtieri, 1742, Index Test. Conch., Pl. 45, upper figure B only, with letterpress (included by Linné among the original references for *Bulla achatina*)].
- [d'Argenville, 1742, La Conchyliologie, p. 270; Pl. 13, fig. E (included by Linné among the original references for *Bulla achatina*)].
- [*Urceus* species 1 Klein, 1753, Tentamen Method. Ostracologicae, p. 47].
- ["Breitwellige *Buccinum*" G. W. Knorr, 1754, Deliciae Naturae Selectae, German Ed. (Nuremberg), 1, p. 54; Pl. B5, fig. 1].
- ["Breede Gevlamde Kink-Hoorn" G. W. Knorr, 1771, Deliciae Naturae Selectae, Dutch Ed. (Dordrecht), 1, p. 26; Pl. B5, fig. 1].
- [Seba, 1758, Rer. Nat. Thesauri, 3, p. 169; Pl. 71, figs. 1-3 and 7-10].
- Bulla achatina* Linné, 1758, Syst. Nat., 10th Ed., 1, p. 728 ("habitat in O. americano"; herewith restricted to Linné's specimen and to the figures cited from Fabius Columna, 1616; Bonanno, 1684; Gualtieri, 1742, upper fig. B only; and d'Argenville, 1742; the figures cited from Gualtieri, 1742, lower fig. B, Lister, 1688, and Klein, 1753, refer in my opinion to *Archachatina marginata*); 1764, Mus. Ludovicae Ulricaе, p. 589 (detailed description of a specimen); 1767, Syst. Nat., 12th Ed., 1, pt. 2, p. 1186 (the new, additional references to Petiver, 1764, and Adanson, 1757, are erroneous); 1771, Natuurlijke Historie, Houttuyn Ed., 1, pt. 16, p. 135. Born, 1778, Rer. Nat. Mus. Caes. Vindobonensis, 1, p. 195. J. S. Schröter, 1779, Geschichte Flussconchylien, p. 301; Pl. 6, fig. 1. Born, 1780, Test. Mus. Caes. Vindobonensis, p. 208 (in part: form  $\alpha$  only; not forms  $\beta$  and  $\gamma$ , nor the figures). J. S. Schröter, 1783, Einleitung Conchylienkenntn., 1, p. 185; 1783, Ueber Innern Bau See-, Erd-, Flussschnecken, p. 40 (inner structure of shell; saw specimens 7 and 6 German inches long). Karsten, 1789, Museum Leskeanum, 1, p. 213 (in part). Gmelin, 1790, in Linné, Syst. Nat., 13th Ed., 1, pt. 6, p. 3431 (in part). Schreibers, 1793, Vers. Vollst. Conchylienkenntniss, 1, p. 92. Turton, 1802 (and 1806, with new title page only), in Linné, System of Nature, Animal Kingdom, 4, p. 355 (in part). Dillwyn, 1817, Deser. Cat. Recent Shells, 1, p. 494. Wood, 1818 (and 1825), Index Testaceologicus, p. 89; Pl. 18, fig. 53. Mawe, 1823, Linnaean Syst. Conch., p. 102. Hanley, 1855, Ipsa Linnaei Conchylia, pp. 210 and 503 (type not in Linné's collection in London). Wood, 1856, Index Testaceologicus, Hanley Ed., p. 95; Pl. 18, fig. 53. Hanley, 1859, Jl. Proc. Linn. Soc. London, Zool., 4, p. 67.
- Buccinum achatinum* O. F. Müller, 1774, Verm. Terr. Fluv. Hist., 2, p. 140 (in part: of the references only those to Fabius Columna, 1616; Bonanno, 1684; d'Argenville, 1742; and Gualtieri, 1742, upper fig. B. Descriptions based on several species of *Achatina*, *Archachatina* and *Limicolaria*).
- [Favanne, 1780, in d'Argenville, La Conchyliologie, 3d Ed., Atlas, Pl. 65, fig. M5 (not a copy of d'Argenville's fig. of 1742)].
- [Chemnitz, 1786, Syst. Conch. Cab., 9, pt. 2, p. 18 (localities given as Guinea and Gold Coast; text in part only; not the figs. 1012-1013, which are subsp. *elegans*; said to be terrestrial)].
- Bulimus achatinus* Bruguière, 1792, Encyclop. Méthod., Vers, 1, pt. 2, p. 358. Bose, 1802 (An X), Hist. Nat. Coq., 4, p. 117.

- [*Chersina tigrina africana* Humphrey, 1797, Museum Calonianum, p. 63 (with *Bulla achatina* Linné as synonym). Not binominal].
- Achatina achatina* Lamarck, 1799 (An VII), Mém. Soc. Hist. Nat. Paris, p. 75 (genotype of *Achatina*). Bosc, 1803, Nouveau Dict. Hist. Nat., 1, p. 133; 1816, *Op. cit.*, 2d Ed., 1, p. 201. Gray, 1847, Proc. Zool. Soc. London, (for 1847), p. 177. Pilsbry, 1904, Man. of Conch., (2), 17, p. 9; Pl. 31, fig. 1 (specimen). Germain, 1908, Jl. de Conchyl., 56, p. 100 (Ivory Coast: Bouroukrou). Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., 32, p. 64. Gruvel, 1912, Ann. Inst. Océanogr. Monaco, 5, pt. 3, p. 143, fig. 19 (Upper and Lower Dahomey. Togo. Southern Nigeria. Eaten by natives and Europeans). Standen, 1917, Jl. of Conch., 17, pt. 5, p. 160 (egg). Lamy, 1929, Jl. de Conchyl., 73, p. 201 (egg). Roux, 1935, Bull. Soc. Sci. Bretagne, 11, (1934), pts. 3-4, p. 106, fig. 3 (ingestion of chalk). Darteville, 1935, Rev. Zool. Bot. Afric., 27, pt. 3, Bull. Cercle Zool. Congolais, 12, pts. 3-4, p. (91) (Ivory Coast). Brunet and Jullien, 1937, Arch. Zool. Gén. Expér., 73, pt. 10, p. 387, figs. III-IV; Pl. 9, figs. 7-8 (heart). Dickinson, 1946, The Aquarium, Philadelphia, 15, p. 152; fig. on p. 151 (living snail in captivity in New Jersey). Andrews, 1948, The Nautilus, 61, pt. 3, p. 95 (oviposition in captivity at Baltimore, Maryland). Hanna, 1948, *Op. cit.*, 62, pt. 1, p. 29. Abbott, 1949, Natural History, New York, 58, pt. 2, p. 71, upper fig. Burton, 1949, Illustrated London News, 214, p. 120, right middle fig.
- Helix (Agathina) achatina* Férussac, 1807, Essai Method. Conchyl., p. 49.
- Helix (Cochlitoma, Achatina) achatina* Férussac, 1821, Tabl. Syst. Moll., Tabl. Limaçons, p. 50 (or 54); 1823, Hist. Nat. Moll. Terr. Fluv., Atlas, Pl. 131, figs. 1-3 (in Livraison 20, with name in Explanation on cover), and Pl. 131A, fig. 1 (in Livraison 21, with name in Explanation on cover); 1832, *Op. cit.*, Atlas, Pl. 131B (in Livraison 28, with name engraved on Plate and also in Explanation on cover).
- Helix (Cochlitoma) achatina* Rang, 1831, Ann. Sci. Nat., 24, p. 30 (common along the entire West African Coast; description of animal and egg).
- Cochlitoma achatina* G. B. Sowerby, 1825, Cat. Shells Earl Tankerville, p. 38.
- Achatina (Achatina) achatina* Germain, 1912, Ann. Inst. Océanogr. Monaco, 5, pt. 3, p. 120 (Dahomey: Abomey), figs. 2A, A' and B (on p. 122; 3 juvenile shells).
- Ampulla flammea* "Bolten" Röding, 1798, Museum Boltenianum, pt. 2, p. 110 (defined by the reference to "Gmel. *Bulla flammea* Sp. 32;" there is no *Bulla flammea* Gmelin, but his Sp. 32 was *Bulla achatina* Linné); 1819, *Op. cit.*, 2d Ed. (by J. Noodt) p. 78.
- Ampulla bombardia* "Bolten" Röding, 1798, Museum Boltenianum, pt. 2, p. 110 (defined by the reference to "Gmel. *Bulla achatina* Sp. 32"); 1819, *Op. cit.*, 2d Ed. (by J. Noodt), p. 78.
- Ampulla lacteae* "Bolten" Röding, 1798, Museum Boltenianum, pt. 2, p. 110 (defined by the reference to "Gmel. *Bulla achatina* Sp. 32"); 1819, *Op. cit.*, 2d Ed. (by J. Noodt), p. 78.
- Achatina variegata* Lamarck, 1801, Syst. Anim. Sans Vert., p. 91 (no locality; new name for *Bulla achatina* Linné). de Roissy, 1805 (An XIII), Hist.



Nat. Moll., **5**, p. 354. Pfeiffer, 1848, Monogr. Helic. Viv., **2**, p. 249. Reeve, 1849, Conch. Icon., **5**, *Achatina*, Pl. 1, fig. 3 only (Sierra Leone). Jay, 1850, Cat. Shells Coll., 4th Ed., pp. 222 and 223. Deshayes, 1851, in Férrussac, Hist. Nat. Moll. Terr. Fluv., **2**, pt. 2, p. 155 (in part); and Expl. of Plates of Atlas, p. 19. Mörch, 1852, Cat. Conch. Yoldi, **1**, p. 20. Pfeiffer, 1853, Monogr. Helic. Viv., **3**, p. 482. Woodward, 1854, Manual of Mollusca, pt. 2, p. 165 and p. 12 of Expl. of Plates; Pl. 12, fig. 22. H. and A. Adams, 1855, Gen. Rec. Moll., **2**, p. 132. Pfeiffer 1857, Syst. Conch.-Cab., **1**, Abt. 13, pt. 1, p. 290 (in part; not the figs.); 1859, Monogr. Helic. Viv., **4**, p. 600. v. Martens, 1860, in Albers, Die Heliceen, 2d Ed., p. 201. A. D. Brown, 1861, Cat. Shells Coll., p. 56. Mörch, 1863, Cat. Conch. Lassen, p. 4. Bielz, 1865, Verzeichn. Moll. Conch.-Samml., 3d Ed., p. 23. Haines, 1868, Cat. Terr. Shells Coll., pp. 68 and 69. Pfeiffer, 1868, Monogr. Helic. Viv., **6**, p. 211. Paetel, 1869, Moll. Syst. Cat., p. 80. Woodward, 1871, Manual of Mollusca, 2d Ed., p. 292; Pl. 12, fig. 22 (all subsequent editions reprints of this). Paetel, 1873, Cat. Conch.-Samml., p. 99. Roeters van Lennep, 1876, Cat. Coll. Shells van Lennep, p. 53. v. Martens, 1876, Monatsber. Ak. Wiss. Berlin, p. 257 (Gold Coast: Acera). Pfeiffer, 1876, Monogr. Helic. Viv., **8**, p. 271. G. R. Batalha, 1878, Cat. Coll. Conchyl. F. R. Batalha, p. 2. Dohrn, 1878, Jahrb. D. Mal. Ges., **5**, p. 155 (Liberia). G. Nevill, 1879, Hand List Moll. Indian Mus., **1**, (1878), p. 145. Kobelt, 1880, Illustriertes Conchylienbuch, **2**, p. 261; Pl. 82, fig. 1. P. Fischer, 1883, Manuel de Conchyliologie, p. 486; Pl. 12, fig. 22. Grasset, 1884, Index Test. Viv. Coll., p. 200. v. Martens, 1886, Sitzungsber. Ges. Naturf. Fr. Berlin, p. 114 (Gold Coast: Abetifi, 150 Kilom. inland, at 700 m.). Martorell y Peña, 1888, Catálogo Colección Conchol. Mus. Martorell, Barcelona, p. 57. Vignon, 1888, Bull. Soc. Mal. France, **5**, p. 70 (Ivory Coast: Grand Bassam). Schepman, 1888, Notes Leiden Mus., **10**, p. 247 (Liberia: Soforé's Place; St. Paul River). Paetel, 1889, Cat. Conch.-Samml., 4th Ed., **2**, p. 241. Bourguignat, 1889, Moll. Afr. Equat., pp. 72 and 74. Büttikofer, 1890, Reisebilder aus Liberia, **2**, pp. 454 and 481. Stearns, 1893, Proc. U. S. Nat. Mus., **16**, p. 327 (Sierra Leone: Freetown). O. F. Cook, 1897, Science, (N. S.), **6**, p. 886 (Liberia. With *Wandolleckia achatinae* as commensal). Boucard, 1901, Cat. Coll. Coquilles Terr., p. 50. Johnston, 1906, Liberia, **2**, p. 861. Julia E. Rogers, 1908, The Shell Book, p. 275. Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 65. Connolly, 1928, Ann. Mag. Nat. Hist., (10), **1**, p. 540 (Sierra Leone: Freetown). Coen, 1945, Catalogo Gasteropodi Polmonati Coll. Coen, p. 42.

*Achatina (Achatina) variegata* Beck, 1837, Index Moll., pt. 1, p. 75.

*Achatina (Archachatina) variegata* Albers, 1850, Die Heliceen, p. 190.

*Achatina (Achatinus) variegata* Pfeiffer, 1856, Malak. Blätt., **2**, (1855), p. 167; 1879, Nomencl. Helic. Viv., p. 264. Römer, 1891, Jahrb. Nassau. Ver. Naturk., **44**, p. 123.

*Achatina (Urceus) variegata* Mörch, 1857, Cat. Coll. Suenson, p. 6.

*Achatina perdix* Lamarek, 1822, Hist. Nat. Anim. Sans Vert., **6**, pt. 2, p. 127 (description of specimens; with *Bulla achatina* Linné as a synonym).

- Children, 1823, Quart. Jl. Sci., London, **15**, p. 240. Stark, 1828, Elements Natural History, p. 56. Menke, 1828, Synopsis Meth. Moll., p. 16; 1829, Verzeichn. Conch.-Samml. Walsburg, p. 7. de Cristofori and Jan, 1832, Consp. Method. Moll., Pars 1, Fasc. 1, p. 4. Potiez and Michaud, 1835, Gal. Moll. Douai, **1**, p. 130. Jay, 1835, Cat. Shells Coll., p. 31; 1836, *Op. cit.*, 2d Ed., p. 42. Schlüter, 1838, Syst. Verz. Conchyliensamml., p. 8. Deshayes, 1838, in Lamarek, Hist. Nat. Anim. Sans Vert., 2d Ed., **8**, p. 294. Jay, 1839, Cat. Shells Coll., 3d Ed., p. 58. Hanley, 1840, Young Conchologist's Book Species, p. 36. Pfeiffer, 1841, Symbolae Hist. Helic., **1**, p. 28. Deshayes, 1844, in Lamarek, Hist. Nat. Anim. Sans Vert., 3d Ed., **3**, p. 374. Leunis, 1844, Synopsis d. Drei Naturreiche, Zool., p. 375. Catlow and Reeve, 1845, Conchologist's Nomenclator, p. 165. Porro, 1846, Coll. Mus. Modiol., Moll. Terr. Fluv., p. 17. Jay, 1850, Cat. Shells Coll., 4th Ed., p. 220. Shuttleworth, 1858, Notitiae Malacologicae, **1**, p. 33 (young shell). Fridrici, 1874, Bull. Soc. Hist. Nat. Metz, **13**, p. 184. G. R. Batalha, 1878, Cat. Coll. Conchyl. F. R. Batalha, p. 1. Leunis, 1883, Synopsis d. Thierk., 3d Ed. (by H. Ludwig), p. 888. Martorell y Peña, 1888, Catálogo Colección Conchol. Mus. Martorell, Barcelona, p. 56. Rethaan Macaré, 1888, Cat. Coll. Coq. Mme Rethaan Macaré, p. 23. Kennard, Salisbury and Woodward, 1931, Smithsonian. Misc. Coll., **82**, No. 17, p. 21 (Children's type of *Achatina*).
- Achatina (Cochlitoma) perdix* Menke, 1830, Synopsis Method. Moll., 2d Ed., p. 28.
- Bulimus (Achatina) perdix* Anton, 1839, Verzeichn. Conch. Samml., p. 44.
- Oncaea perdix* Gistel (or Gistl), 1848, Naturgeschichte d. Thierreichs, p. 168.
- Achatina perdix* "Lamarek" Rang, 1831, Ann. Sci. Nat., **24**, p. 30 (as a synonym of *Helix achatina* Linné; misspelling of *perdix* Lamarek). Gould, 1833, Lamarek's Genera Shells, p. 66. A. and J. B. Villa, 1841, Dispos. Syst. Conch. Terr. Fluv., p. 19.
- Achatina zebra* Schumacher, 1817, Essai Nouv. Syst. Vers Test., p. 201 (in part). de Blainville, 1825, Man. Malac. Conch., p. 456; Pl. 40, fig. 1. Not *Bulimus zebra* Bruguière, 1792.
- Achatina (Achatina) amphora* "Fér." Beck, 1837, Index Moll., pt. 1, p. 75 (Guinea; without description; with a doubtful reference to Seba, 1758, Pl. 71, fig. 1). Jay, 1839, Cat. Shells Coll., 3d Ed., p. 58 (Sierra Leone).
- ?*Achatina fulva* Grasset, 1884, Index Test. Viv. Coll., p. 199 (Ivory Coast: Grand Bassam).

Linné's first description of *Bulla achatina* (1758) was very brief: "B. testa ovata, apertura obovata apiceque sanguineis, columella laevi." It was, however, based on at least one specimen; of which he gives a detailed and recognizable description in Mus. Ludovicae Ulricaë (1764), in addition to a copy of the earlier diagnosis: "Testa magna, ovata, glabra, pellucida, rubra s. alba, fasciis longitudinalibus undulatis fuscis, apice sanguinolento. Apertura magna, figura literae S vel inaequaliter ovata. Labium exterius tenue aequale; interius

longitudinaliter reflexum, adnatum, sanguineum. Basis non emarginata, quamvis obtusa et truncata columella, adeoque dubii generis." I agree with Dollfus and Dautzenberg (1932) that Fabius Columna's (1616) figure, cited by Linné (1758) and copied in my Pl. 11, fig. 2, is the true *Achatina achatina*, as here understood. It shows, not the dwarf race of the species, but an immature shell of the typical form, 71 mm. long, 36 mm. in greatest width, of about 6 whorls. Whether Linné's specimen is still preserved in some Swedish collection, I have been unable to trace. If it were definitely lost, Columna's figure might be selected as the type figure, being the oldest. Of the other references given by Linné, Bonanno's fig. 192 (1684), copied in my Pl. 13, fig. 4, is extremely poor, but seems to be a foreshortened drawing of an immature *A. achatina*, 86 mm. long and 52 mm. wide. Gualtieri's (1742) upper fig. B of Pl. 45,<sup>1</sup> copied slightly reduced in my Pl. 3, fig. 1, is a good representation from the back of a very large *A. achatina*, with a decidedly pointed summit, 178 mm. long, 101 mm. wide (the size may have been exaggerated by the draftsman, although I have seen even larger specimens). d'Argenville's (1742) Pl. 13, fig. E, copied in my Pl. 8, fig. 4, is clearly *A. achatina*, apparently a reduced drawing of the typical race; it is 89 mm. long, 50 mm. wide, of 7 whorls, with the aperture 48 by 24 mm. The remaining figures cited by Linné (1758) are not in my opinion *A. achatina*: Gualtieri's Pl. 45, lower fig. B, represents *Archachatina marginata* (Swainson); Lister's Pl. 579, fig. 34, and the poor copy by Klein, Pl. 3, fig. 60, are *A. marginata suturalis* (Philippi). They are discussed later under these two forms.

Seba's (1758) figs. 1-3 and 7-10 of Pl. 71, one of which is copied in my Pl. 4, fig. 1, are reversed drawings, mostly from the back, of typical *A. achatina*, some adult, others immature.

Favanne's (1780) figure, copied in my Pl. 16, fig. 4, is not, as might be supposed, a copy of d'Argenville's (1742) Pl. 13, fig. E, but represents an entirely different shell, 89 mm. long, 51 mm. wide, of 7 whorls, with the aperture 48 by 25 mm. It is evidently a reduced drawing of an example of typical *A. achatina*.

Röding's (1798) trivial names *bombarda*, *flammea* and *lacteae*, though published without descriptions, were validly defined for nomenclatorial purposes by the references to "Gmelin Sp. 32," which makes them straight synonyms of *A. achatina*. Presumably the names were given to specimens in Bolten's collection, but what became of these shells is unknown.

Lamarck first (1801) introduced the trivial name *variegata*, without a description, but as a substitute for *Bulla achatina* Linné, of which

<sup>1</sup> The accompanying description, which covers both upper and lower figs. B, is copied in my discussion of *Archachatina marginata*.

it is therefore a synonym. Later he discarded *variegata* for *perdix* (1822), adding the following description: "A. testa maxima, ovato-oblonga, ventricosa, decussata, alba, apice rosea; flammis longitudinalibus undulatis spadiceis; columella purpureo-violacea; labro intus alba." The French text also stated that "the sutures are slightly crenulate and the shell very prettily ornamented with beautiful reddish-brown flames." At my request, Dr. G. Mermod sent me the following detailed information on the shells now called *perdix* in the Lamarck Collection at the Geneva Museum. That Museum also owns Lamarck's personal copy of the "Histoire Naturelle des Animaux sans Vertèbres" (often called the "Système"), with marginal manuscript annotations by his daughter Rosalie, as noted in a recent paper by Dr. Mermod (1947, Rev. Suisse Zool., 54, p. 158). According to the marginal note relating to *A. perdix*, Lamarck had three specimens. Dr. Mermod describes the three now present as follows (translated from the French, *in litt.*, 1948): "Specimen 1: 124 mm. long, 68 wide; aperture 76.5 mm. long, 38.5 wide; 8 whorls; length of spire (above body-whorl) 57.5 mm.; of next to last whorl, 23.5; of preceding whorl, 13; of next preceding whorl, 4; of combined first three embryonic whorls, 6; outer lip slightly chipped; shell clothed in a brownish golden-yellow periostracum, covered with growth striae, which are very marked toward the suture, forming as it were lengthened granules; elsewhere on the whorls there are about 20 such growth striae over a space of 1 cm.; the spiral striae, not strongly marked though distinct, difficult to count exactly, cut across the growth striae at rather irregular intervals; they are less marked over the base of the body-whorl; the white ground color bears brown zigzag bands, sometimes confluent, especially in the upper part of the whorls; aperture with a well marked parietal callus, dark roseate, like the columella; outer lip sharp, bluish-white like the aperture inside, broadly rounded in its lower (basal) portion; first whorls of spire roseate. Specimen 2: much larger, 154 mm. long, 88 wide; aperture 87 mm. long, 55 wide; 8 whorls; agrees exactly with the foregoing in markings and color; aperture inside with traces of numerals, unfortunately unreadable, as is often the case for Lamarck's shells. I cannot be sure that this is the shell of which Lamarck gives the dimensions, particularly as it is only 154 mm. instead of 162 mm. long.<sup>1</sup> Specimen 3: bears inside a perfectly readable annotation in Lamarck's own hand (not his daughter's), '*A. perdix*,' which escaped former Curators of the Lamarck Collection,

<sup>1</sup> I propose to select this largest specimen as Lamarck's true type of *A. perdix*, as he stated that his largest examples were nearly 6 inches long. Obviously he was satisfied with an approximation and it is unlikely that a specimen would be exactly 6 French inches long. Moreover, in my experience it is by no means easy to make exact measurements of very large shells. A relatively slight deviation from the true vertical may cause a difference of several millimeters. [J. B.]

including Mr. Paul Godet; the latter identified the shell, I believe correctly, as '*Achatina marginata*, Sénégal ou Afrique occidentale;' unfortunately, this shell, polished with a grindstone, is without periostracum; it is 112 mm. long, 70 wide, the aperture 86 mm. long, 39 wide; 7 whorls; although polished, the last 2 whorls show a continuous impressed line at about 2 mm. below the suture; brown bands colored as in the foregoing 2 shells, but more tortuous, zigzagging, close together; margin of outer lip completely covered outside with the confluent brown bands, which is not true at all of the other 2 shells; outer lip in profile much more sinuous, forming a reversed S; mouth inside, parietal callus, and columella white; columella markedly more curved in profile; first 3 whorls of spire very pale brownish, not roseate; summit of spire distinctly more obtuse, which is not due to the polishing, since the sculpture remains quite distinct."<sup>1</sup>

*Specimens Examined.* SIERRA LEONE: Bwedu (J. Bequaert.-M.C.Z.); Mosente on Lake Kwarko, Kwarko Chiefdom (T. S. Jones.-M.C.Z.); Bumpe Chiefdom (T. S. Jones.-M.C.Z.); Njala (T. S. Jones.-M.C.Z.); Freetown (W. H. and A. H. Brown.-U.S.N.M.). — LIBERIA: Harbel (Firestone Plantation), on the Du (or Dukwa) and Farmington Rivers; Monrovia; Memeh Town; Reputa to Kakata; Salala; Dobli Id.; Degei; Jenne; Kailahun; Bolahun; Sardu Pascia; Vasala; Nekaboo; foot of Mt. Wolagwissi at 2,000 ft.; Belleyella; Pandamai; Popolahun; Lukahzu; Bondualahun; Nyandamolahun; Taninewa; Daugomai; Vanyata; Bellepalamu; Kumbaeta; Mabossu; Zigida; Lakrata (all by J. Bequaert.-M.C.Z.); Ganta (G. W. Harley.-M.C.Z.); Cape Palmas (U.S.N.M.; M.C.Z.); Bavia (J. Büttikofer.-Leid.M.); St. Paul's River (Amst.M.); Mt. Coffee (Curie.-U.S.N.M.). — GOLD COAST: Suhum near Accra; Bawaleshi near Accra; Yensu near Accra (all by J. Bequaert and A. Mead.-M.C.Z.); Oda, 90 miles N. of Accra (G. S. Cansdale.-Chic.M.; also seen there alive by A. Mead); Nsawam (David Fairchild.-M.C.Z.). — SOUTHERN NIGERIA: Lagos (Ac.N.S.Phila.; M.C.Z.).

Previous records of typical *A. achatina*, with precise localities, were from Sierra Leone, Liberia, the Ivory Coast (Grand Bassam; Bouroukrou), the Gold Coast, and Dahomey (Abomey).

<sup>1</sup> Dr. Mermod notes also that specimens 1 and 2 agree with Pilsbry's Pl. 31, fig. 1 (*Achatina achatina* Linné); while specimen 3 agrees with his Pl. 24, fig. 23 (*Archachatina marginata* Swainson), except for the color of the aperture inside, which is much darker in the figure, and for the columella, which is less curved in the figure. Lamarck's Specimen 3 appears to be an immature *A. marginata*, with a sharp, not yet expanded outer lip, which may explain why Lamarck placed it with his other *A. perdir*. Moreover, *A. marginata* was only recognized as a distinct species by Swainson about the time Lamarck wrote his account of *Achatina*. [J. B.]

*Measurements of Adult Shells*

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
194 mm.	106	111	60	8	8	Harbel
191.5	99.5	102	54	8	8	Mt. Coffee
186.5	101	104.5	54	8	8	"
184	117	100	57	8	8	Liberia
172	87.5	85	49	7½	7½	Cape Palmas
167	80	86	43	8	8	West Africa
160	89	86	46	7	7	Taninewa

The nominate race of *A. achatina* is not only the largest, but also the most capacious terrestrial mollusk now living. The capacity of some of our Liberian specimens reaches 500 to 520 cubic cm. Our largest specimen (194 mm.) comes close to the record length of 200 mm. given by Dohrn (1878), also for a shell from Liberia. This area, with its yearlong high temperature, its protracted heavy rainfall and its luxuriant evergreen vegetation of dense forest, seems to offer the optimum environmental conditions for the species.

An abnormal umbilicate specimen, labelled as from "West Africa" (M.C.Z.), is shown in Pl. 39, fig. 3. It is 115 mm. long and 71 mm. wide.

b. *A. ACHATINA ROSEOLABIATA*, new subspecies

Pl. 1, fig. 1; Pl. 12, fig. 2

*Bulla achatina* Shaw and Nodder, 1796, Naturalist's Miscellany, 7, Pl. 248 (no date on Pl.; 2 views of immature shell). Not of Linné, 1758.

Size, shape and sculpture of typical *A. achatina*, the color pattern of dark brown wavy or zigzag stripes being the same. In addition to the columella and the parietal wall, the outer lip also is bright violaceous-pink over a wide inner margin, extending sometimes far into the interior of the mouth. Apex of spire more strongly suffused with rose than usual, as far down as the fifth whorl.

Shaw and Nodder apparently figured an immature specimen of this form, with the outer lip rather extensively violaceous within. The pointed spire refers the figures to a form of *A. achatina* and not to one of the purple-mouthed species of *Archachatina*. One of them is copied in my Pl. 12, fig. 2.

*Specimens Examined.* LIBERIA: Bolahun, holotype, M.C.Z. No. 163513; Jenne, paratype, M.C.Z. No. 163502; foot of Mt. Wolagwissi (about 2000 ft.) near Pandamai, paratype, M.C.Z. No. 163503 (all collected by J. Bequaert).

*Measurements of Adult Shells*

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
181 mm.	101.5	93.5	52	7½		Bolahun; holotype
169	87	92.5	46	7½		Jenne; paratype

c. *A. ACHATINA DEPRAVATA*, new subspecies

## Pl. 2, fig. 1

Size, shape and sculpture of typical *A. achatina*, but without any trace of dark brown wavy stripes; periostracum nearly uniformly straw-colored, with a few darker narrow vertical zones indicating stages of growth. Apex pinkish; columella and parietal wall vinaceous-red as usual.

*Specimens Examined.* LIBERIA: Harbel (Firestone Plantation), on the Du (or Dukwa) River, holotype, M.C.Z. No. 77001 (J. Bequaert). — Also one paratype, without locality, Chic.M. No. 525.

*Measurements of Adult Shells*

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
177 mm.	95	92.5	51.5	7½		Harbel; holotype
152	85	91	46	7		Paratype

d. *A. ACHATINA ELEGANS* (Link)

## Pl. 12, fig. 1; Pl. 14, fig. 1; Pl. 15, fig. 1

*Buccinum achatinum* var.  $\gamma$  O. F. Müller, 1774, Verm. Terr. Fluv. Hist., **2**, p. 141 (no locality; with description, but no references).

[Chemnitz, 1786, Syst. Conch. Cab., **9**, pt. 2, p. 18 (text in part only); Pl. 118, figs. 1012–1013].

*Ampulla achatina* Röding, 1798, Museum Boltenianum, pt. 2, p. 110 (with references to Gmelin sp. 32 $\beta$  and to Chemnitz, Pl. 118, figs. 1012–1013); 1819, *Op. cit.*, 2d Ed. (by J. Noodt), p. 78. Not of Linné, 1758.

*Achatium elegans* Link, 1807, Besch. Natur.-Samml. Rostock, **3**, p. 138 (defined by the reference to Chemnitz, Pl. 118, figs. 1012–1013).

*Helix (Cochlitoma) achatina* Férussac, 1823, Hist. Nat. Moll. Terr. Fluv., Atlas, Pl. 131A, figs. 2–3 (in Livraison 21, with name in Explanation on cover).

*Achatina perdix* Voigt, 1837, Lehrb. d. Zoologie, **3**, p. 396 (with reference to Chemnitz, Pl. 118, figs. 1012–1013). Pfeiffer, 1840, Krit. Register Konch.-Kab., p. 84. Not of Lamarck, 1822.

- Achatina variegata* var. Philippi, 1849, Abb. Besch. Conch., **3**, pt. 5, p. 31 (9 of *Achatina*); Pl. 2 of *Achatina*, fig. 4 (no locality). Reeve, 1849, Conch. Icon., **5**, *Achatina*, Pl. 5, fig. 3b (no locality). Not of Lamarck, 1801.
- Achatina variegata* var.  $\beta$  Pfeiffer, 1853, Monogr. Helic. Viv., **3**, p. 482 (with reference to Philippi's fig. 4).
- Achatina variegata* var. 1 Pfeiffer, 1857, Syst. Conch.-Cab., **1**, Abt. 13, pt. 1, p. 291 (in part); Pl. 2, figs. 1-2 (copies of Chemnitz's Pl. 118, figs. 1012-1013).
- Achatina chaperi* Ancey, 1888, Bull. Soc. Mal. France, **5**, p. 70, footnote (Ivory Coast: Assinie). Bequaert and Clench, 1934, Rev. Zool. Bot. Afric., **26**, pt. 1, p. 113.
- Achatina achatina* var. *chaperi* Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 64.
- Achatina variegata* var. *minor* Morelet, 1888, Jl. de Conchyl., **36**, p. 99 (no locality; briefly defined by comparison with *A. bayoli* Morelet). Not *Achatina panthera* var. *minor* Deshayes, 1851.
- Achatina variegata* var. *gracilis* Preston, 1909, Ann. Mag. Nat. Hist., (8), **3**, p. 183 (West Africa). Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 65. Schouteden, 1936, Rev. Zool. Bot. Afric., **28**, pt. 4, p. 498 (type from Putzeys' Coll., now at Tervuren Mus.). Not *Achatina sennaariensis* var. *gracilis* v. Martens, 1870.
- Achatina (Achatina) achatina* var. *minima* Germain, 1912, Ann. Inst. Océanogr. Monaco, **5**, pt. 3, p. 121 (Dahomey: Abomey. French Guinea: Konakry), fig. 1 (specimen from Abomey). Not *Achatina minima* Siemaschko, 1847.
- Achatina tincta* Gruvel, 1912, Ann. Inst. Océanogr. Monaco, **5**, pt. 3, p. 143 (French Guinea: Konakry; Los Archipelago, particularly Tamara. Eaten by natives). Not of Reeve, 1842.

O. F. Müller (1774) seems to have given the first recognizable description of the race *elegans*: "fulva, vel candida, axi sanguineo; long. 4 unc. [Danish inches=104.5 mm.], lat. 1 unc. 9 lin. [=45.5 mm.]" and (on p. 142): "Testa in  $\gamma$  fulva (decorticata, candida) pellucida, subrubens, duriuscula, pulcherrime longitudinaliter striata; striae subtilissimae confertae creberrime interruptae, ita ut series lineolarum excavatarum transversalium anfractus cingere videantur. Fasciae latae, undulatae fuscae longitudinales. Faux caeruleus, fasciis pellucidibus. Solus axis sanguineus."

Chemnitz (1786, p. 20) stated expressly that, in order to save space, he figured of this well-known snail only a pair of medium-sized specimens: one (fig. 1012) covered with the yellowish periostracum, seen from the back, is 85 mm. long, 53 mm. wide; the other (fig. 1013), shown in front view, is polished and denuded, 83 mm. long, 45 mm. wide, the aperture 47 by 27 mm. He added that some of his other specimens were up to 7 German inches (=183 mm.) long, these being of the typical form of the species. Both figures are copied in my



Pl. 12, fig. 1, and Pl. 14, fig. 1. Link may have had a specimen, the present whereabouts of which is unknown; his name is validated in any case by the reference to Chemnitz's figures; of these fig. 1012 is herewith taken as the type figure of *elegans*. Gmelin's *Bulla achatina*  $\beta$  (1790, p. 3432) covers references to figures of typical *achatina*, as well as to Chemnitz's figs. 1012-1013. Philippi (1849) pointed out the similarity between Chemnitz's fig. 1012 and his own shell, which was 93 mm. long, 50 mm. in greatest width, with the aperture 50 by 27 mm. Reeve's (1849) shell, although appearing perfectly full-grown, is one of the smallest known of the species, being only 61 mm. long, 34 mm. in greatest width, the aperture 34 by 18 mm.

Ancey gave no measurements of his unfigured *chaperi*, barely defining it by the statement that it is "always of small size." I have been unable to trace one of his actual types, although I saw some shells, without a locality, at the Brussels Museum which may have come from him.

Morelet's var. *minor* was described incidentally as follows (translated from the French): "The second form. [= *minor*], much more ventricose, has a more lengthened and much less obtuse spire; as a result its aperture is more dilated; the color and particularly the ornamentation are very different and although the sculpture is similar in both species, it does not appear the same, since *A. variegata* [var. *minor*] seems to be distinctly rugose to the eye, whereas the other species [= *A. bayoli*], more finely engraved, looks smooth." No measurements were given.

Preston's *gracilis* was very briefly described: "Shell less swollen and proportionately much narrower than is the case with typical *A. variegata*; the whorls are also rather more convex and the painting less regular. Alt. (about) 120, diam. maj. (about) 58 mm." I saw the unfigured type in Putzeys' collection in 1933; it is now at the Congo Museum, Tervuren (Belgium).

The best description published of subsp. *elegans* is that given by Germain for his *minima* (translated from the French): "Shell medium-sized, rather elongate, ovoid; spire of 8 moderately convex whorls, regularly increasing, divided by almost linear sutures; apex obtuse, almost smooth; body-whorl large, with the greatest convexity a little below mid-length; aperture elongate subpyriform, very acute above, broadly rounded below and outwardly, equal to about half the total length of the shell; columella curved inwardly, abruptly truncate at base. The apex is almost smooth; the first whorls show well-marked vertical striae, wrinkled at the sutures, wavy, rather close together, and cut by fine spaced spiral striae; the body-whorl has rather coarse irregular vertical striae, with only a few spiral striae near the suture.

The color is as variable as in typical *A. achatina*." Measurements are given of 5 shells: length respectively 80, 97, 100, 105, and 120 mm.; greatest width respectively 46, 50, 52, 59, and 60 mm.; lesser width respectively 36, 44, 45, 49, and 52 mm.; aperture respectively 44, 53, 56, 53, and 59 mm. long and 22, 27, 28, 30, and 35 mm. wide. The types could not be seen at the Paris Museum in 1933; but some have been traced there since by Dr. E. Fischer, who sent me a photograph of one of them, 120 mm. long, and presented one of these cotypes to the M.C.Z.

Subsp. *elegans* agrees with the nominate race in shape, color and sculpture, differing only in the smaller size for the same number of whorls in adult shells. Often, but not always, the apical whorls are whitish, without any trace of pink. Such dwarfs occur sporadically throughout the range of the species, almost always together with the larger form, seemingly showing no preference either for a particular geographical section or for a special environment. They may predominate, however, in certain localities. They do not seem to intergrade with the large specimens, so that some genetic difference may be involved.

If the name *elegans* is to be rejected owing to some technicality in present or future Rules of Nomenclature, the name *chaperi* Ancy will have to be used instead for this dwarf race.

*Specimens Examined.* LIBERIA: "Coast of Malaguette" (U.S.N.M.); Bolahun (J. Bequaert.-M.C.Z.); Ganta (G. W. Harley.-M.C.Z.); Suah Koko, ovipositing (J. Bequaert.-M.C.Z.).— DAHOMEY: Abomey, cotypes of var. *minima* (A. Gruvel.-Par.M.; M.C.Z.).— SOUTHERN NIGERIA: Oloki Meji, Ibadan (J. C. Bridwell.-Bish.M.; M.C.Z.).— Also several specimens merely labelled "West Africa", including the type of *gracilis* (Terv.M.; M.C.Z.).

There are also reliable records from French Guinea and the Ivory Coast.

#### *Measurements of Adult Shells*

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
150 mm.	84	76	44	7½		Oloki Meji
132	70	70	40	7¾		Suah Koko
115.5	63	66	32	7½		Ganta
107	56	58	29.5	7½		West Africa
102	55	57	29	7½		Bolahun
98	51	53.5	26.5	7½		Abomey
97	50.5	53	28	7		Liberia
69	39	39	29	6½		West Africa

e. *A. ACHATINA MONOCHROMATICA* Pilsbry

Pl. 10, fig. 2; Pl. 13, fig. 1; Pl. 19, fig. 1; Pl. 75, fig. 3

- ? *Bulimus fulvus* Bruguière, 1792, Encycl. Méthod., Vers, **1**, pt. 2, p. 359 (no locality; description of a specimen; also a reference to Lister, 1688, Synopsis, Pl. 582, fig. 35a, which, however, is *A. fulica* Bowdich, not Bruguière's *fulvus*). Bosc, 1802 (An X), Hist. Nat. Coq., **4**, p. 120.
- Achatina (Achatina) fulva* "Bruguière" Beck, 1837, Index Moll., pt. 1, p. 76 (with reference to Férussac's Pl. 124; no individual figures cited, but figs. 3-4 presumably intended).
- ? *Achatina fulva* Pilsbry, 1904, Man. of Conch., (2), **17**, p. 47 (in part: the description translated from Bruguière, but not most of the references).
- ? *Helix (Cochlitoma) fulvescens* Férussac, 1821, Tabl. Syst. Moll., Tabl. Limaçons, p. 49 (or p. 53) (no locality; no description; with *Bulimus fulvus* Bruguière as a synonym, to which I herewith restrict the name; also with a reference to Lister's Pl. 582, fig. 35a, which is *A. fulica* Bowdich).
- Achatina variegata* Reeve, 1849, Conch. Icon., **5**, *Achatina*, Pl. 5, fig. 3c (no locality). Not of Lamarek, 1801.
- Achatina variegata* var.  $\beta$  Pfeiffer, 1853, Monogr. Helic. Viv., **3**, p. 482 (with references to Reeve's fig. 3c and to Deshayes' Pl. 124, figs. 3-4).
- Achatina variegata* var. 2 Pfeiffer, 1857, Syst. Conch.-Cab., **1**, Abt. 13, pt. 1, p. 291.
- Achatina variegata* var. *unicolor* Deshayes, 1851, in Férussac, Hist. Nat. Moll. Terr. Fluv., Explanation of Plates in Atlas, p. 18, for Pl. 124, figs. 3-4 (no name on Plate); described without name as a small unicolorous variety in Vol. **2**, pt. 2, p. 157. According to Kennard, Pl. 124 was published after Férussac's death by Deshayes, presumably in 1851; but this is seemingly contradicted by Beck's citing it in 1837. Not *Achatina unicolor* C. B. Adams, 1849.
- Achatina cyanea* Roeters van Lennep, 1876, Cat. Coll. Shells van Lennep, p. 51 (*nomen nudum*). "Albers" Paetel, 1889, Cat. Conch.-Samml., 4th Ed., **2**, p. 239 ("Angola"); no description nor reference. *Nomen nudum*).
- Achatina achatina* var. *monochromatica* Pilsbry, 1904, Man. of Conch., (2), **17**, p. 10 ("Angola"); Pl. 32, fig. 3 (type). Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 64.
- Achatina (Achatina) achatina* var. *monochromatica* Germain, 1912, Ann. Inst. Océanogr. Monaco, **5**, pt. 3, p. 122 (French Guinea: Konakry. Dahomey: Abomey).
- Achatina monochromatica* Bequaert and Clench, 1934, Rev. Zool. Bot. Afric., **26**, pt. 1, p. 114.

The description of *Bulimus fulvus* Bruguière (1792), based on a specimen, reads (translated from the French): "Bulimus, testa obovata, fulva longitudinaliter obsolete striata, columella rosea. Differs from the preceding two species [*Achatina zebra* (Bruguière) and *A. achatina* (Linné)] in: (1) the shell, although with the same number of whorls, being a little more elongate and less ventricose; (2) the striae which cover it being all longitudinal [vertical], inconspicuous and without

any trace of transverse [spiral] striae; (3) the aperture being shorter than half the length of the shell, the left [outer] lip being very thin and not colored, while the columella has a beautiful incarnate tint as in the *Bulime perdrix* [*A. achatina*], but a little less deep; finally in the outside color, which is fulvous throughout without any mixture of another color. All other parts of the shell as in the preceding two species." Unfortunately no measurements are given. The first of the two citations, to Lister's Pl. 582, fig. 35a, is clearly erroneous, as this figure represents *A. fulva* Bowdich. It is, moreover, distinctly striped vertically, not unicolorous. Bruguière also cites with doubt O. F. Müller's *Buccinum achatinum* var. *c* [or  $\gamma$ ]; but this is described as having vertical undulating fuscous streaks and appears to be *A. achatina elegans* Link. So far as I could trace, Bruguière's type is lost. As pointed out by Pilsbry (1904), his *monochromatica* fits Bruguière's description of *B. fulvus* better than any other known *Achatina*. Although I fully agree with this, I hesitate to introduce the name *fulva* for it. So much is certain, however, that the name cannot be applied to any of the East African *Achatinae*, as Deshayes (1838; 1851) and his successors did. Deshayes' description and the Plate 124, figs. 1-2, of Férussac's Atlas, which he cites in support of it, are of *Achatina fulva*. The pale columella and the markings of the shell could not possibly fit Bruguière's description.

The small unicolorous race of *A. achatina* was well figured by Reeve (1849), his specimen being 96 mm. long, 53 mm. in greatest width, with the aperture 53 by 29 mm. Deshayes' (1851) specimen (Pl. 124, figs. 3-4) is slightly smaller, 83 mm. long, 47 mm. in greatest width, with the aperture 48 by 25 mm. One of Deshayes' figures is copied in my Pl. 75, fig. 3. This form, recognizably described by Pfeiffer in 1853 and 1857, is found in several collections labelled "*cyanea* Albers," a manuscript name published, but not validated by Paetel (1889). I saw Paetel's specimen at the Berlin Museum in 1933 and recognized it as var. *monochromatica* Pilsbry. It now bears the obviously erroneous locality label "Algoa Bay", although Paetel listed it from "Angola."

Pilsbry's description of var. *monochromatica* was presumably based on one of these old specimens: "Shell somewhat smaller [than typical *A. achatina*], white under the smooth and glossy olive-yellow cuticle, which is uniform except for some faintly darker streaks marking growth-stages, and a faint peripheral belt. Suture distinctly margined. Aperture smaller than in *achatina*, colored the same. Length 120, diam. 65, aperture 66 mm." I have seen the type (Ac.N.S.Phila. No. 78483), shown in my Pl. 19, fig. 1. It has 7 whorls and agrees with the measurements given (the original figure is 5 mm. too short). Pilsbry states correctly that this shell meets the requirements of

Bruguère's description of *B. fulvus* better than the East African form (a variant of *A. fulica* Bowdich) which later authors have associated with the name. There is, however, too much uncertainty about the matter to replace the name *monochromatica* by the earlier *fulva*. The lack of any information about the size of Bruguère's shell is particularly disturbing. It would seem strange that the author called attention to the more elongate shape as compared with *A. achatina*, and not to the more obvious size. For this reason the possibility cannot be ignored that his *B. fulvus* might have been a specimen of the large unicolorous race which I describe as *A. achatina depravata*.

Germain (1912) recorded *monochromatica* from French Guinea and Dahomey. I could not see these specimens at the Paris Museum in 1933; but Dr. E. Fischer has recently found the lot from Abomey and has kindly sent me two of them, with permission to retain one for the M.C.Z. These specimens agree in every respect with Pilsbry's type of *monochromatica*, as well as with the similar shells called "*cyanea*" in some collections, being entirely devoid of even traces of wavy dark streaks. At least one exact locality is now known for this race. Whether the shells Germain mentioned from French Guinea also belong here must be left undecided for the present.

Subsp. *monochromatica* includes diminutive adult examples, nearly uniformly yellowish-fulvous or straw-colored, entirely devoid of the usual dark-brown vertical streaks or zigzag markings. Columella and parietal wall are bright rose-colored to purplish when fresh.

*Specimens Examined:* DAHOMEY: Abomey (A. Gruvel.-Par.M.; M.C.Z.). — In addition I have seen Pilsbry's holotype (Ac.N.S.Phila. No. 78483) and several specimens in various museums (M.C.Z.; U.S.N.M.; A.M.N.H.; Hamb.M.; Brus.M.; Berl.M.; Brit.M.). All seem to be from old collections and may have come originally from the same source. None bear a reliable locality. A few are labelled "Angola", almost certainly by error as no form of true *A. achatina* has ever been reliably collected there so far as I know. One shell at M.C.Z. is labelled "Sierra Leone", a more likely locality, in view of Germain's record from French Guinea, although the occurrence in both these countries needs to be confirmed.

#### Measurements of Adult Shells

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
103.5 mm.	54.5	57	28.5	7¾		Abomey
101	54	53	29	7¾		Brussels Mus.
96	51	49	28	7½		M.C.Z. No. 97934
90	51	50	27	7½		Brussels Mus.
80	49.5	47	24	7		M.C.Z. No. 75564

It may be noted that Pilsbry's type is appreciably larger than any of the specimens I have measured for the foregoing table, although it is considerably smaller than the unicolorous race which I call subsp. *depravata*.

f. A. *ACHATINA TOGOËNSIS* Bequaert and Clench

Pl. 2, fig. 2; Pl. 5, fig. 2; Pl. 7, fig. 2; Pl. 39, fig. 1

*Achatina* (?) *hamillei* v. Martens, 1893, Mitth. Deutsch. Schutzgeb., 6, pt. 3, p. 216 (Togo: Bismarekburg). Not of Petit, 1859.

*Achatina togoënsis* Bequaert and Clench, 1934, Rev. Zool. Bot. Afric., 26, pt. 1, p. 112 (Togo: Bismarekburg); Pl. 1, figs. 1 (paratype), 2 (holotype), 3 (paratype), and 4 (sculpture of holotype X 4).

"Shell broadly ovate, moderately thick and solid, uniformly and slightly shiny. Color pale olive-brown, with narrow, rather evenly spaced, oblique, chestnut-brown axial stripes, which are partly even, partly broken up into a fine zig-zag or occasionally into small spots (especially on the lower half of the whorls); on the body-whorl the stripes do not reach the columella; the first two and a half whorls are whitish, unstriped; on the next two whorls the stripes are faint, becoming gradually bolder; columella white, in the upper part slightly bluish; aperture pale bluish inside and showing the brownish stripes by transparence. Apex subobtusate, not drawn out. Whorls  $7\frac{1}{4}$  (holotype), slightly convex, gradually increasing in size; sutures scarcely indented, slightly depressed on the body-whorl, very finely wrinkled. Spire broad, top-shaped, produced at an angle of  $57^\circ$ . Body-whorl about 78 per cent of the total shell. Aperture oval, slightly oblique, widest about the middle. Palatal lip (peristome) thin and simple, broadly rounded at the base. Parietal wall glazed bluish-white. Columella short, broad, almost straight, simple throughout, very obliquely truncate, the broad truncation placed a short distance above the basal margin of the aperture. First two whorls microscopically granular in the youngest shell seen, partly worn smooth in older shells; remaining whorls decussately sculptured to the naked eye through the intersection of rather regularly spaced and moderately deep spiral lines with strong axial growth-wrinkles; on the third whorl this produces a fine beading, on the succeeding whorls regular, oblique rows of axial welts; the decussation is much fainter above the sutures and is lacking over the lower half of the body-whorl, which shows only faint growth-wrinkles." (Bequaert and Clench, 1934).

*Specimens Examined.* Togo: Bismarekburg, holotype (Berl.M. No. 47176, collected by Conradt), and 2 paratypes (R. Büttner, 1891.-

Berl.M. No. 43356 and M.C.Z. No. 98688). Also one immature paratype from Togo (E. Kling.—Berl.M. No. 42362).

The specimens collected by R. Büttner were the shells doubtfully referred to *A. hamillei* by v. Martens in 1893. *A. fulica hamillei* is strictly East African.

Although originally described as a distinct species, a study of the several variations in size and color of *A. achatina* has now convinced me that *togoënsis* is at most a subspecies. It is very similar to subsp. *elegans*, but lacks all trace of rose or violaceous color on the columella and parietal wall.

*Measurements of Adult Shells*

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
89.5 mm.	48.6	50	26	7¼		Holotype
89	49.2	51.3	27.6	7¼		Paratype
72.5	40.6	41.8	22.6	7		"

g. *A. ACHATINA BAYOLI* Morelet

Pl. 6, fig. 1; Pl. 9, fig. 1

*Achatina bayoli* Morelet, 1888, Jl. de Conchyl., **36**, p. 97 (Ivory Coast: Assinie); Pl. 1, fig. 4 (2 views of type).

*Archachatina bayoli* Pilsbry, 1905, Man. of Conch., (2), **17**, p. 118; Pl. 22, figs. 9–10 (after Morelet). Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 66.

*Archachatina (Megachatinops) bayoli* Bequaert and Clench, 1936, Rev. Zool. Bot. Afric., **29**, pt. 1, p. 86.

Morelet's original description (French text translated): "T. oblonge ovata, ventricosula, solidula, confertim striata et superne usque ad peripheriam (praeter nucleum) impressionibus aequidistantibus granulata, nitida, luteo-fulva, in ultimo anfractu strigis maculisque nigricantibus irregulariter picta, in superioribus confertim flammulata vel strigata. Columella vix arcuata, oblique truncata, pulchre purpurea. Anfr. 6½ convexi, ultimo medio obsoletissime angulato, spiram superante. Spira conoidea, obtusa, nucleo livido, laevigato. Apertura ovalis, intus pallide lilacina, opalina, flammulis maculisque translucens. Perist. acutum, tenue. — Longit. 66; diam. 30. Apert. 36 mill. longa, 20 lata. The shape is that of a somewhat elongate ovoid; the shell is therefore ventricose with a mediocre spire, the whorls of which are convex and the summit obtuse. The suture which joins them is simple, but strongly impressed. The columella, scarcely arched, is

obliquely truncate; it is striking for its bright purple color, which extends, but fades over the parietal wall of the aperture. The shell, of moderate thickness, rather thin in some specimens, is engraved with distinct, closely set striae, crossed at right angles by other less distinct and more spaced striae, forming a lengthened granulation, which usually is reduced to a simple striation on the second half of the last whorl. Sometimes, however, the ornamentation persists on the dorsal face to the end of the shell. The color is yellowish fulvous, on which stand out sharply dark brown striae and flammules, as well as spaced and very irregular small spots. This ornamentation, less distinct on the whorls preceding the last, but more closely set, more regularly spaced, is visible by transparence inside the aperture, which is tinged a very pale, slightly opaline lilac. On account of a certain analogy of size, proportions and colors, this shell may be compared to *Achatina papyracea*, *A. siderata* and *A. knorri*; but it could not be confused with the variety *minor* of *A. variegata*, for the similarity which seems to be noted between these shells vanishes as soon as one compares them. The second form, much more ventricose, has a more elongate and much less obtuse spire; as a result, its aperture is more dilated. Its coloration and especially its ornamentation are very different, and, although the sculpture of the surface is analogous in the two species, the effect is not the same, for *A. variegata* seems to the eye markedly rugose, whereas the other form, more finely chiseled, appears smooth. Finally in this one the suture is not margined." Several specimens were collected by Dr. Bayol and sent to Chaper, who deposited the type specimen at the Ecole des Mines in Paris. The others seem to have been distributed freely, for paratypes are found in various collections. I have seen some of these, but not the holotype. Morelet's figure is copied in my Pl. 9, fig. 1.

*A. bayoli* has thus far been placed in *Archachatina*, no doubt under the influence of Morelet's suggestion that his species showed some analogy to *papyracea*, *siderata* and *knorri*. However, the resemblance is very slight and indicates no true relationship. In particular, the nepionic whorls are not in the least dome-shaped and do not point to the abnormally large egg characteristic of *Archachatina*. The summit, although somewhat broader than in typical *A. achatina* (which may be correlated with the dwarfed size), is nevertheless obtusely pointed. Notwithstanding Morelet's statement to the contrary, the sculpture is essentially that of *A. achatina*. It is somewhat weaker than in the nominate subspecies, but it differs little in this respect from some of the other subspecies. The most distinctive features of *bayoli* appear to be the relatively narrower shape and more fusiform outline, as well as the peculiar arrangement of the color markings. The spire is



scarcely more narrowed than the base. This is the smallest race of *A. achatina*; but there is some doubt in my mind that even Morelet's largest specimen, apparently figured by him, was actually full-grown. The few specimens I have seen were all clearly immature. The largest of these was 56 mm. long, 30 mm. in greatest width, of 6 whorls, with the aperture 33.5 by 15.5 mm.

*Specimens Examined.* IVORY COAST: Assinie (one paratype, received from Ancey.—U.S.N.M.; 3 specimens collected by C. Alluaud, named by P. Dautzenberg.—Terv.M.; M.C.Z.; one paratype, sent by Chaper to Connolly.—Brit.M.; one specimen bought from Preston.—Leid.M.). According to Dr. E. Fischer (*in litt.*, 1949), the collection of the "Journal de Conchyliologie," now deposited at the Paris Museum, also contains an immature paratype, 48 mm. long.

#### ACHATINA (ACHATINA) BALTEATA Reeve

*A. balteata* is the only known representative in Upper Guinea of a complex of superficially similar species, with large, elongate-ovate to spindle-shaped shells, much more slender than *A. achatina*, fairly uniformly olivaceous-yellow, yellowish-brown or pale chestnut, sometimes with darker chestnut or mahogany streaks or blotches or with hydrophanous areas in the periostracum. The sculpture, characteristic of each species, consists of various types of wavy lines or granulations, particularly diagnostic on the body-whorl of full-grown shells. In 1934 (Amer. Mus. Novitates, No. 705, pp. 1-16) Bequaert and Clench published the first attempt to define the species on the basis of the sculpture. Further study of additional material and particularly of certain types in European Museums, has led me now to modify the nomenclature adopted in 1934 and has enabled me to include some other species or races in the same group. Their classification now stands as follows.

1. *A. balteata* Reeve, with the subsp. *infrasusca* v. Martens. Fully discussed in the present paper.

2. *A. iostoma* Pfeiffer, 1854 (Synonyms: *A. tiara* Preston, 1900; *A. hessei* C. R. Boettger, 1913; and *A. gruweli* Dautzenberg, 1921). See the 1934 paper. *A. hessei* is now believed to be not separable from *A. iostoma*.

3. *A. bandeirana* Morelet, 1866 (Synonym: *A. bandeirana capacior* C. R. Boettger, 1927). See the 1934 paper.

4. *A. dohrniana* Pfeiffer, 1870. Closely related to *A. balteata* and *A. iostoma*, but with the columella more twisted and very obliquely truncated at the base. The sculpture is stronger than in *balteata*, but

weaker than in *iostoma*, being well visible with the naked eye and just felt by touch. Moreover, while it is distinctly granulose on the early whorls, on the upper part of the body-whorl it consists of elongate, vertical welts, arranged fairly uniformly in spiral rows and vertical lines, becoming bead-like only below the periphery.

5. *A. stuhlmanni* v. Martens, 1892 (Synonyms: *A. rugosa* Putzeys, 1898; and *A. osborni* subsp. *hylaecae* C. R. Boettger, 1927); with subsp. *chapini* Bequaert and Clench, 1934. See the 1934 paper. A study of the holotype and an immature paratype of *stuhlmanni* at the Berlin Museum, in 1933, and a comparison with two paratypes of *rugosa* (both from the type locality Micici), as well as with the holotype and paratype of *hylaecae* at the Hamburg Museum, shows that neither of the two last-named differs, even subspecifically.

The sculpture of *A. balteata* is a fine to medium-sized granulation, covering practically the entire shell. On the youngest specimen seen, 47.5 mm. in length, of about 5 whorls, the nepionic shell, of about  $2\frac{1}{2}$  whorls, is unicolorous pale straw-yellow, decussately and minutely granulose, except for the smooth first half-whorl (Pl. 71, fig. 1). On the first post-nepionic whorl appear vertical, straight or slightly wavy, spaced, light-brown streaks, distinct as far as the fourth whorl, then gradually fading, not being present except as traces beyond the fifth whorl in the nominate race of the species. In subsp. *infracusca*, these dark streaks are not only more marked and more mahogany-brown, but extend to the body-whorl of full-grown shells, at least as blotches or as half-streaks above the periphery. In full-grown shells, the granulation of the early whorls of the spire is well-marked and uniform, the beads being placed in distinct spiral rows, but less regular vertical lines. It is so delicate that it often imparts a silky appearance to the summit of the shell. On the penultimate whorl the granulation is much less regular, being interrupted by many smooth or wrinkled areas. On the body-whorl the granulation, though present, becomes more confused (Pl. 17, fig. 3), the growth-lines being coarser than the beads. On the upper half of the body-whorl, close to the outer lip, there are 25 to 30 beads over a vertical distance of about 1 cm. The granulation of the body-whorl is barely visible with the naked eye, but cannot be felt by touch. There is no trace of wavy sculpture, either vertical or spiral, the beads being too coarse. This species also lacks hydrophanous areas of the periostracum, even in the best preserved and freshest shells seen. In immature shells, up to 70 mm. long, the last whorl is more or less angular at the periphery, which usually shows a narrow spiral, light-brown streak, the latter sometimes present on the body-whorl of the adult.

*A. balteata* has an unusual discontinuous distribution, which is difficult to explain. The main range, where the species is fairly common in several localities, is Lower Guinea, from Cameroon to Central Angola (Novo Redondo and Golungo Alto), extending in the Congo Basin to the Upper Uele country. Originally it was described, however, from Gambia and there appears to be no valid reason to doubt that the types were actually taken there, as there are also two reliable records from Sierra Leone. Yet in the vast intervening area, from Liberia to Southern Nigeria, it has never been observed, so far as I am aware. Moreover, a most careful comparative study of specimens from Lower Guinea and the Sierra Leone-Gambia area, discloses no appreciable difference. It is here suggested that the colonies in the western section of Upper Guinea are isolated and the progeny of accidental or perhaps intentional introduction by man of living snails from the main Lower Guinea range.

#### a. Typical *A. BALTEATA*

Pl. 17, figs. 1 and 3; Pl. 18, fig. 2;

Pl. 41, fig. 1; Pl. 71, fig. 1; Pl. 77, fig. 4

*Achatina fulva* Pfeiffer, 1848, Monogr. Helic. Viv., **2**, p. 251 (in part: measurements and reference to Pl. 11, figs. 3-4 of Syst. Conch.-Cab., **1**, Abt. 13, pt. 1, later recognized by Pfeiffer to represent *A. balteata*). Not *Bulimus fulvus* Bruguière, 1792; nor *Achatina fulva* Beck, 1837.

*Achatina balteata* Reeve, 1849 (February), Conch. Icon., **5**, *Achatina*, Pl. 2, fig. 7 (banks of the River Gambia). Jay, 1850, Cat. Shells Coll., 4th Ed., p. 216. Deshayes, 1851, in Férussac, Hist. Nat. Moll. Terr. Fluv., **2**, pt. 2, p. 164, and Explan. of Plates, p. 19; Atlas, Pl. 132, figs. 3-4 (2 views of one shell) and 5 (detail of sculpture) (Plate published after Férussac's death, presumably in 1851). Pfeiffer, 1853, Monogr. Helic. Viv., **3**, p. 487; 1857, Syst. Conch. Cab., **1**, Abt. 13, pt. 1, p. 304; Pl. 11, figs. 3-4 (specimen). Plate published without explanation or corresponding text in 1841). Gruner, 1857, Cat. Coll., p. 25. Morelet, 1858, Séries Conchyl., **1**, p. 20 (Gaboon). Pfeiffer, 1859, Monogr. Helic. Viv., **4**, p. 603. v. Martens, 1860, in Albers, Die Heliceen, p. 201. A. D. Brown, 1861, Cat. Shells Coll., p. 55. Bielz, 1865, Verzeichn. Moll. Conch.-Samml., 3d Ed., p. 23. Morelet, 1867, Voy. Welwitsch, Moll. Terr. Fluv., (1868), p. 65 (Angola: Golungo Alto; District of Novo Redondo). Haines, 1868, Cat. Terr. Shells Coll., p. 67 ("Liberia"). Pfeiffer, 1868, Monogr. Helic. Viv., **6**, p. 217. Paetel, 1869, Moll. Syst. Cat., p. 80; 1873, Cat. Conch.-Samml., p. 99. Fridrici, 1874, Bull. Soc. Hist. Nat. Metz., **13**, p. 184. Pfeiffer, 1876, Monogr. Helic. Viv., **8**, p. 275. v. Martens, 1876, Monatsber. Ak. Wiss. Berlin, p. 258; Pl. 2, fig. 2 (animal. Cameroon: Victoria). Roeters van Lennep, 1876, Cat. Coll. Shells van Lennep, p. 53. G. R. Batalha,

1878, Cat. Coll. Conchyl. F. R. Batalha, p. 1. v. Martens, 1882, Jahrb. D. Mal. Ges., **9**, p. 245 (Portuguese Congo: Chinchoxo). Grasset, 1884, Index Test. Viv. Coll., p. 199. Vignon, 1888, Bull. Soc. Mal. France, **5**, p. 69 (Gaboon). Martorell y Peña, 1888, Catálogo Colección Conchol. Museo Martorell, Barcelona, p. 56. Bourguignat, 1889, Moll. Afr. Equat., p. 78. Paetel, 1889, Cat. Conch.-Samml., 4th Ed., **2**, p. 239. Stearns, 1893, Proc. U. S. Nat. Mus., **16**, p. 326 (Sierra Leone: Freetown). Boucard, 1901, Cat. Coll. Coq. Terr., p. 49. Pilsbry, 1904, Man. of Conch., (2), **17**, p. 30 (Gaboon); Pl. 4, fig. 27 (after Reeve). Nobre, 1909, Bull. Soc. Portugaise Sc. Nat., **3**, Suppl. 2, p. 89 (Angola: Golungo Alto; Novo Redondo; Cazenge; Loanda; Quilombo; forests of Mupépé; forests of Zembe; region of Selles; Gumba; Hambo; Supa; interior of Benguella).<sup>1</sup> Hidalgo, 1910, Mem. Soc. Españ. Hist. Nat., **1**, No. 29, p. 508 (Spanish Guinea: Cabo San Juan). Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 65. Germain, 1911, Bull. Mus. Hist. Nat. Paris, **17**, p. 223 (French Congo: Marvisch River; Makoua; Ivindo River). C. R. Boettger, 1913, Ann. Soc. Zool. Mal. Belgique, **47**, (1912), p. 94 (Belgian Congo: Upoto, in 20° E.). Germain, 1913, Bull. Mus. Hist. Nat. Paris, **19**, p. 353, fig. 71 (young shell. French Equatorial Africa: M'Baiki in Lobaye District; Fort Rousset); 1916, Ann. Mus. Civ. Genova, **47**, p. 238 (French Congo: Fernand Vaz. Cameroon: Buea, 800 to 1200 m.). Pilsbry, 1919, Bull. Amer. Mus. Nat. Hist., **40**, p. 78. Dautzenberg, 1921, Rev. Zool. Afric., **9**, pts. 1-2, p. 87 (Cameroon: Yaunde, 700 m.). Connolly, 1928, Ann. Mag. Nat. Hist., (10), **1**, p. 540 (Sierra Leone: Freetown). Bequaert and Clench, 1934, Amer. Mus. Novitates, No. 705, p. 8, figs. 4-5 (Gambia: Bathurst. Cameroon: Kribi; Lolodorf. Belgian Congo: Ngayu). Coen, 1945, Catalogo Gasteropodi Polmonati Coll. Coen, p. 42. Not of Gould, 1850.

*Achatina* (*Archachatina*) *balteata* Albers, 1850, Die Heliceen, p. 190.

*Achatina* (*Achatinus*) *balteata* Pfeiffer, 1856, Malak. Blätt., **2**, (1855), p. 168; 1879, Nomencl. Helic. Viv., p. 265.

*Achatina monetaria* Morelet, 1867, Voy. Welwitsch, Moll. Terr. Fluv., (1868), p. 63 (Angola: region of Selles, in the interior of Novo Rodondo District); Pl. 8, fig. 2 (type). Pfeiffer, 1876, Monogr. Helic. Viv., **8**, p. 272. Grasset, 1884, Index Test. Viv. Coll., p. 199. Bourguignat, 1889, Moll. Afr. Equat., p. 75. Paetel, 1889, Cat. Conch.-Samml., 4th Ed., **2**, p. 340. Pilsbry, 1904, Man. of Conch., (2), **17**, p. 19; Pl. 5, fig. 6 (after Morelet). Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 65. Germain, 1925, Mission Rohan-Chabot, **4**, pt. 3, p. 216 (says it is probably an abnormal *A. balteata*). Dartevelle, 1948, Bull. Service Géolog., Léopoldville, Congo Belge, No. 3, (1947), p. 110, footnote.

*Achatina* (*Achatinus*) *monetaria* Pfeiffer, 1879, Nomencl. Helic. Viv., p. 264.

*Achatina papyracea* Vignon, 1888, Bull. Soc. Mal. France, **5**, p. 71 (Gaboon). Not of Pfeiffer, 1845. According to Ancey, *Op. cit.*, p. 71, footnote, a specimen of *A. balteata*.

<sup>1</sup> Some of Nobre's localities no doubt were based on specimens of *Achatina bandeirana* Morelet, which he regarded as synonymous with *A. balteata*, an opinion with which I do not agree.

- Achatina iostoma* form *albina* O. Boettger, 1905, *Nachrichtsbl. D. Mal. Ges.*, **37**, p. 170 (Cameroon: Nongo Madiba on the Bali Road).
- Achatina balteata* var. *vidaleti* Germain, 1913, *Bull. Mus. Hist. Nat. Paris*, **19**, p. 354 (French Equatorial Africa: precise locality not given, but presumably from Fort Rousset, where Vidalet collected his other specimens of *A. balteata*).
- Achatina rugosa* Pilsbry, 1919, *Bull. Amer. Mus. Nat. Hist.*, **40**, p. 76 (in part: specimens from Ngayu, Belgian Congo, only). Not of Putzeys, 1898.

Original description of *A. balteata* Reeve (1849): "Achat. testa acuminato-oblonga, subfusiformi, crassiuscula, anfractibus octo ad novem, subplicato-striatis, undique creberrime minute granulatis, columella peculiariter arcuata, et contorta, abrupte truncata; flavescente, fasciis castaneis longitudinalibus apicem versus tincta, fascia spirali interrupta, subindistincta, medio cingulatis, columella et aperturæ fauce caerulescente-alba. Shell acuminately oblong, somewhat fusiform, rather thick, whorls eight to nine in number, slightly plicately striated, very closely minutely granulated, columella peculiarly arched and twisted, abruptly truncated; yellowish, stained towards the apex with chesnut longitudinal bands, and encircled round the middle with a rather indistinct interrupted spiral band, columella and interior of the aperture bluish-white. Very beautifully minutely granulated throughout, and characterized by a faint spiral band, in a manner which obtains some specific importance on account of its singularity." The original figure is copied in my Pl. 18, fig. 2. The two adult cotypes, from the Cuming Collection, which I saw at the British Museum in 1933, are much alike. They have the characteristic sculpture which I have described for *balteata*. The upper half of the body-whorl lacks all trace of dark brown vertical streaks. The figure of the type is 125 mm. long, 56 mm. in greatest width, with the aperture 59 by 30 mm., being relatively narrower than average.

Original description of *A. monataria* Morelet (1867): "T. ovato-acuta, crassa, ponderosa, albido-livida, epidermide tenui, fulvescente, induta; spira contabulata, mucronata, apice acuta, carneola; anfr. 8, priores convexiusculi, minutissime granulati, 3 ultimi infra suturas horizontaliter planati, deinde convexiusculi; ultimus permagnus, deorsum ruditer et crebre granuloso-plicatus, spiram valde superans; columella crassa, alba, leviter arcuata, supra basim aperturæ oblique truncata; apertura ampla, subverticalis, sinuato-ovalis, intus lactea; perist. obtusum, rectum, extus fusco limbatum, margine externo superne breviter sinuoso, cum altero callo lato, crasso, albido, juncto. Longit. 142; diam. 65 mill." The following additional descriptive notes are translated from the French: "The specimen we have seen is unfortunately without periostracum, which judging from the remnants

must have been fulvous, variegated with some darker longitudinal streaks. The species is remarkable for its solidity and the spire arranged in tiers. The first whorls are regularly developed and form a rather sharp cone; the last three are swollen below the sutures, where there is a horizontal flattening which makes the shell somewhat scalariform. It cannot be decided from a single specimen whether this peculiarity is constant or merely accidental. The body-whorl is ventricose and ends in a broad, calloused aperture, with thickened margins and milky-white interior. The right margin [outer lip] is slightly dilated toward its insertion and margined with brown outside; the columella is arcuate, solid, ending in an oblique truncation and provided with a strong callosity over its entire length. The shell is engraved with distinct, closely set, granulose, more or less regular striae, more pronounced, as often happens, near the sutures." The type and only known specimen of *monetaria* is at the British Museum, where I saw it in 1933. It is a very old, bleached and worn shell, apparently picked up in or near a native settlement. Its peculiar shape is clearly abnormal. The sculpture, so far as preserved, is that of *balteata*, of which I regard it as a synonym, following Germain's (1925) suggestion. It is one of the largest specimens of the species on record. Morelet's figure is copied in my Pl. 41, fig. 1.

Germain (1913) gave the following brief description (translated from the French) of his var. *vidaleti*, based entirely on color: "The coloration [of *balteata*] also is variable. As a rule greenish-yellow in young shells, where the columella moreover is often tinged with violet, it turns more or less dark chestnut in the adult. However, some medium-sized specimens (95 mm. long, 50 mm. in greatest width, 42 mm. in lesser width) retain the pale yellowish-chestnut color with the violaceous columella. These specimens are the variety *ex colore* which I call var. *vidaleti*." On my visit to the Paris Museum in 1933 I was unable to examine the types of this variety. There is, however, nothing in the description to justify the retention of the name for a race of *balteata*. It was clearly based on immature specimens. In all young *balteata* the columella is partly violaceous, while in fully adult specimens this color tends to disappear; but even in some full-grown shells from Gambia the columella is blotched with purplish.

O. Boettger's *A. iostoma* form *albina* was based on specimens "almost unicolorous olive-yellow or olive-brown and with streaks on the upper whorls only; in addition often somewhat larger and more slender." A study of four of the types at the Senckenberg Mus. (Frankfort), in 1933, disclosed that they were *A. balteata*, not *A. iostoma*, so far as the sculpture is concerned. It is moreover impossible to separate them from the nominate race of *balteata*. An immature paratype is shown in my Pl. 77, fig. 4.

*A. balteata* has been used by certain African native tribes for monetary purposes. Morelet (1867, Voy. Welwitsch, Moll. Terr. Fluv., p. 47) relates that, in Angola, the shells are cut into disks, pierced in the center and put up in strings, to be used as money. According to C. R. Boettger (1913), at Upoto (Lisala), Belgian Congo, the shell is sawed lengthwise by the natives, the halves serving as currency.

*Specimens Examined.* Several merely labelled "West Africa" (U.S.N.M.). — GAMBIA: without precise locality (2 cotypes at B.M., others at M.C.Z., Amst.M., Berl.M.); Bathurst (Carn.M.; M.C.Z.). — SIERRA LEONE: Freetown (U.S.N.M.). — CAMEROON: Bafia (E. D. Horner.—M.C.Z.); Buea (P. Preuss.—Berl.M.; M.C.Z.); Kribi (G. Schwab.—M.C.Z.); Nongo Madiba on Bali Road (R. Rohde.—Types of *f. albina* at Frankf.M. and M.C.Z.); Lolodorf (A. J. Good.—Carn.M.; M.C.Z.). — FRENCH CONGO: Franceville (Terv.M.); Ombouet (C. R. Aschemeyer.—U.S.N.M.); Rembokotou (C. R. Aschemeyer.—U.S.N.M.); Sámkita, Ogowé River (M.C.Z.); Gaboon River (Berl.M.). — BELGIAN CONGO: Luvituku (Terv.M.); Kitobola (Terv.M.); Eala (J. Bredo.—Terv.M.); Leverville (Mrs. Tinant.—Terv.M.); Ngayu (Lang and Chapin.—A.M.N.H.; M.C.Z.).

The species is also reliably recorded from the Portuguese Congo, Angola, Spanish Guinea and the interior of French Equatorial Africa (Fort Rousset, 0° 30' S., 16° E.). Ngayu (1° 40' N., 27° 40' E.) is the easternmost locality known. Haines' (1868) indication "Liberia" I regard as wholly unreliable.

#### Measurements of Adult Shells

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
148.5 mm.	73	81	38		9	Rembokotou
140.5	67	74.5	37		9	"West Africa"
138	68	74	40.5		9	Bathurst
137	62	67	33		9	Gaboon
133	65	69	38.5		9	Gambia
131	67.5	71	35		8½	Gaboon
124	62	65.5	36.5		7¾	Ngayu
120	60.5	61	30.5		8¾	"
114	57.5	64	34.5		7½	"
113	57	57	30		8½	Freetown
110	50	53.5	26		8½	Gaboon
105	51	52.5	28		8	"West Africa"

b. *A. BALTEATA INFRAFUSCA* v. Martens

Pl. 44, fig. 1; Pl. 51, figs. 1-2

*Achatina dimidiata* v. Martens, 1889, Conch. Mitth., **3**, pts. 1-2, p. 17 (French Congo: mouth of Gaboon River); Pl. 42, figs. 1-1a (front view of type and detail of sculpture). Not *Achatina dimidiata* E. A. Smith, 1878.

*Achatina infrafusca* v. Martens, 1897, Deutsch-Ost-Afrika, **4**, Besch. Weichth., p. 89 (new name for *A. dimidiata* v. Martens, 1889).

*Achatina balteata* var. *infrafusca* Pilsbry, 1904, Man. of Conch., (2), **17**, p. 32 (French Congo: Gaboon, with specimens transitional to typical *balteata*); Pl. 4, figs. 22-23 (after v. Martens). Kobelt; 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 65. C. R. Boettger, 1913, Ann. Soc. Zool. Mal. Belgique, **47**, (1912), p. 94 (in part: only shell from French Congo: Quillo River, N. of Loango);<sup>1</sup> 1932, Sitzungsber. Ges. Naturf. Fr. Berlin, p. 303 (French Congo: Lambarene). Bequaert and Clench, 1934, Amer. Mus. Novitates, No. 705, p. 11, fig. 6 (Belgian Congo: Lukolela. French Congo: Lambarene on Ogowe River).

Original description of *A. dimidiata* v. Martens (1889) (German text translated): "Testa fusiformi ovata, imperforata, rugosostriata, undique granulata, granulis spiratim seriatis, supra fulva, strigis castaneis plus minusve flexuosis vel abbreviatis picta, infra unicolor castanea; spira conica, sutura simplice; anfr.  $8\frac{1}{2}$  vix convexiusculi, primi albi, sequentes magis confertim strigati; apertura dimidiam longitudinem non aequans, sinuato-ovalis, intus coerulescens, peristomate tenui recto castaneo, columella arcuata, coerulescenti-alba, basi attenuata, distincte truncata. Long. 120, diam. 60, apert. long. 59, diam. 32 mill. Shell between spindle-shaped and ovate, imperforate, wrinkled striate, covered everywhere with granulations placed in spiral rows; yellowish-brown above the suture and the periphery, with a few usually zigzag or briefly interrupted streaks; below the periphery (hence visible only on the body-whorl) uniformly chestnut-brown; at the limit between the two colors with occasional darker spots. Spire rather sharply conical;  $8\frac{1}{2}$  almost flat whorls, the apical two unicolorous white, the next with numerous streaks. Aperture somewhat less than half the total length, ovate, but obliquely narrowed above and below, bluish inside; outer margin thin, straight, dark brown inside; columellar margin somewhat curved, bluish, narrowed below and then transversely truncate." I have seen the holotype at the Berlin Museum in 1933. It has the characteristic sculpture of *balteata*. The original figure is copied in my Pl. 44, fig. 1.

<sup>1</sup> The shells from Banana, Belgian Congo, referred by C. R. Boettger in 1913 to *infrafusca* were later described by him as *Achatina bandeirana cupacior*, a form which I now regard as not separable from typical *A. bandeirana* Morelet.



As noted in the general description of the species, subsp. *infracusca* differs from the nominate race only in the color markings, the chestnut vertical streaks continuing to the upper half of the body-whorl. There are, however, transitional specimens between the two forms, which seem to occur together in some localities. Too little is known as yet of the distribution to decide whether the subspecies should really be kept separate or merely considered a synonym. It has been claimed that *infracusca* has a proportionately shorter and broader shell than typical *balteata*, but this is not borne out by the original measurements nor by the specimens I have seen.

*Specimens Examined.* CAMEROON: Etome (P. Dusén.—Stock.M.; M.C.Z.).—FRENCH CONGO: Gaboon River (holotype and another shell at Berl.M.; M.C.Z.; U.S.N.M.; A.N.S.Phila.); Lambarene, Ogové River (Mrs. L. Russell.—A.N.S.Phila.).—BELGIAN CONGO: Lukolela (J. P. Chapin.—A.M.N.H.); Inkongo near Lusambo (Terv. M.); Luluabourg (P. Callewaert.—Terv. M.).—Also an umbilicate abnormal shell from the Gaboon (Pl. 51, fig. 2) at M.C.Z.

#### Measurements of Adult Shells

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
152 mm.	68.5	75	37	9		Lukolela
142	75	78.5	40	9		Gaboon
137.5	70	70	39	9		"
135	66	70.5	35	8 $\frac{2}{3}$		"
132	65	73	32.5	9		"
116	61	63	31.5	Apex broken		Lambarene

## 2. Subgenus PINTOA Bourguignat

*Achatina* subg. *Pintoa* Bourguignat, 1889, Moll. Afr. Equat., p. 80 (for *Achatina pfeifferi* Dunker, *A. semidecussata* Menke, *A. capelloi* Furtado, *A. zebriola* Morelet [= *zebriolata*], *A. polychroa* Morelet, and *A. colubrina* Morelet). Type by designation of Pilsbry, 1904, Man. of Conch., (2), 17, p. 24: *Achatina pfeifferi* Dunker, 1845.

It is not clear whether Bourguignat intended to give *Pintoa* generic or subgeneric status. He defined the group as follows: "Spire elongate obtuse. Spiral growth slow. Aperture oval or semicircular, rather small, never reaching half the height of the shell. Columella short" (translated from the French). The name is here restricted to what appears to be a fairly natural group of small species, 55 mm. or less

in length, usually slender in outline and with relatively short aperture, shaped more like *Limicolaria*, but with distinctly truncate columella. In addition, the sculpture is as in *Achatina*, proper, with the newly hatched nepionic shell finely and regularly granulose (except for the smoothish first half-whorl) and the post-nepionic whorls at least partially decussate. As a rule the early post-nepionic whorls are markedly granulose, while the later ones bear vertical lengthened welts separated by distant spiral grooves. Sometimes the sculpture becomes less pronounced on the body-whorl of full-grown shells, particularly below the periphery. *A. semisculpta*, here included in *Pintoa*, is in shape clearly transitional to *Achatina*, proper.

The following five species are decidedly granulose on the nepionic whorls at least of the best preserved specimens I have examined. It is possible that in some of the species which I place in the sequel in the subgenus *Leptocalina*, the nepionic shell may be granulose when newly hatched; in which case they will have to be transferred to *Pintoa*.

1. *A. parthenia* Melvill and Ponsonby, 1903.
2. *A. penestes* Melvill and Ponsonby, 1893.
3. *A. pfeifferi* Dunker, 1845 (Synonym: *A. ivensi* Furtado, 1886); with subsp. *eugrapta* Pilsbry, 1919.
4. *A. polychroa* Morelet, 1866.
5. *A. semisculpta* Pfeiffer, 1845.

Of the other species originally included by Bourguignat in *Pintoa*, *A. semidecussata* Menke has a broad, dome-shaped summit, for which reason I have transferred it to my new subgenus *Tholachatina*, in *Archachatina*. *A. capelloi* Furtado has the nepionic whorls unquestionably smooth, while most of the remainder of the shell is coarsely decussate, so that I relegate it to the subgenus *Lissachatina*. *A. zebriolata* Morelet and *A. colubrina* Morelet, also with smooth nepionic whorls, seem to belong to the subgenus *Leptocalina*.

### 3. Subgenus TRIPACHATINA Bourguignat

*Tripachatina* Bourguignat, 1889, Moll. Afr. Equat., p. 73. Monotypic for *Achatina vignoniana* Morelet, 1874.

- According to Bourguignat, the subgenotype is "remarkable for the oblique and weak columellar truncation and the open umbilical perforation, which is limited by a strong angle forming an obtuse crest." It should be added that the general shape of the shell is that of a young *A. achatina* and that the nepionic whorls are densely granulose almost from the very start. The few known specimens of the only species included, *A. vignoniana*, seem to have all been part of the original lot,

collected at some unknown locality in the interior of the Gaboon. These specimens, the largest of which measures 105 mm. in length, appear to be all immature and it is a question whether the umbilicus might not be completely closed in the fully adult shell. One of the smaller specimens is shown in my Pl. 69, fig. 1. The original figure of the type is copied in my Pl. 17, fig. 2. The species was described from the Vignon Collection. The present whereabouts of the figured type is unknown; it is not at the Paris Museum (Dr. E. Fischer, *in litt.*, 1949).

#### 4. LISSACHATINA, new subgenus

Nepionic whorls of newly hatched snails without granulation or decussated sculpture, either completely smooth or with faint vertical wrinkles; in older shells these early whorls are sometimes corroded and irregularly pitted or rugose. Post-nepionic whorls granulose or decussate; the sculpture sometimes very weak or evanescent on the body-whorl of adult shells. Apex of full-grown shell either of the usual conical shape or more or less drawn out into a narrow nipple, in which case the nepionic whorls may eventually break off. Most species are large or medium-sized, broadly ovate, elongate ovate or spindle-shaped; a few are slender and shaped like *Pintoa* or *Limicolaria*, differing from the former in the smooth nepionic whorls and from the latter in the truncate columella.

Subgenotype: *Achatina fulica* Bowdich, 1822.

Since in some species of *Achatina*, proper, and of *Pintoa*, the decussate sculpture of the nepionic whorls often wears off with age, a careful study of very young shells is essential to place the species correctly. I have seen young shells of most of the forms listed below. Some others, included because they appear to be closely related to species unquestionably with a smooth nepionic shell, should be studied again in the very early stages.

The synonyms of the species more fully treated in the present paper, will be discussed at some length. The synonymy of the others, as indicated in the following list, is only tentative.

1. *A. albicans* Pfeiffer, 1853.
2. *A. albopicta* E. A. Smith, 1878. See below.
3. *A. allisa* Reeve, 1849. See below.
4. *A. bayoniana* Morelet, 1867 (author's correction of *bayaona* Morelet, 1866).
5. *A. bloyeti* Bourguignat, 1889 (Synonyms: *A. fatalis* v. Martens, 1895; *A. retzii* d'Ailly, 1910).
6. *A. capelloi* Furtado, 1886 (Synonyms: *A. morrelli* Preston, 1905;

and *A. rhodesiaca* var. *lanceolata* Melvill and Standen, 1907); with subsp. *rhodesiaca* Melvill and Standen, 1907 (Synonyms: *A. rhodesiaca* var. *leucopasa* Melvill and Standen, 1907; *A. morrelli* var. *kafuensis* Melvill and Standen, 1907; and *A. schoutedeni* Dautzenberg and Germain, 1914).

7. *A. connollyi* Preston, 1912.

8. *A. craveni* E. A. Smith, 1881 (Synonyms: *A. kirkii* E. A. Smith, December, 1880, not of Craven, March, 1880; *A. jacobii* Da Costa, 1906; *A. ovata* Da Costa, 1907; *A. zebrina* Da Costa, 1907); with subsp. *arctespirata* Bourguignat, 1889 (Synonym: *A. fulminatrix* v. Martens, 1895); subsp. *randabeli* Bourguignat, 1889; and subsp. *virgulata* Da Costa, 1907.

9. *A. delorioli* Bonnet, 1864. See below.

10. *A. fulica* Bowdich, 1822. See below.

11. *A. glaucina* E. A. Smith, 1899.

12. *A. glutinosa* Pfeiffer, 1853 (Synonym: *A. petersi* v. Märtens, 1860).

13. *A. immaculata* Lamarck, 1822 (Synonym: *A. mariei* Ancey, 1894).

14. *A. iredalei* Preston, 1910. See below.

15. *A. johnstoni* E. A. Smith, 1899.

16. *A. kilimae* Dautzenberg, 1908. Position uncertain.

17. *A. lactea* Reeve, 1842. See below.

18. *A. layardi* Pfeiffer, 1858.

19. *A. panthera* Férussac, 1832. See below.

20. *A. reticulata* Pfeiffer, 1845. See below.

21. *A. spekei* Dohrn, 1864 (Synonym: *A. thomsoni* E. A. Smith, 1880). Pl. 62, fig. 3; Pl. 81, figs. 2 and 3.

22. *A. vassei* Germain, 1918.

23. *A. yalaensis* Germain, 1936.

24. *A. zanzibarica* Bourguignat, 1879. See below.

#### East African Species of *Lissachatina*

##### ACHATINA (LISSACHATINA) FULICA Bowdich

When full-grown, the shell of *A. fulica* consists of from 7 to 9 (very exceptionally 10) whorls, with a moderately swollen body-whorl and a sharply conical spire, which is distinctly narrowed but scarcely drawn out at the apex. The outline varies greatly, even in the same colony, from very slender to moderately obese, the broader specimens tending to be shorter for the same number of whorls. All whorls are

decidedly convex, due to the broadly impressed sutures. The aperture is relatively short, even in the broadest specimens, being always shorter than the spire, often considerably so. The outer lip is usually sharp and thin, rarely somewhat thickened or even slightly expanded in very old specimens; it is very convex, evenly curved into a regular semi-ellipse, and inserted on the body-whorl at a sharp, open angle, the upper part of the body-whorl being scarcely or not flattened behind the lip. The columella is more or less concave, sometimes rather weakly so, in which case it may be slightly or even much twisted; it tends to be more concave in the broader shells. It should be noted that in *A. fulica* all stages, from the nepionic shell on, have the umbilical slit completely closed and the columella truncate. In all specimens seen, which on general shape and sculpture were referable to *A. fulica*, both columella and parietal callus are white or bluish-white, without any trace of pink. The importance which I attach to this feature will be more fully discussed under *A. fulica hamillei* and *A. panthera*.

The newly hatched, nepionic shell is 5 to 5.5 mm. long and about 4.5 mm. wide, of  $2\frac{1}{2}$  nearly smooth whorls, without any granulation or decussation and with only the weakest traces of vertical wrinkles (Pl. 19, figs. 3 and 4). The first half post-nepionic whorl is more distinctly wrinkled vertically, but not yet decussate; after this the vertical growth-striae become gradually stronger and are now cut by spiral engraved lines into elongate, vertical welts; at first weak, the decussation gains in strength on the fourth and fifth whorls, where it is visible to the naked eye, after which it decreases again, being superficial on the sixth and usually lacking on the seventh and succeeding whorls. In young shells, the periostracum of the early post-nepionic whorls shows in addition to the decussation a superficial, microscopic criss-cross texture, as if a finely woven cloth had been pressed onto the surface; but no trace of this remains on older shells. In the largest full-grown adult shells, of 7 to 9 whorls, the body-whorl is nearly even, the growth-striae being very low or superficial, except below the suture where they form short, strong folds, very lightly crenulating the irregular sutural line. When the periostracum is fresh and intact, the terminal whorls appear not only smooth, but also glossy. The ground color and markings vary greatly and will be discussed under the several races. When present in the adult, the darker markings appear almost at once on the first post-nepionic whorl as faint, vertical, straight, pale-brown streaks; in very young shells these streaks stop at the periphery, forming there slightly deflected spots.

The egg is broadly ellipsoidal, 5 to 5.5 mm. by 4 to 4.5 mm., slightly

larger in subsp. *hamillei* than in the nominate race, white or slightly yellowish, with a very thin and brittle calcareous shell. In controlled breeding carried on by Mr. D. B. Langford in Guam, shells 1 week old, of about 3 whorls, were nearly 6 mm. long (Pl. 19, fig. 3); they reached 9 mm., with  $3\frac{1}{2}$  whorls, at 2 weeks; 14 mm., with 4 whorls, at 3 weeks; 16.5 mm., with  $4\frac{1}{3}$  whorls, at 4 weeks; 22 mm., with  $4\frac{1}{2}$  whorls, at 5 weeks; 27.5 mm., with nearly 5 whorls, at 6 weeks; 31 mm., with  $5\frac{1}{3}$  whorls, at 7 weeks; 35.5 mm., with  $5\frac{1}{2}$  whorls, at 8 weeks; 46 mm., with 6 whorls, at  $2\frac{1}{2}$  months; 75 mm., with  $6\frac{1}{3}$  whorls, at 3 months; and 92 mm., with slightly over  $6\frac{1}{2}$  whorls, at 5 months. Although these 5 month old snails were as yet far from full-grown, they mated and started laying eggs. The species may be sexually mature even before being 5 months old. The largest shell I have seen from Guam is 131 mm. long, for  $8\frac{1}{3}$  whorls. Later growth, after sexual maturity is reached, appears to be very slow and the snail may live for several years. Doeters van Leeuwen (1932) relates that a specimen, brought alive from Singapore, was kept in captivity in Java for 9 years, reaching 4 inches in length when it died. Mr. G. S. Dun, Entomologist to the Department of Agriculture, Territory of Papua-New Guinea, has recently given me some valuable information on *Achatina fulica* in his area (*in litt.*, 1949). After noting that near Rabaul, New Britain, the snail sometimes reaches as much as 175 mm. in length, he writes: "It is of interest to note that these very large specimens are fast becoming increasingly rare. When I first went to New Britain, over two years ago, these large individuals were quite common in a number of localities. At one particular locality adjacent to Keravat, the vanguard of the snails' approach was largely comprised of the very large specimens. At this spot they had arrived from a nearby Japanese camp where they were cultured. Eighteen months ago it was possible to collect the very large snails in dozens daily. Now, however, when specimens are required, it may take several days to collect a single large snail. As these individuals are evidently of a considerable age, it occurred to me that the Japanese may have had a forcing diet for them which they are now unable to obtain naturally and subsequent generations are consequently smaller. Caged specimens that I have reared from the egg stage and are now over two years old, have failed to exceed  $3\frac{1}{2}$  ins., while many of them are less than 3 ins."

Pilsbry (1904, p. 57) first suggested that the original home of *A. fulica* was the coastal area of continental East Africa, an opinion to which I fully subscribe. This coastal area is nowadays inhabited by the subsp. *hamillei*, which I regard as the ancestral stock of the species. Here it occurs from southern Abyssinia and the southern half of Italian Somaliland, through Kenya Colony and Tanganyika Territory, as far

as northern Portuguese East Africa. The northernmost reliable record appears to be in  $7^{\circ} 30' N.$ , the southernmost in about  $17^{\circ} S.$  Inland it extends 150 to 500 miles from the coast. The small islands off the East African coast, including Zanzibar and Pemba, where it now lives, I consider as part of the original range, their flora and fauna being mainly continental. It was most probably transported by man from the East Coast to Madagascar. Its later dispersal by man to Mauritius, Asia and the Pacific is a matter of historic record, more fully presented under the nominate race of the species.

The habits of *A. fulica* are essentially those of the other species of *Achatina*. It is, however, not as strictly terrestrial as *A. achatina*. In a paper published as a separate issue of this Bulletin, Dr. F. X. Williams presents his observations on the behavior, food preferences, mating, parasites, and predators of *A. fulica hamillei* in East Africa.

The first, very brief observations on the animal of a species of *Achatina* were by de Blainville on a preserved specimen of *A. fulica* collected by Quoy and Gaimard in Mauritius about 1820-1822. He wrote (1824, Dict. Sci. Nat., **32**, p. 250, referring to the snail as "Agathine zèbre"): "We have observed in the animal a sort of interruption of the collar, at the junction of right and left sides, as well as a projection of the columellar muscle producing the truncation of the columella of the shell." Lesson (1831) gave a fairly complete description of the animal (as *A. couroupa*), together with a good figure drawn from life in Mauritius: "The animal of this *Achatina* is very robust, large, very fleshy, with a foot ending in a point, convex above, everywhere much areolate and very dark, sombre violaceous. The eyes are globular, yellow, borne on two long cylindrical peduncles, dilated at their insertions. The two labial tentacles are swollen at the tip, half again shorter than the foregoing and also more voluminous at their insertions. The mouth is covered over by an upper festoon, deeply divided in the middle, thus forming two very prominent covering lobes." The anatomy of this species, now treated at length by Dr. A. R. Mead, was first described by Quoy and Gaimard (1831), together with a good account of the external features of the animal, but with rather crude figures.

*Synopsis of Subspecies.* Disregarding mere abnormalities, some 20 names have been proposed for various variants of *A. fulica*, this species being extremely variable in size and shape, and to some extent also in texture and color. After studying extensive series of nearly 1000 adult shells and many immatures, from a variety of places, I am able to recognize by name five forms only. Some of these are rather poorly defined and might perhaps better be sunk as synonyms; they are retained here as a concession to prevailing practice and in order to

prevent that they be described again under some new name. All forms are given subspecific status for purely nomenclatorial reasons, although several are not geographically segregated and they are not all of equal value.

A. Boldly marked with vertical streaks of dark-chestnut or blackish-brown on a pale dirty-white or yellowish background, often also with small scattered spots; the dark streaks sometimes confluent, particularly on the body-whorl, which may be nearly all dark-chestnut.

1. Medium-sized to large shells, 100 to 200 mm. in length when full-grown, usually rather heavy. Elongate-oval, slender or moderately swollen on the average, the whorls decidedly convex, broadly concave at the deep sutures. Body-whorl and aperture relatively short. Typical *A. fulica*.

2. Averaging usually larger than the nominate race. Broadly to very broadly oval, the whorls moderately convex and more shallowly concave at the sutures. Body-whorl and aperture relatively longer. Subsp. *hamillei*.

3. Small shells, when full-grown less than 60 mm. in length, shaped much like the nominate race. Subsp. *coloba*.

B. 4. Shell white, the periostracum uniformly or nearly uniformly olivaceous-yellow to pale golden-yellow, occasionally with a few darker, straw-yellow streaks. Size and shape of subsp. *hamillei*. Subsp. *rodatzki*.

C. 5. Whorls more or less distinctly divided into two areas: one uniformly dark buff above the periphery, the other much paler, light brown, below the periphery. Rarely faint traces of darker streaks or blotches in the upper buff area. Apparently known only from immature shells. Subsp. *castanca*.

#### a. Typical *A. FULICA*

Pl. 7, fig. 1; Pl. 16, fig. 3; Pl. 19, fig. 3; Pl. 20, fig. 2;  
 Pl. 21, fig. 2; Pl. 22, fig. 1; Pl. 23, fig. 4; Pl. 24, fig. 2;  
 Pl. 25, fig. 1; Pl. 26, fig. 2; Pl. 27, fig. 2; Pl. 28, fig. 2;  
 Pl. 29, figs. 1-2; Pl. 30, fig. 2; Pl. 31, figs. 1-2;  
 Pl. 32, figs. 1-2; Pl. 33, fig. 2; Pl. 34, fig. 2; Pl. 35,  
 fig. 1; Pl. 36, figs. 1-2; Pl. 37, fig. 4; Pl. 38, fig. 3

[Lister, 1688, Method. Conchyl. Liber Quartus, Pl. 582, fig. 35a; and Pl. 578, fig. 33].

[Seba, 1758, Rer. Nat. Thesauri, 3, p. 169; Pl. 71, figs. 4-5].

?*Bulla achatina*  $\gamma$  Born, 1780, Test. Mus. Caes. Vindobonensis, p. 209 (no locality); Pl. 10, fig. 2 (unrecognizable; apparently a dead, weathered shell).

*Bulimus zebra* Bruguière, 1792, Encycl. Méthod., Vers, 1, pt. 2, p. 357 (in



part: reference only to Seba, Pl. 71, figs. 4-5; also specimens collected by Bruguière at Foulepointe, Madagascar).<sup>1</sup>

*Ampulla kambeul* "Bolten" Röding, 1798, Museum Bolttenianum, pt. 2, p. 110 (in part: reference to Lister, Pl. 578, fig. 33, only); 1819, *Op. cit.*, 2d Ed., (by J. Noodt), p. 78 (in part, as before).<sup>2</sup> Not *Bulimus kambeul* Bruguière, 1789.

[*Helix* (*Cochlitoma*) *fulica* Férussac, 1821 (? May), Tabl. Syst. Moll., Tabl. Limaçons, p. 49 (or p. 53) ("Ile de France" = Mauritius; no description; with a doubtful reference to Lister's Pl. 578, fig. 33)]. *Nomen nudum*, not being validly defined.

[*Helix* (*Cochlitoma*) *borbonica* Férussac, 1821 (? May), Tabl. Syst. Moll., Tabl. Limaçons, p. 49 (or p. 53) ("Ile de Bourbon" = Réunion; no description nor reference)]. *Nomen nudum*.

*Achatina fulica* "Lamarck" Bowdich, 1822 (February), Elements of Conchology, 1, Pl. 13, fig. 3 (with name in accompanying Explanation of Plate; no locality or description). Deshayes, 1838, in Lamarck, Hist. Nat. Anim. Sans Vert., 2d Ed., 3, p. 297, footnote (says it is the correct name for *A. mauritiana* Lamarck); 1844, *Op. cit.*, 3d Ed., 3, p. 375, footnote. Porro, 1846, Coll. Mus. Modiol., Moll. Terr. Fluv., p. 17. Pfeiffer, 1848, Monogr. Helic. Viv., 2, p. 254. Reeve, 1849, Conch. Icon., 5, *Achatina*, Pl. 2, fig. 8; Pl. 3, fig. 8b; Pl. 11, fig. 8c (umbilicate abnormality) (Mauritius). Philippi, 1849, Abb. Beschreib. Conch., 3, pt. 5, p. 30 (p. 8 of *Achatina*); Pl. 2 (of *Achatina*), fig. 3 (Madagascar). Petit, 1850, Jl. de Conchyl., 1, p. 76 (Madagascar). Deshayes, 1851, in Férussac, Hist. Nat. Moll. Terr. Fluv., 2, pt. 2, p. 162, and Expl. of Plates of Atlas, p. 18. Mörch, 1852, Cat. Conch. Yoldi, 1, p. 20. Pfeiffer, 1853, Monogr. Helic. Viv., 3, p. 488. Woodward, 1854, Manual of the Mollusca, pt. 2, p. 160, fig. 90 (radula). J. E. Gray, 1855, Cat. Pulmonata Brit. Mus., 1, p. 3, fig. 2 (radula). Benson, 1858, Jl. de Conchyl., 7, pp. 266-268 (introduced from Mauritius to Calcutta in April, 1847). Pfeiffer, 1859, Monogr. Helic. Viv., 4, p. 603. v. Martens, 1860, in Albers, Die Heliceen, 2d Ed., p. 201. Morelet, 1860, Séries Conchyl., 2, p. 70 (Madagascar. Réunion. Mauritius. Comoros). A. D. Brown, 1861, Cat. Shells Coll., p. 55. Deshayes, 1863, in Maillard, Notes Ile Réunion, 2d Ed., 2, Annex E, p. 90 (Réunion). Mörch, 1863, Cat. Conch. Lassen, p. 4. Kefenstein, 1864, in Bronn's Classen u. Ordnungen d. Thier-Reichs, 3, pt. 2, Pl. 95, fig. 23 (radula after Woodward). Mörch, 1865, Jl. de Conchyl., 13, p. 386 (jaw; radula). Bielz, 1865, Verzeichn. Moll. Conch.-Samml., 3d Ed., p. 23. v. Martens, 1866, Sitzungsber. Ges. Naturf. Fr. Berlin, p. 16 (umbilicate abnormality from Seychelles). Haines, 1868, Cat. Terr. Shells Coll., p. 67.

<sup>1</sup> *Bulimus zebra* Bruguière was a composite species originally. The trivial name was restricted to the South African *Achatina zebra* by Férussac (1821, Tabl. Syst. Moll., Tabl. Limaçons, p. 50 (or 54), and 1832, Hist. Nat. Moll. Terr. Fluv., Atlas, Pl. 133, in Livr. 28, with name printed on the Plate), Reeve (1842; 1849), Krauss (1848), and Pilsbry (1904).

<sup>2</sup> In order to forestall any future attempt to use the trivial name *kambeul* for *Achatina fulica*, I herewith restrict *Ampulla kambeul* Röding, which was a composite species, to the shell represented by Röding's first reference to "Martini 1024, 1025" (i.e. Chemnitz, 9, Pl. 119, figs. 1024-1025). These figures are in my opinion *Limnicolaria kambeul* (Bruguière, 1789).

Pfeiffer, 1868, *Monogr. Helic. Viv.*, **6**, p. 217. v. Martens, 1869, in v. d. Decken's *Reisen Ost-Afrika*, **3**, pt. 1, p. 58 (Seychelles); Pl. 2 (Mollusca), figs. 1a (normal shell) and 1b-c (umbilicate abnormality). Paetel, 1869, *Moll. Syst. Cat.*, p. 80. G. Nevill, 1869, *Proc. Zool. Soc. London*, p. 64 (Seychelles: Mahé; Praslin; Silhouette; a smaller, thinner form than in Mauritius); 1870, *Jl. Asiatic Soc. Bengal*, **39**, pt. 4, p. 414 (Réunion). Paetel, 1873, *Cat. Conch.-Samml.*, p. 99. Fridrici, 1874, *Bull. Soc. Hist. Nat. Metz*, **13**, p. 184. v. Martens, 1876, *Jahrb. D. Mal. Ges.*, **3**, p. 250 (Comoros: Anjouan). Pfeiffer, 1876, *Monogr. Helic. Viv.*, **8**, p. 275. Roeters van Lennep, 1876, *Cat. Coll. Shells van Lennep*, p. 53. Liénard, 1877, *Cat. Faune Mal. Maurice*, pp. 54 and 90 (Mauritius. Seychelles: Mahé; Praslin). Morelet, 1877, *Jl. de Conchyl.*, **25**, p. 335 (Comoros: Anjouan). G. R. Batalha, 1878, *Cat. Coll. Conchyl. F. R. Batalha*, p. 2. Clessin, 1878, *Jahrb. D. Mal. Ges.*, **5**, pp. 179, 181, 183, and 184. Morelet, 1879, *Jl. de Conchyl.*, **27**, p. 315. G. Nevill, 1879, *Hand List Moll. Indian Mus.*, **1**, (1878), p. 145. Kobelt, 1880, *Illustrirtes Conchylienbuch*, **2**, p. 263; Pl. 81, fig. 1 (figure possibly of another species). v. Martens, 1880, in Möbius, *Beiträge Meeresfauna Mauritius Seychellen*, p. 197. Crosse, 1881, *Jl. de Conchyl.*, **29**, p. 196 (Madagascar: Nossi-Comba). Morelet, 1883, *Op. cit.*, **31**, p. 210 (Comoros: Mayotte). Grasset, 1884, *Index Test. Viv. Coll.*, p. 199. Martorell y Peña, 1888, *Catálogo Colección Conchol. Museo Martorell, Barcelona*, p. 56. Bourguignat, 1889, *Moll. Afr. Equat.*, p. 76. Paetel, 1889, *Cat. Conch.-Samml.*, 4th Ed., **2**, p. 239. Crosse and Fischer, 1889, in Grandidier, *Hist. Phys. Nat. Madagascar*, **25**, *Moll.*, Atlas, pt. 1, Pl. 20, fig. 1; Pl. 21, fig. 1. Brancsik, 1893, *Jahresh. Naturw. Ver. Trencsöner Comit.*, **15-16**, (1892-1893), p. 204; Pl. 6, fig. 6 (anatomy figured, but not described, of scalariform specimen from Madagascar: Sualala on Bali Bay). Dautzenberg, 1893, *Bull. Soc. Zool. France*, **18**, p. 79 (Seychelles: Praslin). Cooke, 1895, *Cambridge Natural History*, **3**, p. 211, fig. 107D (jaw), and p. 279. v. Martens, 1898, *Mitt. Zool. Mus. Berlin*, **1**, pt. 1, p. 30 (Seychelles). Boucard, 1901, *Cat. Coll. Coq. Terr.*, p. 49. Pilsbry, 1904, *Man. of Conch.*, (2), **17**, p. 55; Pl. 36, figs. 18 (specimen), 19 (specimen from Mauritius), and 20 (specimen from Madagascar); Pl. 37, figs. 22 (umbilicate, after v. Martens, 1869), 23 (specimen from Calcutta), and 24 (after Reeve). Sykes, 1905, *Proc. Mal. Soc. London*, **6**, pt. 5, p. 266 (umbilicate specimens from Mauritius and Seychelles). Ancey, 1906, *Bull. Scient. France Belgique*, **40**, p. 190 (sinistral). Anandale, 1907, *Rec. Indian Mus.*, **1**, pp. 176-177 (common near Calcutta). E. A. Smith, 1908, *Proc. Mal. Soc. London*, **8**, pt. 1, p. 1 (sinistral). Kobelt, 1910, *Abh. Senckenberg. Naturf. Ges.*, **32**, pp. 65, 90, 93, and 95. Rolle, 1910, *Op. cit.*, **32**, p. 193; Pl. 17, figs. 3 and 4 (abnormal shells). Pearson, 1910, *Spolia Zeylanica*, **7**, p. 110 (Ceylon: Moragalla; shell 6½ inches long). Green, 1910, *Op. cit.*, **7**, p. 56 (Ceylon: very common in the Beruwala region); 1910, *Circ. Agric. Jl. R. Bot. Gard. Ceylon*, **5**, No. 7, pp. 55-64; Pl.; 1911, *The Zoologist*, (4), **15**, pp. 41-45 (egg. Introduced in Ceylon probably some 10 years before); Pl. 2. Connolly, 1912, *Ann. South Afr. Mus.*, **13**, pt. 5, p. 188 (only specimen ever taken in South

Africa was found in a garden at Durban, Natal, about 1911). Dautzenberg, 1914, Bull. Soc. Zool. France, **39**, p. 57 (sinistral). Standen, 1917, Jl. of Conch., **15**, pt. 5, p. 160 (egg). Paiva, 1919, Rec. Indian Mus., **16**, pp. 19–28 (attacked by the lampyrid, *Lamprophorus tenebrosus*, in India). Odhner, 1919, Arkiv f. Zool., **12**, No. 6, p. 44 (Madagascar: Fénérive. Comoros: Mayotte). Annandale, 1919, Nature, (London), **104**, pp. 412–413. Hutson, 1920, Tropical Agriculturist, **55**, pp. 217–225, figs. 1–3 (on p. 220) (spread in Ceylon; attacked by *Lamprophorus tenebrosus*). Germain, 1921, Mém. Soc. Zool. France, Vol. Suppl., pp. 183 and 464 (egg); Pl. 10, figs. 1–2 (scalariform abnormality); Pl. 11, fig. 1 (umbilicate type of *A. rediviva* Mabille); Pl. 12, figs. 1–2 (2 paratypes of *A. rediviva*). Paravicini, 1922, Teysmannia, **33**, p. 24; Pl. 1, fig. 1 (not yet in Dutch East Indies). South, 1922, Malayan Agric. Jl., **10**, p. 267; 1923, *Op. cit.*, **11**, p. 253 (first occurrence in Federated Malay States). Jarrett, 1923, Singapore Naturalist, **1**, pt. 2, pp. 73–76 (occurrence in Malay Peninsula). Hutson and Austin, 1924, Dept. Agric. Ceylon, Bull. **69**, pp. 1–16; Pl. (*Lamprophorus tenebrosus* attacking this snail in Ceylon). v. d. Meer Mohr, 1924, De Tropische Natuur, **13**, pp. 26–27, fig. 1 (not yet in Dutch East Indies). South, 1924, Malayan Agric. Jl., **12**, pp. 36 and 229; 1925, *Op. cit.*, **13**, p. 201. (Anonymous), 1925, Jaarboek Dept. Landbouw Nijverheid Handel, Batavia, p. 61 (snails found in soil brought with plants to Java from Ceylon). South, 1926, Malayan Agric. Jl., **14**, pp. 157 and 231–241 (spread in Malay Peninsula). Spence, 1926, Jl. of Conch., **18**, pt. 2, p. 53 (sinistral from Mauritius). Paravicini, 1926, Arch. f. Molluskenk., **53**, pt. 4, p. 185. Pereira, 1926, Year-Book Dept. Agric. Ceylon, p. 62 (spread in Ceylon). (Anonymous), 1927, Malayan Agric. Jl., **15**, p. 149. v. d. Meer Mohr, 1927, De Tropische Natuur, **16**, pp. 206–208, fig. 1 (not yet in Dutch East Indies). Bertrand, 1928, Tropical Agriculturist, **71**, pt. 3, pp. 151–152 (damage to soil cover crops in Ceylon; control). Smedley, 1928, Malayan Naturalist, **2**, pt. 1, p. 47 (spread in Malay Peninsula). Birkinshaw, 1928, Malayan Agric. Jl., **16**, p. 154 (spread to Perak, Johore, and Kelantan in Malay Peninsula). Corbett, 1929, *Op. cit.*, **17**, p. 275 (spread to Johore and Kelantan). Doscas, 1929, *Op. cit.*, **17**, p. 287. Lamy, 1929, Jl. de Conchyl., **73**, p. 201 (egg). Haas, 1929, Zool. Jahrb., Abt. Syst., **57**, pp. 396 and 411 (Comoros: Convalescence, 1900 m., Great Comoro; Moheli; Ambarahani Mt., Moheli; Chumaduni Id.; Cercle de Bambao, Anjouan. Madagascar: Sahana in the East). Dammerman, 1929, Agricultural Zoology Malay Archipelago, p. 119, fig. 51. Connolly, 1931, Jl. of Conch., **19**, pt. 4, p. 103. Jarrett, 1931, Hong Kong Naturalist, **2**, pt. 4, pp. 262–264 (occurrence near Amoy, China, in 1931; in Sarawak, Borneo since 1928); Pl. 3 (2 views of one shell); 1932, *Op. cit.*, **3**, pt. 1, p. 70. Docters van Leeuwen, 1932, *Op. cit.*, **3**, pt. 1, p. 71 (snail kept alive for 9 years). Grandidier and Petit, 1932, Zoologie de Madagascar, p. 192. Corbett, 1933, Malayan Agric. Jl., **21**, pp. 77–79 (further spread in Malaya). Laidlaw, 1933, Jl. Malayan Branch R. Asiat. Soc., **11**, pt. 2, p. 215. Leeftmans and v. d. Vecht, 1933, Algemeen Landbouweekblad v. Nederl.-Indië, **17**, pt. 47, pp. 878–881, fig. 1 (Rhio

Archipelago: Poelau Bintan. Java: Kebajoran, 12 Kilom. from Batavia); 1933, *De Bergcultures*, **7**, pt. 21, pp. 579-584, figs. 1-3; Pl., figs. 1-2; 1933, *Landbouw, Landbouwkundig Tijdschr. Nederl.-Indië*, **8**, (1932-1933), pt. 10, pp. 668-677; Pl., figs. 1-2. Leefmans, 1933, *Op. cit.*, **9**, (1933-1934), pt. 6, pp. 289-298 (control in Java). Germain, 1934, C. R. 67<sup>e</sup> Congrès Soc. Savantes (for 1934), Sciences, pp. 123 and 128. v. Benthem Jutting, 1934, *Jl. of Conch.*, **20**, pt. 2, p. 43 (occurrence in East Indies). Dupont, 1935, *Trans. R. Soc. Arts Sci. Mauritius, Ser. C*, No. 3, (1933-1934), p. 138 (Seychelles: Mahé; Silhouette; Praslin). v. d. Meer Mohr, 1935, *Natur und Volk*, **65**, pp. 62-67 (Sumatra: in 1933 at Tandjong Poera, 65 Kilom. W. of Medan; introduced 12 years before), figs. 1-8 (egg; radula). Viader, 1937, *Mauritius Inst. Bull.*, **1**, pt. 2, p. 86. Heubel, 1937, *De Bergcultures*, **11**, pt. 47, pp. 1667-1669 (spread in Sumatra: Lampong Districts); 1938, *Op. cit.*, **12**, pt. 14, pp. 400-401 (spread in southern Sumatra). Beeley, 1938, *Jl. Rubber Res. Inst. Malaya*, **8**, pt. 2, pp. 130-139, Pl. Pemberton, 1938, *Hawaiian Planters' Record*, **42**, pp. 135-140 (first occurrence in Hawaii in 1936); 2 Pls. Corbett, 1938, *Malayan Agric. Jl.*, **26**, pp. 276-279 (control in Malaya). Connolly, 1939, *Ann. South Afr. Mus.*, **33**, pt. 1, p. 325. Dias and Thamoheram, 1939, *Tropical Agriculturist*, **92**, pt. 4, pp. 222-223 (control in Ceylon). Pemberton, Williams and Sukimura, 1939, *Proc. Hawaiian Ent. Soc.*, **10**, pt. 2, pp. 187 and 190 (occurrence in Hawaii). Feij, 1940, *De Bergcultures*, **14**, pt. 35, pp. 1112-1114 (occurrence in South Sumatra; control). Cotton, 1940, *South Australian Naturalist*, **20**, pt. 4, p. iii of inside back cover (occurrence in Ceylon). v. d. Meer Mohr, 1940, *De Tropische Natuur*, **29**, pp. 145-148 (occurrence in Sumatra: Medan; Lampong Districts; Palembang); 1941, *Op. cit.*, **30**, p. 173 (occurrence in Sumatra: Atjeh). Kaburaki, 1941, *Proc. 6th Pacific Sci. Congr. (Berkeley, 1939)*, **4**, (1940), p. 230 (introduction into Formosa and Japan). Kuroda, 1941, *Mem. Fac. Sci. Agric. Taihoku Imp. Univ.*, **22**, No. 4, p. 142 (Formosa: "very common in the arable regions"). Esaki and Takahashi, 1942, *Kagaku Nanyo [Sci. South Sea]*, **4**, pt. 3, pp. 16-25 (introduction into Formosa, Japan, the Palaus, Ponape, Tinian, Rota, Yap, and Saipan).<sup>1</sup> Kennard, 1943, *Mauritius Inst. Bull.*, **2**, pt. 3, p. 127 (synonymy). Fernando, 1946, *Ceylon Jl. Sci., B, Zoology*, **23**, pt. 2, pp. 97-104, figs. 1-9 (storage of galactogen and glycogen by the snail). R. H. Baker, 1946, *Trans. 11th North Amer. Wildlife Conference*, p. 211 (occurrence in Rota, Saipan, Tinian, and Guam). Krauss, 1947, *Proc. Hawaiian Ent. Soc.*, **13**, pt. 1, p. 9 (occurrence in Guam, Rota, Tinian, Saipan, and Ponape; also said to occur near Manila). (Anonymous), 1947, *Pacific Islands Monthly*, **18**, pt. 2, p. 75 (occurrence in New Ireland and New Britain). v. Benthem Jutting, 1948, *Chronica Naturae*, **104**, pt. 5, p. 137. Herklots, 1948, *Food and Flowers, Bull. Agric. Dept. Hong Kong Govt.*, No. 1, pp. 1-4, fig. on p. 1 (Sarawak. Southern China: Amoy; Hong Kong). Hanna, 1948, *The*

<sup>1</sup> The original of this article, entirely in Japanese, was shown to me by Mr. Yoshio Kondo in Honolulu. I have perused an English résumé in *Biological Abstracts*, **22**, for 1948, p. 2615.

- Nautilus, **62**, pt. 1, pp. 29-30. v. d. Meer Mohr, 1948, *Chronica Naturae*, **104**, pt. 6, pp. 178-179 (spread in Sumatra from 1940 to 1948). Hubert, 1948, *Op. cit.*, **104**, pt. 6, p. 192, 2 figs. (scalariform abnormality from Java). van Weel, 1948, *Op. cit.*, **104**, pts. 8-9, pp. 241-243, pt. 10, pp. 278-280 (spread and economic importance), and pt. 12, pp. 335-336 (habits; food; growth; longevity; oviposition). Abbott, 1948, *The Nautilus*, **62**, pt. 1, pp. 31-34 (spread in the Orient and Pacific; occurrence in Siam); 1949, *Natural History*, New York, **58**, pt. 2, pp. 68-71, 2 figs. on p. 68 and lower fig. on p. 71. van Weel, 1949, *Chronica Naturae*, **105**, pt. 1, pp. 25-27 (control), and pt. 2, pp. 53-55 (enzymes of digestive gland). Louisa C. Williams, 1949, *Scientific Monthly*, **68**, p. 199. Ley, 1949, *Frontiers*, Philadelphia, **13**, pt. 5, p. 140. v. d. Meer Mohr, 1949, *Treubia*, Buitenzorg, **20**, pt. 1, pp. 1-10 (oviposition and rate of reproduction in Sumatra). (Anonymous), 1949, *Pacific Islands Monthly*, **19**, pt. 9, p. 6. Mead, 1949, *Atlantic Monthly*, **184**, pt. 2 (for August), pp. 38-42. d'Emmerez de Charmoy and Gebert, 1921, *Bull. Ent. Res.*, **12**, pt. 2, p. 182 (damage to cotton seedlings in Mauritius). Reh, 1925, in Sorauer, *Handbuch der Pflanzenkrankheiten*, 4th Ed., **4**, p. 73. Y. Matsui, 1942, *Kagaku Nanyo* [Sci. South Sea], **5**, pt. 1, pp. 137-143 (nocturnal habits in the Palaus). S. Hatai and K. Genji, 1943, *Op. cit.*, **5**, pt. 2, pp. 1-19 (ecology and growth in the Palaus). Allan, 1949, *Australian Mus. Mag.*, **9**, pt. 11, pp. 374-377, fig. (live snail on ship at Sydney in 1948). Zuk, 1949, *Museum and Art Notes*, Vancouver, B. C., (2), **1**, pt. 1, p. 34 (live snail on ship at Vancouver in 1949). v. d. Meer Mohr, 1949, *Chronica Naturae*, **105**, pt. 11, p. 290 (damage to tobacco in Serdang District, N. E. Sumatra). Bryan, 1949, Report Insect Control Committee Micronesia 1947-1948, pp. 7-9, fig. on p. 13 (introduction of East African natural enemies in Hawaii). Vosburgh, 1950, *National Geographic Magazine*, **117**, p. 155 (occurrence in Formosa). Clench, 1950, *News Bull. Ann. Rept. Amer. Mal. Union for 1949*, p. 3.
- Cochlitoma fulica* G. B. Sowerby, 1825, *Cat. Shells Earl Tankerville*, p. 38.
- Helix* (*Cochlitoma*) *fulica* Férussac, 1827, *Bull. Univ. Sci. Nat.*, **10**, p. 203 (description of umbilicate abnormality collected by Rang in Mauritius. Réunion. Madagascar: Ste Marie); 1832 (August 4), *Hist. Nat. Moll. Terr. Fluv.*, Atlas, Pl. 124A, fig. 1 (Plate issued by Férussac in *Livr.* 23, with the name in a printed sheet of Explanation).
- Achatina* (*Archachatina*) *fulica* Albers, 1850, *Die Heliceen*, p. 190.
- Achatina* (*Achatinus*) *fulica* Pfeiffer, 1856, *Malak. Blätt.*, **2**, (1855), p. 168; 1879, *Nomencl. Helic. Viv.*, p. 266. Römer, 1891, *Jahrb. Nassau. Ver. Naturk.*, **44**, p. 123.
- ? *Achatina* (*Achatina*) *fulica* Semper, 1874, *Reisen Arch. Philippinen*, Section 2, *Wiss. Res.*, **3**, pt. 2, p. 143; Pl. 12, fig. 17 (jaw, radula, and anatomy of a specimen supposedly from Calcutta; says that a specimen from Zanzibar agreed with it in every respect).<sup>1</sup>

<sup>1</sup> According to Dr. A. R. Mead, the anatomy as described by Semper agrees with that of *A. panthera*, not with that of *fulica*. There is no evidence that *A. panthera* was ever carried to India and its occurrence in Zanzibar is very uncertain. Semper's localities appear to have been erroneous in both cases.

- Agathina fulica* G. Dollfus, 1899, Bull. Soc. Géol. France, (2), **27**, p. 395 (regards it as a rather recent introduction by man into Madagascar from the African mainland).
- ["Agaatslak" Witkamp, 1941, De Tropische Natuur, **30**, pt. 7, pp. 105-108 (occurrence in Dutch Borneo: Koetai)].
- ["Giant African Snail" (Anonymous), 1946, News Bull. Dept. Agric. Commerce Manila, **1**, Nos. 6-7, p. 65; 1947, *Op. cit.*, **1**, No. 11, p. 114 (occurrence and control in the Philippines)].
- ["Giant Snail" (Anonymous), 1947, Pacific Islands Monthly, **18**, pt. 2, p. 33 (New Britain: Kokopo District); 1947, *Op. cit.*, **18**, pt. 3, p. 22 (occurrence in the Marshalls); 1948, *Op. cit.*, **18**, pt. 7, p. 24 (New Britain: Rabaul); 1948, *Op. cit.*, **18**, pt. 12, p. 40; 1948, *Op. cit.*, **19**, pt. 3, p. 49].
- Achatina mauritiana* Lamarek, 1822 (April), Hist. Nat. Anim. Sans Vert., **6**, pt. 2, p. 129 ("Ile de France" = Mauritius. With description and reference to Férussac's *Helix fulva*, 1821, Tabl. Syst. Moll., Tabl. Limaçons, p. 49 (or 53), No. 347, but not to a figure). Menke, 1829, Verzeichn. Conch.-Samml. Walsburg, p. 7. Quoy and Gaimard, 1831, in Dumont d'Urville, Voy. Astrolabe, Zool., **2**, p. 152; 1834, *Op. cit.*, **3**, pp. 843 and 879 (Explanation of Plates); Atlas, Pl. 11, figs. 10-11 (2 views of shell with animal), 12 (head in front), 13-15 (anatomy); Pl. 49, fig. 21 (anatomy) (specimens from Mauritius). Oken, 1835, Allgem. Naturgesch., **5**, pt. 1, p. 425. Jay, 1836, Cat. Rec. Shells, 2d Ed., p. 42. Deshayes, 1838, in Lamarek, Hist. Nat. Anim. Sans Vert., 2d Ed., **8**, p. 297. Jay, 1839, Cat. Shells Coll., 3d Ed., p. 58. Dufo, 1840, Ann. Sci. Nat., (2), **14**, Zool., p. 198 (Seychelles: Mahé. Animal; egg; umbilicate abnormality). Pfeiffer, 1841, Symbolae Hist. Helic., **1**, p. 28. A. and J. B. Villa, 1841, Dispos. Syst. Conch. Terr. Fluv., p. 19. Sganzin, 1843, Mém. Soc. Hist. Nat. Strasbourg, **3**, pt. 2, Cat. Coq. Iles de France, etc., p. 17 (Réunion. Mauritius). Deshayes, 1844, in Lamarek, Hist. Nat. Anim. Sans Vert., 3d Ed., **3**, p. 375. Leunis, 1844, Synopsis d. Drei Naturreiche, Zool., p. 375. Catlow and Reeve, 1845, Conchologist's Nomenclator, p. 165. Keferstein, 1864, in Bronn's Classen u. Ordnungen d. Thier-Reichs, **3**, pt. 2, Pl. 99, fig. 12 (anatomy, after Quoy and Gaimard). Leunis, 1883, Synopsis d. Thierkunde, 3d Ed., (by H. Ludwig), p. 888.
- Achatina (Achatina) mauritiana* Beck, 1837, Index Moll., pt. 1, p. 76 (Madagascar. Mauritius).
- Achatina mauriciana* "Lesson" J. E. Gray, 1859, in Mrs. M. E. Gray, Figures Moll. Anim., **4**, p. 116 (Syst. Arrangement) (Explanation of Pl. 75 of Vol. 1, 1859, copies of Lesson's figures of his *A. couroupa*).
- Achatina acuta* Lamarek, 1822 (April), Hist. Nat. Anim. Sans Vert., **6**, pt. 2, p. 129 ("Sierra Leone", erroneous locality). Menke, 1830, Synopsis Meth. Moll., 2d Ed., p. 28. Deshayes, 1838, in Lamarek, Hist. Nat. Anim. Sans Vert., 2d Ed., **8**, p. 296 (refers to it Férussac's Pl. 124A, figs. 2); 1844, *Op. cit.*, 3d Ed., **3**, p. 375. Catlow and Reeve, 1845, Conchologist's Nomenclator, p. 163. Pfeiffer, 1848, Monogr. Helic. Viv., **2**, p. 251. Reeve, 1849, Conch. Icon., **5**, *Achatina*, Pl. 3, fig. 11 (Mauritius). Mörch, 1852, Cat. Conch. Yoldi, **1**, p. 20. Pfeiffer, 1853, Monogr. Helic. Viv., **3**,

- p. 488. H. and A. Adams, 1855, Gen. Rec. Moll., **2**, p. 132. Pfeiffer, 1859, Monogr. Helic. Viv., **4**, p. 603. A. D. Brown, 1861, Cat. Shells Coll., p. 55. Haines, 1868, Cat. Terr. Shells Coll., p. 67. Pfeiffer, 1868, Monogr. Helic. Viv., **6**, p. 218; 1876, *Op. cit.*, **8**, p. 275. Roeters van Lennep, 1876, Cat. Coll. Shells van Lennep, p. 54. Angas, 1877, Proc. Zool. Soc. London, p. 527 (Madagascar: Ekongo on S. E. coast). G. R. Batalha, 1878, Cat. Coll. Conchyl. F. R. Batalha, p. 1. Kobelt, 1880, Illustriertes Conchylienbuch, **2**, p. 263. Grasset, 1884, Index Test. Viv. Coll., p. 199. Paetel, 1889, Cat. Conch.-Samml., 4th Ed., **2**, p. 239. Boucard, 1901, Cat. Coll. Coq. Terr., p. 48. Pilsbry, 1904, Man. of Conch., (2), **17**, p. 40. Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 64. Coen, 1945, Catalogo Gasteropodi Polmonati Coll. Coen, p. 42.
- Helix (Cochlitoma) acuta* Férussac, 1832 (August 4), Hist. Nat. Moll. Terr. Fluv., Atlas, Pl. 124A, figs. 2 (2 views of one shell; Pl. issued by Férussac in Livr. 23, with name in printed explanatory sheet, but without locality).
- Achatina (Achatinus) acuta* Pfeiffer, 1856, Malak. Blätt., **2**, (1855), p. 168; 1879, Nomencl. Helic. Viv., p. 266. Römer, 1891, Jahrb. Nassau. Ver. Naturk., **44**, p. 123.
- Achatina fulvescens* Gray, 1825, Ann. of Philosophy, (N.S.), **9**, p. 414 (no locality; no description; defined by the references to Lister, Pl. 582, fig. 35a, and to Born, Pl. 10, fig. 2). Not of Férussac, 1821.
- Achatina maculata* Deshayes, 1830, Encyclop. Méthod., Vers, **2**, p. 12 (no locality). Catlow and Reeve, 1845, Conchologist's Nomenclator, p. 164. Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 65. Not of Swainson, 1821.
- Achatina couroupa* Lesson, 1831, in Duperrey, Voyage Autour du Monde La Coquille, Zool., **2**, pt. 1, p. 318 (Mauritius and Réunion, where it is said to have been introduced from Madagascar); Atlas, Moll., Pl. 9, figs. 2 (animal in shell), 2' (shell), and 2'' (head in front). Reichenbach, 1842, Land- Süßwasser- u. See- Conchylien, p. 26; Pl. 6, fig. 156. Catlow and Reeve, 1845, Conchologist's Nomenclator, p. 164.
- Achatina borbonica* "Férussac" Lesson, 1831, in Duperrey, Voyage Autour du Monde La Coquille, Zool., **2**, pt. 1, p. 318 (as a synonym of *A. couroupa* Lesson; apparently first valid use of the name).
- Achatina mauritiana* var. *borbonica* "Férussac" Beck, 1837, Index Moll., pt. 1, p. 76 (no locality; with brief description: "ventricosior; lituris fuscis confluentibus").
- Achatina zebra* var. *macrostoma* Beck, 1837, Index Moll., pt. 1, p. 75 (no locality; no description; defined by the reference to Seba, Pl. 71, figs. 4-5).
- Achatina fulva* Deshayes, 1838, in Lamarck, Hist. Nat. Anim. Sans Vert., 2d Ed., **8**, p. 309 (synonymizes with it *A. maculata* Deshayes); 1844, *Op. cit.*, 3d Ed., **3**, p. 379. Catlow and Reeve, 1845, Conchologist's Nomenclator, p. 164. Pfeiffer, 1848, Monogr. Helic. Viv., **2**, p. 251 (in part; not the measurements, which are based on Pl. 11, figs. 3-4 of Syst. Conch.-Cab.). Reeve, 1849, Conch. Icon., **5**, *Achatina*, Pl. 3, fig. 10 ("East Africa"). Deshayes, 1851, in Férussac, Hist. Nat. Moll. Terr. Fluv., **2**, pt. 2, p. 157 ("?Sénégalie"), and Expl. of Plates, p. 18; Atlas, Pl. 124, figs. 1-2 (2

- views of one shell; Pl. published without name by Deshayes after Férussac's death, presumably in 1851). Pfeiffer, 1853, Monogr. Helic. Viv., **3**, p. 488 (description of shell figured by Reeve, Pl. 3, fig. 10). H. and A. Adams, 1855, Gen. Rec. Moll., **2**, p. 132. Pfeiffer, 1859, Monogr. Helic. Viv., **4**, p. 603. v. Martens, 1860, in Albers, Die Heliceen, 2d Ed., p. 201. Deshayes, 1863, in Maillard, Notes Ile Réunion, 2d Ed., **2**, Annex E, p. 90 (Réunion). Haines, 1868, Cat. Terr. Shells Coll., p. 67. Pfeiffer, 1868, Monogr. Helic. Viv., **6**, p. 218; 1876, *Op. cit.*, **8**, p. 275. Roeters van Lennep, 1876, Cat. Coll. Shells van Lennep, p. 53. Clessin, 1878, Jahrb. D. Mal. Ges., **5**, p. 183. Rethaan Macaré, 1888, Cat. Coll. Coq. Mme Rethaan Macaré, p. 23. Paetel, 1889, Cat. Conch.-Samml., 4th Ed., **2**, p. 239. Bourguignat, 1889, Moll. Afr. Equat., p. 78 (cites Férussac's Pl. 124, figs. 1-2). Brancsik, 1891, Jahresh. Naturw. Ver. Trencsener Comit., **13-14**, (1890-1891), p. 153 (Madagascar: Nossi-Bé). v. Martens, 1897, Deutsch-Ost-Afrika, **4**, Beschalte Weichth., p. 90 (cites Férussac's Pl. 124, figs. 1-2). Boucard, 1901, Cat. Coll. Coq. Terr., p. 49. Comber, 1906, Jl. Bombay Nat. Hist. Soc., **17**, pt. 1, p. 218 (India: Rajkot). Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 65. Not *Bulinus fulvus* Bruguière, 1792.
- Agathina fasciata* Deshayes, 1831, Dict. Class. Hist. Nat., **17**, p. 121 (Explanation of Pl. 85 of Atlas, showing shell and animal; said to be common at Mauritius, where it is called "couroupa").
- Achatina (Archachatina) fulva* Albers, 1850, Die Heliceen, p. 190.
- Achatina (Achatinus) fulva* Pfeiffer, 1856, Malak. Blätt., **2**, (1855), p. 168; 1879, Nomencl. Helic. Viv., p. 266.
- Achatina mauritiana* var. *sinistrosa* Grateloup, 1840, Actes Soc. Linn. Bordeaux, **11**, (1839-1840), No. 55, p. 164 (Madagascar).
- Achatina mauritiana* var. *sinistrorsa* Grateloup, 1841, Actes Soc. Linn. Bordeaux, **11**, (1839-1840), No. 56, p. 415 (Madagascar); Pl. 2, fig. 6.
- Achatina fulica* monstr. *sinistrorsum* "Ancey" Dautzenberg, 1911, Jl. de Conchyl., **58**, (1910), p. 316.
- Achatina fulica* var. *monstrorsa* Liénard, 1877, Catal. Faune Mal. Maurice, p. 54 (Mauritius; no description). *Nomen nudum*.
- Achatina fulica* var. *scularioides* G. Nevill, 1879, Hand List Moll. Indian Mus., **1**, (1878), p. 145 (Mauritius; no description). *Nomen nudum*.
- Achatina fulica* var. *umbilicata* [G. Nevill, 1879, Hand List Moll. Indian Mus., **1**, (1878), p. 145 (shells from Mauritius, without description. *Nomen nudum*)]. Rolle, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 193 (shell from Mauritius; with reference to Reeve's Pl. 11, fig. 8c).
- Achatina fulica* monstr. *umbilicatum* Dautzenberg, 1911, Jl. de Conchyl., **58**, (1910), p. 316 (shells from Madagascar, Mauritius, Seychelles).
- Achatina panthera* Crosse and Fischer, 1889, in Grandidier, Hist. Phys. Nat. Pol. Madagascar, **25**, Moll., Atlas, pt. 1, Pl. 20, figs. 2 (2 views of one shell). Not of Férussac, 1832.
- Achatina rediviva* Mabilie, 1901, Bull. Soc. Philom. Paris, (9), **3**, (1900-1901), pt. 2, p. 57 ("Ile de France" = Mauritius). Types figured by Germain, 1921.
- ?*Achatina panthera* var. *chrysotherma* Pilsbry, 1904, Man. of Conch., (2), **17**,



p. 46 (Mauritius; received from Cuming); Pl. 41, figs. 5-6 (2 cotypes, one from the back, the other in front view). Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 65.

*Achatina fulica* var. *canaliculatum* Dautzenberg, 1911, Jl. de Conchyl., **58**, (1910), p. 315 (based on Rolle's Pl. 17, fig. 3, of 1910).

*Achatina fulica* monstr. *scalaris* Dautzenberg, 1911, Jl. de Conchyl., **58**, (1910), p. 316 (shells from Madagascar, Seychelles: Mahé, and without locality; refers to it also Rolle's Pl. 17, fig. 4, of 1910).

*Achatina panthera* var. *leucostyla* (Anonymous), 1946, The Sphere, (London), **187**, p. 400 (occurrence in New Guinea: Hansa Bay. Also said to have been introduced in New Britain and New Ireland. Not the figures: the shell shown is *A. fulica hamillei*; the eggs are those of a species of *Archachatina*).

*Achatina panthera* var. *leucostyla* (Anonymous), 1948, Pacific Islands Monthly, **18**, pt. 6, p. 71 (New Guinea: Madang. New Britain: Rabaul. New Ireland: Kavieng). Not of Pilsbry, 1904.

*Achatina* sp. Godwin-Austen, 1908, Proc. Mal. Soc. London, **8**, pt. 3, p. 147 (spread near Calcutta in 1876-1877; also at Rajmahal, 170 miles from Calcutta).

*Achatina courouya* Keferstein, 1864, in Bronn's Classen u. Ordnungen d. Thier-Reichs, **3**, pt. 2, Pl. 99, fig. 4 (animal after Lesson. Name in accompanying Explanation of Plate; misspelling of *couroupa* Lesson).

Kennard (1943) has shown that the trivial name *fulica* was first validly proposed by Bowdich (1822), although it was published with a figure only, without a description. This figure, copied in my Pl. 24, fig. 2, is extremely poor, and there is no indication that it was either natural size or reduced. It appears to be an original drawing of a shell, not a copy of an earlier figure; but the type specimen which it shows is lost, so far as known. It is possible to match the figure fairly well with immature examples of *fulica* from Mauritius, assuming that it was reduced. Although no locality was given, the shell came presumably from Mauritius, as did most, if not all, *fulica* found in collections at that time. Férussac's specimen, which I saw at the Paris Museum in 1933, but which is not the type of the species, came from Mauritius, as well as the type of *A. mauritiana* Lamarck. If a type locality is to be designated for the nominate race of *A. fulica*, I propose to take as such Mauritius. As pointed out by Kennard, if Bowdich's figure were ruled unrecognizable or were referred to another species, what is now universally called *fulica* would have to bear the name *A. mauritiana* Lamarck (1822), which antedates the next use of *fulica* by Férussac in 1827 and 1832.

Original description of *A. mauritiana* Lamarck (1822): "A. testa ovato-conica, longitudinaliter striata, albido-lutescente; strigis longitudinalibus confertis rufo-fuscis; spira apice acutiuscula; apertura

albida; labro margine interiore fusco." Length given as 4 inches [=108 mm.]. Dr. G. Mermod states (*in litt.*, 1948) that Lamarck originally had three specimens, one of them in poor condition ("fruste"), according to a marginal note in his own copy of the "Histoire Naturelle", but that there are now only two specimens labelled *A. mauritiana* in the Lamarck Collection at the Geneva Museum. One, of about  $7\frac{1}{2}$  whorls, is 83 mm. long, 45 mm. wide, with the aperture 46 by 26 mm.; it is white with brown streaks, somewhat zigzag-like on the penultimate whorl, straight and confluent on the body-whorl, the earliest whorls creamy-white. The other shell is 89 mm. long, 44 mm. wide, with the aperture 46.5 by 25 mm., and is colored like the first. In both the aperture inside, the columella and the outer lip are pale violaceous-white, the parietal callus is weak and the columella is rather markedly twisted. One of the shells has retained the periostracum intact, yolk-yellow, verging to brown. As neither specimen reaches 4 inches, Dr. Mermod suggests that the third, missing shell might have been about that size. Although none of Lamarck's specimens of *mauritiana* have ever been figured, there is little doubt about his species being *A. fulica*, as Deshayes (1838) first recognized.

It may be appropriate to point out that my synonymy of *A. fulica* does not include *Achatina mauritiana* Potiez and Michaud, 1835 (Gal. Moll. Douai, 1, p. 129; Pl. 11, figs. 11-12, two views of one shell). The figures show a pattern of bold, broad, zigzag-like streaks on the body-whorl, which I have never seen in any specimen of *fulica*, or any of its races. They appear to have been drawn from a specimen of *Achatina tineta* Reeve, with which species they agree in shape as well as in pattern.<sup>1</sup>

Original description of *A. acuta* Lamarck (1822): "A. testa ovato-conica, elongata, apice acuta, tenuissime decussata, alba; flammis longitudinalibus rubro-castaneis, inferne confertis, subcoalitis, superne separatis; apertura alba." The following remarks are in French: "Beautiful shell, quite distinct in shape and brightly colored. Length, about 5 inches" [=135 mm.]. Lamarck's type is now at the Geneva Museum, where it was examined at my request by Dr. G. Mermod, with the following result. According to a marginal note in Lamarck's own copy of the "Histoire Naturelle", he had only one specimen, the one now at Geneva, bearing written inside a "5" corresponding with the number of *A. acuta* in the book. It has 9 whorls and is 124 mm. long, 57 mm. in greatest width, with the aperture 62 by 32 mm. As

<sup>1</sup>The text and plates of Vol. 1 of the "Galerie des Mollusques de Douai", are generally cited as of 1838, the date printed on the title-page. According to a statement by G. Michaud (1879, *Jl. de Conchyl.*, 27, p. 11), the work appeared in parts, each consisting of a number of plates with the corresponding text. The actual date of publication of each part is the one printed on the plates issued in it. Plate 11 is dated November, 1835.

Pilsbry (1904) correctly inferred, the shell has been polished, at least over the lower portion. It is the original to Férussac's Pl. 124A, figs. 2, one of which is copied in my Pl. 7, fig. 1. They are faithful reproductions, although 3 mm. shorter than the shell. Moreover, Férussac used the name *Helix (Cochlitoma) acuta* in the explanatory sheet issued with this Plate in 1832. The figures have the usual shape of the nominate race of *A. fulica* and can be matched with some specimens I have seen from Mauritius and the Pacific. The sculpture is that of *fulica* and the columella is white with a slight bluish tinge on the colored figure. Most probably Lamarck's specimen came from Mauritius, as did the type of his *A. mauritiana*.

Original description of *A. maculata* Deshayes (1830) (French text translated): "A. testa ovato-oblonga, ventricosa, obsolete striata, apice obtusa; anfractibus octonis, ultimis fulvo fuscis; maculis fuscis majoribus vel strigis longitudinalibus ornatis, superioribus albidescentibus, flammis fuscatis instructis; apertura spira brevior; columella contorta, alba; labro intus albo, margine interiore fusco. It has relationships with most of the large species [placed at that time in *Achatina*]. It differs at first glance by the more lengthened, less ventricose shape, the much shorter aperture, longer and more convex whorls, the more pointed apex. It has in addition distinctive color. When covered with the periostracum, it is greenish-brown, interrupted by white or dark-brown, longitudinal [vertical], irregularly spaced areas. Toward the apex the ground color is more divided, alternating with more numerous white areas, and changes gradually to brown, flame-like streaks, which decrease little by little and disappear completely at the white tip. There are nine whorls, convex, rounded, smooth or with some obsolete, longitudinal [vertical] striae. The aperture is shorter than the spire; it is bell-shaped, completely white inside, except for the right margin [outer lip], which is very thin, sharp and of the outside color. The columella is entirely white, strongly sinuous in the middle; the basal truncation is not very deep; the columella is shorter than the anterior portion of the right margin. It is 13½ cm. or nearly 5 inches long."<sup>1</sup> I have been unable to trace the present whereabouts of Deshayes' type. Possibly the original name label was destroyed, when the author synonymized it, erroneously in my opinion, with *Bulimus fulvus* Bruguière. See the discussion of *A. achatina monochromatica*. In 1838, in a slightly modified version of the original description, Deshayes gives the length of the type as 140 mm. and now adds the width, as 65 mm. (under *A. fulva*). In 1851, he published an entirely new account (under *A. fulva*), based on several specimens, and stated

<sup>1</sup> "treize millimètres et demi" in the text is an obvious slip of the pen for "treize centimètres et demi," as Deshayes' later accounts show.

that he sent to Cuming the specimen which Reeve (1849) figured as *A. fulva*. He concluded by saying that "The largest specimen which we know is 130 mm. in length and 65 mm. in diameter." He referred to the species Pl. 124, figs. 1-2, of the Atlas to Férussac's work. This Plate was published by himself after Férussac's death, and there is a possibility that it may represent the original type of *A. maculata*, as the measurements are about those indicated for his largest shell in 1851. One of these figures is copied in my Pl. 32, fig. 2. Reeve's figure (copied in my Pl. 32, fig. 1) is of a smaller shell, 120 mm. long, 60 mm. wide, more boldly streaked on the body-whorl. Both figures can be matched among large series of the nominate race of *A. fulica*.

Original description of *A. couroupa* Lesson (1831) (translated from the French): "This *Achatina* varies oddly in size and color. Sometimes a uniform pale chestnut, it may also turn to chestnut with yellow flame-like spots, and then to fair tawny with irregular yellowish flammules, this last condition being the one most commonly found. It is oval, with a lengthened and conical spire, of 7 whorls, the last the largest and very ventricose. The surface is unevenly and almost vertically striate, and the whorls, united by a linear furrow, have on their margins a sort of shagreened suture from which the striae start. The whorls of the spire are slightly convex and end in an obtuse tip. The aperture is high, moderately wide, with a sharp right lip, and curved into a semicircle, while the left lip is replaced by a rolled up and ascending fold of the columella, smooth, bare, and truncate at the top. The average and usual size is 4 inches [=108 mm.] in length by 20 lines [=45 mm.] in height [diameter]. The aperture is 2 inches [=54 mm.] in height by 13 lines [=29 mm.] in greatest width. Its boldest color is tawny fair with unequal flame-like markings or ill-defined fasciae of deep chestnut. The tip of the spire is most often whitish, with elongate chestnut maculations, brownish in the center and tawny at the margins. When very young the shell is tawny, speckled with chestnut on the last whorl only, the spots on the spire being scarcely indicated. At this age the shell is also more ventricose and much less elongate for its size." What became of the type or types of *A. couroupa* is unknown. Although many of Lesson's types are at the Paris Museum, no shell labeled "*couroupa*" is to be found there now (Dr. E. Fischer, *in litt.*, 1949). One of the original figures is shown in my Pl. 34, fig. 2; it is 114 mm. long, 58 mm. wide, with the aperture 63 by 32 mm., and is a rather obese typical *fulica*. Lesson knew that his species was identical with *A. mauritiana* Lamarck, which he cites in the synonymy, together with *A. castanea* Lamarck, *A. borbonica* Férussac, *A. fulica* Férussac, and *A. zebra* Férussac.

Original description of *A. panthera* var. *chrysoderma* Pilsbry (1904):

"Shell thin and light; white with a few narrow stripes or with diffused patches of red-brown under a bright yellow cuticle on the last whorl, the spire white with broad red-brown streaks, fading on the left. Whorls  $7\frac{1}{2}$  or 8. Aperture fleshy-white within, the columella narrow, delicate. Columella and parietal wall covered with a thin white callous. Length 126, diam. 58, aperture 68 mm. Length 115, diam. 56, aperture 62 mm. Apparently mature, yet thin and light, with a thin, white columellar callous." The author referred doubtfully to this form Reeve's *A. fulica* on Pl. 2, fig. 8 (1849), and *A. acuta* on Pl. 3, fig. 11 (1849). Both these figures represent shells from Mauritius and are in my opinion of the nominate race of *A. fulica*. I have examined the types of *chrysoerma* (originally received from Cuming). They are rather large specimens of a form of *A. fulica*, in unusually fresh condition, which accounts for the bright periostracum. If the locality "Mauritius" were to be trusted, they would be referable to the nominate race of the species. The specimens agree, however, better in size and shape with average large shells of the continental *A. fulica hamillei*. It is not impossible that the locality Mauritius was fictitious, as was so often the case for shells distributed by Cuming. For this reason I am listing *chrysoerma* doubtfully as a synonym of typical *fulica*.<sup>1</sup> The two cotypes (Ac.N.S.Phila. No. 4241), respectively 128 and 117 mm. long, are shown in my Pl. 31, figs. 1 and 2.

Original description of *A. rediviva* Mabilie (1901): "Testa magna, late umbilicata, crassa, solida, ovoidea, parum nitente, sub epidermite luteola, decidua, albescente; strigisque rufis, latis, undique strigata, striis longitudinalibus parum perspicuis; spira conico-elata; apice obtuso; anfractibus 7 primis convexo-depressis, sensim et regulariter crescentibus, sutura lineari separatis; ultimo maximo, turgidissimo, fere dimidiam partem altitudinis aequante, ad aperturam paululum descendente, versus suturam sat regulariter crispato; apertura sub-recta, ovato elongata, margine columellari incrassato, ad umbilicum revoluta; externo longe arcuato; columella crassa, torta, ad basin truncata. Alt. 77-82. Diam. 58-67 mill." As recognized by Germain (1921), who figured the types, this supposed species was based on three umbilicate abnormalities of *A. fulica*. I saw these specimens also at the Paris Museum in 1933. A similar shell is shown in my Pl. 20, fig. 2. Pilsbry had previously (1904) placed *A. rediviva* in the synonymy of *A. fulica*.

Specimens of the nominate race of *A. fulica* seem to have reached Europe, probably from Madagascar, from the Seventeenth Century

<sup>1</sup> Germain (1921, p. 180) misunderstood Pilsbry's description, as he states that "the columella, which is narrow and delicate, is also tinted with fleshy-pink." The columella of both types is pure white. Moreover, Pilsbry included his *chrysoerma* among the forms of supposed *panthera* with white columellar margin.

on. The earliest recognizable figures are Lister's (1688) Pl. 578, fig. 33, copied in my Pl. 16, fig. 3, and Pl. 582, fig. 35a, copied in my Pl. 29, fig. 2. Seba's (1758) Pl. 71, figs. 4-5, show two views of one shell, one of the views reproduced in my Pl. 30, fig. 2. Born's (1780) Pl. 10, fig. 2, was drawn from a poorly preserved example and is scarcely recognizable, although it was most probably also *A. fulica*. A copy of this figure would serve no useful purpose.

The nominate, insular race of *A. fulica* is on the average smaller and more slender than the subsp. *hamillei* of the East African mainland, as shown by a comparison of the tables of measurements in the present paper. Most shells do not reach over 120 mm. in length and 55 mm. in greatest width. It varies, however, greatly in size and shape, and it is possible to select exceptional specimens of *hamillei* and of typical *fulica* that fairly agree in both respects. Correlated with the generally more slender outline, the spire of most nominate *fulica* is relatively higher and the aperture shorter, particularly in the largest shells which are usually also the most slender. The wide range of variation in the same territory is well shown by the 3 specimens figured from Madagascar by Crosse and Fischer (1889). One (Pl. 20, fig. 1) is very slender, 104 mm. long and 46 mm. wide; the second (Pl. 21, fig. 1) is moderately elongate, but very large, 146 mm. long, 67 mm. wide; the third (Pl. 20, fig. 2) is short and broad, 91 mm. long and 50 mm. wide (agreeing well with an average *hamillei*), and for this reason was mistaken for an *A. panthera*. The color and pattern exhibit as much variation as size and shape, and it is difficult to find two specimens that are alike in this respect, even in the same colony. In the lighter specimens the ground color is yellowish-brown; this is crossed by broad mahogany or chestnut-brown, vertical streaks, unevenly spaced and of varying width, straight or slightly curved, usually frayed at the edges and occasionally somewhat wavy. The streaks are, as a rule, more distinct on some of the early post-nepionic whorls and tend to fade or to coalesce on the body-whorl. In the darkest specimens the chestnut streaks have fused to cover most of the surface, particularly on the body-whorl, which may then be described as blackish-chestnut with a few narrow, yellowish, vertical streaks. In these dark shells the penultimate and earlier whorls usually preserve the original pattern described above. Sometimes the frayed edges cut deeper into the dark streaks and produce a pattern of irregular, transverse, flame-like spots, very variable in size and shape, giving the shell a speckled rather than a streaked appearance. In a series from Koror Id., in the Palaus, most of the shells are very poorly marked with a few chestnut blotches on a fulvous-yellowish background, perhaps owing to an abnormal or diseased condition. The periostracum is rarely intact in full-grown

shells, but when present it is bright yellow to olivaceous-yellow. After the periostracum is removed, the dark pattern stands out more boldly. The brown vertical streaks are very pale on the first post-nepionic whorls. They are entirely lacking on the nepionic shell, which is at first yellowish-white, later turns almost pure white. The inside of the aperture, the glazed parietal wall, and the columella are white, usually with a slight bluish tinge. Some shells have a more or less distinct blackish-brown margin on the inner edge of the outer lip, but this is far from being a common feature in the adult.

*Specimens Examined.* MADAGASCAR: without precise locality (Amst.M.; Ac.N.S.Phila.; Berl.M.; Terv.M.; Brus.M.); Bemangidy, Post Manantenina, Fort Dauphin District, Tulear Province (H. Hoogstraal.-M.C.Z.); 40 miles N.W. of Mananjary (W. D. Mateer.-M.C.Z.). — MAURITIUS: without precise locality (U.S.N.M.; A.M.-N.H.; Ac.N.S.Phila.; M.C.Z.; Amst.M.; Brus.M.; Berl.M.; Leid.M.; Brit.M.). — REUNION: without precise locality (M.C.Z.). — COMORO IDS.: without precise locality (M.C.Z.); Anjouan (Berl.M.); Moheli (Berl.M.). — SEYCHELLES: without precise locality (Berl.M.; M.C.Z.). — INDIA: Calcutta (Berl.M.; M.C.Z.). — CEYLON: without precise locality (Berl.M.); Colombo (M.C.Z.). — MALAY PENINSULA: Singapore (W. D. Jellison.-M.C.Z.); Ipoh, Perak (A. E. C. Doscas.-M.C.Z.); Penang (M.C.Z.). — SUMATRA: Palembang (C. T. Brues.-M.C.Z.). — JAVA: Batavia (J. Knock, 1938; J. Sandground, 1939.-M.C.Z.). — PHILIPPINES: Pasay near Manila, Luzon (P. de Mesa.-M.C.Z.). — BISMARCK ARCHIPELAGO: Keravat near Rabaul, New Britain (G. S. Dun.-M.C.Z.). — MARIANAS: Saipan (L. Gates; J. T. Gregory, 1946; H. S. Dybas; W. H. Lange.-Bish.M.; Chic.M.; M.C.Z.); Guam (D. B. Langford, 1946.-Bish.M.; M.C.Z.); Tinian (W. Nutting; J. Helmick; W. H. Lange; R. T. Abbott.-M.C.Z.); Rota (W. H. Lange.-M.C.Z.). — CAROLINES: Ulalu [Romanum], Truk area (D. Anderson, Sept. 1947.-Bish.M.). — PALAU IDS.: Koror (D. B. Langford, 1946; F. X. Williams, 1948.-M.C.Z.); Peleliu (H. S. Dybas, 1945.-Chic.M.); Babelthuap (F. X. Williams, 1948.-M.C.Z.). — OKINAWA JIMA (LOO CHOO IDS.): Toyama (C. Parsons, 1945); F. N. Young.-M.C.Z.); Baten Ko (S. L. Kimball.-Bish.M.); Suga, Motobu Mura (F. N. Young.-M.C.Z.); Itokazu (F. G. Werner, 1945.-M.C.Z.). — HAWAIIAN IDS.: Kalihi Valley, Honolulu, Oahu (D. Bryant, 1940.-Bish.M.; M.C.Z.); Pauoa Valley, Honolulu, Oahu (D. T. Fullaway, July 1938.-Bish.M.); Kahala, Honolulu, Oahu (D. T. Fullaway, Jan. 1940.-Bish.M.); Honolulu, Oahu (C. E. Pemberton, 1948.-M.C.Z.); Kaneohe, Oahu (T. S. Uaeda, March 1942; Y. Kondo, Jan. 1848; J. Bequaert, April 1949.-Bish.M.; M.C.Z.). — NEW GUINEA: Hansa Bay (G. S. Dun, 1949.-M.C.Z.). — According to recent reports (1949), the snail

is now very abundant on Chichi Jima, one of the Bonins, in 27° 2' N. Mr. R. T. Abbott also informs me that the U.S.N.M. has a large series collected by L. C. Bulkley at Trang, Siam, in 1937 or 1938. Dr. F. Haas writes me (Jan. 1950) that the Chic.M. has 2 *A. fulica* collected at Setul, Setul Prov., Siam, by C. C. Sanborn, in August, 1949. During the summer of 1949 Dr. A. R. Mead and Mr. Yoshio Kondo found the snail also on Haha Jima, in the Bonins, and on Pagan and Agiguan, in the Marianas. Its introduction in Ponape and Yap was reported by Esaki and Takahashi (1942).

*Geographical Distribution.* Whether *Achatina fulica* (and *A. panthera*) should be regarded as truly indigenous (autochthonous) or as human importations in Madagascar is difficult to decide. In 1761-1763, Le Gentil (1779, Voyage dans les Mers de l'Inde, etc., 2, p. 412) found *Achatina* in several localities in Madagascar, as shown by the following extract from his account of the land shells (translated from the French): "I found on the peninsula of Fort Dauphin some very beautiful snails shaped like *Buccinum*. They have a thin lip, are 3½ to 4 inches long and only about half that wide in the upper portion, consisting of 8 greyish-white whorls crossed by large fire-colored bands. They live in thorny thickets of a kind very common at Fort Dauphin. These snails have 4 horns; when they retire into their house, they close the entrance with a rather dense tissue or kind of operculum made of a sticky fluid which they sometimes exude. This operculum is easily destroyed as it crumbles between the fingers. I found several of them alive closed up in this fashion. Breaking their operculum awoke them, and they wandered about the room in which they were put for nearly a fortnight, after which they closed up again. After four months in this condition, they were still alive. Another species of snail is also found, similar in many respects to the foregoing, but once again larger; it has a very thick lip and is less common. I found none of it with the animal or with the original color. Perhaps this snail is only the first species having died of old age." In the same work he states later (2, p. 471), where he describes Antongil Bay: "I also found the species of *Buccinum* snail of which I spoke at the article of Fort Dauphin. Apparently this snail is spread along the entire coast. I saw some at Foulpointe, at Sainte Marie islet and at Marotte islet.<sup>1</sup> Later some were given to me at Mauritius which came from Mozambique. These were once again larger than those I obtained in Madagascar." From these statements *Achatina*, possibly of two species, were common about 1760 in Madagascar; the smaller snails mentioned were clearly *A. fulica*; the larger ones may have been

<sup>1</sup> Marotte is a very small islet in Antongil Bay.



*A. panthera*. Germain (1921, Ann. de Paléontologie, 10, p. 53) is strongly of the opinion that both *A. fulica* and *A. panthera* are recent arrivals in Madagascar and most probably accidental introductions by man. This he concludes from the absence of remains of *Achatina* in late Pleistocene deposits of the island, some of them containing terrestrial shells in fair abundance. Collections of these shells, which he examined, belonged mostly to characteristic endemic recent Madagascar snails, often scarcely separable from them. G. Dollfus (1899) previously expressed the same opinion as Germain. Although I am inclined to agree with them, it should be pointed out, nevertheless, that some fossil remains attributed to *Achatina* have been recorded by Newton (1895, Quart. Jour. Geol. Soc. London, 51, pt. 1, pp. 72 and 87) from supposedly Pleistocene ("Quaternary") deposits capping a hill at Ambohimarina in northern Madagascar. Some of these remains were definitely referred to *A. panthera*. I am unable to evaluate the significance of this find. It may well be that these fossils were actually not as old as Newton believed.

It seems an established fact that *A. fulica* did not occur in Mauritius much before the year 1800. It was not there in 1760-1769, when Le Gentil spent considerable time in this island. A few years later Bernardin de St. Pierre, who lived there some time, does not mention it in his well-known relation (1773, Voyage à l'Isle de France). This book contains (vol. 1, pp. 147-151) a long list of marine, fluviatile and terrestrial snails, which the author seems to have collected with predilection. Yet no mention is made of anything resembling *A. fulica*, a snail he could hardly have missed. The earliest published account I was able to trace of *Achatina* in Mauritius, is by Bosc in 1803 (Nouveau Dict. Hist. Nat., 1, p. 134; translated from the French): "I have heard from an inhabitant of Mauritius that the wife of a governor of the island, ailing of the chest, had on doctors' orders fetched from Madagascar many of these snails [*Achatina*, referred by error to *A. achatina* by Bosc], since there were none in this part of the colony.<sup>1</sup> She died shortly after and the snails spread over the island, increasing to the extent of becoming a calamity. They have been hunted several times, but they are even now very common." Lesson also (1831) found *A. fulica* (which he called *A. couroupa*) very common when he visited Mauritius in 1824. At the time of Quoy and Gaimard's (1831) visit in 1828, the snail had become a pest. They note that "one cannot travel without seeing heaps of their shells at the edges of the fields." They mention also that the shells showed numerous variations "which probably may have led to exaggerate the number of species."

<sup>1</sup> The same tale is recounted by several later writers, such as Férussac (1827), Lesson (1831), and Benson (1858).

In more recent years its economic importance seems to have become negligible there, as I can find no further complaints about it in the recent literature dealing with the mollusks of Mauritius. It might perhaps be worth investigating how this change was brought about.

From Mauritius *A. fulica* reached Réunion a few years later, as Férussac (1821 and 1827) saw specimens from there. In 1840 Dufó recorded it from the Seychelles. The earliest mention from the Comoros is by Morelet in 1860. According to Benson (1858), it was first carried from Mauritius to India in April, 1847, when he released some of the snails in the garden of the Asiatic Society of Bengal, at Calcutta. In 1848, Hutton took some of the Calcutta snails to Mussoori, in the foothills of the Himalayas.

At first the spread of the snail in southern Asia was very slow. It was reported in 1910 from Ceylon by E. E. Green, who relates that some living specimens had been liberated about 1900 near Watawala by one Oliver Collett. By 1910 the snail was particularly abundant in the Kalutara area. Early in 1922 it was observed in several localities of the Malay Peninsula, particularly in Singapore (Jarrett, 1923), Perak, Johore and Kelantan (Birkinshaw, 1928); but F. W. South (1926) believes that it may have been in Malaya since 1910 or 1911. It was introduced in Sarawak, Borneo, about 1928 (Jarrett, 1931), in Dutch Borneo about 1939 (Witkamp, 1941), and in Southern China near Amoy in 1931 (Jarrett, 1931) and from there to Hong Kong about 1941 (Herklots, 1948). It had reached Siam by 1937-1938, according to R. T. Abbott (*in litt.*). Up to 1932 it was thought not to occur anywhere within the Dutch East Indies, but it had actually been introduced some time before, probably about 1921, into Sumatra, although it was not noticed there until July, 1933, near Tandjong Poera, 65 Kilom. N.E. of Medan (v. d. Meer Mohr, 1935 and 1940). Toward the end of 1932 or early in 1933 it was found in the Rhio Archipelago and near Kebajoran, Java (Leefmans and v. d. Vecht, 1933). Esaki and Takahashi (1942) state that it was brought from Singapore to Formosa in January, 1932, and that its introduction and rearing were forbidden there in 1936; but, according to Kuroda (1941), it is now very common in the cultivated sections of Formosa. Esaki and Takahashi also mention that the snail was brought to Japan proper in 1925, carried from there to the Palau Ids. in 1938, and later also to Ponape, Tinian, Rota, Yap and Saipan. It is now extremely abundant in most of these Micronesian islands. Kaburaki asserts (1941) that, although the snail was often brought to Japan since 1936, it did not become established there "owing to the unfavorable climatic conditions." This does not apply, however, to the Loo Choo Ids., where the Americans found *A. fulica* to be fairly common in 1945 in

Okinawa. Possibly this island may be the northernmost point reached at present by the snail (nearly 27° N.). It was carried from Formosa to the Philippines during the Japanese occupation (1943-1945) and is now found at various places near Manila.<sup>1</sup> The earliest known occurrence in Hawaii was in 1936 (Pemberton, 1938). Although drastic control measures were taken almost at once, it spread rapidly in Oahu, where it is now a serious agricultural problem. According to Pemberton, 12 snails had been imported from Japan in November, 1936, to Makawao, Maui. In April, 1938, six snails of the Maui stock were transported to Honolulu, but these were promptly destroyed. The present *Achatina* colonies of Oahu appear to be the progeny of two snails brought to Honolulu from Formosa in 1936. In April, 1949, I could find no trace of the several foci of *fulica* at one time present within the city limits of Honolulu; but a moderate number of snails were observed in the eastern section of Oahu, near Kaneohe, during a visit made with Mr. Yoshio Kondo and Mr. P. W. Weber. R. T. Abbott (1948) relates that the snail was imported accidentally with *Pandanus* leaves into Guam from Saipan in 1946; a year later it had spread over most of the southern half of the island. Anonymous reports in "The Sphere" (1946) and the "Pacific Islands Monthly" (1948) mention its occurrence in British New Guinea (Madang and Hansa Bay) and the Bismarck Archipelago (New Ireland and New Britain). In a recent letter to Mr. R. T. Abbott (June, 1949), Mr. G. S. Dun, Entomologist at the Department of Agriculture, Territory of Papua-New Guinea, states that there are at present only three original points of infestation in that area. The first, at Hansa Bay on the North-East Coast of New Guinea, extends some 20 miles along the coast and some 10 miles inland. The second, in New Britain, is limited to the northern half of the Gazelle Peninsula. The third, in New Ireland, spread from Kavieng on the most northerly tip a limited distance down the western and about 40 miles down the eastern coast.

The foregoing account shows that the spread of *A. fulica* from its original continental African home and Madagascar to the islands of the Indian Ocean, India; the Orient, the East Indies and the Pacific Islands is entirely due to transport by man, usually deliberate, in a few cases accidental. Furthermore all later importations may be traced back ultimately to the first introduction from Madagascar into Mauritius, some 150 years ago.

According to R. T. Abbott (1948), a few live *A. fulica* were found in 1946 or 1947 in gardens at San Pedro, California, presumably intro-

<sup>1</sup> Various anonymous reports (1946; 1947). Mr. R. T. Abbott informs me that the occurrence of the snail in the Philippines is mentioned by Abada in a mimeographed Bulletin of the Bureau of Education in Manila (1946, 6, 8, No. 19075).

duced accidentally from the Pacific area. Although the snails were promptly destroyed, they caused much apprehension locally and induced the Department of Agriculture of the state to enforce stringent measures in order to prevent further importations. As a result the snail was intercepted on several later shipments of military supplies returned from the Pacific Islands. It is, in my opinion, extremely doubtful that *A. fulica* could ever become established in California or elsewhere in the continental United States, to judge from the present distribution and the ecology of this snail. Like most other Achatininae, *A. fulica* is for all practical purposes a typical tropical snail. The known distribution in its original East African home, between lat. N.  $7^{\circ} 30'$  and lat. S.  $17^{\circ}$ , is well within the tropics. This is true also for most of the areas to which it has spread, with the exceptions of Okinawa and the Bonins (lat. N.  $26^{\circ}$  to  $27^{\circ}$ ). The latter have an unusually warm climate for the latitude, owing to the powerful hot Northern Equatorial Current. Wherever it occurs, the snail keeps to the hot lowlands and the warm temperate lower slopes of the mountains. It evidently needs a combination of a constantly high temperature, well above freezing the year round, and much humidity at least during part of the year, the drier months being spent in dormant estivation. At the same time it is averse to sunshine, exposure to the direct rays of the sun killing it off rapidly. Conditions essential to the permanent survival of *A. fulica* do not seem to occur anywhere in the continental United States, no part of which is completely free at all times of winter frosts; while, in addition, most of the warmer areas are deficient in rainfall or lack protection against the sun. Nevertheless controlled experiments, under strict supervision, but under natural conditions in a presumably favorable area, are called for in order to determine once and for all whether or not the snail could survive the winter and reproduce freely in the United States. Meanwhile it might be unwise to relax present measures to prevent its importation.

The real danger of further spread of the snail would seem to be to Central and South America and the West Indies, where many sections apparently offer ideal conditions for its permanent establishment and its possibly becoming a major agricultural pest. It is nevertheless remarkable that during the past four and a half centuries no African species of *Achatina* or related genera has become established in the New World tropics, although some live specimens must occasionally have been transported across the tropical Atlantic.

*Measurements of Adult Shells*

Length	Greatest		Aperture		Whorls	Locality
	Width	Length	Length	Width		
171 mm.	81	74	42.5	8 $\frac{2}{3}$		Locality unknown
151	73	70	38.5	8		Keravat
131	59	62	30.5	8		Guam
128	57.5	59	32	8		Honolulu
118	52.5	55	28.5	8		Colombo
118	54	56	28.5	8		Perak
116.5	63	60.5	33	7 $\frac{3}{4}$		Guam
112	59	56	31	7 $\frac{3}{4}$		Mauritius
112	55	55.5	30.5	7 $\frac{1}{2}$		Honolulu
111.5	46	53	25	7 $\frac{1}{2}$		Mauritius
109.5	51	52	28	8		Singapore
106	55.5	55	29	7 $\frac{1}{2}$		Honolulu
106	53.5	54.5	30	7 $\frac{3}{4}$		Okinawa
105	52	52.5	27	7 $\frac{1}{2}$		Mauritius
103.5	55.5	52	31	7 $\frac{3}{4}$		Rizal
103.5	51	52	26	7 $\frac{1}{2}$		Babelthuap
102	49	49	28	7 $\frac{1}{2}$		Mauritius
101.5	45	49	25	7 $\frac{1}{2}$		"
101	52	53	29.5	7 $\frac{1}{2}$		Penang
100	51	50.5	27	7 $\frac{1}{2}$		Mauritius
98	50	52	27	7 $\frac{3}{4}$		Manila
98	46	48.5	24.5	7 $\frac{1}{2}$		Bemangidy
97	52	50	25.5	7 $\frac{1}{2}$		Koror
91.5	40	44	22	7 $\frac{1}{3}$		Comoros
91	48	49	26.5	7 $\frac{1}{3}$		Manila
89	43	44	23	7 $\frac{1}{2}$		Koror
88	42.5	46	22	7		Saipan
86.5	44	44.5	23.5	7		Batavia
85	45	46.5	22	7 $\frac{1}{2}$		Koror
80.5	43	42.5	22	7 $\frac{1}{3}$		Rota
77.5	40.5	41.5	21.5	7		Koror
75	41	41	21	7		"
72	37.5	38.5	19	7		"

The largest shell seen (171 mm.) is very slender, approaching in shape Deshayes' (1851, in Férussac) Pl. 124, figs. 1-2, but with the spire more drawn out.

The average length of the nominate race of *fulica* is about 110 mm., with an average greatest width of about 50 mm. My measurements show that relatively slender shells predominate in this race. Specimens over 120 mm. in length are scarce. Some of the largest were figured by the early writers. Deshayes' Pl. 124, fig. 1, is 133 mm. long and

67 mm. wide, but is fairly matched by a shell from Guam (M.C.Z.). Reeve's Pl. 3, fig. 11 (as *A. acuta*, from Mauritius) is 136.5 mm. long, 61 mm. wide. Crosse and Fischer's Pl. 21, fig. 1 (from Madagascar) exceeds both of these, being 146 mm. in length and 67 mm. in greatest width. No doubt these shells had been selected for their unusual size, which has a special appeal to collectors. F. W. South (1926) states that in Malaya the full-grown snail averages 4 to 5 inches, with an occasional specimen  $6\frac{1}{2}$  inches (170 mm.) in length. In some of the Pacific Islands, notably in the Palaus, *A. fulica* is usually stunted; the average length of 10 specimens, apparently adult (of 7 to  $7\frac{1}{2}$  whorls), from Koror Id., is about 83 mm.; the dwarfed condition may be due to a disease of the snails. Two of these shells are shown in my Pl. 25, fig. 1, and Pl. 36, fig. 1.

An unusually broad shell from Perak (Pl. 23, fig. 4) is not included in my table of measurements; it is 98.5 by 57 mm. and seems to be somewhat deformed. Abnormal shells are, moreover, by no means rare in collections, no doubt because of the abundance of the snails in certain localities. Most of these seem to come from Mauritius, however; and I have as yet seen no sinistral, umbilicate or scalariform specimens from the Orient or the Pacific. Pl. 20, fig. 2, shows an umbilicate, and Pl. 22, fig. 1, a scalariform shell, both from Mauritius.

Mr. Yoshio Kondo informs me (*in litt.*, Nov. 1949) that in 1949 he obtained a sinistral *A. fulica* on Pagan, in the Marianas. This appears to be the third, or possibly fourth, sinistral specimen known of the species. The first was reported by Grateloup (1840, 1841) from Madagascar. Smith's (1908) specimen from the British Museum (locality not given) may have been Grateloup's. Spence (1926), however, had another shell from Mauritius. The other references to sinistrality in *fulica*, by Ancey (1906) and Dautzenberg (1911, 1914), were based on Grateloup's record.

#### b. *A. FULICA CASTANEA* Lamarck

Pl. 7, fig. 3; Pl. 22, fig. 4; Pl. 54, fig. 3

*Achatina castanea* Lamarck, 1822 (April), Hist. Nat. Anim. Sans Vert., 6, pt. 2, p. 130 (no locality). Deshayes, 1838, in Lamarck, *Op. cit.*, 2d Ed., 8, p. 297; 1844, in Lamarck, *Op. cit.*, 3d Ed., 3, p. 375. Catlow and Reeve, 1845, Conchologist's Nomenclator, p. 163. Pilsbry, 1904, Man. of Conch., (2), 17, p. 54; Pl. 15, fig. 8 only (after Férussac's Pl. 125, fig. 5). Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., 32, p. 65.

*Helix (Cochlitoma) zebrina* Férussac [1821 (May ?), Tabl. Syst. Moll., Tabl. Limaçons, p. 49 (or p. 53) (no locality; no description; no reference). *Nomen nudum*]; 1823 (September 27), Hist. Nat. Moll. Terr. Fluv., Atlas,

Pl. 125, figs. 3-4 (2 views of one shell) and 5 (another specimen) (Plate published in Livr. 20, with name printed on cover). Kennard, 1942, Proc. Mal. Soc. London, **25**, pt. 1, p. 15.

*Achatina fulica* var.  $\beta$  Pfeiffer, 1848, Monogr. Helic. Viv., **2**, p. 254 (with *A. zebrina* Férussac as a synonym and a reference to Férussac's Pl. 125, figs. 3-5).

Original description of *A. castanea* Lamarck: "A. testa ovata, ventricosa, tenuissime striata, nitida, castanea, apice albida; suturis linea alba marginatis; labro intus albo." The following remarks are added in French: "The upper half of the last whorl is a beautiful chestnut, while the lower half is a paler russet. Length, 2 inches 8 lines." [= 72 mm.]. Dr. G. Mermod writes that the only specimen now labelled *castanea* in Lamarck's collection at the Geneva Museum and evidently the type of this race, is 67 mm. long, 39 mm. wide, with the aperture 39 by 20 mm. It is the specimen figured by Férussac on the latter's Pl. 125, fig. 5, as v. Martens (1897) and Pilsbry (1904) surmised. Dr. Mermod says: "This figure is a faithful reproduction, except for the color of the upper portion of the body-whorl which is too dark on the figure. It may be noted, in addition, that the transverse dividing line between the two contrasting colors of the body-whorl corresponds also to a very blunt carina, distinct especially on the prolongation of the suture over the whorl. The aperture is white, somewhat violaceous-pinkish; the area of the callus [parietal wall], almost non-existent, is dark brown." No locality was originally given, either by Lamarck or by Férussac. In view of the fact that Férussac had received specimens of *A. fulica* from Madagascar, Mauritius and Réunion, it seems reasonable to assume that the originals to his Pl. 125, figs. 3-5, came from this insular area. I have reached the conclusion that the two shells he figured were dwarfed or immature specimens of a peculiar color phase of *A. fulica*, with which they agree in outline and apparently also in sculpture. The slight carination at the periphery of the last whorl, noted by Dr. Mermod, would seem to indicate that this specimen at any rate (fig. 5) was immature. The shell shown in figs. 3-4 is somewhat transitional to the usual color pattern of *fulica*, and I have seen specimens from Saipan, Rota and elsewhere exhibiting a tendency toward the production of narrow, incomplete streaks or even toward a division of the body-whorl into two zones of contrasting color. None I have seen, however, show the broad dark-brown parietal callus and outer edge of the columella, which I regard as characteristic for *castanea*. These are also present in Lamarck's type (as noted by Dr. Mermod), shown in Férussac's fig. 5 from the back only. It is mainly owing to this peculiarity that I retain *castaneae* as a distinct subspecies of *A. fulica*, and refer to it both specimens shown in

Férussac's Pl. 125, figs. 3-5. These figures are copied in my Pl. 17, fig. 3, Pl. 22, fig. 4, and Pl. 54, fig. 3.

I do not include in my bibliography of *A. fulica castanea* references to v. Martens' *Achatina castanea* (1897, Deutsch-Ost-Afrika, 4, Beschalte Weichth., p. 88; lower 2 figs. on p. 87, 2 views of a shell from the cultivated zone at the foot of Mt. Kilimanjaro, Tanganyika Territory). These figures were copied by Pilsbry (1904, Man. of Conch., (2), 17, Pl. 15, figs. 7 and 9) and by Germain (1923, Voy. Afr. Orient. Angl. 1913 G. Babault, p. 74, fig. 24). They represent a shell differing in shape and sculpture from any form of *A. fulica* I am acquainted with, and also lacking the dark brown parietal callus of true *castanea*. I have seen this specimen at the Berlin Museum in 1933. It appears to be a form or color phase of *A. bloyeti* Bourguignat. I have seen specimens of *bloyeti*, similarly colored, collected by Mr. A. Loveridge at Kibwezi and other localities of Kenya Colony toward Mt. Kilimanjaro.

My interpretation of Lamarek's *castanea* as an unusual color form of *A. fulica* must necessarily remain tentative, as I have as yet seen no actual shell that agrees exactly with either of Férussac's specimens.

#### c. *A. FULICA COLOBA* Pilsbry

##### Pl. 27, fig. 3

*Achatina fulica* var. *coloba* Pilsbry, 1904, Man. of Conch., (2), 17, p. 58 (no locality); Pl. 37, fig. 21 (holotype). Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., 32, p. 65.

Original description of *A. fulica* var. *coloba* Pilsbry (1904): "Similar to *fulica* in shape and texture, but differing in the extremely small size. Yellowish, copiously streaked with red-brown, the streaks unequal, narrow and straight on the last whorl, wider on the penult.; whorls 7, the last three puckered below the sutures. Length 58, diam. 30.5, aperture 29 mm. Based upon two adult shells, 54 and 58 mm. long and a young specimen." I have seen the two type specimens at Ac.N.S.Phila. (No. 30266), the one figured by Pilsbry (58 mm.) being shown in my Pl. 27, fig. 3. They are now labelled "West Africa", clearly an erroneous locality, since they are merely dwarf specimens of *A. fulica*, as Pilsbry recognized. I retain the name provisionally with subspecific status, as I can throw no further light on it at present. All other small adult specimens of *fulica* I have seen were considerably larger than Pilsbry's shells, the smallest being 72 mm. long. They are clearly connected by gradually larger adults with specimens of average size of the nominate race, being also found in the same localities with larger shells.



d. *A. FULICA HAMILLEI* Petit

Pl. 15, fig. 2; Pl. 19, figs. 2 and 4; Pl. 40, fig. 3; Pl. 42, fig. 1;  
 Pl. 43, fig. 1; Pl. 45, fig. 2; Pl. 46, fig. 2; Pl. 47, figs. 1 and 3;  
 Pl. 48, fig. 1; Pl. 49, fig. 2; Pl. 50, figs. 1-2; Pl. 55, fig. 3;  
 Pl. 78, figs. 2-3; Pl. 79, fig. 2; Pl. 80, figs. 1-3 and 5

*Achatina hamillei* Petit, 1859, Jl. de Conchyl., **7**, p. 384 ("West Coast of Africa, probably near Gambia;" erroneous locality); Pl. 13, fig. 3. v. Martens, 1860, in Albers, Die Heliceen, 2d Ed., p. 201. Pfeiffer, 1868, Monogr. Helic. Viv., **6**, p. 212; 1876, *Op. cit.*, **8**, p. 272. E. A. Smith, 1881, Proc. Zool. Soc. London, p. 282; Pl. 32, fig. 10 (Tanganyika Territory: Usambara). Pelseener, 1886, Bull. Mus. Hist. Nat. Belgique, **4**, p. 104 (Tanganyika Territory: between the East Coast and Lake Tanganyika). Bourguignat, 1889, Moll. Afr. Equat., p. 75. v. Martens, 1897, Deutsch-Ost-Afrika, **4**, Beschalte Weichth., p. 86, upper 2 figs. on p. 87 (Zanzibar Id.: Mojoni. Tanganyika Territory: Tanga; between Simbaweni and Koo in Usegua; Mkurumu in the Masai Steppe); 1897, Arch. f. Naturgesch., **63**, pt. 1, p. 54; 1897, Mitt. Naturh. Mus. Hamburg, **14**, p. 114 (1901, Zool. Ergebn. Küstengebiete Ost-Afrika Reise Stuhlmann, **2**, pt. 15, p. 4). E. A. Smith, 1899, Proc. Zool. Soc. London, p. 590 (Nyasaland. Tanganyika Territory: Usambara). Ancey, 1902, Jl. de Conchyl., **50**, p. 273 (Tanganyika Territory: valley of the Malagarazi River in Unyanyembe. Says Petit's type came most probably from Zanzibar or the East African coast). Pilsbry, 1904, Man. of Conch., (2), **17**, p. 53; Pl. 8, figs. 21 (after Petit) and 22 (after E. A. Smith). Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 65. Menezel-Ben-Tovim, 1934, Arch. f. Naturgesch., (N. F.), **3**, pp. 64, 87, and 112 (cutaneous glands; Semper's glands). Germain, 1935, Mem. Est. Mus. Zool. Univ. Coimbra, Ser. I, No. 80, p. 40 (Portuguese East Africa: Nova Choupanga near Chemba). Frömming, 1940, Arch. f. Molluskenk., **72**, pp. 158-160; 1941, *Op. cit.*, **73**, pp. 151-154 and 195-200 (food preferences in captivity).

*Achatina (Achatinus) hamillei* Pfeiffer, 1879, Nomencl. Helic. Viv., p. 264.

*Achatina hammillei* Paetel, 1889, Cat. Conch.-Samml., 4th Ed., **2**, p. 239 (misspelling of *hamillei*).

*Achatina panthera* v. Martens, 1859, Malak. Blätt., **6**, p. 214 (var. with white columella from Portuguese East Africa: Querimba Ids.); 1879, Monatsber. Ak. Wiss. Berlin, p. 737 (in part: shells from Querimba Ids.). Bourguignat, 1879, Deser. Moll. Egypte Abyssinie Zanzibar, p. 9 (Nasimoya in Zanzibar). v. Martens, 1897, Deutsch-Ost-Afrika, **4**, Beschalte Weichth., p. 84 (var. with white columella from Zanzibar Id. and Tanganyika Territory: Bagamoyo); 1897, Arch. f. Naturgesch., **63**, pt. 1, p. 54. Neville and Anthony, 1906, Bull. Soc. Philom. Paris, (9), **8**, pt. 6, p. 295, fig. 2 (dead, weathered shell from near Lake Rudolf); 1906, Bull. Mus. Hist. Nat. Paris, **12**, p. 410. Piersanti, 1941, Missione Biologica Sagan-Omo, **12**, (Zoologia, 6), p. 272; Pl., fig. 26 (Southern Abyssinia: mouth of the Omo River in Lake Rudolf). Not of Férussac, 1832.

- Achatina fulica* Gibbons, 1879, Jl. of Conch., **2**, p. 143 (Zanzibar Id.). Pfeiffer, 1889, Jahrb. Hamburg. Wiss. Anst., **6**, pt. 2, p. 24 (Zanzibar Id. Tanganyika Territory: Bagamoyo). v. Martens, 1897, Deutsch-Ost-Afrika, **4**, Beschalte Weichth., p. 89 (Zanzibar Id.); 1897, Arch. f. Naturgesch., **63**, pt. 1, p. 54; 1897, Mitt. Naturh. Mus. Hamburg, **14**, p. 114 (1901, Zool. Ergebn. Küstengebiete Ost-Afrika Reise Stuhlmann, **2**, pt. 15, p. 4) (Zanzibar Id.). Connolly, 1925, Trans. R. Soc. South Africa, **12**, pt. 3, p. 169 (Portuguese East Africa: S. of Mt. Dedza near Nyasaland border); 1928, Atti Soc. Nat. Mat. Modena, (6), **7**, (or vol. **59**), p. 127 (Italian Somaliland: between Gumbo and Bieja). Haas, 1929, Zool. Jahrb., Abt. Syst., **57**, pp. 389 and 392 (specimens from Pemba Id., Fundu Id. near Pemba, Mafia Id., Lamu Id.). Bacci, 1939, Ann. Mus. Civ. Genova, **58**, p. 335, fig. 1 (anatomy. Italian Somaliland: Magala Umberto I on Uebi River; Baidao). Burton, 1949, Illustrated London News, **214**, p. 120, top fig. (alive in London, from East Africa). Not of Bowdich, 1822.
- Achatina letourneuxi* Bourguignat, 1879, Descr. Moll. Egypte Abyssinie Zanzibar, p. 8 (Nasimoya in Zanzibar). Kobelt, 1881, Synopsis Moll. Viv. Test. 1879 Promulgat., p. 137. Bourguignat, 1889, Moll. Afr. Equat., p. 79 (Zanzibar Id.; "Zanguebar" = coast of Tanganyika Territory; "Coast of the Benadir" = southern section of Italian Somaliland). Paetel, 1889, Cat. Conch.-Samml., 4th Ed., **2**, p. 240. v. Martens, 1897, Deutsch-Ost-Afrika, **4**, Beschalte Weichth., p. 84; 1897, Arch. f. Naturgesch., **63**, pt. 1, p. 54. Pilsbry, 1904, Man. of Conch., (2), **17**, p. 49. Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 65.
- Achatina panthera* var. *nasimoyensis* Bourguignat, 1879, Descr. Moll. Egypte Abyssinie Zanzibar, p. 9 (no locality; presumably from Nasimoya in Zanzibar). Pilsbry, 1904, Man. of Conch., (2), **17**, p. 44. Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 66.
- Achatina milne-edwardsiana* Révoil, 1885, Bull. Soc. Mal. France, **2**, p. 98 (Italian Somaliland: valley of Uebi River above Gueledi, 4 days travel from Mogadischu [or Mogdishu], type locality. Tanganyika Territory: Usagara); Pl. 5 (paratype from Usagara). Paetel, 1889, Cat. Conch.-Samml., 4th Ed., **2**, p. 240. Ancy, 1894, Mém. Soc. Zool. France, **7**, p. 220. v. Martens, 1895, Ann. Mus. Civ. Genova, **35**, p. 64 (Italian Somaliland: between Bardera and Brava on the Juba River); 1897, Deutsch-Ost-Afrika, **4**, Beschalte Weichth., p. 83 (refers to it also a shell from Portuguese East Africa: Querimba Ids.); 1897, Arch. f. Naturgesch., **63**, pt. 1, p. 54. Pilsbry, 1904, Man. of Conch., (2), **17**, p. 38; Pl. 14, fig. 4 (after Révoil). Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 65. H. Wagner, 1940, Veröffentl. D. Kolonial Uebersee Mus. Bremen, **3**, pt. 1, p. 93, fig. 1 on p. 96 (Tanganyika Territory: Arusha-Chini near Mt. Kilimanjaro); 1941, Rivista Biol. Colon., **4**, pt. 3, p. 119, fig. 4 on p. 127; 1941, Ann. Mus. Nat. Hungarici, Zool., **34**, p. 82; Pl. 2, fig. 3. Burton, 1949, Illustrated London News, **214**, p. 120.
- Achatina milne-edwardsi* Bourguignat, 1889, Moll. Afr. Equat., p. 79.
- Achatina pantherina* v. Martens, 1897, Mitt. Naturh. Mus. Hamburg, **14**, p. 114 (1901, Zool. Ergebn. Küstengebiete Ost-Afrika Reise Stuhlmann,

- 2, pt. 15, p. 4) (in part: shell from Zanzibar Id. with white columella).  
Not of G. Nevill, 1879.
- Achatina panthera* var. *neumannii* v. Martens, 1897, Deutsch-Ost-Afrika, **4**, Beschalte Weichth., p. 84, fig. (Zanzibar Id.: Jambiani); 1897, Arch. f. Naturgesch., **63**, pt. 1, p. 54. Pilsbry, 1904, Man. of Conch., (2), **17**, p. 45; Pl. 42, fig. 9 (after v. Martens). Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 66.
- Achatina panthera* var. *leucostyla* Pilsbry, 1904, Man. of Conch., (2), **17**, p. 45 (Kenya Colony: Wasin Id., close to the Coast, S. of Mombasa); Pl. 39, fig. 33 (cotype); Pl. 40, figs. 2 (cotype) and 3 (cotype). Kobelt, Abh. Senckenberg. Naturf. Ges., **32**, p. 65. d'Ailly, 1910, in Sjöstedt, Kili-mandjaro Meru Exped., **1**, Abt. 6, p. 21 (Tanganyika Territory: Tanga).
- Achatina leucostyla* Pilsbry, 1905, Man. of Conch., (2), **17**, pp. xi and xiii of Introduction (animal; anatomy); pp. 216, 226, and 232 (as a species); Pl. 64, figs. 65-66 (anatomy).
- Achatina* (*Achatina*) *leucostyla* Dautzenberg and Germain, 1914, Rev. Zool. Afric., **4**, pt. 1, p. 25 (Tanganyika Territory: Dar-es-Salaam).
- Achatina panthera leucostyla* Haas, 1929, Zool. Jahrb., Abt. Syst., **57**, p. 389 (Tanganyika Territory: Mafia Id.).
- Achatina fulva* E. A. Smith, 1894, Proc. Mal. Soc. London, **1**, pt. 4, p. 165 (Kenya Colony: Mkonumbi near Witu). Not *Bulimus fulvus* Bruguière, 1792.
- Achatina acuta* C. R. Boettger, 1947, Arch. f. Molluskenk., **76**, p. 97; Pl. 2, fig. 6 (Tanganyika Territory: in Pleistocene deposits on the Garussi River, N.W. of Lake Njarasa [=Nyaraza or Eyasi]; also Recent shells from Amani). Not of Lamarck, 1822.

Original description of *A. hamillei* Petit (1859) (French text translated): "A. testa conico-ovata, ad basim ventricosa, strigis castaneis undatis picta: spira acuminata; anfractibus 7-8, subrotundatis, superioribus plus minusve subtiliter decussatis, ultimo sublaevigato, ad suturam marginato: columella contorta, truncata; caerulescente albida: labro simplici. Length, 90 mm.; width, 50 mm. Shell ovate-conical, rather ventricose, with a relatively short and acuminate spire; upper whorls slightly decussate; columella and inside of aperture bluish-white; right margin [outer lip] thin. The color of the shell, covered with a strong periostracum, approaches that of *A. marginata* Swainson, but that species has the right margin [outer lip] thick and the spire obtuse, whereas our shell has the right margin [outer lip] thin and the spire more pyramidal. The color of the columella also differs; there is one whorl more." Described from a single type, which I saw in the collection of the "Journal de Conchyliologie," in 1933, when it was in the custody of the late Mr. P. Dautzenberg. This collection is now in the care of Dr. E. Fischer-Piette, who sent me the photograph of my Pl. 78, fig. 2. The original figure is copied in my Pl. 19, fig. 2. The

type is an immature, medium-sized specimen of the common continental East African form of *A. fulica*, lacking the nepionic whorls. It can be matched with immature specimens collected by Dr. F. X. Williams in Zanzibar (compare my Pl. 80, fig. 2). The periostracum is usually well preserved in young shells of this species. E. A. Smith (1881) recognized *hamillei* correctly in a shell from Usambara. His figure, copied in my Pl. 48, fig. 1, is of nearly average size and shape for this race, 128 mm. long, 70 mm. wide, with the aperture 69 by 37 mm.; the coloration is somewhat unusual, but I have seen very similar shells among Dr. Williams' material. Other writers have occasionally recognized *hamillei* and v. Martens (1897) gave a good figure of a specimen from Tanga. The true relations of *hamillei* to *A. fulica* and its identity with the supposed *A. panthera* with white columella (*A. panthera* var. *leucostyla* Pilsbry) were, however, overlooked.

Original description of *A. letourneuxi* Bourguignat (1879) (French text translated): "Testa valde elongata, parum tumida, sat ponderosa, opaca, nitida, in supremis luteola ac deinde rosacea, in medianis albida, in ultimis luteo-olivacea, ac flammulis rufo-castaneis (supremi exclusi), in ultimo obscure rufo-subolivaceis, ornata; ad apicem laevigata, ad caeteris paulatim striata plicataque et ad ultimum lamellosa (praecipue circa suturam), tandem ad medianos sulcis minutissimis argutissime decussata; spira producta, elongata, acuminata; apice obtusiusculo; anfractibus 9 convexiusculis, sutura (inter inferiores sulcosa) separatis; ultimo oblongo-convexo, relative mediocri, dimidiam altitudinis non attingente; apertura fere verticali, ovali, intus albido-margaritacea; margine externo arcuato-convexo; columella arcuata, basi tenuata ac mediocriter truncata; peristomate acuto, intus in margine externo pallide rufo-castaneo; callo albido, sat crasso. Alt. 118 mill.; diam. 50 mill.; alt. apert. 53 mill.; diam. ap. 30 mill. Can only be placed near *A. panthera* [name erroneously used by Bourguignat for *A. fulica hamillei*] for the sum total of its characters, but *letourneuxi* is more slender in all its parts, more elongate, less ventricose, the aperture relatively smaller, less developed; the columella is more elongate, more curved, less robust and more narrowed toward the base (in "*panthera*" the columella, more voluminous, thicker, has in its median portion a slight swelling caused by the torsion of the axis); the spire, more acuminate, more elongate, is markedly more slowly coiled over the upper whorls; finally the body-whorl appears to descend more toward the insertion of the outer margin." The holotype, which I saw at the Paris Museum in 1933, is an elongate *hamillei*, with well-preserved periostracum. It is shown in my Pl. 80, fig. 1. Although such slender shells are more typical of the nominate race of *A. fulica*, some occur

occasionally in populations of subsp. *hamillei* in Zanzibar and on the neighboring mainland.

Original description of *A. panthera* var. *nasimoyensis* Bourguignat (1879) (translated from the French): "A relatively small form, 90 mm. long, 47 mm. wide, with the aperture 50 by 26 mm., differing from the type [supposedly from *panthera*, but actually compared with *fulica hamillei*] only in being proportionately smaller in all parts. The body-whorl seems to be, however, more convex, considering the proportions, and the spire slightly more acute." The holotype was obtained in the locality Nasimoya presumably, together with the type of *A. letourneuxi*, and with specimens of *A. fulica hamillei* (called erroneously *A. panthera* by Bourguignat) of the usual size, 123 mm. long, 62 mm. wide.<sup>1</sup> Similar variation in size and shape is common in any fairly large series of *hamillei* from any given locality and is purely individual. I could not see the actual type at the Paris Museum in 1933, but was shown instead a specimen from Guededi, Italian Somaliland, labelled in Bourguignat's hand "*Achatina nasimoyensis*" with a manuscript varietal name meaning "larger". This specimen differed in no way from *A. f. hamillei*. Dr. E. Fischer (*in litt.*, 1949) has since found the true type and sent me the photograph shown in my Pl. 79, fig. 2.

Original description of *A. milne-edwardsiana* Révoil (1885): "Testa maxima, oblongo-elongata, solida, ponderosa, opaca, nitida, striatula, ad suturam in medianis rugosa, in ultimo fimbriata aut crispulato-tuberculosa ac prope aperturam lineis duabus spiralibus decussata; — ad superiores uniformiter albido-rosacea, in caeteris albido-vinosa et flammulis latis vinoso-violaceis plus minusve saturatis ornata; — spira elongata, acuminata, ad summum acuta; — anfractibus 10 convexiusculis, regulariter crescentibus, sutura impressa separatis; — ultimo relative mediocri, dimidiam altitudinis non aequante, convexo, circa suturam leviter subcompressiusculo, ad aperturam tumido-rotundato, ad insertionem subito deflexo; — apertura vix obliqua, lunata, subvato-rotundata, externe bene convexa, intus albo-margaritacea; — peristomate recto, obtuso, superne ad insertionem crasso, ad basin leviter acutiusculo; — columella brevi, robusta, contorta valde curvata inferne valide truncata (sinus truncaturae externe sulcum sat productum praebens); marginibus callo crasso alboque junctis." The unfigured holotype from the Uebi Valley was 143 mm. long, 64 mm. wide, with the aperture 60 by 40 mm. The figured paratype, from Usagara, was much larger, 190 mm. long, 94 mm. wide; on the figure the

<sup>1</sup> Mr. A. Loveridge informs me that there is a locality Nasimoya in the Island of Zanzibar, a point about which there appears to have been some doubt. In the "Guide to Zanzibar" (1939 Edition), recently obtained by Dr. F. X. Williams, it appears with the spelling "Mnazi Mmoja" as a suburban section at the southern outskirts of the town of Zanzibar.

aperture is 70 by 55 mm. In the additional French remarks it is stated that the species is "remarkable for its large size, its elongate shape, its relatively small, oval aperture, very rounded outwardly, and its short, very curved, twisted and strongly truncate columella." I have not seen this paratype, the figure of which is copied in my Pl. 40, fig. 3, slightly reduced. It is the largest specimen on record, not only for subsp. *hamillei*, but for the species *fulica* as a whole. It seems to show a slit along the outer or left margin of the columella; this is not, as might be supposed, a true columellar slit, but an adventitious groove produced in old age by the unusual thickening of the columella. I have observed it also in some old *hamillei* sent from the coast of Kenya Colony by Dr. F. X. Williams. Dr. E. Fischer sent me a photograph (my Pl. 78, fig. 3) of a shell labelled *A. milne-edwardsiana* at the Paris Museum, where I saw it in 1933. Although from the type locality, Guedi, it could not well be the holotype mentioned by Révoil, as it is only 118 mm. long. The columella of this shell is white, a point not mentioned in the original description, although the parietal wall is said to be of that color. Connolly (1928) concluded that *milne-edwardsiana* was based on unusually large *A. fulica*. Like *A. letourneuxi* it covers in my opinion elongate individuals of the subsp. *hamillei*.

Original description of *A. panthera* var. *neumannii* v. Martens (1897) (translated from the German): "In general with the characters of *A. panthera*, but the aperture is pure white and strikingly thickened, the outer margin almost a little bent outwardly and inside with a lip-like, somewhat uneven, but not sharply set off swelling; the margin of the columella strongly curved above, then straight, and also very thick, as is also the callus on the parietal wall. Length 126, width 62, aperture 64 mm. Probably a local form, remaining small, although very old." v. Martens' original figure is reproduced in my Pl. 15, fig. 2. I have examined the holotype and only known specimen at the Berlin Museum in 1933. It is an unusually heavy *A. fulica hamillei*, with abnormally thickened outer lip and columella, which accounts for the truncation being obsolete. Dr. F. X. Williams obtained a similar abnormal *hamillei* near Mombasa. That this is not a local Zanzibar form of the species is shown by the large series of *hamillei* collected by Dr. Williams in this Island.

Original description of *A. panthera* var. *leucostyla* Pilsbry (1904): "Shell elongate, rather solid, weakly plicatulate. Last whorl dusky-olive colored with some darker and lighter streaks, violaceous where worn; preceding whorl or two white, boldly striped with dark brown stripes, often interrupted; preceding whorls yellowish-white or pink, narrowly striped with brown. Whorls  $8\frac{1}{2}$ , the first  $2\frac{1}{2}$  smooth and glossy, uniform. Aperture sky-blue within, with a dark purple-brown

border within the acute lip-edge. Columella and parietal callous blue-white. Length 143, diam. 63, aperture 72 mm. Length 107, diam. 50, aperture 56 mm. Length 105, diam. 53, aperture 60 mm. Remarkable for its very dark color, 27 specimens collected agreeing in this. The spire shows the typical *panthera* pattern. It is larger than *A. le-tourneuxi* Bgt., and judging from the description, it is smoother." The author later (1905, p. 216) stated that "This form proves to be so different in genitalia from *A. panthera* that it will stand as a species." I have studied the type material of *leucostyla* at Ac.N.S.Phila. It consists of several specimens of what I regard as the common continental race of *A. fulica*, for which the oldest name appears to be *hamillei* Petit, as shown above. They can be matched with specimens in the long series collected by Dr. F. X. Williams in Zanzibar Id. and near Mombasa. These series also include small, immature shells agreeing with Petit's original figure of *hamillei*. The largest of the cotypes of *leucostyla* (Ac.N.S.Phila. No. 81980), actually 146 mm. long, is shown in Pilsbry's Pl. 40, fig. 3, and in the photograph of my Pl. 47, fig. 1.

The continental East African *A. fulica hamillei* is on the average a larger and bulkier shell than the nominate, insular race of the species, so that if extremes of shape or size are compared, one might be tempted to regard them as two distinct species. The sculpture, color of the columella and type of pattern are, however, the same. It is also possible to select specimens of both races that are practically alike in shape and size. Fullgrown *hamillei* often reach 130 mm. or more in length, the largest individuals having one-half to two whorls more than those of average size. The spire is often much shorter in proportion to the total length than in nominate *fulica*, the body-whorl longer and broader, and the aperture longer, relatively narrower and with a less convex outer lip. All these features are extremely variable, even in the same locality. In small or medium-sized shells the columella is as a rule moderately concave; in some very large, old shells it may be very deeply curved, with the lower end somewhat produced forward. The color and pattern are as variable as in nominate *fulica*. When the periostracum is well-preserved, it is pale olivaceous to golden-yellow; after it wears off, the ground color is white, often with a bluish tinge, particularly on the body-whorl. The chestnut to blackish-brown vertical streaks are as in nominate *fulica*. Usually the terminal two-thirds or half of the body-whorl are almost unstreaked, sometimes with a sharply defined streak corresponding to the black margin of the aperture at an earlier stage of growth. Such a shell is shown in E. A. Smith's (1881) beautiful figure, copied in my Pl. 48, fig. 1. The inner blackish-brown margin of the outer lip is more often present in *hamillei* than in

nominate *fulica*. The nepionic and early post-nepionic whorls are usually white or yellowish-white, as in nominate *fulica*; in a series at all stages of growth, collected by Dr. F. X. Williams in Zanzibar Id., the summit is intensely roseate, down to the sixth whorl and persisting even in adult shells. In all *hamillei* seen the columella and parietal wall are white or bluish-white.

The animal of *A. f. hamillei* was observed in captivity at the M.C.Z., living specimens having been sent by Dr. F. X. Williams from Zanzibar and Mombasa, for dissection. Externally it is much like an enlarged helicid snail. The foot is long and broad and may expand greatly on the sides and extend longitudinally. The upper surface is divided by many coarse and fine impressed lines into an irregular network, the appearance of which changes with the degree of extension. On each side of the upper part of the mouth there is a lobe-like retractile projection. Of the two pairs of retractile tentacles the anterior are the shorter and the posterior can extend much farther and bear the eyes at the tips. The animal is very dark, almost black over the upper surface.

A study of the large series of *Achatina* collected in Zanzibar Id. and the coastal districts of Kenya Colony and Tanganyika Territory, by Dr. F. X. Williams and Mr. A. Loveridge, and some of the types of the named species and varieties discussed above, has led me to the conclusion that all the supposed *A. panthera* with a white columella recorded from this area were specimens of what is here called *A. fulica hamillei*. I have seen as yet no specimens from this area with the characteristic shape and sculpture and the violaceous-red columella of true *A. panthera*. Specimens of *panthera* may be found occasionally in Museums labelled "Zanzibar"; but these are old specimens and their localities are not reliable. In any case, neither Gibbons (1879) nor, more recently, Dr. F. X. Williams found any *panthera* on the Island, although Dr. Williams had been urged to be on the lookout for large *Achatina* with a reddish columella. I also refer to subsp. *hamillei* all the shells from continental East Africa, Zanzibar and the other coastal islets, which previous authors have been calling *fulica*. As stated before, I restrict the name *fulica*, in a subspecific sense, to the shells of the Malagasy Region and the introductions from there to India, the Orient and the Pacific. Moreover, I regard *hamillei* as the ancestral stock of the species, from which the nominate race *fulica* was derived by insular isolation at a comparatively recent date.



*Measurements of Adult Shells*

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
162 mm.	78	77	45	9		Changamwe
154	73	73	38	8½		Malindi to Shanzu
153	76	70	37	8½		" "
147	70	69.5	37	8½		Shanzu
143	73	72.5	41	8½		Mombasa
141	80	72	45.5	8		Mkonumbi
138.5	67.5	70	33	8½		Shanzu
138	71	73	41	8½		Mombasa
136	69	71	34.5	8½		Malindi to Shanzu
135	67	70	38.5	8½		Mombasa
131.5	70	71.5	38	8½		Changamwe
130	63	65	35	8		Zanzibar Id.
129	72	68.5	40.5	8½		Mombasa
128.5	67	61.5	35	8½		"
126	65	67	36	8		"
124.5	63.5	64.5	35	8		"
121	62	66.5	32	8		"
116.5	58	59.5	33	7¾		Zanzibar Id.
115.5	57	62.5	31.5	7½		Mombasa
111	61.5	60	35	7½		"
108.5	57	57.5	30	7½		"
108	64	60	34.5	7½		"
107.5	52	56	27	7½		Zanzibar Id.
105.5	55	59.5	29	7½		"
101	52	53.5	28	7¾		"
98	55.5	58	32	7½		"
86	45.5	48.5	24.5	7½		"
73	41.5	40	21.5	7		"

*Specimens Examined.* KENYA COLONY: Mombasa (J. Bequaert; J. P. Chapin; L. Burgeon; F. X. Williams.—M.C.Z.; Ac.N.S.Phila.; U.S.N.M.; A.M.N.H.; Terv.M.); Wasin Id.,<sup>1</sup> cotypes of *leucostyla* (C.Eliot.—Ac.N.S.Phila.); Malindi (F. X. Williams.—U.S.N.M.; M.C.Z.); Changamwe near Mombasa (U.S.N.M.; M.C.Z.); Witu (A. Loveridge.—M.C.Z.); Mkonumbi near Witu (A. Loveridge.—M.C.Z.); Lamu Id. (A. Loveridge.—U.S.N.M.); Malindi to Shanzu (F. X. Williams.—U.S.N.M.; M.C.Z.); Kilindini (A. Loveridge.—M.C.Z.); Shimba Hills, 15 to 20 miles N. of Mombasa (U.S.N.M.; Terv.M.). — TANGANYIKA TERRITORY: Kitaya, Ruvuma River (A. Loveridge.—M.C.Z.); Tanga (J. Sandground; F. X. Williams.—Berl.M.; U.S.N.M.);

<sup>1</sup> The only map on which I have found Wasin Id. places it close to the coast near Vanga (or Wanga) and Shimoni, and apparently as a dependency of Kenya Colony.

M.C.Z.); Siga Caves near Tanga (A. Loveridge.-M.C.Z.); Amboni Estate near Tanga (A. Loveridge.-M.C.Z.); Magrotto near Tanga (A. Loveridge.-M.C.Z.); Mikindani (A. Loveridge.-M.C.Z.); Masai Steppe (Berl.M.); Bagamoyo (Berl.M.); Dar-es-Salaam (J. Bequaert; A. Loveridge.-M.C.Z.; Terv.M.). — ZANZIBAR ID.: (F. X. Williams; E. L. Petersen.-U.S.N.M.; M.C.Z.; Brus.M.); Mojoni (Berl.M.); Chwaka Bay (F. X. Williams.-U.S.N.M.; M.C.Z.). — PEMBA ID.: (A. Voeltzkow.-Berl.M.). — PORTUGUESE EAST AFRICA: Angoxe (M.C.Z.).

The southernmost locality known for *A. f. hamillei* is Chemba, on the Zambesi River (about 17° S.), and the northernmost, the mouth of the Omo River into Lake Rudolf (about 5° N.).

The average length of available specimens of *A. f. hamillei* is about 124 mm. and the average width about 64 mm. So far as I can find, only one recorded specimen exceeds in length the largest one I have seen (162 mm.). This is the paratype of Révoil's *milne-edwardsiana*, which reached 190 mm. in length. The holotype of this species was, however, not unusually large, being only 143 mm. long. Mr. G. W. Jeffery recently wrote to Dr. F. X. Williams that he obtained at Kilifi (between Mombasa and Malindi) a specimen over 7 inches (178 mm.) long and 3 inches (76 mm.) wide.

#### e. *A. FULICA* RODATZI Dunker

Pl. 3, fig. 3; Pl. 11, fig. 4; Pl. 30, fig. 1; Pl. 44, fig. 2; Pl. 52, fig. 1; Pl. 53, figs. 2-3; Pl. 54, fig. 1

*Achatina rodatzii* Dunker, 1852, Zeitschr. f. Malakoz., **9**, p. 127 (Id. of Zanzibar).

Pfeiffer, 1853, Monogr. Helic. Viv., **3**, p. 483. H. and A. Adams, 1855, Gen. Rec. Moll., **2**, p. 132. Dunker, 1857, in Pfeiffer, Novit. Conchol., **1**, p. 97; Pl. 27 (2 views of type). Pfeiffer, 1859, Monogr. Helic. Viv., **4**, p. 601; 1868, *Op. cit.*, **6**, p. 212. Haines, 1868, Cat. Terr. Shells Coll., p. 68. Pfeiffer, 1876, Monogr. Helic. Viv., **8**, p. 273. Gibbons, 1879, Jl. of Conch., **2**, p. 143 (Id. of Zanzibar). Pfeiffer, 1889, Jahrb. Hamburg. Wiss. Anst., **6**, pt. 2, p. 24 (Tanganyika Territory: between Kikoka and Rosako in Usaramo; Msere on Wami River). Paetel, 1889, Cat. Conch.-Samml., 4th Ed., **2**, p. 240. Bourguignat, 1889, Moll. Afr. Equat., p. 76. v. Martens, 1897, Deutsch-Ost-Afrika, **4**, Beschalte Weichth., p. 85 (Tanganyika Territory: a young presumably of this form from Usambara); 1897, Arch. f. Naturgesch., **63**, pt. 1, p. 54; 1897, Mitt. Naturh. Mus. Hamburg, **14**, p. 114 (1901, Zool. Ergebn. Küstengebiete Ost-Afrika Reise Stuhlmann, **2**, pt. 15, p. 4).<sup>1</sup> Pilsbry, 1904, Man. of Conch., (2), **17**, p. 60;

<sup>1</sup> The shell from Bagamoyo (F. Stuhlmann), referred by v. Martens to *A. rodatzii*, was seen at the Hamburg Museum. I regard it as belonging to *A. bloeyi* Bourguignat, the sculpture being much too strong, particularly on the body-whorl, for *rodatzii*.

Pl. 45, fig. 3 (after Dunker). Germain, 1905, Bull. Mus. Hist. Nat. Paris, **11**, p. 255 (eastern part of Tanganyika Territory); 1908, Rés. Scientif. Voy. Afrique Foà, p. 631. Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 66.

*Achatina (Achatinus) rodatzii* Pfeiffer, 1856, Malak. Blätt., **2**, (1855), p. 168; 1879, Nomencl. Helic. Viv., p. 265.

*Achatina chrysoleuca* Pilsbry, 1897 (November 23), Proc. Ac. Nat. Sci. Philadelphia, **49**, p. 357 (Southern Abyssinia: Tulu Didirko, about 4° 4' N., 39° 36' E., at 3,580 ft., E. of Lake Stefanie); 1904, Man. of Conch., (2), **17**, p. 59 (also Anglo-Egyptian Sudan: Magois, about 5° 30' N., 35° E., an immature shell); Pl. 16, fig. 13 (holotype); 1905, *Op. cit.*, (2), **17**, p. ix, fig. 6 (radula), and pp. xii-xiii (anatomy), of Introduction; Pl. 64, figs. 64 and 68 (anatomy). Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 65.

*Achatina erlangeri* v. Möllendorff and Kobelt, 1902, Nachrichtsbl. D. Mal. Ges., **34**, p. 180 (Italian Somaliland: Wabbi [Uebi or Webbi] Valley; Ganale Valley). Pilsbry, 1904, Man. of Conch., (2), **17**, p. 59. Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, pp. 18 and 65; Pl. 2, fig. 1 (paratype); Pl. 3, fig. 1 (holotype). Connolly, 1928, Atti Soc. Nat. Mat. Modena, (6), **7**, (or vol. **59**), p. 127 (Italian Somaliland: between El Sai and Torda); 1928, Proc. Zool. Soc. London, p. 180. Haas, 1932, Senckenbergiana, **14**, p. 176 (figured holotype, paratype figured by Kobelt, Pl. 2, fig. 1, and four other paratypes, all from Ganale Valley, at Senckenberg Museum).

*Achatina daroliensis* Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, pp. 19 and 65 (Southern Abyssinia: Daroli); Pl. 11, figs. 1-2 (2 views of holotype) Connolly, 1928, Atti Soc. Nat. Mat. Modena, (6), **7**, (or vol. **59**), p. 12 (Italian Somaliland: Genale; Baidoa; Bardera); 1928, Proc. Zool. Soc. London, p. 180. Haas, 1932, Senckenbergiana, **14**, p. 176 (holotype at Senckenberg Museum). Bacci, 1941, Ann. Mus. Civ. Genova, **41**, p. 133 (Italian Somaliland: Baidoa).

Original description of *A. rodatzii* Dunker (1852): "A. testa elongata ovato-conica, apice acuta, crassiuscula, tota alba, epidermide pallide olivacea vestita; anfractibus  $8\frac{1}{2}$  parum convexis, sutura haud profunda vix crenulata divisis, ad longitudinem obsolete plicatis, superioribus transversim decussatis subreticulatis et granosis, ultimo dorso  $\frac{3}{5}$  totius longitudinis testae aequante; apertura ovali superne acuta; columella parum arcuata, basi oblique truncata; peristomate acuto. Long. fere 5'' [=131mm.], latit. max. 2'' 3'' [=59 mm.], long. apert. 2'' 7'' [=67.5 mm.], latit. ejusdem 1'' 3'' [=33 mm.]. Species haec magna unicolor alba statu integro epidermide pallide olivacea induta, habitu maxime accedit ad *Achatinam acutam* Fér., a qua tamen praesertim differt anfractibus minus convexis, sutura vix crenulata, columella parum arcuata, flammis strigisque omnino deficientibus. *Achatina lactea* Reeve testa solida multo minore, sculptura

in anfractu ultimo granulato-decussata, ratione anfractuum et aperturæ forma facile distingui potest." Dunker had originally two specimens, both in his collection; but their present whereabouts is unknown. In 1857 he repeated the original description (with a German translation), making a few changes: the spire was now called "sub-acuta," the aperture "lactea", and the description of the outer lip was omitted. He also remarked that the color of the periostracum was somewhat too bright in the 2 figures of his Pl. 27, which are copied in my Pl. 30, fig. 1, and Pl. 54, fig. 1, two views of one shell. As these figures are exactly of the length given in the original description, they may be taken to represent the holotype. It should be noted that the lighter and darker blotches of my copies are merely areas where the periostracum was only partly preserved and do not correspond to markings. Likewise the transverse lines on the body-whorl are not due to sculpture, but are slightly darker yellow lines of the periostracum. I have observed a similar spiral zonation or striping of lighter and darker yellow in some of the *rodatzi* found by Dr. F. X. Williams in Zanzibar Id.

Original description of *A. chrysolucea* Pilsbry (1897): "Shell ovate, with conic spire, in general contour like *A. variegata* [*A. achatina* Linné]. Solid and strong, though not very thick. White, with a thin golden-brown cuticle, which is deciduous over the greater part of the shell, remaining behind the aperture and in the depressions between longitudinal plications elsewhere; later  $1\frac{1}{2}$  whorls immaculate, the next earlier with spaced, somewhat zig-zag and rather broad brown streaks, the next earlier narrowly streaked, the streaks straight. Whorls of the spire soiled white. Whorls  $6\frac{1}{2}$  (the apical whorls truncated, perhaps 1 or  $1\frac{1}{2}$  whorls being thereby lost), moderately convex, the last quite convex. Surface shining, finely decussated on the spire, the sculpture hardly visible to the naked eye, and gradually becoming obsolete, the spirals lost on the latter  $1\frac{1}{2}$  whorls, which are somewhat coarsely plicatulate. Sutures even above, weakly and irregularly serrate below. Aperture a little exceeding half the length of the shell, pure white within, subvertical, acuminate above, deeply excised by the body-wall; outer lip rather regularly arcuate, but less curved above, simple; columella short, cylindric, very deeply concave on the front and the side toward aperture, abruptly truncated at base, delicate flesh-tinted; parietal wall with a thin, transparent varnish. Alt. 105, diam. 58 mm. Longest axis of aperture 60, greatest width of cavity 33 mm. It is an ivory-white shell, with some inconspicuous marking on the spire. The cuticle is largely deciduous." The author's later description (1904) has a few changes, the most important of which are: the shell is said to be moderately solid and is now compared with *A.*

*hamillei* and *A. petersi*; the finely decussate sculpture is restricted to the antepenultimate whorl; the outer lip is thin and acute. The following remarks are added: "There is a little prominence at the periphery, and there are some oblique flattened places above it on the last whorl. The columella is very short and sinuous. *A. petersi* is a thinner shell than *chrysoleuca*, differently colored, with finer vertical sculpture and far more spiral grooving on the last whorl." It is also stated that the type specimen was collected alive. I have examined Pilsbry's holotype (Ac.N.S.Phila. No. 68113), shown in my Pl. 44, fig. 2. It appears to be an extremely obese and relatively short specimen of the almost unicolorous race of *A. fulica*, covered with a golden-yellow periostracum, described by Dunker as *A. rodatzii*. The series of *rodatzii* collected by Dr. F. X. Williams on Zanzibar Id. bridge the gap between the slender type of Dunker and the obese type of Pilsbry's *chrysoleuca*. These unicolorous shells show occasionally traces of darker, yellowish-brown vertical streaks, particularly on the earlier whorls, as described by Pilsbry. v. Martens (1897) notes their presence in a young *rodatzii* from Usambara, and furthermore that one of Dunker's original figures of the type shows traces of them. Both Gibbons (1879) and Dr. F. X. Williams found *rodatzii* in Zanzibar in the same colonies with normally marked *A. fulica hamillei*, though in smaller numbers; and Gibbons suspected that the two were very closely related.

Original description of *A. erlangeri* v. Möllendorff and Kobelt (1902): "T. imperforata, conoideo-ventricosoblonga, solidissima, ponderosa, indistincte plicato-striatula, fere laevigata, nitidula, alba. Spira fere exacte conica apice acutula, glabro, hyalino. Anfr.  $7\frac{1}{2}$  convexiusculi, ultimus magnus, spiram multo superans, bene convexus. Apertura fere verticalis, subauriformis, basi subeffusa; peristoma rectum, obtusum, columella, sat torta, basi oblique valde truncata. Diam. 68, alt. 122.5, apert. lat. 41, long. 65.5, alt. 60 mm." In 1910 Kobelt added the following description (translated from the German): "Shell completely imperforate, large and heavy, elongate conical, somewhat ventricose, indistinctly plicately striate, looking almost smooth, fairly shiny, unicolorous white; no traces of periostracum or markings in any of the numerous specimens seen. Spire almost exactly conical; apex rather pointed, smooth, strongly shiny.  $7\frac{1}{2}$  somewhat convex whorls, the body-whorl large, much longer than the spire, distinctly convex. Aperture almost vertical, nearly ear-shaped, compressed and somewhat gutter-shaped at the base; outer lip straight, obtuse; columella distinctly twisted, strongly truncate at the base." I made a careful study of the type series of *erlangeri* at the Senckenberg Museum in 1933. The holotype (No. 4852), labeled "Ganale-Tal",

is an unusually heavy shell, collected dead and weathered. It had been broken in life and repaired by the animal, so that it may be somewhat abnormal. It is the original to Kobelt's Pl. 3, fig. 1 (copied in my Pl. 52, fig. 1). Several of the paratypes are also weathered shells; but a few have portions of the pale yellowish periostracum preserved, showing that *erlangeri* belongs to the albino race *rodatzii*. One of these relatively fresh paratypes is now at M.C.Z. (my Pl. 53, fig. 3). I have seen additional paratypes at the Berlin Museum. The sculpture and general shape of all these shells are those of *A. fulica*.

Original description of *A. daroliensis* Kobelt (1910): "Testa imperforata, ovato-acuminata, solida, ? albida spira rufescente, striis in anfractibus superis subtilibus, sulcis spiralibus microscopicis subgranulosis, sculptura spirali evanescente. Spira conica lateribus vix convexiusculis, sutura impressa, inter anfractus inferos irregularis, subtiliter crenulata, obsolete albomarginata. Anfractus  $7\frac{1}{2}$  convexiusculi, celeriter accrescentes, apicales laeves, ultimus  $\frac{3}{5}$  altitudinis occupans, subventroso-rotundatus. Apertura ovata, fere verticalis, supra acuminata, faucibus albido-rosaceis, marginibus callo tenuissimo vix junctis, externo acuto, tenui, basali sat longe ultra truncaturam columellae contortae producto. Alt. 77, diam. 42, alt. apert. obl. 43 mm." The following additional description is translated from the German: "Shell imperforate, acuminate ovate, not particularly drawn out in length, solid, both available specimens collected dead and white with reddish spire, the upper whorls finely and densely striate and very finely granulate through microscopic spiral lines, the body-whorl with coarse rib-striae and without spiral sculpture below the periphery. Spire conical with scarcely convex sides and a smooth, rather sharply rounded apex. Suture somewhat impressed, irregular between the lower whorls, weakly crenulate, with a very indistinct pale margin.  $7\frac{1}{2}$  slightly convex whorls, rapidly increasing, the body-whorl occupying three-fifths of the total length when measured from the back and somewhat roundly swollen. Aperture not very large, ovate, acute above, reddish inside; the insertions of the margins are connected by a glazed layer, which is very thin but distinctly delimited outwardly; the outer lip is thin, sharp, moderately rounded, the basal margin acutely rounded and extended considerably beyond the truncation of the strongly twisted columella. Undoubtedly related to *A. erlangeri*, but differing considerably in the manner of coiling." An examination of the holotype and paratype and a comparison with the type series of *A. erlangeri*, at the Senckenberg Museum, in 1933, showed that *daroliensis* was apparently based on immature shells, collected dead and bleached, of *erlangeri*. Hence *daroliensis* also is here included in the synonymy of *A. fulica rodatzii*. One of the original

figures is copied in my Pl. 3, fig. 3. The reddish color of the spire and of the inside of the aperture, mentioned by Kobelt, is due to staining by foreign material.

The subsp. *rodatzii* agrees in size, shape and sculpture with average specimens of *A. f. hamillei*, and is equally variable in outline. It is little more than the albino race of *hamillei*. Even in fresh and living specimens, some of which were under observation at the M.C.Z., the shell material is pure white, and covered with a thin, deciduous, pale olivaceous-yellow to golden-yellow periostracum, with a few darker yellow or duller vertical streaks or lines, seemingly corresponding to arrests in growth. Some specimens also show a faint zonation or spiral striping of darker and lighter yellow in the periostracum of the body-whorl. The inside of the aperture, including the inner margin of the outer lip, the columella, the thin glazed callus of the parietal wall, and the summit of the spire are milky-white.

Connolly (1928, p. 126) refers to *A. daroliensis* a fresh specimen, from Genale, which he describes as follows (translated from the Italian): "Of 7 whorls and agreeing perfectly in dimensions with Kobelt's type, being scarcely one millimeter smaller in length as well as in width. The color is leather-yellow with reddish flames and spots on the 4th, 5th and 6th whorls, gradually decreasing in number until they disappear on the body-whorl." I have seen similarly colored specimens in our lots of *hamillei* from Zanzibar Id. and the Mombasa area. They are evidently transitional between *A. f. hamillei* and *A. f. rodatzii*. A more interesting connecting specimen is an immature shell from Voi (A. Loveridge), at M.C.Z. It is 88.5 mm. long, 43 mm. wide, of  $6\frac{1}{2}$  whorls, with the aperture 41.5 by 23 mm. Except for the white parietal wall and columella, it resembles somewhat Férussac's Pl. 125, figs. 3-4 of *H. zebrina* (= *A. fulica castanea* Lamarck). The shell is white, covered with a golden-yellow periostracum, worn off in places, and with a few narrow, widely spaced, straight or slightly wavy vertical russet-brown streaks (Pl. 55, fig. 3). It was found with normal *rodatzii*.

*Specimens Examined.* SOUTHERN ABYSSINIA: Tulu Didirko, E. of Lake Stefanie, holotype of *chrysoleuca* (A. D. Smith.-Ac.N.S.Phila.); Daroli River, 7° 30' N., 40° 30' to 42° E., holotype and paratype of *daroliensis* (C. v. Erlanger.-Frankf.M.). — ITALIAN SOMALILAND: without precise locality (Brus.M.); Ganale Valley, holotype and paratypes of *erlangeri* (C. v. Erlanger.-Frankf.M.; Berl.M.; M.C.Z.; Brit.M.). — KENYA COLONY: Voi (A. Loveridge.-M.C.Z.); South Creek on Mt. Garguess, 3600 ft. (E. Heller.-U.S.N.M.; M.C.Z.); Camp on Tana River (U.S.N.M.; M.C.Z.); between Mt. Eudoto and Tana River (E. A. Mearns.-U.S.N.M.; M.C.Z.); Shanzu, 8 miles N.

of Mombasa (F. X. Williams.—U.S.N.M.; M.C.Z.).—TANGANYIKA TERRITORY: Madabado Mts. in the Masai Steppe (Glauning.—Berl.M.; M.C.Z.); Ruaha (Prittwitz and Gaffron.—Berl.M.).—ZANZIBAR ID.: (J. S. Gibbons; F. X. Williams.—M.C.Z.; U.S.N.M.; Brus.M.; A.M.—N.H.); Chwaka Bay (F. X. Williams.—M.C.Z.).

Although often found in the same localities or even in the same colonies with *A. f. hamillei*, from which it is evidently derived, the albino race *rodatzii* appears to be most frequent in the drier or semi-desertic portions of the general area covered by the species. It reaches farther north ( $7^{\circ} 30' N.$ ) on the African continent than any of the other forms of *A. fulica*.

The M.C.Z. has an abnormal *A. f. rodatzii*, from "East Africa", very broadly and deeply umbilicate (Pl. 53, fig. 2). It is 118 mm. long, 68 mm. wide, of nearly 8 whorls, with the aperture 60 by 34 mm. It shows traces of injury in two areas of the penultimate whorl, which may explain the deformity.

#### Measurements of Adult Shells

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
148 mm.	70	70	36	8	8	Shanzu
142	66	70.5	35	8	8	"
134	66.5	61	36	8	8	Tana River
130	67	70.5	37	8	8	Zanzibar Id.
120	62.5	66	33	$7\frac{2}{3}$	$7\frac{2}{3}$	Shanzu
117	62	69	31	$7\frac{1}{2}$	$7\frac{1}{2}$	Zanzibar Id.
113	61	62	33	$7\frac{1}{2}$	$7\frac{1}{2}$	"
110	54	56.5	30	$7\frac{1}{2}$	$7\frac{1}{2}$	"
109	58	60	31	$7\frac{1}{2}$	$7\frac{1}{2}$	Ganale; paratype of <i>erlangeri</i>
106	53	59	30	$7\frac{1}{3}$	$7\frac{1}{3}$	Zanzibar Id.
98	50	54	28	7	7	"

Some of the larger specimens in this table agree well with Dunker's type of *rodatzii* in size and proportions; while others, among the smaller ones, come closer to Pilsbry's *chrysoleuca*.

#### ACHATINA (LISSACHATINA) LACTEA Reeve

Pl. 24, fig. 3; Pl. 48, fig. 2

*Achatina lactea* Reeve, 1842 (November), Proc. Zool. Soc. London, (for 1842), p. 55 ("Zanzibar"); 1842 (month ?), Conch. System., 2, p. 86; Pl. 177, fig. 6 (type). Catlow and Reeve, Conchologist's Nomenclator, p. 165.



- Pfeiffer, 1848, Monogr. Helic. Viv., **2**, p. 252. Reeve, 1849, Conch. Icon., **5**, *Achatina*, Pl. 12, fig. 4 (type). Pfeiffer, 1853, Monogr. Helic. Viv., **3**, p. 487. H. and A. Adams, 1855, Gen. Rec. Moll., **2**, p. 132. Pfeiffer, 1859, Monogr. Helic. Viv., **4**, p. 603; 1868, *Op. cit.*, **6**, p. 217; 1876, *Op. cit.*, **8**, p. 275. Paetel, 1889, Cat. Conch.-Samml., 4th Ed., **2**, p. 240. v. Martens, 1897, Deutsch-Ost-Afrika, **4**; Beschalte Weichth., p. 82; 1897, Arch. f. Naturgesch., **63**, pt. 1, p. 54. Pilsbry, 1904, Man. of Conch., (2), **17**, p. 35; Pl. 16, fig. 12 (after Reeve, 1842). Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 65. Connolly, 1928, Atti Soc. Nat. Mat. Modena, (6), **7**, (or vol. **59**), p. 126 (Italian Somaliland: Garbauèn in Obbia District; between El Sai and Torda; between Gumbo and Bieja; Uardavèl in the drainage of the Uebi Scebeli; Bur Buduleca; Bur Cal-ie-Corar; Tiglielgól). Cox, 1930, Monogr. Geol. Dept. Hunterian Mus., Glasgow Univ., **4**, p. 149 (Kenya Colony: post-Pliocene fossil in raised reef S. E. of Mombasa Id., about  $\frac{1}{4}$  mile N. of Ras Serani). Nardini, 1933, Paleontographia Italica, **32**, Suppl. 1, p. 179 (Italian Somaliland: Pleistocene fossils; plain of Gumbo; Amarr Gegeb near Mogadischu; Bohal Dablarrez in Obbia District; caves near Mogadischu, on road to Afgoi; hospital of Mogadischu); Pl. 22 (or 17), figs. 2 (adult) and 3a-b (2 views of immature). Bacci, 1939, Ann. Mus. Civ. Genova, **58**, p. 337, fig. 2 (anatomy. Italian Somaliland: Afgoi, W. of Mogadischu); 1941, *Op. cit.*, **61**, p. 132 (Italian Somaliland: 50 Kilom. inland from Itala; between Bugda Acable and El Dubbo; Buloburti). Coen, 1945, Catalogo Gasteropodi Polmonati Coll. Coen, p. 42.
- Achatina (Achatinus) lactea* Pfeiffer, 1856, Malak. Blätt., **2**, (1855), p. 168; 1879, Nomencl. Helic. Viv., p. 265.
- Achatina marioni* Ancey, 1881, Le Naturaliste, (1), **3**, p. 414 (Kenya Colony: "Elai Country in the interior of Zanguebar, at a higher latitude than Zanzibar"); 1885, Bull. Soc. Mal. France, **2**, p. 140 (locality here said to be "Elai Country, between Brava and Lake Victoria"; the type lot comprised several specimens, all found dead). Bourguignat, 1889, Moll. Afr. Equat., p. 74. Paetel, 1889, Cat. Conch.-Samml., 4th Ed., **2**, p. 240. Pilsbry, 1904, Man. of Conch., (2), **17**, p. 39. Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 65. Fulton, 1922, Proc. Mal. Soc. London, **15**, pt. 1, p. 26. Not *Achatina marioni* Matheron, 1868.
- Achatina fulica* var. *solida* de Angelis, 1900, in de Angelis and Millosevich, Sec. Sped. Bottego, Studio Geolog., (Rome), p. 147 (Italian Somaliland: hill near Brava); Pl. 3, fig. 7.
- Achatina fulica* var. *ponderosa* "de Angelis" Connolly, 1928, Atti Soc. Nat. Mat. Modena, (6), **7**, (or vol. **59**), p. 150 (error for var. *solida* de Angelis).
- Achatina fulica* Piersanti, 1941, Missione Biologica Sagan-Omo, **12**, (Zoologia, 6), p. 271; Pl., fig. 26 (Southern Abyssinia: mouth of Omo River in Lake Rudolf). Not of Bowdich, 1822.
- [*Achatina lactea elongata* Coen, 1945, Catalogo Gasteropodi Polmonati Coll. Coen, p. 42 (without description. Italian Somaliland: subfossil at Mogadischu). *Nomen nudum*].

Original description of *A. lactea* Reeve (1842): "Ach. testa oblongo-ovata, solida, intus extusque quasi fossili, lactea, epidermide levidensi sparsim induta; spira regulari, anfractibus longitudinaliter striatis, lineisque minutis circumdatis; apertura suboblonga, labro solidiusculo. Long.  $4\frac{1}{10}$ ; lat.  $2\frac{1}{10}$  poll. [105.5 and 53 mm.]. This beautiful shell, which is in a perfectly live state, and covered with a slight scattered epidermis, is of a rich uniform cream-color, without the least indication of any pattern; the whorls are very fully striated longitudinally, the striae rather irregularly following the growth of the shell; and they are again characterized by having a number of fine lines running around the upper half of them in an opposite direction. The columella, the aperture, indeed the entire shell, both inside and out, is of rich cream-color, and by this alone it cannot fail to be recognised." As Reeve cites with this original description Pl. 177, fig. 6, of his Conch. System., published without a description but with the name, it is possible that this Plate may have appeared first. This first figure, copied in my Pl. 48, fig. 2, is 102 mm. long, 55 mm. wide, with the aperture 56 by 28 mm. and the earliest whorls broken off. The second figure of the type (1849), although clearly drawn from the same shell, is slightly larger, 105 mm. long, 53 mm. wide, with the aperture 58 by 28 mm.; it is also not as yellowish as the first figure, at least in the copy seen. I saw the type at the British Museum in 1933 and it agrees in every respect with the two figures.

Original description of *A. marioni* Ancey (1881); "Long. 113; lat. 66 mill. Ovato-elongata, crassa, solida, omnino lutescente-albida, nitens, pergranulata ( $2\frac{1}{2}$  primis anfr. exceptis). Spira apice obtusa, anfr. 8, rapide crescentibus, convexis, ultimo coeteris majore, rotundato; omnibus, primis exceptis, strigis irregularibus spirialibus et longitudinalibus, in parte supera praesertim anfractuum impressis, granigeris et decussatis. Apertura simplice, ovali, truncata, non expansa aut reflexa; marginibus callo micante crassissimo junctis. Parte interiore pallide lutea." The following additional remarks are translated from the French: "It is close to *A. reticulata* Pf., of Guinea, but differs in the fewer whorls, the color, the smaller size, the much finer granulation, and the lack of rugosities on these granulations. The shell is also less elongate." In 1885 Ancey added a few notes, based on the type series (translated from the French): "Like *A. reticulata*, which it resembles somewhat, although it is colorless, much shorter, more strongly conical and much smaller, *A. marioni* is provided with coarse granulations on the last three whorls; these granulations are produced by longitudinal striae being cut by horizontal striae, rather indistinct. This sculpture stops at the lower part of the penultimate whorl, near the suture, or at least becomes very weak. It changes also

below the middle of the body-whorl to another similar but much finer sculpture, the granulations becoming then much less marked. This transformation is rather abrupt. The penultimate whorl of *A. marioni* tends to be rather strongly swollen. The shell material is calcareous and quite thick. The truncation of the columella is strong and oblique." *A. marioni* seems to have been overlooked by v. Martens when he wrote his account of the Mollusks of East Africa (1897). Ancey stated at first (1881) that the type was at the Marseilles Museum of Natural History. I have not seen this shell. In his later account (1885), however, he mentioned that the original lot comprised several specimens, all found dead. Some of these were evidently retained in his collection and later found their way elsewhere, probably after his death through G eret. I saw one of these paratypes in the Putzeys Collection, in 1933, and it is now at the Tervuren Museum. I recognized at the time that it agreed in every respect with *A. lactea*, although Ancey's measurements exceed somewhat those of Reeve's type. There is, therefore, no need to coin a new name for the homonym which Ancey had inadvertently introduced.

*A. fulica* var. *solida* was very briefly defined by de Angelis (1900) as being similar to v. Martens Pl. 2, fig. 1 (representing *A. fulica*), in v.d. Decken's "Reisen in Ost-Afrika" (1868), but very thick and with a peculiar sculpture. Length, 115 mm.; width, 50 mm.; aperture, 50 by 31 mm. The shell is readily recognized from d'Angelis' figure as *A. lactea*, with which species Connolly (1928) synonymized it. The present location of the type is unknown. Piersanti's (1941) figure of a supposed *A. fulica* from the mouth of the Omo River, likewise shows the characteristic sculpture of *A. lactea*; this shell was 110 mm. long, 58 mm. wide, of 8 whorls, with the aperture 50 by 30 mm.

*A. lactea* is here discussed because it is likely to be confused with *A. fulica*, particularly the unicolorous race, *A. f. rodatzki*, although it is very distinct owing to the coarse, bead-like sculpture of body-whorl and penultimate whorl. It is a moderately large, thick and heavy shell, 90 to 120 mm. long, regularly acuminate-ovate, in outline somewhat intermediate between *A. fulica* and *A. panthera*. The whorls, particularly the last, are more convex than in *panthera*; but the subsutural upper portion of the body-whorl is somewhat flattened as in that species. Early whorls somewhat drawn out, smooth; later whorls with regular spiral rows of granulations, either bead-like or slightly lengthened vertically. The sculpture is particularly coarse on the upper third of the body-whorl some distance above the periphery, being well visible to the naked eye. At and below the periphery the granulations are superficial and irregular, although traces are present even near the base and at the columella. All specimens I have seen, some of

them evidently collected alive, were pure white or slightly stained yellowish (probably through the lateritic soil), but completely deprived of periostracum.

*Specimens Examined.* ITALIAN SOMALILAND: Benadir District, 2 specimens (Ac.N.S.Phila.); Elai Country, in the hinterland of Brava, paratype of *A. marioni* (Terv.M.). — ZANZIBAR ID.: holotype of *lactea* (Brit.M.); several additional specimens, apparently distributed by Cuming (Copenh.M.; M.C.Z.; Berl.M.).

Although several examples (including Reeve's type) are labelled "Zanzibar" in collections, there is no certainty that *A. lactea* lives now or ever lived on that island. It is reliably known only from the coastal area of Northeast Africa, from southern Somaliland to Mombasa, a section formerly included in what was called "Zanguebar," and at one time part of the domain of the Sultan of Zanzibar. The Mombasa record by Cox (1930) is based only on Post-Pliocene fossils which could stand more careful study. Piersanti's specimen, from the mouth of the Omo River, would extend the area of the species to 600 miles from the Coast. This might indicate that the Elai Country (not found thus far on any of my maps), the type locality of Ancey's *A. marioni*, may have been a considerable distance inland.

#### Measurements of Adult Shell

Length	Greatest		Aperture		Whorls	Zanzibar (?)
	Width	Length	Width	Length		
97 mm.	52	51.5	28	7 $\frac{1}{4}$		

#### ACHATINA (LISSACHATINA) PANTHERA (Férussac)

When full-grown, the shell of *A. panthera* has 8 to 9 whorls and is large, capacious and fairly heavy, often reaching over 140 mm. in length and 80 mm. in greatest width. It is regularly acuminate-ovate, with a broadly conical and relatively short spire, the summit not particularly drawn out. It varies relatively little, small specimens having about the same outline as large ones. More slender individuals are exceptional. The whorls of the spire are moderately convex, the sutures being narrow and slightly depressed. The body-whorl is very large, two-thirds or more of the total length of the shell, somewhat saccate toward the base, very gradually narrowed toward the spire and flattened at the suture, particularly over the terminal third. The aperture is elongate-ovate, very long, usually over half the total length of the shell and longer than the spire. The outer lip is sharp, thin or slightly thickened, frequently somewhat expanded, sometimes mark-

edly so in old shells; it is moderately convex, more curved below than above, being decidedly flattened where it joins the body-whorl at a narrow sharp angle. The columella is long, weakly concave to nearly straight. The sculpture, much coarser than that of *A. fulica*, furnishes in my opinion one of the most reliable specific characters. The nepionic whorls are smooth in all specimens seen; but I have not examined newly hatched or very young shells. On the earliest post-nepionic whorls the vertical growth-striae are fine and cut by very fine, irregularly spaced, engraved spiral lines. Beginning with the fourth whorl, the decussation gradually grows stronger, producing vertically elongate welts on the much heavier growth-striae. On the body-whorl the vertical striae change to strong, close-set low ridges, extending fairly regularly from the suture to the base, producing a coarsely plicatulate surface, very different from the nearly even body-whorl of *A. fulica*. The decussation continues, though weaker, over the upper half of the body-whorl, but fades away behind the outer lip; there are also slight traces of it in the lower half, below the periphery. Toward the sutures the growth-striae become even coarser, also on the penultimate whorl, producing strong subsutural folds; the suture itself is irregular and superficially crenulate.

The color and pattern appear to be fairly uniform, more so than in *A. fulica*. The periostracum is rarely preserved in adult shells. The earliest 3 to 3½ whorls are unicolorous white. The ground color of the remainder of the shell is yellowish or bluish-white to buff. On the latter part of the third whorl faint, spaced, vertical, light brown streaks appear; these become broader and bolder, mahogany to chestnut-brown, from the sixth whorl on, sometimes russet with a purplish tinge; they are often irregular or jagged at the edges, sometimes zig-zag-like or broken up into confluent patches; in addition the pale areas of the body-whorl often show small brownish blotches or spots. In all boldly marked, normal specimens which I refer to *panthera* on the strength of the general shape, outline of body-whorl and aperture, and coarse sculpture, the columella and the callus of the parietal wall are vinaceous-pink; in most large adult shells the outer lip also has a broad rose-colored inner edge. The pink color may, of course, fade and eventually disappear in dead, bleached shells; but often some suggestion of it remains. I have as yet seen no true *fulica* (or any of its races) with a pink columella, although I readily admit that such specimens are not an impossibility. On the other hand, with the exception of the depauperate albino form *aniourtourensis*, of Madagascar, no fresh true *panthera* were observed with a white columella. The so-called *panthera* with a white columella, which I have studied in various collections, had the shape and sculpture of *fulica* and were

usually *A. fulica hamillei*. I have referred to the latter race nearly all published records of such specimens, as they were mostly based on shells from continental East Africa or Zanzibar.

Because of the frequent confusion with *A. fulica*, the exact area inhabited at present by *A. panthera* is as yet difficult to determine. It is further complicated by the fact that the specific limits between *A. panthera*, *A. layardi* Pfeiffer and *A. immaculata* Lamarck are at present ill-defined. All true *panthera* I have seen thus far came from Madagascar, Mauritius, southern Nyasaland, and Portuguese East Africa. There are also reliable records from Réunion, the Seychelles, the Comoros and the eastern border sections of Southern Rhodesia and of Transvaal. Connolly (1939) discounts rightly the supposed occurrence of this species at Port Elizabeth. The continental area would seem to extend along the East Coast from the Island of Mozambique (15° S.) to Lourenço Marques (Rikatla, 25° 45' S.) and to stretch inland some 150 to 200 miles. Most old collections have specimens of true *panthera* labelled "Zanzibar"; but I regard this as an erroneous locality. Neither J. S. Gibbons (1879) nor Dr. F. X. Williams (1948) saw any true *panthera* in that island. As I have indicated in the discussion of *A. fulica*, I do not regard *A. panthera* as truly indigenous in the islands of the Malagasy Region where it now occurs. I believe it was introduced by man into Madagascar at a comparatively recent date, notwithstanding Newton's (1895) record of supposedly Pleistocene fossil specimens from that island. According to Benson (1858) it was brought from Madagascar to Mauritius in 1847. The earliest record from Réunion is by Deshayes (1863), from the Comoros by Haines (1848) and from the Seychelles by Dautzenberg (1893). It is remarkable that the species never spread beyond this area, as did its companion, *A. fulica*.

So far as my material goes, *A. panthera* appears to be much less variable than *A. fulica*. I have retained Pfeiffer's *lamarckiana* as subspecifically distinct, mainly in order to call attention to the synonymy of the name. It should be noted, however, that both *Achatina immaculata* Lamarck (1822) and *Achatina layardi* Pfeiffer (1858) may eventually prove to be only subspecifically separable from *A. panthera* (Férussac, 1832). If this were true, the species as a whole would have to be called *A. immaculata*, Lamarck's name being the oldest of the three. I do not have at present the material nor the time to go into this problem. The peculiar shell described by Crosse as *A. antourouensis*, I regard as the dwarf albino subspecies of *panthera*.

## a. Typical A. PANTHERA

Pl. 5, fig. 3; Pl. 34, fig. 1; Pl. 38, fig. 2;

Pl. 56, fig. 2; Pl. 57, fig. 1; Pl. 58, fig. 3

- Helix (Cochlitoma) panthera* Férussac [1821, Tabl. Syst. Moll., Tabl. Limaçons, p. 49 (or p. 53) (no locality; without description or reference; *nomen nudum*); 1832 (?August 4), Hist. Nat. Moll. Terr. Fluv., Atlas, Pl. 126, figs. 1-2 (Plate with name engraved, published by Férussac in Livr. 28).
- Achatina panthera* Deshayes, 1838, in Lamarck, Hist. Nat. Anim. Sans Vert., 2d Ed., 8, p. 309. Pfeiffer, 1841, Symbolae Hist. Helic., 1, p. 28. Deshayes, 1844, in Lamarck, Hist. Nat. Anim. Sans Vert., 3d Ed., 3, p. 379. Catlow and Reeve, 1845, Conchologist's Nomenclator, p. 165. Pfeiffer, 1848, Monogr. Helic. Viv., 2, p. 252. Reeve, 1849, Conch. Icon., 5, *Achatina*, Pl. 3, fig. 12 (Madagascar). Deshayes, 1851, in Férussac, Hist. Nat. Moll. Terr. Fluv., 2, pt. 2, p. 159, and Expl. of Plates, p. 18. Pfeiffer, 1853, Monogr. Helic. Viv., 3, p. 487. H. and A. Adams, 1855, Gen. Rec. Moll., 2, pp. 131 and 132; Pl. 73, fig. 3 (specimen with animal). Benson, 1858, Jl. de Conchyl., 7, p. 267 (said to have been introduced in Mauritius from Madagascar in 1847). Pfeiffer, 1859, Monogr. Helic. Viv., 4, p. 603; 1860, Syst. Conch.-Cab., 1, Abt. 13, pt. 1, p. 327; Pl. 28, fig. 1. v. Martens, 1860, in Albers, Die Heliceen, 2d Ed., p. 201; 1860, Malak. Blätt., 6, p. 214 (Portuguese East Africa: Mozambique District). Morelet, 1860, Séries Conchyl., 2, p. 69 (Madagascar: Port Léven on N. E. coast, 12 leagues S. of Cape Amber). Deshayes, 1863, in Maillard, Notes Ile Réunion, 2d Ed., 2, Annex E, p. 90 (Réunion). Bielz, 1865, Verzeichn. Moll. Conch.-Samml., 3d Ed., p. 23. Dohrn, 1865, Proc. Zool. Soc. London, p. 232 (Portuguese East Africa: Mozambique; Zambesi River). Pfeiffer, 1868, Monogr. Helic. Viv., 6, p. 217. Haines, 1868, Cat. Terr. Shells Coll., p. 68 (Comoros). Paetel, 1869, Moll. Syst. Cat., p. 80. G. Nevill, 1870, Jl. Asiatic Soc. Bengal, 39, pt. 4, p. 414. Paetel, 1873, Cat. Conch.-Samml., p. 99. Fridrici, 1874, Bull. Soc. Hist. Nat. Metz, 13, p. 184. Pfeiffer, 1876, Monogr. Helic. Viv., 8, p. 275. Roeters van Lennep, 1876, Cat. Coll. Shells van Lennep, p. 54. Liénard, 1877, Cat. Faune Mal. Maurice, p. 54. Clessin, 1878, Jahrb. D. Mal. Ges., 5, pp. 179, 181, and 183. Morelet, 1878, Jl. de Conchyl., 26, p. 171 (according to Dupont introduced some 20 years ago and now supplanting *A. fulica* in Mauritius). Gibbons, 1879, Jl. of Conch., 2, p. 143 (Portuguese East Africa: Mozambique Id.; Inhambane. Epiphragm; egg). v. Martens, 1879, Monatsber. Ak. Wiss. Berlin, p. 737 (Portuguese East Africa: Tette); 1880, in Möbius, Beiträge Meeresfauna Mauritius Seychellen, p. 198. Crosse, 1881, Jl. de Conchyl., 29, p. 196; Pl. 8, fig. 2 (epiphragm. Madagascar: Nossi-Bé). Grasset, 1884, Index Test. Viv. Coll., p. 199. Ancey, 1885, Bull. Soc. Mal. France, 2, p. 139 (sinistral from Madagascar). Amaudrut, 1886, Bull. Soc. Philom. Paris, (7), 10, p. 107 (nervous system). Martorell y Peña, 1888, Catálogo Colección Conchol. Museo Martorell, Barcelona, p. 56. Paetel, 1889, Cat. Conch.-Samml., 4th Ed., 2, p. 240. O. Boettger, 1889, Nachrichtsbl. D. Mal. Ges., 21, p. 42 (Madagascar:

Loucoubé in Nossi-Bé). Bourguignat, 1889, Moll. Afr. Equat., p. 75. v. Martens, 1889, Sitzungsber. Ges. Naturf. Fr. Berlin, p. 164 (Transvaal: Queens River near Barberton; Lebombo Mts. between Barberton and Delagoa Bay); 1890, *Op. cit.*, p. 86 (Transvaal: Kapaiva). E. A. Smith, 1891, Proc. Zool. Soc. London, p. 310. Dautzenberg, 1893, Bull. Soc. Zool. France, **18**, p. 79 (Seychelles: Mahé). Ancey, 1894, Mém. Soc. Zool. France, **7**, p. 219 (Nyasaland: outflow of Shiré River, 3 Kilom. S. of Lake Nyasa). Newton, 1895, Quart. Jl. Geol. Soc. London, **51**, pt. 1, pp. 72 and 87 (Madagascar: in Pleistocene deposits capping the hill of Ambohimarina, 1400 ft., in the N. part of the Id.). Ancey, 1897, The Nautilus, **10**, p. 105 (sinistral, Mauritius). Sturany, 1898, Denkschr. Ak. Wiss. Wien, Math.-Naturw. Cl., **67**, p. 592. v. Martens, 1897, Deutsch-Ost-Afrika, **4**, Beschalte Weichth., p. 83 (Portuguese East Africa: Quilimane); 1897, Arch. f. Naturgesch., **63**, pt. 1, p. 54; 1898, Mitt. Zool. Mus. Berlin, **1**, pt. 1, pp. 22 and 30 (Seychelles: Mahé, from sea-level to 400 m.). Wiegmann, 1898, *Op. cit.*, **1**, pt. 1, p. 85, figs. on p. 86; Pl. 4, figs. 5-6 (anatomy of snails from Mahé). Melvill and Ponsonby, 1898, Proc. Mal. Soc. London, **3**, pt. 3, p. 178. Boucard, 1901, Cat. Coll. Coq. Terr., p. 49. Pilsbry, 1904, Man. of Conch., (2), **17**, p. 41; Pl. 38, fig. 31 (after Férussac, Pl. 126); Pl. 39, fig. 32 (specimen from Madagascar; called *A. panthera lamarckiana* in Expl. of Plates, p. 226); Pl. 42, fig. 8 (epiphragm, after Brancsik); 1905, *Op. cit.*, (2), **17**, p. xii of Introduction; Pl. 62, figs. 22-24 (radula, jaw, after Wiegmann); Pl. 63, figs. 30-32 (anatomy, after Wiegmann). Sykes, 1905, Proc. Mal. Soc. London, **6**, pt. 5, p. 270 (sinistral). Ancey, 1906, Bull. Scient. France Belgique, **40**, p. 190 (sinistral). Julia E. Rogers, 1908, The Shell Book, p. 275. Sykes, 1909, Trans. Linn. Soc. London, Zool., (2), **13**, pt. 1, p. 63 (Seychelles: Mahé at Trois-Frères, 1500 ft., and Chateau Margot; Praslin; Silhouette). Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, pp. 65, 90, 93, and 95. Rolle, 1910, *Op. cit.*, **32**, p. 191; Pl. 17, figs. 1a-b (2 views of scalariform abnormality from Mauritius) and 2 (sinistral, Mauritius). Connolly, 1912, Ann. South Afr. Mus., **11**, pt. 3, p. 197 (Southern Rhodesia: Sebakwe). Simroth, 1912, in Bronn's Klassen u. Ordnungen d. Tier-Reichs, **3**, Abt. 2, Book 2, Pulmonata, p. 564; Pl. 35, figs. 9-10 (anatomy, after Wiegmann). Dautzenberg, 1914, Bull. Soc. Zool. France, **39**, p. 57 (sinistral). Standen, 1917, Jl. of Conch., **15**, pt. 5, p. 160 (egg). Germain, 1918, Bull. Mus. Hist. Nat. Paris, **24**, p. 364 (Portuguese East Africa: Andrada); 1921, Mém. Soc. Zool. France, Vol. Suppl., p. 178 (Mauritius. Réunion); Pl. 10, figs. 3-4 (2 views of sinistral shell); Pl. 11, fig. 2 (umbilicate abnormality); Pl. 13, figs. 5-6 (2 views of monstr. *angulatum*). Connolly, 1925, Jl. of Conch., **17**, pt. 9, p. 263 (Rodriguez Id.); 1925, Trans. R. Soc. South Africa, **12**, pt. 3, p. 166 (Portuguese East Africa: Querimba Ids.; Quilimane; Tette; Inhambane; Rikatla; Andrada; Amatongas; Chinde; headwaters of Rio Tristão, Macequece District). Haas, 1929, Zool. Jahrb., Abt. Syst., **57**, pp. 396 and 411 (Comoros: Anjouan; Mayotte. Madagascar: Mananava, Antongil Bay, in E. part; Ste Marie de Madagascar; Andranohinaly, in S.W. part; Mojanga, in W. part). Connolly, 1931, Jl. of Conch., **19**, pt. 4,



- p. 103. Grandidier and Petit, 1932, Zoologie de Madagascar, p. 192. Germain, 1934, C. R. 67e Congrès Soc. Savantes, (1934), Sciences, pp. 123 and 128; 1935, Mem. Est. Mus. Zool. Univ. Coimbra, Ser. I, No. 80, p. 38 (Portuguese East Africa: Nova Choupanga near Chemba). Dupont, 1935, Trans. R. Soc. Arts Sci. Mauritius, Ser. C, No. 3, (1933-1934), p. 138 (Seychelles: Mahé; Silhouette; Praslin). Viader, 1937, Mauritius Inst. Bull., **1**, pt. 2, p. 86. Connolly, 1939, Ann. South Afric. Mus., **33**, pt. 1, p. 322 (earlier records repeated; adds Southern Rhodesia: Umtali; Mandellaras. Two shells labelled Port Elizabeth were either introduced or wrongly labelled). Burton, 1949, Illustrated London News, **214**, p. 120.
- Achatina* (*Archachatina*) *panthera* Albers, 1850, Die Heliceen, p. 190.
- Achatina* (*Achatinus*) *panthera* Pfeiffer, 1856, Malak. Blätt., **2**, (1855), p. 168; 1879, Nomencl. Helic. Viv., p. 265. Römer, 1891, Jahrb. Nassau. Ver. Naturk., **44**, p. 123.
- Achatina zebra* Sganzin, 1843, Mém. Soc. Hist. Nat. Strasbourg, **3**, pt. 2, Cat. Coq. Iles de France, etc., p. 17 (Madagascar). Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 90. Not of Bruguière, 1792.<sup>1</sup>
- Achatina lamarckiana* Dohrn, 1865, Proc. Zool. Soc. London, p. 232 (Portuguese East Africa: Mozambique; Zambesi River). Not of Pfeiffer, 1847.
- Achatina zebra* var.  $\gamma$  Pfeiffer, 1853, Monogr. Helic. Viv., **3**, p. 482 (with *A. eburnoides* "Sganzin" as synonym).
- "Achatine eburnoide" Sganzin, 1843, Mém. Soc. Hist. Nat. Strasbourg, **3**, pt. 2, Cat. Coq. Iles de France, etc., p. 17 (scalariform abnormality; 2 shells from Ste Marie de Madagascar).
- Achatina eburnoides* Pfeiffer, 1853, Monogr. Helic. Viv., **3**, p. 482 (as a synonym of *A. panthera* var.  $\gamma$ ).
- Achatina perdix* de Man, 1877, Recherches Faune Madagascar Dépendances, Pt. 5, Livr. 3, pp. 2 and 18 (Madagascar: Nossi Bé). Not of Lamarek, 1822.
- ? *Achatina* (?) *panthera* de Man, 1877, Recherches Faune Madagascar Dépendances, Pt. 5, Livr. 3, pp. 2 and 18 (Madagascar: Pasandava Bay): Pl. 3, fig. 19.<sup>2</sup>
- Achatina pantherina* "Férussac" Roeters van Lennep, 1876, Cat. Coll. Shells van Lennep, p. 53. G. Nevill, 1879, Hand List Moll. Indian Mus., **1**, (1878), p. 145 (Mauritius; no description; error for *panthera* Férussac). v. Martens, 1897, Mitt. Naturh. Mus. Hamburg, **14**, p. 114 (1901, Zool. Ergebn. Küstengebiete Ost-Afrika Reise Stuhlmann, **2**, pt. 15, p. 4) (in part: specimen from Portuguese East Africa: Quilimane, with reddish columella).
- Achatina panthera* var. *sinistrorsa* Grasset, 1884, Index Test. Viv. Coll., p. 199 (Mauritius; no description).

<sup>1</sup> Bruguière's *Bulimus zebra* was originally a mixture of *A. panthera* from Madagascar and *A. zebra* (of later authors) from South Africa. The name was later restricted to the South African species.

<sup>2</sup> Although the colored figure shows a white columella, a feature which I have never seen myself in true *panthera*, the general shape and rough sculpture of strong growth-striae seem to refer this shell to *panthera* and not to *fulica*. Possibly the figure was made from a shell with discolored or faded columella.

- Achatina* (*Achatinus*) *fulva* O. Boettger, 1890, *Nachrichtsbl. D. Mal. Ges.*, **22**, p. 87 (Madagascar: Nossi-Bé at Loucoubé and Tafondro. — According to Haas, 1929, these shells were *A. panthera*). Not *Bulimus fulvus* Bruguière, 1792, nor *A. fulva* Beck, 1837.
- Achatina mossambica* Brancsik, 1893, *Jahresh. Naturw. Ver. Trencsener Comit.*, **15-16**, (1892-1893), p. 116 (Portuguese East Africa: Id. of Mozambique); Pl. 6, figs. 2 and 2a-b (anatomy only); Pl. 10, figs. 2a-b (outer and inner views of epiphragm).
- Achatina lechaptouisi* Ancey, 1894, *Mém. Soc. Zool. France*, **7**, p. 220 (Portuguese East Africa: Mozambique).
- ? *Achatina* sp. like *layardi* Newton, 1895, *Quart. Jl. Geol. Soc. London*, **51**, pt. 1, pp. 72 and 87 (Madagascar: Pleistocene deposits capping the hill of Ambohimarina, 1400 ft., in N. part of the Island).
- Achatina panthera* monstr. *sinistrorsum* Dautzenberg, 1909, *Jl. de Conchyl.*, **57**, p. 41; Pl. 1, fig. 3 (Mauritius); 1911, *Op. cit.*, **58**, (1910), p. 315.
- Achatina panthera* monstr. *angulatum* Dautzenberg, 1911, *Jl. de Conchyl.*, **58**, (1910), p. 314; Pl. 14, fig. 1 (Mauritius). Germain, 1921, *Mém. Soc. Zool. France*, Vol. Suppl., p. 181; Pl. 13, figs. 5-6 (2 views of one shell).
- Achatina panthera* monstr. *canaliculatum* Dautzenberg, 1911, *Jl. de Conchyl.*, **58**, (1910), p. 314 (no locality; 2 shells).
- Achatina panthera* monstr. *umbilicatum* Dautzenberg, 1911, *Jl. de Conchyl.*, **58**, (1910), p. 315; Pl. 14, fig. 3 (Mauritius; Madagascar).
- Achatina panthera* monstr. *contabulatum* Dautzenberg, 1911, *Jl. de Conchyl.*, **58**, (1910), p. 314 (specimen without locality; refers to it also Rolle's Pl. 17, figs. 1a-b of 1910).
- Achatina panthera* monstr. *compressum* Dautzenberg, 1911, *Jl. de Conchyl.*, **58**, (1910), p. 315; Pl. 14, fig. 2 (Madagascar; Mauritius).<sup>1</sup>
- Achatina panthera* var. *mossambica* Kobelt, 1910, *Abh. Senckenberg. Naturf. Ges.*, **32**, p. 65.
- Achatina panthera* var. *berevoensis* Clench and Archer, 1930, *The Nautilus*, **43**, p. 85 (Madagascar: forest between Mahabo and Berevo; Berevo; 10 miles S. of Berevo; no type locality and no holotype selected).

Pilsbry (1904) and Germain (1921) also cite de Montfort's figure of *Achatinus* (1810, *Conchyl. Systém.*, **2**, p. 418), but not the accompanying text, in the synonymy of *A. panthera*. In my opinion this figure is unrecognizable and bears only a superficial resemblance to *A. panthera*.

Although Férussac gave no description of his *Helix panthera*, he published the trivial name validly in 1832 in the engraved caption of his Pl. 126. The two figures of this plate (one of which is copied in my Pl. 58, fig. 3) are the type figures of the species and are two views of one shell. Fig. 1 is 151 mm. long, 75 mm. in greatest width, with

<sup>1</sup> Dautzenberg credits some of his names of abnormalities to Rolle. It should be noted that Rolle gave a name in print only to *A. fulva* var. *umbilicata*; although he may have distributed some of the others with manuscript names.

the aperture 75 by 41 mm. The type specimen may yet be in existence in some collection, but I have been unable to trace it thus far.<sup>1</sup> It could not be shown to me at the Paris Museum in 1933 and it has not been found there since (Dr. E. Fischer, *in litt.*, 1949). Fortunately Férussac's figures leave no doubt as to the identity of the species.

The first formal description, by Deshayes (1838), is as follows (French text translated): "A. testa ovato-oblonga, solida, apice obtusa albo-grisea; strigis longitudinalibus fusco violaceis vel flavis ornata; anfractibus convexis ultimo spira brevior; apertura ovata, albo-coerulea; columella contorta, labroque roseis. Fine and large shell, which has some analogy in shape with *Achatina fulva* [Deshayes' *A. fulva* was *A. fulica*], but is in proportion shorter and more ventricose. There are 8 whorls to the spire, which are convex, with the suture simple, smooth or scarcely striate by the growth additions. The apex is obtuse and whitish. On the succeeding whorls some fulvous flammules appear; these become broader and darker on the penultimate whorl; but on the body-whorl they form broad zones of a very intense brown, often shading by scarcely perceptible stages into the ash-gray background. The aperture is oval, oblong, bluish-white inside, white along the right margin [outer lip]; the left margin [parietal wall] and the columella are a beautiful rose color. The columella, strongly twisted on itself, has its end [base] produced forward and outward. It is much shorter than the right margin [outer lip] and its truncation is deep. This shell, one of the largest of the genus, is 15 cm. long and 75 mm. wide." It may be noted that the measurements and description fit Férussac's Plate 126 nicely. This does not necessarily mean, however, that Deshayes saw Férussac's type specimen, as the description may have been written from the figures.

Original description of *A. mossambica* Brancsik (1893) (German text translated): "T. solidissima, ovato-oblonga, ventricosa, longitudinaliter sulcato striata, nitida; livide fulva, striis ac apice pallidioribus, anfractibus superis rufi flammulatis, caeteris irregularibus flammulis ac maculis fulvo-coerulescentibus; columella truncata, rosea, apertura oblongo-ovalis, intus rosacea, interdum caerulescens; peristoma simplex, crassum, margine columellari late calloso, rosaceo; spira conica, acutiuscula; anfractus 8 convexiusculi, 3-7 striis transversis reticulatis, ultimus longitudinem spirae multo superans." Dimensions of 7 specimens in mm.: 1. Length, 168; width, 55; length of aperture, 95 ("exempl. ventricosissimum"). 2. L., 158; w., 49; 1. of a.,

<sup>1</sup> Germain (1935, p. 39, footnote) says that "the type of Férussac's *A. panthera* has the parietal margin and the columellar margin white." This can hardly be reconciled with Férussac's Pl. 126 where both columella and parietal wall are fairly uniformly reddish. Germain's measurements of the "figured" type were probably taken from Férussac's figures, the length given (120 mm.) being a misprint or slip for 150 mm.

87. 3. L., 152; w., 45; l. of a., 88 ("exempl. minus crassum"). 4. L., 146; w., 44; l. of a., 81. 5. L., 145; w., 44; l. of a., 79. 6. L., 141; w., 38; l. of a., 71 ("exempl. angustissimum"). 7. L., 137; w., 38; l. of a., 83 ("exempl. minus crassum"). "Very ventricose, with conical, rather acute spire, readily separated at first glance from *A. panthera*. The columellar margin of the aperture is much less obtusely curved inward in the middle than in *panthera* and all margins are colored pink, this color acquiring a bluish tinge inside. The striation particularly on the body-whorl is very coarse." The present location of the cotypes is unknown. The description was, however, clearly based on typical specimens of *A. panthera*, which is common in the region of Mozambique, and with which Pilsbry (1904) first synonymized it.

Original description of *A. lechaptouisi* Ancey (1894) (French text translated): "Testa solida, crassa, parum nitida, ovata, superne conico-attenuata, ventricosa, lineis incrementi passim rudibus exarata et, summo excepto, striis spiralibus in supremis anfractibus approximatis et granulos efficientibus, in inferioribus magis remotis et e medio ad basin obsolete notatis reticulata, sordide albida, fusco et caerulescentigriseo late irregulariterque flammeata et maculosa, apice pallido, minuto. Spira conica, anfractibus 7, sutura irregulariter impressa separati, convexiusculi, regulariter crescentes; ultimus maximus, ovato-ventrosus, caeteros longitudine superans. Apertura magna, basi subpatula, intus albescens, ad marginem exterum roseo-tincta; columella crassa, oblique ad basin truncata, fere recta, vix contorta, cum callo parietali crasso rosea. Long. 125, lat. 75, alt. apert. 77 mill. This well characterized species has the general color of *panthera*, but has a very peculiar appearance owing to the length of the body-whorl; in this respect, but in this only, it has a certain analogy with *variegata* [*A. achatina*] of the West Coast of Africa." I have been unable to trace the present whereabouts of Ancey's type. As noted by Pilsbry (1904), *lechaptouisi* is "exactly equivalent to *mossambica*, except in being a little smaller." It was probably based on an immature shell.

Original description of *A. panthera* var. *berevoensis* Clench and Archer (1930): "Shell acutely ovate, moderately solid, the ground color of the nuclear whorl whitish shading off into a pinkish buff on the body whorl, and marked throughout by somewhat irregular chocolate streaks. Nearly every streak on the body whorl is washed on the right with deep neutral grey. Surface covered with axial striae. Each whorl covered with fine spiral lines with the exception of the body whorl where they appear only in a region extending about 15 mm. below the suture. Whorls  $6\frac{1}{2}$  to 7. Aperture obliquely ovate, bluish grey within, outer lip slightly buff pink, columella and parietal

callus white tinged on the outer lip with coral red. Columella sharply truncate, slender, and curved outwards. Base of lip quite flaring, lip itself marginate. This variety differs from *A. panthera*, *s. s.* as figured by Férussac, Prodr., p. 49, no. 349; Hist., pl. 126, and as figured by Pilsbry, M. of C. (2), Vol. 17, p. 41, pl. 38, fig. 31, 1904, in the following respects: The shell is smaller, the pinkish buff ground color is spread over the body whorl contrasting with the lighter ground color of the species proper; the streaks are further apart and set in straighter lines, and contrast with those of *A. panthera*, by the less pronounced wash of neutral grey on the right; the axial striae are not so deep, while the spiral lines on the last whorl differ in being confined to a narrow subsutural area, as compared with *A. panthera* where they may be absent, or if present are scattered at irregular distances. The spire is slightly less acute; the aperture narrower as regards its length, and less ovate. The columella is slenderer, and from a side view is more concave than *A. panthera*." The measurements given for 3 cotypes are respectively: length, 133, 122 and 122 mm.; width, 71, 68 and 68; length of aperture, 68, 63 and 66 mm.; width of aperture, 40, 35 and 35.5. This form has not been figured thus far. I have studied all three cotypes. They are in poor condition and apparently immature. The best preserved example, from Bérévo (M.C.Z. No. 31077), is 122 mm. long and clearly abnormal, the summit being very broad as if the early whorls had been crushed in and repaired by the animal; it shows more traces of pink on the columella than either of the others. The shell from 10 miles S. of Bérévo (M.C.Z. No. 31079) is 120 mm. long, very bleached, with the columella almost white. The specimen from between Mahabo and Bérévo (M.C.Z. No. 31078), herewith selected as the lectotype and shown in my Pl. 5, fig. 3, also bleached and with nearly white columella, is otherwise the most normal shell; it measures 132 mm. in length, 71 mm. in greatest width, of  $7\frac{1}{2}$  whorls, with the aperture 71.5 by 40 mm. I can find no characters by means of which these specimens could be separated from the nominate race of *panthera*.

*Specimens Examined.* MADAGASCAR: without precise locality in most collections (M.C.Z.; A.M.N.H.; Ac.N.S.Phila.; U.S.N.M.; Amst.M.; Leid.M.; Brus.M.; Berl.M.); Bérévo, cotype of *berevoensis* (F. R. Wulsin.—M.C.Z. No. 31077); between Mahabo and Bérévo, cotype (now selected as lectotype) of *berevoensis* (F. R. Wulsin.—M.C.Z. No. 31078); 10 miles S. of Bérévo, cotype of *berevoensis* (F. R. Wulsin.—M.C.Z. No. 31079); Nossi-Bé (Berl.M.). — PORTUGUESE EAST AFRICA: Mozambique (E. L. Layard.—A.M.N.H.; M.C.Z.); Lumbo near Mozambique (A. Loveridge.—M.C.Z.); Villa Machado R. Allen and R. M. de Schauensee.—Ac.N.S.Phila.). — Also many

specimens in various collections labelled "East Africa" and some "Zanzibar", the latter locality in my opinion open to question; I have seen no specimens that had been reliably collected in Zanzibar Id., and neither Gibbons nor Williams found it there; in the early days many shells were labelled from "Zanzibar" because they had been shipped from there to Europe, although they actually came from some part of the East African coast.

There are published records, apparently reliable, of the large nominate race of *panthera* from the extreme eastern sections of Nyasaland, Southern Rhodesia and Transvaal, although in this area it seems to be replaced in certain localities by the small race *lamarckiana*. All the specimens I have seen from Mauritius were *lamarckiana*. The species has been recorded from the Comoros, Réunion, and the Seychelles; but I have seen no specimens from there and do not know what race is involved.

#### Measurements of Adult Shells

Length	Greatest		Aperture		Whorls	
	Width	Length	Width			
163.5 mm.	85	91	49	8		Mozambique
161	85	87	49	8		Lumbo
154	79	89	41.5	8		East Africa
153	83	82	44.5	8		Mozambique
137	73	75.5	38	7½		Madagascar

The largest specimens on record appear to be the one at the British Museum measured by Connolly (1939), locality not given, 195 mm. long, 92 mm. wide; and the cotype of *mossambica*, the length of which is given by Brancsik (1893) as 168 mm.

Abnormal shells appear to be rather frequent in this species and several authors have described them, as listed in the bibliography. A sinistral example is shown in my Pl. 38, fig. 2, and a scalariform shell in my Pl. 56, fig. 2.

It should be emphasized that there is at present no reliable evidence of *A. panthera* occurring outside East Africa, Madagascar, the Mascarenes and the Seychelles. This species was not introduced into Southern Asia, the East Indies or the Pacific Islands. The few references in popular writings to its supposed occurrence in the latter area were due to a confusion with *A. fulica*. They may have been caused by *A. leucostyla* being originally described by Pilsbry as a variety of *A. panthera*. As shown previously in this paper, *leucostyla* was based on specimens of the continental East African race of *A. fulica*, for which the oldest valid name appears to be *hamillei* Petit.

b. *A. PANTHERA LAMARCKIANA* Pfeiffer

Pl. 35, figs. 2-3; Pl. 38, fig. 1; Pl. 55, fig. 2; Pl. 76, fig. 2

- Achatina lamarckiana* Pfeiffer, 1846 (January 26), Proc. Zool. Soc. London, (for 1846), p. 115 (interior of the Id. of Madagascar); 1847 (April), Ann. Mag. Nat. Hist., **19**, p. 269 (copy of original description); 1848, Monogr. Helic. Viv., **2**, p. 253; 1853, *Op. cit.*, **3**, p. 483. H. and A. Adams, 1855, Gen. Rec. Moll., **2**, p. 132. Pfeiffer, 1859, Monogr. Helic. Viv., **4**, p. 601. v. Martens, 1860, in Albers, Die Heliceen, 2d Ed., p. 201. Haines, 1868, Cat. Terr. Shells Coll., p. 67. Pfeiffer, 1868, Monogr. Helic. Viv., **6**, p. 213; 1876, *Op. cit.*, **8**, p. 273. Clessin, 1878, Jahrb. D. Mal. Ges., **5**, p. 179. Grasset, 1884, Index Test. Viv. Coll., p. 199. Paetel, 1889, Cat. Conch.-Samml., 4th Ed., **2**, p. 240. E. A. Smith, 1891, Proc. Zool. Soc. London, p. 310. Boucard, 1901, Cat. Coll. Coq. Terr., p. 49. Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 90.
- Achatina (Achatinus) lamarckiana* Pfeiffer, 1856, Malak. Blätt., **2**, (1855), p. 168; 1879, Nomencl. Helic. Viv., p. 265. Römer, 1891, Jahrb. Nassau. Ver. Naturk., **44**, p. 123.
- Achatina lamarkiana* A. D. Brown, 1861, Cat. Shells Coll., p. 55. Paetel, 1869, Moll. Syst. Cat., p. 80; 1873, Cat. Conch.-Samml., p. 99. Roeters van Lennep, 1876, Cat. Coll. Shells van Lennep, p. 53.
- Achatina lamarcki* Germain, 1918, Bull. Mus. Hist. Nat. Paris, **24**, p. 365.
- Achatina panthera* var. *minor* Deshayes, 1851, in Férussac, Hist. Nat. Moll. Terr. Fluv., Explanation of Plates of Atlas, p. 19; Atlas, Pl. 132, figs. 1-2 (2 views of one shell; no locality. Plate published, without name, by Deshayes, after Férussac's death, presumably in 1851). Godet, in Junod, 1899, Bull. Soc. Vaudoise Sci. Nat., (4), **35**, No. 133, p. 278 (no description; defined by the reference to Férussac's Pl. 132, figs. 1-2. Portuguese East Africa: Rikatla. Egg).<sup>1</sup> Connolly, 1939, Ann. South Afric. Mus., **33**, pt. 1, p. 323 (Portuguese East Africa: Rikatla; Macequeece District. Southern Rhodesia: Mt. Selinda; Selinda Forest).
- Achatina panthera* var. E. A. Smith, 1899, Proc. Zool. Soc. London, p. 589; Pl. 34, fig. 1 (Nyasaland: Zomba). Pilsbry, 1904, Man. of Conch., (2), **17**, p. 44; Pl. 38, fig. 30 (after E. A. Smith).

Original description of *A. lamarckiana* Pfeiffer (1847): "Ach. testa ovato-conica, solida, ponderosa, ruditer plicata, in fundo albido strigis fulminatis nigricantibus et castaneis, maculisque rufis variegata; spira conica, pallida, apice obtusiusculo; anfractibus 8 convexiusculus, supremis lineis spirilibus obsolete decussatis, ultimo ventroso, spiram superante; columella arcuata, purpureo-callosa, supra basin aperturæ oblique et leviter truncata; apertura ovali, intus margaritacea, caerulelescente, saturatius marmorata; peristomate fusco-limbato, marginibus

<sup>1</sup> Some authors credit the name *minor* to Junod; but it seems clear, from the introductory remarks by Junod, that all names were given by Godet, who moreover cites Férussac as the author of the name.

callo purpureo junctis. Long. 103, diam. 52 mill." In 1848 Pfeiffer added to this diagnosis that the aperture was 58 mm. long and 34 mm. wide. The unfigured type came from the Cuming Collection, later mostly acquired by the British Museum. No specimen labelled "*lamarckiana*" is now to be found there, so that the type must be considered lost.<sup>1</sup> According to the measurements it was a dwarf example of *panthera*, being even smaller than the one figured by Deshayes (as var. *minor*). In 1853, Pfeiffer cites Deshayes' Pl. 132, figs. 1-2, in the synonymy of *lamarckiana*. If the dwarf specimens are to be given varietal or subspecific status they should be called *lamarckiana*. Pilsbry (1904) pointed out that, at the time he described *lamarckiana*, Pfeiffer believed that true *panthera* had a white columella. He was deceived by his specimen of *panthera* (described by him in 1848, p. 253, and figured in 1860, Pl. 28, fig. 1) having a bleached columella. Moreover, in his figure the columella is not pure white, but is faintly tinged with roseate, at any rate in the copies of the Conchylien-Cabinet I have examined. This figure has the shape and coarse sculpture of *panthera* and its size (132 mm.) is that of the nominate race.

Connolly (1939) gives the following account of the dwarf race of *A. panthera*: "The form actually mentioned by Junod is referred to that figured on Pl. 132 of Deshayes' *Histoire*, which measures alt. 108, lat. 57; apert. alt. 59, lat. 30; last whorl 85 mm., and his varietal name seems applicable to the beautiful race from Nyasaland figured by Smith, which shows the typical *panthera* colour pattern and most brilliant rosy peristome and columellar region, is extremely solid with unusually thick lip, and columellar truncation less pronounced than in the larger form. Its dimensions are very constant in such localities as those wherein I have noticed its occurrence, and I have no evidence of its ever having been collected in company with the larger form. An example from Mt. Selinda measures: alt. 95, lat. 44; apert. alt. 46.4, lat. 23.3; last whorl 70 mm."

It seems to have been generally overlooked that the varietal name *minor* was first applied to this dwarf form by Deshayes in 1851, figs. 1-2 of Pl. 132 in the Atlas to Férussac's work being the type figures for both Deshayes' and Godet's names. One of Deshayes' figures is copied in my Pl. 76, fig. 2. Smith's (1899) variety from Zomba was "small and rather slender in comparison with the typical form figured by Férussac. The largest specimen is only 125 mm. in length, although consisting of  $8\frac{1}{2}$  whorls, the number possessed by a large typical

<sup>1</sup>The original label may have been destroyed by Cuming, since as early as February, 1849, Reeve treated *lamarckiana* as a synonym of *panthera*. Reeve then figured also an example from the Cuming Collection, but of the nominate race, 136 mm. long.



example from Mozambique, 157 mm. long. A very small specimen, which probably would not have grown larger, has a length of only 93 mm." Godet (1899) gave no measurements of his Rikatla shells.

Pilsbry (1904, p. 45) noted that similar dwarf specimens of *panthera* occur also in Madagascar. One of these he describes as follows: "smaller than the typical form, solid, rather narrow, of a dull livid or purplish shade with narrow, crowded, indistinct mottling. Columella and inner edge of lip rose. Outer lip thickened within. Length 115, diam. 55, aperture 59 mm. A similar shell has been figured by Deshayes in Férussac, Pl. 132, figs. 1-2." In this connection it may be noted that although Deshayes gave no locality, the shell which was figured on his Pl. 132 most probably came from Madagascar. In the rather limited material of *panthera* which I have seen, the dwarf form predominates among the shells from Madagascar and Mauritius, and is the only one present from Nyasaland.

*Specimens Examined.* MADAGASCAR: without precise locality (M.C.Z.).—MAURITIUS: without precise locality in many collections (M.C.Z.; A.M.N.H.; U.S.N.M.; Ac.N.S.Phila.; Berl.M.; etc.).—PORTUGUESE EAST AFRICA: Inhambane (M.C.Z.); Cape Delgado (M.C.Z.).—NYASALAND: Mtimbuka at the southern end of Lake Nyasa, 1949 (A. Loveridge.—M.C.Z.); Blantyre, 1948 (A. Loveridge.—M.C.Z.); 40 miles East of Blantyre, 1949 (A. Loveridge.—M.C.Z.); Mt. Chiradzulu, 3900 ft. (A. Loveridge.—M.C.Z.); Cholo Mountains, 20 miles South of Blantyre (A. Loveridge.—M.C.Z.); MacDonald's Camp, Vipya Plateau, 6000 ft., Mombera District (A. Loveridge.—M.C.Z.); Kasonga, Zomba Plateau, 5000 ft. (A. Loveridge.—M.C.Z.).

The smaller race of *A. panthera* occurs also in certain localities of Southern Rhodesia.

#### Measurements of Adult Shells

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
138 mm.	64	70	35		8½	Blantyre
118	63	64	34		7½	Mauritius
115.5	54	60	28		7½	No locality
114	56	60.5	31		7½	40 mi. E. Blantyre
111	59	60	34		7½	Madagascar
110	56	60	31.5		7½	"
104.5	54	58	28.5		7½	Mauritius
101	51	58.5	26.5		7½	Inhambane
100	53	60	29		7½	Mauritius
93	45	49	24		7½	"
92	52	54	28		7	"
89	45.5	48.5	23.5		7	"
82	42.5	43	23		7	Madagascar

The small specimen from Madagascar figured by Pilsbry (1904, Pl. 39, fig. 32), 120 mm. long, was evidently also of the dwarf race here called *lamarckiana*. The measurements listed above give for the subsp. *lamarckiana* an average length of 105 mm. and an average width of 53 mm.; while my measurements of nominate *panthera* give corresponding figures of 153 mm. and 80 mm. The relations between the two races of *panthera* appear therefore to be of much the same type as those existing between nominate *A. fulica* and its subsp. *hamillei*.

c. *A. PANTHERA ANTOURTOURENSIS* Crosse

Pl. 25, fig. 4; Pl. 79, fig. 1

*Achatina antourturensis* Crosse, 1879, Jl. de Conchyl., **27**, p. 340 (Madagascar: Antourtour in Nossi-Bé); 1881, *Op. cit.*, **29**, p. 197; Pl. 8, fig. 1 (type). Kobelt, 1881, Synopsis Moll. Viv. Test. 1879 Promulgat., p. 137. Grasset, 1884, Index Test. Viv. Coll., p. 199. Crosse and Fischer, 1889, in Grandidier, Hist. Phys. Nat. Pol. Madagascar, **25**, Moll., Atlas, pt. 1, Pl. 20, figs. 3 (2 views of type). Pilsbry, 1904, Man. of Conch., (2), **17**, p. 46; Pl. 35, fig. 16 (after Crosse and Fischer, 1889). Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 65.

*Achatina antourturensis* Paetel, 1889, Cat. Conch.-Samml., 4th Ed., **2**, p. 239.

*Achatina anturturensis* O. Boettger, 1890, Nachrichsbl. D. Mal. Ges., **22**, p. 82.

Original description of *A. antourturensis* Crosse (1879): "T. im<sup>r</sup> perforata, oblongo-conica, sat tenuis sed solidula, longitudinalite striato-plicata, transversim subdistanter et vix conspicue striatula' haud nitens, sub epidermide pallide lutea, decidua, fere omnino deficiente, unicolor, alba; spira sat elongata, apice planato, medio vix concaviusculo; sutura sat irregulariter impressa, sublaciniata, anfractus  $7\frac{1}{2}$ , convexiusculi, regulariter accrescentes, embryonales primi 2 laeves, nitiduli, ultimus subdescendens, spirae longitudinem paulo superans, infra medium subinflatus, basi rotundatus, leviter attenuatus; apertura angulato-ovata, piriformis, intus nitida, unicolor, alba; peristoma simplex, nitidum, album, marginibus callo crassiusculo, concolore junctis, columellari arcuato, dilatato, reflexiusculo, basi truncato, basali rotundato, subincrassato, externo vix crassiusculo. — Longit. 90, diam. maj. 41 mill." Crosse's later description (1881) is a literal translation of the Latin diagnosis. I saw the figured holotype in 1933 in the collection of the "Journal de Conchyliologie," when it was in the custody of the late Mr. P. Dautzenberg. It is now in the care of Dr. E. Fischer-Piette, who sent me the photograph shown in my Pl. 79, fig. 1. Although this form has not been found

again, so far as I know, it was originally taken in some number, as it was distributed to several collections, where I saw paratypes. All these shells are very similar. The original figure (1879) is copied in my Pl. 25, fig. 4.

*A. antourtourensis* appears to be a depauperate albino race of *A. panthera*, remarkable not only for the total lack of color in the material of the shell, the very pale dirty-yellowish periostracum, and the pure white columella, but also for the small size, slenderness and lightness. The outline (particularly the relative length of body-whorl and spire), the shape of the aperture, and the type of sculpture are those of *panthera*, not of *fulica*.

*Specimens Examined.* MADAGASCAR: Antourtour in Nossi-Bé, figured holotype and several paratypes (Par.M.; Brus.M.; Leid.M.; M.C.Z.; Ac.N.S.Phila.; A.M.N.H.).

*Measurements of Adult Shell*

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
86 mm.	42	46.5	23	7½		Antourtour, paratype

ACHATINA (LISSACHATINA) ZANZIBARICA Bourguignat

Pl. 1, fig. 2; Pl. 4, fig. 2; Pl. 16, fig. 1; Pl. 36, fig. 3; Pl. 37, figs. 3 and 5; Pl. 41, fig. 2; Pl. 47, fig. 2; Pl. 59, fig. 2; Pl. 73, fig. 4; Pl. 77, fig. 5; Pl. 78, fig. 1; Pl. 79, figs. 3-4

*Achatina zanzibarica* Bourguignat, 1879, Descr. Moll. Egypte Abyssinie Zanzibar, p. 5 (Nasimoya in Zanzibar). Kobelt, 1881, Synopsis Moll. Viv. Test. 1879 Promulgat., p. 138. Bourguignat, 1889, Moll. Afr. Equat., p. 75. Paetel, 1889, Cat. Conch.-Samml., 4th Ed., 2, p. 241. v. Martens, 1897, Deutsch-Ost-Afrika, 4, Beschalte Weichth., p. 86 (Tanganyika Territory: Bagamoyo; Buloa [=Bulwa] near Tanga; Usambara; Masai Steppe; Lake Jipe; Kitothai, S. W. of Sadi Makangele in S. E. section); 1897, Arch. f. Naturgesch., 63, pt. 1, p. 54; 1897, Mitt. Naturh. Mus. Hamburg, 14, p. 114 (1901, Zool. Ergebn. Küstengebiete Ost-Afrika Reise Stuhlmann, 2, pt. 15, p. 4). Pilsbry, 1904, Man. of Conch., (2), 17, p. 51. Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., 32, p. 66. Thiele, 1911, Wiss. Ergebn. D. Zentr.-Afr. Exped. (1907-1908), 3, p. 205. C. R. Boettger, 1913, Proc. Mal. Soc. London, 10, pt. 6, p. 351; Pl. 16, fig. 2 (cotype of *A. usambarensis* Rolle). Germain, 1916, Bull. Mus. Hist. Nat. Paris, 22, p. 255 (Tanganyika Territory: Kipatimu in Kilwa district; Kiwiro in Mahenge district); 1935, Mem. Est. Mus. Zool. Univ. Coimbra, Ser. I, No. 80, p. 40, footnote. Reh, 1925, in Sorauer, Handbuch der Pflanzenkrankheiten, 4th Ed., 4, p. 73 (damaging plants in Tanganyika Territory).

- Leptocala* (*Leptocallista* ?) *zanzibarensis* "Bourguignat" Coen, 1945, *Catalogo Gasteropodi Polmonati Coll. Coen*, p. 43 ("Kuriro" = Kwiwo, Tanganyika Territory). Misspelling of *zanzibarica*.
- Achatina lhotellerii* Bourguignat, 1879, *Descr. Moll. Egypte Abyssinie Zanzibar*, p. 7 (Nasimoya in Zanzibar). Kobelt, 1881, *Synopsis Moll. Viv. Test.* 1879 Promulgat., p. 137. Bourguignat, 1889, *Moll. Afr. Equat.*, p. 73. Ancey, 1902, *Jl. de Conchyl.*, **50**, p. 273, fig. 1 on p. 274 (specimen named by Bourguignat from Tanganyika Territory: Mswa in Ukuere).
- Achatina zanzibarica* var. *lhotellerii* v. Martens, 1897, *Deutsch-Ost-Afrika*, **4**, Beschalte Weichth., p. 86 (Tanganyika Territory: Usambara). Pilsbry, 1904, *Man. of Conch.*, (2), **17**, p. 53. Kobelt, 1910, *Abh. Senckenberg. Naturf. Ges.*, **32**, p. 66. C. R. Boettger, 1913, *Proc. Mal. Soc. London*, **10**, pt. 6, p. 351; Pl. 16, fig. 3.
- Achatina lhotelleriei* Paetel, 1889, *Cat. Conch.-Samml.*, 4th Ed., **2**, p. 240.
- Achatina zanzibarica ihotellerii* Loveridge, 1928, *Proc. Zool. Soc. London*, p. 126 (viviparity. Tanganyika Territory: Amani).
- Achatina usambarensis* Rolle, 1895, *Nachrichtsbl. D. Mal. Ges.*, **27**, p. 100 (Tanganyika Territory: Nguelo in Usambara). Cotype figured by C. R. Boettger, 1913.
- Achatina usambarica* v. Martens, 1897, *Deutsch-Ost-Afrika*, **4**, Beschalte Weichth., p. 86 (misspelling of *usambarensis* Rolle; as a synonym of *A. zanzibarica*).
- Achatina zanzibarica* var. *naegelei* C. R. Boettger, 1913, *Proc. Mal. Soc. London*, **10**, pt. 6, p. 351; Pl. 16, fig. 4 (Tanganyika Territory: Kwiwo near Mahenge).
- Achatina kilimae* var. *rollei* C. R. Boettger, 1913, *Proc. Mal. Soc. London*, **10**, pt. 6, p. 351; Pl. 16, fig. 1 (Tanganyika Territory: Bulwa [=Buloa near Tanga], in Usambara).
- Achatina madaziniana* Clench and Archer, 1930, *Occ. Papers Boston Soc. Nat. Hist.*, **5**, p. 299 (Tanganyika Territory: Madazini, holotype; Itende, paratype); Pl. 16, fig. B (holotype). (?) C. R. Boettger, 1947, *Arch. f. Molluskenk.*, **76**, p. 100; Pl. 2, fig. 7 (Tanganyika Territory: in Pleistocene deposits on the Garussi River, N.W. of Lake Njarasa [=Nyaraza or Eyasi]).
- Achatina* sp. Vosseler, 1906, *Berichte Land-Forstwirtschaft, Amani*, **2**, pt. 7, p. 406 (damaging sisal at Amani). Kränzlin, 1909, *Der Pflanzer, Tanga*, **5**, p. 182 (damaging crops in East Africa). Morstatt, 1911, *Op. cit.*, **7**, p. 72 (damaging crops in East Africa). The snails observed by these authors were referred to *A. zanzibarica* by Reh (1925).

Original description of *A. zanzibarica* Bourguignat (1879): "Testa oblongo-tumida, in medio ventrosa, utrinque attenuata, parum ponderosa, obscure passim subtranslucida, nitida, ad superiores rosacea, ad tres inferiores epidermide luteo (epidermis sat fugax, facile squamans), in ultimo saturatiore, induta, et strigis ad apicem fulvo-flammulatis, ad medianos atro-castaneis flammulato-fulguratis,

inter se confluentibus, in ultimo prope aperturam castaneo-olivaceo-flammulatis, eleganter ornata; in supremis laevigata, in medianis valide costata (costae praesertim in antepenultimo penultimoque sulcis longitudinalibus decussatae), in ultimo ample plicatula (plicae obtusae, passim evanidae ac hebetes) et circa suturam eleganter plicosa; spira regulariter acuminata, relative parum producta; apice rosaceo, obtuso, submamillato; anfractibus 8 convexis, regulariter crescentibus, sutura (inter ultimos subplicosa) separatis; ultimo oblongo, amplo, dimidiam altitudinis superante; apertura leviter obliqua, acuminato-oblonga, intus intense caerulescente, externe exacte convexa, inferne attenuata, non dilatata; columella subcaerulea, fere recta, leviter contorta, basi abrupte truncata; callo tenui, subdiaphano ac subcaeruleo. Alt. 117 mill., diam. 57 mill.; alt. apert. 65, diam. ap. 30." The following additional notes are translated from the French: "It resembles most *A. schweinfurthi*, from which it differs in the smaller size, the less elongate spire (the swollen part of *zanzibarica* is exactly at about half-length; in *schweinfurthi* it is more basal, instead of being median it is pronounced at about two-thirds of the height measured from the apex), the body-whorl being longer than half the total height (in *schweinfurthi* it is the opposite), the more oblong aperture, which is more acuminate above, the whitish not bluish inside, the less arched columella, etc." I saw the unfigured holotype at the Paris Museum in 1933 and, after comparing it with the type of *lhotellerii*, recognized it as a slightly more obese example of the same species. It is shown in Pl. 79, fig. 3, a photograph received from Dr. E. Fischer.

Original description of *A. lhotellerii* Bourguignat (1879), translated from the French: "Species of the same shape as *A. zanzibarica* and having about the same sum total of characters, but differing nevertheless in: 1. The smaller size in all parts (97 mm. high, 49 in diameter, with the aperture 56 by 24). 2. The less ventricose shape, so that it seems a little more elongate. 3. The less convex whorls. 4. The shorter, more acuminate spire. 5. The more elongate-ovate penultimate whorl and the less swollen body-whorl. 6. The relatively more elongate, less wide aperture, which is whitish inside, tinged in places with horny or light bluish. 7. The outer margin less convex, particularly in the lower portion, which makes the aperture look more narrowed at the base. 8. The more regular flammulae, which do not join on the penultimate whorl as those of *zanzibarica*. 9. The truncation at the base of the columella not so abrupt and not having as pronounced a siphon-like appearance." The unfigured holotype, seen at the Paris Museum in 1933, proved to be a somewhat more slender specimen of *zanzibarica*. Both variants in shape, as well as some others, are among

the fairly large series of this species collected by Mr. A. Loveridge in Usambara. Ancey's (1902) rather poor figure was drawn from an unusually large shell for the species; but an example from Amani, collected by J. Vosseler and received from the Berlin Museum as *A. zanzibarica*, is about the same size (114 mm.). A photograph of Bourguignat's holotype, recently received from Dr. E. Fischer, is reproduced in my Pl. 78, fig. 1.

Original description of *A. usambarensis* Rolle (1895): "T. ovata, solidula, ruditer costato-striata, costis aperturam versus majoribus, irregularibus, spiraliter irregulariter impresso-sulcata, strigis luteo castaneis fulminulatis in anfractibus superis angustioribus in inferis latis maculisque transversis interdum sagittiformibus ornata. Spira conica, apice obtusulo. Anfractus 8-9 convexiusculi, sutura impressa inter inferos crenulata discreti, ultimus subelongatus celerius descendens,  $\frac{3}{5}$  altitudinis occupans. Apertura ovata, supra acuminata, intus albido-coerulea strigis translucens; columella callo tenuissimo nitido in pariete aperturali vix conspicuo induta, basi exciso-truncata, basin testae haud attingens. Alt. 110, diam. 55, alt. apert. obl. 60 mm." The following remark is added in German: "In appearance like *A. fulica*, but quite distinct in color and sculpture." The present location of the unfigured type, corresponding to Rolle's measurements, is not known. The only figure in existence is that of a cotype (at Frankfurt-M.) by C. R. Boettger (1913), only 93 mm. long, 45 mm. wide, with the aperture 59 by 21.5 mm. This figure is copied in my Pl. 16, fig. 1. Both v. Martens (1897) and C. R. Boettger synonymized *usambarensis* with *zanzibarica*, I believe correctly. Boettger's specimen was much more slender than Rolle's holotype and the figure can be duplicated among the *A. zanzibarica* I have seen from Amani. On the other hand, two shells at U.S.N.M., bought from Rolle as *A. usambarensis* var., from the type locality (Nguelo) and therefore possibly paratypes, have more the proportions of the holotype, being respectively 90.5 and 91 mm. long, 50 and 49.5 mm. wide, of  $7\frac{1}{2}$  whorls, with the aperture 54 and 53 mm. by 25 and 26 mm.

Original description of *A. kilimae* var. *rollei* C. R. Boettger (1913): "Differt a typo colore et pictura. Testa flava, flammulis nigro-brunneis ornata; flammulae in medio anfractuum interdum zigzag-formes, confluentesque. Anfractus superiores subtiliter rosaceae. Testa indistincte granulata, subnitens, solida. Long. 88, diam. 43 mm.; apertura, alt. 47.5, lat. 25.5 mm. This new variety differs from the typical *Achatina kilimae* in colour and painting. The shell is straw-yellow, ornamented with blackish chestnut stripes, which in the median zone of the whorls sometimes become zigzag, flammulate, and confluent. The upper whorls are pale roseate, but never so intensely

coloured as in *A. zanzibarica* Bourg. and its allies. The granulation of the shell is not so distinct as in that species, and the shell has more lustre and is heavier. I have also a specimen before me which is rather more elongated." I have not seen the holotype, described from C. R. Boettger's own collection. The original figure, copied in my Pl. 59, fig. 2, agrees well with some of the *zanzibarica* collected by Mr. A. Loveridge and Dr. F. X. Williams in Usambara and Uluguru.

Original description of *A. zanzibarica* var. *naegelei* C. R. Boettger (1913): "Differt a typo figura minore et graciliore et anfractibus rapidius accrescentibus; testa flava, flammulis brunneis ornata. Long. 78, diam. 38 mm.; apertura, alt. 39, lat. 20 mm. This variety differs from the type in being smaller and more slender, even than var. *hotellerii* Bourg.; the whorls increase more rapidly than in the type. The shell is straw-yellow ornamented with chestnut stripes. The shape of the new form is quite different from that of the type of *A. zanzibarica* Bourg., and nobody, seeing only these two forms, would suppose that they belong to the same species. The variety *hotellerii* Bourg., however, is intermediate between them. We now see that *A. zanzibarica* is a species, the shape of which varies from tumid ovate to slender ovate. All forms clearly show that they belong to one species by their upper whorls being intensely roseate, by being not very heavy, and by other features mentioned in Bourguignat's diagnosis." The description was based on a single specimen in C. R. Boettger's collection. I have not seen this type. The original figure, copied in my Pl. 1, fig. 2, can be duplicated among the individual variants of some of the lots of *zanzibarica* at M.C.Z., particularly those collected by Mr. A. Loveridge near Tanga. This latter lot shows all transitions from slender specimens (Pl. 4, fig. 2) to such with obese body-whorl (Pl. 37, fig. 3). The collections of the M.C.Z. contain also 2 shells from Kwirow, one 61 mm. long, of  $6\frac{1}{3}$  whorls, the other 86 mm. long, of  $7\frac{1}{2}$  whorls, which I cannot separate from some *zanzibarica* of about the same age.

Original description of *A. madaziniana* Clench and Archer (1930): "Shell acutely ovate, imperforate, rather thin but strong. Nuclear whorl pinkish buff. All following whorls as far as body-whorl having pinkish buff ground color. Beginning at second whorl from nuclear whorl and continuing to edge of aperture surface covered with rather straight, longitudinal, liver brown flames set apart at irregular intervals from each other, but tending to fuse together on the last fifth of the body-whorl. Ground color of body-whorl cinnamon buff. Nuclear whorl smooth, slightly flattened. Beginning at the second whorl from the nuclear whorl and continuing to the aperture, surface covered with axial striae at first light, but on the body-whorl becoming rather definite growth lines. These striae and growth lines are intersected over

most of the surface by spiral lines set apart at rather irregular distances. These lines are obsolescent on the lower half of body-whorl. From fourth whorl from apex to edge of aperture there is a series of rough subsutural folds. Whorls 7. Aperture acutely ovate. Interior translucent, showing the color pattern of exterior. Outer and basal margins very sharp. Columella long, almost straight and sharply truncate. Parietal wall almost completely lacking a callus. Alt. 87, diam. 44.5, ap. length 49.5, ap. width 23 mm. (holotype). Alt. 76, diam. 40.5, ap. length 43, ap. width 22 mm. (paratype).” Both types at the M.C.Z. are immature. After comparing them with specimens of *A. zanzibarica* of approximately the same age, that is of about the same number of whorls ( $6\frac{1}{4}$  to  $6\frac{1}{2}$ ), I am unable to find reliable differences and I am forced to include *madaziniana* also among the synonyms of that variable species. The holotype is shown from a new photograph in my Pl. 77, fig. 5. The Pleistocene shells referred by C. R. Boettger (1947) to *madaziniana* do not seem to have been true *zanzibarica*. The figure appears to be of an immature *A. fulica hamillei*, full-grown specimens of which were recorded from the same locality as *A. acuta*.

*A. zanzibarica* is a medium-sized, rather thin and light species, 80 to 135 mm. long when full-grown. Adult shell usually elongate-ovate, widest at about the lower third, with a short, narrow, regularly conical spire, as a rule sharply set off from the inflated body-whorl. Of the  $6\frac{1}{2}$  to  $7\frac{1}{2}$  whorls, those of the spire fairly closely coiled, very gradually increasing in width and length, moderately convex, separated by deeply impressed but narrow sutures. Apex obtusely pointed. Body-whorl over two-thirds, sometimes even up to three-fourths of the total length of the shell in front view, markedly more convex than the penultimate whorl. Aperture long and comparatively narrow, half or more of the total length of the shell, semi-elliptical, with evenly curved outer margin. Inside bluish-white, showing the darker outside markings through the translucent shell. Outer lip thin, sharp, often with a dark border within. Parietal wall covered with a very thin, bluish-white glaze. Columella bluish-white, long and narrow, usually straight or nearly so, more rarely slightly concave, sometimes weakly twisted or folded in the upper portion, obliquely truncate some distance from the base of the aperture. The sculpture of the very young shell is described in detail below. In the adult it is often nearly completely worn off on the early whorls, as far down as the fourth. The latter is finely decussated by numerous transverse engraved lines crossing the fine closely-set vertical growth-striae at fairly even intervals. This sculpture is coarser and less regular on the fifth and sixth whorls, consisting of vertical series of elongate welts. It gradually



becomes less pronounced on the body-whorl, being as a rule very superficial over the last half or third behind the outer lip, and is even weaker at and below the periphery, although traces of the welts persist even near the columella. In addition to this coarser sculpture, the periostracum of well preserved shells shows a microscopic "weave" pattern of impressed criss-cross lines. The growth-striae are coarser, more fold-like in the upper part of the body-whorl, where they are set off, as a rule, by an irregular, deeply impressed line, producing a slightly crenulate or bead-like subsutural area. Normally, the ground color is straw-yellow or brownish-yellow, sometimes with whitish-yellow patches; the summit is either roseate or dirty-white, both conditions seemingly occurring in apparently fresh shells of the same colony. The fourth whorl shows the first traces of dark markings, as pale brown, straight, slightly bent or wavy vertical streaks. These become gradually darker and bolder, mahogany to chocolate-brown, on the succeeding whorls, from the latter half of the fifth on. On the penultimate and body-whorl the streaks are often very broad, but irregular, jagged at the edges, broken up into patches or confluent. Two shells in a lot of otherwise normal ones, from Magrotto (Pl. 41, fig. 2), are nearly unicolorous pale straw-yellow, with a few darker yellow vertical lines and a milky-white apex, and are evidently albinos. In the same lot transitional stages of partly marked shells connect them with normally marked individuals. The lot from Iloilo also contains a unicolorous straw-yellow example.

The species is variable in outline, even among adult shells, which accounts for the several named varieties. All of these are here regarded as individual variants, since they are found in one locality if a sufficiently large series is available, and are also linked by transitions. An unusually slender and 2 more normally shaped shells, all from Magrotto, are shown in Pl. 4, fig. 2, Pl. 37, fig. 3, and Pl. 41, fig. 2.

*A. zanzibarica* is noteworthy for being one of the few Achatininae that are truly ovoviviparous.<sup>1</sup> Mr. A. Loveridge found at Amani three adults, one dead, the other two alive, containing respectively 55, 72, and 27 young snails considerably beyond the nepionic stage. These are brownish-ivory (without the roseate hue of the apex of their mothers), at first unicolorous, but marked beyond the third whorl, above the periphery, with vertical, slightly bent, light chestnut-brown streaks. They consist of  $3\frac{1}{4}$  to  $3\frac{1}{2}$  whorls and are 8.5 to 11.2

<sup>1</sup> G. H. Clapp (1897, *The Nautilus*, **11**, p. 69) reported finding three embryonic shells, about 8 mm. in diameter, in a dead example of *Archachatina crawfordi* (Morelet). G. C. Robson found rather advanced young snails in an undetermined *Limicolaria*, from S. W. Uganda (1912, *Proc. Mal. Soc. London*, **10**, pt. 1, p. 32), but was uncertain as to whether this was a case of true viviparity.

mm. long, 6.5 to 8.5 mm. wide, with the aperture 5.7 to 7.5 by 3.6 to 5 mm. The first  $1\frac{1}{2}$  to 2 whorls, apparently formed in the egg, are smooth or with extremely fine vertical wrinkles. Spiral engraved lines, placed at irregular intervals, appear on the latter part of the second whorl, cutting across the growth-wrinkles. The decussation gradually grows stronger, being more distinct beyond the third whorl than on the corresponding area of full-grown snails. Another shell from Magrotto, 89 mm. long, was found estivating, the aperture closed with the customary brittle, calcareous, white epiphragm. It contained 9 young shells of the size and with the sculpture as described above. Unhatched eggs, taken from some live snails at Amani, are pale yellowish, ellipsoidal, 9.1 mm. long and 6.5 mm. wide.

*Measurements of Adult Shells*

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
120 mm.	59	68	32		$7\frac{3}{4}$	Iloilo
116	61	67	34		$7\frac{1}{2}$	Mt. Rungwe
114	52	60.5	30.5		$7\frac{1}{2}$	Amani
108	57.5	62	30		$7\frac{1}{4}$	Mt. Rungwe
105	51.5	57	27		$7\frac{1}{4}$	Amani
103	52.5	60.5	27		$7\frac{1}{4}$	Mt. Rungwe
101	51	53	27		$7\frac{1}{2}$	Amani
98	50	52	28		$7\frac{1}{2}$	"
96	46	49.5	25		7	"
94.5	47	49	25		$7\frac{1}{4}$	"
94.5	46	52	25		$7\frac{1}{2}$	Magrotto
92	45	51	23.5		7	Amani
89	43	49	23.5		7	Magrotto
88	43	48.5	21.5		$7\frac{1}{2}$	Amani
86	43.5	47	23		$7\frac{1}{2}$	Kwiro
86	37.5	45.5	18.5		$7\frac{1}{2}$	Magrotto
85.5	41	46.5	21		$7\frac{1}{4}$	Kizerui
82.5	39.5	47	21		7	Amani
81	43	41.5	23.5		$6\frac{3}{4}$	Lutundi

*Specimens Examined.* KENYA COLONY: Mt. Mbololo, 4400 ft. (É. Heller; A. Loveridge.—U.S.N.M.; M.C.Z.). — TANGANYIKA TERRITORY: Amani, Usambara Mts., 3000 ft. (J. Vosseler; A. Loveridge; F. X. Williams.—M.C.Z.; Berl.M.); Kizerui, Usambara Mts., 4000 ft. (A. Loveridge.—M.C.Z.); Lutindi, Usambara Mts., 4000 ft. (A. Loveridge.—M.C.Z.); Nguelo, Usambara Mts., 2 probable paratypes of *usambarensis* (U.S.N.M.); Magrotto near Tanga (A. Loveridge.—M.C.Z.); Siga Caves near Tanga (A. Loveridge.—M.C.Z.); Vituri,

Uluguru Mts., 2500 ft. (A. Loveridge.-M.C.Z.); Nyange, Uluguru Mts., 3000 ft. (A. Loveridge.-M.C.Z.); Bagilo, Uluguru Mts., 5000 ft. (A. Loveridge.-M.C.Z.); Kwiro near Mahenge, type locality of *naegelei* (G. Naegele.-M.C.Z.); Ilolo, at the foot of Mt. Rungwe, 4600 ft. (A. Loveridge.-M.C.Z.); Mt. Rungwe (R. Boulton.-Ac.N.S.Phila.; Carn.M.; M.C.Z.); Madazini near Kilosa, holotype of *madaziniana* (A. Loveridge.-M.C.Z. No. 53185); Itende near Kilosa, paratype of *madaziniana* (A. Loveridge.-M.C.Z. No. 53186); Mikindani (A. Loveridge.-M.C.Z.); Mbanja Airfield near Lindi (A. Loveridge.-M.C.Z.).

Both *A. zanzibarica* and *A. lhotellerii* were described from Nasimoya (or Mnazi Mmoja), a suburban section of the City of Zanzibar. This original habitat needs to be confirmed. All recent records are from the opposite mainland in Kenya Colony and Tanganyika Territory, where the species appears to be widely distributed.

Ancey's figured example (1902, as *lhotellerii*) was 118 mm. long, 56.5 mm. wide, with the aperture 57.5 by 32.5 mm. This and the largest shells of the foregoing table are close to Bourguignat's type, which was 117 mm. long. The largest specimen recorded is one mentioned by v. Martens (1897), 134 mm. long, 62 mm. wide, with the aperture 71 mm. long.

An abnormal shell, apparently adult and shown in my Pl. 79, fig. 4, found at Amani with normal examples, is remarkable for the nearly total lack of truncation at the base of the columella. It is 81.5 mm. long, 43 mm. wide, of  $6\frac{3}{4}$  whorls, with the aperture 45.5 by 24 mm.

#### ACHATINA (LISSACHATINA) ALLISA Reeve

##### Pl. 63, fig. 3

*Achatina allisa* Reeve, 1849 (February), Conch. Icon., **5**, *Achatina*, Pl. 5, fig. 15 (supposedly from "Cape Palmas, West Africa"). Pfeiffer, 1853, Monogr. Helic. Viv., **3**, p. 489. H. and A. Adams, 1855, Gen. Rec. Moll., **2**, p. 132. Pfeiffer, 1859, Monogr. Helic. Viv., **4**, p. 603. v. Martens, 1860, in Albers, Die Heliceen, 2d Ed., p. 202. Pfeiffer, 1868, Monogr. Helic. Viv., **6**, p. 218. Paetel, 1869, Moll. Syst. Cat., p. 80; 1873, Cat. Conch.-Samml., p. 99. Pfeiffer, 1876, Monogr. Helic. Viv., **8**, p. 276. Paetel, 1889, Cat. Conch.-Samml., 4th Ed., **2**, p. 239. Pilsbry, 1904, Man. of Conch., (2), **17**, p. 33; Pl. 35, fig. 17 (after Reeve). Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 65.

*Achatina (Achatinus) allisa* Pfeiffer, 1856, Malak. Blätt., **2**, (1855), p. 168; 1879, Nomencl. Helic. Viv., p. 266. Römer, 1891, Jahrb. Nassau. Ver. Naturk., **44**, p. 123.

Original description of *A. allisa* Reeve (1849): "Achat. testa elongato-oblonga, subcylindracea, anfractibus septem, oblique subtiliter granato-striatis, infra suturas tenue crenulatis, apertura parviuscula; columella arcuata, subcontorta, abrupte truncata; olivaceo-lutescente, maculis rufo-castaneis oblongis hic illic irregulariter inquinata. Shell elongately oblong, somewhat cylindrical, whorls seven in number, obliquely finely granosely striated, finely crenulated beneath the sutures, aperture rather small; columella arched, slightly twisted, abruptly truncated; olive-yellow, here and there irregularly bedaubed with reddish chesnut blotches. This species may be readily distinguished from any of those hitherto described, by its oblong cylindrical form and peculiar style of irregular blotching. The aperture is proportionably smaller and narrower than in the allied species." Reeve's figure, copied in my Pl. 63, fig. 3, is 77 mm. long, 33 mm. wide, with the aperture 36 by 18 mm. The type and only definitely known specimen, from the Cuming Collection, is now at the British Museum, where I saw it in 1933. Unfortunately I was not aware at the time of its possible relations to *A. iredalei* Preston, so that I failed to compare it with that species. The locality "Cape Palmas" is no doubt one of Cuming's many errors. No shell even remotely resembling *A. allisa* has been collected during the past century in West Africa. I am strongly inclined to regard it as an unusually slender example of the East African *A. iredalei*, although none of the many specimens which I have seen of that species matches Reeve's figure either in shape or in design. It seems scarcely possible that *allisa* might be *A. spekei* Dohrn, a species which I shall discuss more fully under *A. iredalei*. *A. capelloi* Furtado (= *A. morelli* Preston) is another species which may have to be considered in attempting to settle the identity of *A. allisa*.

ACHATINA (LISSACHATINA) DELORIOLI Bonnet

Pl. 4, fig. 4

*Achatina deLorioli* Bonnet, 1864, Rev. Mag. Zool., (2), 16, p. 279 (supposedly from "Brazil", an erroneous locality); Pl. 22, figs. 1-1a (*Achatina lorioli* on Plate).

*Cochlitoma delorioli* Pilsbry, 1904, Man. of Conch., (2), 17, p. 82; Pl. 28, fig. 41 (after Bonnet).

*Achatina lorioli* Pfeiffer, 1868, Monogr. Helic. Viv., 6, p. 218; 1876, *Op. cit.*, 8, p. 276. Paetel, 1889, Cat. Conch.-Samml., 4th Ed., 2, p. 240.

*Achatina (Achatinus) lorioli* Pfeiffer, 1879, Nomencl. Helic. Viv., p. 266.

Original description of *A. deLorioli* Bonnet (1864) (translated from the French): "Shell thin, transparent, obtuse, marked with slightly

oblique striae, rather strong on the body-whorl; finer at the summit of spire, where they are crossed by other spiral striae also very little visible; the last 2 or 3 whorls covered with a rather dark fulvous periostracum, lighter at the summit and toward the umbilical region; spire of 7 slightly rounded whorls with slightly wavy sutures; body-whorl semi-globulose, marked with large, lengthened, irregular dark brown spots, which do not reach the ends of the whorls; sometimes these spots are decidedly oblique and disappear toward the summit of the spire. Aperture oval, with very thin margins, violaceous-white inside, but yellowish by transparence, the outside spots being well visible; columella whitish. Height, 72; width, 32 mm." On the original figurè, copied in my Pl. 4, fig. 4, the aperture is 36 mm. long and 13 mm. wide. The present whereabouts of the type is unknown; but the locality "Brazil" was undoubtedly erroneous and the shell came most probably from East Africa. The species is here included because of its obvious relations to *A. iredalei* and possibly to *A. allisa*. Pfeiffer (1868) wrote from the figure that its shape was very similar to that of *A. vestita*, from Natal, but that it differed in the much less obtuse spire and the simple suture. Pfeiffer's remarks may have induced Pilsbry to place *delorioli* in *Cochlitoma* and to suggest that the draughtsman may have made the apex too narrow. However, the figure agrees well with some of the more slender examples of *A. iredalei* I have seen, while the pattern shown is often found in that species. Nevertheless, it would seem unwise to adopt the name *delorioli* for *A. iredalei*, until something definite can be known of the type and until the identity of *A. allisa* can also be settled.

#### ACHATINA (LISSACHATINA) IREDALEI Preston

Pl. 13, fig. 3; Pl. 14, fig. 3; Pl. 57, fig. 2; Pl. 60, fig. 2;  
Pl. 61, figs. 3-4; Pl. 64, fig. 2; Pl. 65, fig. 3; Pl. 77, fig. 2

*Achatina iredalei* Preston, 1910, Ann. Mag. Nat. Hist., (8), **6**, p. 533; Pl. 9, fig. 20 (Kenya Colony: Shimbi [=Shimba] Hills, [15 to 20 miles N. of Mombasa]). Germain, 1920, Voy. Afr. Orient. Angl. 1912-1913 G. Babault, p. 245 (in Expl. of Plates); Pl. 2, figs. 1-2 (2 colored views of paratype).

*Achatina allisa* Pfeiffer, 1865, Syst. Conch.-Cab., **1**, Abt. 13, pt. 1, p. 367; Pl. 44, figs. 7-8 (2 views of a shell from Zanzibar Id.). Gibbons, 1879, Jl. of Conch., **2**, p. 143 (Zanzibar Id.: a dead shell, doubtfully referred to this species from a cave on an islet between Bawri Id. and Chapani). (?) G. Nevill, 1879, Hand List Moll. Indian Mus., **1**, (1878), p. 145 (doubtful identification of a shell from "Africa"). Not of Reeve, 1849.

*Achatina allisa* var.  $\beta$  Pfeiffer, 1853, Monogr. Helic. Viv., **3**, p. 489 (with de-

scription of a shell from Zanzibar Id.; also a reference to Pl. 44, figs. 7-8 of Syst. Conch.-Cab., which was as yet unpublished). v. Martens, 1897, Deutsch-Ost-Afrika, 4, Beschalte Weichth., p. 92; 1897, Arch. f. Naturgesch., 63, pt. 1, p. 54.

*Achatina (Achatinus) allisa* var. Pfeiffer, 1879, Nomencl. Helic. Viv., p. 266.

Original description of *A. iredalei* Preston (1910): "Shell ovately fusiform, moderately solid, the earlier whorls pink, the latter covered with a brownish periostracum, and painted with broad, irregular, somewhat distant and occasionally much broken, transverse chestnut bands and flame-markings; whorls 7, regularly increasing, rather flattened, decussately sculptured, the sculpture becoming obsolete towards the base; sutures impressed, crenellate and narrowly margined below; columella bluish-white, a very thin callus joining it with the sutural region just inside the aperture, slightly excavated, descending nearly vertically; labrum simple, acute; aperture rather narrowly, elongately ovate, interior of shell bluish-white. Alt. 101, diam. 41 mm. Aperture: alt. 48, diam. 29 mm." The large specimen shown in Preston's original figure, copied in my Pl. 14, fig. 3, may be taken as the holotype. It is now at the British Museum, where I saw it in 1933. I have also seen paratypes, from the original lot, in several collections, one being at the M.C.Z. There is no difficulty about recognizing this species.

The bleached shell which Pfeiffer (1853) described and later figured as a variety of *allisa* and the shell which Gibbons (1879) referred doubtfully to that species, both came from the Island of Zanzibar. I consider that they were *A. iredalei*, which is common on that island. I also list here doubtfully the specimen which G. Nevill (1879) called *A. allisa*.

*A. iredalei* is one of the smaller species of the genus, averaging about 80 mm. in length when full-grown. Shell often fairly thick and heavy, very regularly elongate-ovate, sometimes almost spindle-shaped, widest at or slightly below mid-length, with a short, broad, regularly conical spire, the cone continuous with the upper part of the body-whorl. All of the  $6\frac{3}{4}$  to  $7\frac{1}{3}$  whorls moderately and about equally convex, the body-whorl not much more so than the whorls of the spire, except in unusually broad and short examples; all whorls separated by slightly impressed sutures. Apex obtusely pointed; upper 3 or 4 whorls somewhat more closely coiled; the others gradually increasing in width and length. Body-whorl about three-fourths of the total length of the shell in front view. Aperture long and comparatively narrow, about half of the total length of the shell or slightly more, semi-elliptical, with very evenly curved outer lip. Inside pure white

or slightly bluish. Outer lip normally thin, sharp, white along inner margin. Parietal wall with a mere trace of a bluish-white glaze. Columella pure white or faintly bluish, long and narrow, very weakly concave or nearly straight, obliquely truncate some distance from the base. First  $1\frac{1}{2}$  to 2 (nepionic) whorls, as studied on young shells hatched in the uterus (see below), entirely smooth; next early whorl at first with superficial vertical wrinkles only; beginning with the latter part of the third whorl, the wrinkles become closely-set growth-striae, and fine, spiral engraved lines appear. Decussation well-marked from the fifth whorl on, consisting then of vertically elongate granulation; as a rule best developed on the upper half of the body-whorl (7th), and consisting here of very long, unequal, vertical welts, placed in irregular vertical and spiral rows; the welts often bifid, either at the upper or at the lower ends. Growth-striae coarser below the sutures, producing a fine, irregularly crenulated sutural line; sub-sutural area often set off by a transverse depression or line. Below the periphery of the body-whorl, decussation much weaker in most shells, often almost wanting, although the growth-striae are well marked down to the base and the columella. In some examples the decussation of the body-whorl almost as strong below as above the periphery, although such shells do not otherwise differ from more normal ones in the same colony. Periostracum, when well preserved, showing in addition to the decussation at least traces of a "weave" type, criss-cross microsculpture, usually best seen on the lower half of the whorls. This microsculpture is present in the paratype at M.C.Z. Ground color deep straw-yellow to golden-yellow, with a very variable pattern of dark chestnut or mahogany-brown, vertical markings. In a few shells, streaks complete or nearly complete from suture to suture and, on the body-whorl, from suture to base, but of unequal width and more or less jagged at the edges. More often streaks incomplete or broken up into spots or blotches, usually stopping rather abruptly at the periphery. The number and size of the markings vary to such an extent that scarcely two shells are alike. Some examples have only traces of them and a few from Siga Caves and Kibarini are unicolorous brownish-yellow. Summit of the shell as a rule intensely roseate; sometimes dirty-white even in the same lot with pink-tipped shells (possibly faded in life).

A shell from Zanzibar Id., collected alive by Dr. F. X. Williams, is unusual in having the outer lip much thickened, evidently through old-age accretions to the inner margin; these deposits of lime have nearly obliterated the columellar truncation. The shell is fully adult, of  $6\frac{3}{4}$  whorls, but only 68 mm. long and 34.5 mm. wide (Pl. 77, fig. 2).

Like *A. zanzibarica*, *A. iredalei* appears to be ovoviviparous. At any

rate, an adult shell, found dead by Mr. A. Loveridge at Ngatana, contained several young shells, larger and of more whorls than at the nepionic stage. They are 9 to 9.5 mm. long, of about  $3\frac{1}{2}$  whorls. They showed conclusively that the nepionic shell of this species is perfectly smooth (Pl. 65, fig. 3).

*A. iredalei* is sometimes labelled in collections *A. allisa* Reeve. As noted before, *iredalei* may eventually be shown to be a synonym either of *A. allisa* or of *A. delorioli*, or perhaps of both; but this cannot at present be proved conclusively. I prefer therefore to use a name about the identity of which there can be no doubt, particularly in view of the fact that it is one of the few species now well-known anatomically. I have also seen *A. iredalei* under the name *A. albopicta*, a species which had not been properly recognized thus far. *A. iredalei* is closely related to *A. zanzibarica* Bourguignat. Although these two species are distinct enough when full-grown, they are often puzzling when immature, particularly as both sometimes occur in the same locality. The much narrowed and drawn-out summit of the spire of *zanzibarica* is then its most reliable distinguishing feature.

*A. iredalei* might perhaps be confused also with *A. spekei* Dohrn (1864, Proc. Zool. Soc. London, p. 117), described from East Africa, "near Lake Victoria"; but the type and immature paratype, at the British Museum, are labelled "East Africa, from the Central Plateau, 6° S. lat.", which places the type locality in Tanganyika Territory. The types are figured here for the first time in Pl. 81, figs. 2 and 3. I studied them at the British Museum in 1933 and concluded that they were conspecific with *A. thomsoni* E. A. Smith (1880, Ann. Mag. Nat. Hist., (5), 6, p. 428; 1881, Proc. Zool. Soc. London, p. 283; Pl. 33, fig. 12), the type of which I also compared, and which then becomes a synonym. Smith's original figure of *thomsoni* is copied in my Pl. 62, fig. 3; his type locality was also vaguely given as "between Lake Nyasa and the East Coast," which could be in Tanganyika Territory, Nyasaland or Portuguese East Africa. Specimens from the Chirinda Forest, Southern Rhodesia (M.C.Z.), which I refer to *A. spekei*, differ decidedly from *A. iredalei* in being regularly spindle-shaped, with the upper (subsutural) portion of the body-whorl rather flattened, as well as in the slightly different sculpture and the relatively shorter spire.

*Specimens Examined.* KENYA COLONY: Shimba Hills near Mombasa, holotype (Brit.M.) and paratypes (M.C.Z.; Brit.M.; Terv.M.; Frankf.M.; Leid.M.; U.S.N.M.); Gedi Ruins, 10 miles S. of Malindi (F. X. Williams.-U.S.N.M.; M.C.Z.); Witu (A. Loveridge.-M.C.Z.); Ngatana on Tana River (A. Loveridge.-M.C.Z.); Diani Beach, P. O. Ukunda, S. of Mombasa (F. X. Williams.-M.C.Z.; U.S.N.M.); Ma-



lindi (F. X. Williams.-M.C.Z.); Kibarini Experiment Station, near Kilifi (F. X. Williams.-U.S.N.M.; M.C.Z.).—TANGANYIKA TERRITORY: Siga Caves near Tanga (A. Loveridge.-M.C.Z.); Songo-Songo Id., in the Mafia Group (A. Voeltzkow.-Berl.M.; Frankf.M.; M.C.Z.); Ibondo Id., in the Mafia Group (O. Baumann.-Brit.M.; M.C.Z.).—ZANZIBAR ID.: Kizimbani (F. X. Williams.-M.C.Z.); Chwaka Bay (F. X. Williams.-U.S.N.M.; M.C.Z.).—PEMBA ID.: (A. Voeltzkow.-Berl.M.).

*Measurements of Adult Shells*

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
92 mm.	38.5	45	21	7½		Pemba
90	44	45.5	24	7		Ngatana
87	43.5	50	24.5	7		Diani Beach
86	43	46.5	22.5	7¼		Shimba, paratype
84	40	39.5	23	7½		Ngatana
83	40	42	22	7		Diani Beach
81.5	40.5	45.5	22.5	7		Witu
80.5	41	44	21	7		Shimba, paratype
77.5	35	37	19	7		Siga Caves
77	37	41.5	20	6½		Ngatana
76.5	38	42	21.5	7		Diani Beach
74.5	36.5	39	21	7		Zanzibar Id.
73	34	37	18	7		Siga Caves
72	36.5	38	19.5	7		Zanzibar Id.
71	31.5	37.5	15.5	6½		Songo Songo
70.5	33	34.5	17.5	6½		Diani Beach
69	35.5	34.5	19.5	7		Siga Caves
68	33.5	33	17.5	6¾		Zanzibar Id.
66.5	29	33.5	14.5	6½		Songo Songo
64	32	34	17	6¾		Diani Beach

The holotype is slightly larger (101 mm.) than any specimen I have measured. The paratype figured by Germain (1920) is about average, 80 mm. long, 37.5 mm. wide, with the aperture 44 by 20.5 mm.

ACHATINA (LISSACHATINA) ALBOPICTA E. A. Smith

Pl. 5, fig. 4; Pl. 12, fig. 3; Pl. 21, figs. 1 and 3; Pl. 24, fig. 4; Pl. 27, fig. 1; Pl. 40, fig. 2; Pl. 42, fig. 2; Pl. 43, fig. 2; Pl. 52, fig. 2; Pl. 58, fig. 2; Pl. 63, fig. 2; Pl. 65, fig. 1; Pl. 66, fig. 2; Pl. 67, fig. 3; Pl. 81, fig. 6

*Achatina albopicta* E. A. Smith, 1878, Quart. Jl. Conch., 1, pt. 15, p. 346 (no locality; "probably African"). Kobelt, 1879, Synopsis Moll. Viv. Test.

- 1878 Promulgat., p. 89. Paetel, 1889, Cat. Conch.-Samml., 4th Ed., **2**, p. 239. Ancey, 1902, Jl. de Conchyl., **50**, p. 278, fig. on p. 279 (no locality; fig. of a specimen, not the type).
- Cochlitoma albopicta* Pilsbry, 1904, Man. of Conch., (2), **17**, p. 88; Pl. 13, fig. 43 (after Ancey). Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 66.
- Achatina albopicta* var. *β subumicolor* Ancey, 1902, Jl. de Conchyl., **50**, p. 279 (no locality; with brief description).
- Achatina pilsbryi* d'Ailly, 1910, in Sjöstedt, Kilimandjaro Meru Exped., **1**, Abt. 6, p. 20; Pl. 1, figs. 27-30 (Tanganyika Territory: at the Mkulumusi Caves near Tanga, Usambara).

Original description of *A. albopicta* E. A. Smith (1878): "Shell rather solid and heavy, ovate, acuminate above or in the direction of the apex. The colors are about equally divided, and consequently the ground color may be termed either white or dark-brown; in the former case it would be streaked and blotched with brown and in the latter with white. The streaking and blotching are very irregular, but decidedly display a tendency for an oblique direction parallel with the lines of growth. Whorls  $7\frac{1}{2}$ , rather convex, and ornamented over the entire surface with narrow, elongate granules, which like the coloring also follow the direction of the incremental lines or striae. The last whorl is not very ventricose, but extends or is produced some distance below the truncated end of the columella. The aperture is about as long as half the entire length of the shell, of an irregular, elongate, oval form, acute superiorly, very white within, being covered with a thick shelly deposit of that hue. The columella is only slightly arched, also clothed with a white callosity extending upwards over the whorl as far as the extremity of the outer lip. Its truncation is rather abrupt and narrow. The nearest ally of this species appears to be *A. kraussi* Rve. It differs from it, however, in having a more elongate and acuminate spire, the more varied and irregular character of the blotching and the strongly marked granular sculpture." This description is preceded by a Latin diagnosis, which appears to be a condensed version of the English text, hence is not copied here. The dimensions are given as "Long. 84 mill.; diam. 37; apert. long. 43; diam. 22." Ancey (1902) gave a few additional notes on this species (translated from the French): "Recently (October, 1901) I had occasion to examine the type at the British Museum, and I have noticed that the specimen described must have lost the periostracum, so that the name which Smith gave scarcely fits fresh specimens, in which the ground color is not white, but a rather dull yellow. The shell, moreover, has little gloss. The species is well recognizable by the convexity of the whorls, notably near the suture. I figure a specimen of the typical form. I

have a second specimen, which may be a variety *β subunicolor*, with the shell almost entirely yellow with a few designs or macules, especially on the upper whorls." The specimen figured by Ancey, presumably natural size, is smaller than Smith's type, being 66 mm. long, 34 mm. wide, with the aperture 34 by 18.5 mm. It is evidently immature, consisting of about 6 whorls. I examined Smith's type at the British Museum in 1933. It is figured here for the first time (Pl. 81, fig. 6). It is somewhat worn, but shows nevertheless clearly the outstanding characteristic of the species, the sculpture consisting of coarse elongate granules or welts which cover the entire surface, as noted by Smith. They extend on the body-whorl of the adult below the periphery to the base of the shell, a peculiarity which this species shares only with *A. reticulata*. Neither Smith nor Ancey knew the locality of their specimens.

Original description of *A. pilsbryi* d'Ailly (1910): "Testa conico-ovata, solidula, sericeo-nitidula, summum versus saturate rosacea, apice mamillato, anfractus embryonales unicolores, sequentes duo fasciis rufescentibus, angustis, aequidistantibus, oblique ad sinistram abeuntibus vel flexuosis, superne rarissime bifurcatis ornati, ceteri sub periostraco pallido olivaceo, in ultimo saturatiore, albescentes, strigis flammulisque fusco-castaneis, in peripheria latoribus plerumque fulguratis interdum in maculas dissolutis picta; spira regulariter conico; anfr. 7 convexiusculi, regulariter accrescentes, ultimus basi attenuatus; sutura impressa, inter anfractus quatuor ultimos rugosoplicata lineaque fortiter impressa marginata; anfr. embryonales laevigati, sequentes leviter plicato-striatis, ultimi tres fortiter plicis incrementalibus ad suturam validioribus et lineis impressis spiralibus in ultimo sat distantibus et infra peripheriam infirmioribus, plicas incrementi in rectangula superne saepe bipartita in parte superiore anfractuum pervalida praesertimque ibi longitudinaliter inter se non regulariter continuata, transformantibus, praeterea superficies tota, summo excepto, oculo nudo haud conspicue regulariter densissimeque decussatim cancellata. Apertura parum obliqua, acuminato-oblonga, dimidium longitudinis testae paulum superans, intus lacteo-caerulea, flammulis externis translucens; peristoma simplex, acutum, intus fusco-castaneo-limbatum, marginibus callo eburneo extus distincte terminato picturam parietis pellucide exhibente junctis, margine externo regulariter curvato; columella stricta, sursum vix tortuosa, abrupte truncata, basin aperturae non attingens, callo porcellaneo, sursum in pariete aperturali dilatato, incrassata. Long. 74, diam. 39; apert. long.  $40\frac{1}{2}$ , lat.  $20\frac{1}{2}$  mm." I saw the holotype and two paratypes at the Stockholm Museum in 1933. As d'Ailly suspected, they are immature shells. The species has not been mentioned since it was

described. As listed above, it is a synonym of *A. albopicta*. The original figure of the type in front view is copied in my Pl. 63, fig. 2.

*A. albopicta* appears to have been generally overlooked or confused with other East African species, owing to the extraordinary variation in shape and the wide range of size. Immature examples may be mistaken for young or slender *A. zanzibarica* or *A. iredalei*, or possibly even *A. craveni* E. A. Smith. On the other hand, very large, full-grown specimens could readily be regarded as slender or dwarfed *A. reticulata*, to which species *A. albopicta* is no doubt most closely related. Fortunately Dr. F. X. Williams collected several hundred examples in one locality, ranging all the way from newly hatched to adult and even giant, old shells. Without the transitional stages, it might have been very difficult, if not impossible, to recognize all of these shells as belonging to one species. For this reason I have figured a selected series of stages of growth, from the nepionic shell to one of the largest adults seen. The latter (Pl. 27, fig. 1), 166 mm. long, had to be slightly reduced to fit in the format of this Bulletin. Moreover, Dr. Williams also sent us some live snails of both *A. albopicta* and *A. reticulata*. Their dissection disclosed to Dr. A. Mead significant anatomical differences, removing all doubts as to their specific distinctness.

When full-grown, *A. albopicta* averages about 130 mm. in length for  $8\frac{1}{2}$  whorls, but may exceptionally reach 176 mm. for as many as 10 whorls (the apical ones in this case almost always lost). Adult shell thick, opaque, solid, but moderately heavy, elongate-oval, with the greatest width at the lower third. Upper third, or spire, forming a regular, usually very slender cone, with strongly convex whorls (the later ones more so than those at the apex), separated by deeply impressed sutures. Early whorls when preserved forming a bluntly pointed apex, often broken off in large or old examples. Body-whorl sharply set off from the spire, about two-thirds of the total length of the shell, evenly but very strongly convex. Aperture relatively short and broad, much less than half and often only one-third of the total length of the shell, semi-elliptical, with strongly but evenly curved outer margin. Inside white. Outer lip simple, moderately thick, usually sharp at the edge. Parietal wall with a distinct white callus. Columella long, thick, white, moderately concave, strongly truncate close to the base. In older shells, first 3 to  $4\frac{1}{2}$  whorls smooth or worn smooth (original sculpture described below); succeeding whorls decussate. Closely-set, strong vertical growth-wrinkles are cut at fairly regular intervals by deep spiral engraved lines or grooves, visible to the naked eye from the sixth whorl on; this produces regular vertical and spiral rows of elongate welts, usually simple, rarely bifid; they are

much stronger and fold-like below the sutures. Sculpture strongest on the body-whorl, where it extends equally over the entire surface from suture to base. It is of the same type as that of *A. reticulata*, but slightly weaker and the welts lack the puckering visible in that species. In most adult shells periostracum almost completely worn off; if preserved, with the criss-cross or "weave" microsculpture of younger shells. Apical 3 whorls, when present, pale roseate; light brown vertical streaks appear on the latter half of the third whorl and continue darker over the fourth. Remainder of shell variegated white and mahogany-brown, the white areas being more yellowish when the periostracum is preserved. The dark pattern is extremely variable, sometimes of fairly complete, straight or wavy, narrow or broad, vertical streaks, more often jagged at the edges or broken up into transverse or anastomosing blotches, or even into small spots.

*A. albopicta* is oviparous. Dr. F. X. Williams found at Diani Beach a snail 130 mm. long, which had deposited 330 eggs in one set. Reproduction starts even before the snail is half-grown; one shell, 71 mm. long, of 7 whorls, found dead, contained some well-developed eggs. A few eggs were laid by the imported live specimens observed in captivity at Cambridge (M.C.Z.). The egg is regularly ellipsoid, 6.3 to 6.8 mm. long and 4.6 to 5.2 mm. wide, light saffron-yellow when freshly laid. The newly hatched, embryonic (or nepionic) shell (Pl. 21, fig. 3) is about 5.2 mm. long and 4 mm. wide, of  $2\frac{1}{2}$  whorls, which are completely smooth and colorless. Sculpture appears on the latter half of the first post-nepionic whorl (beginning of fourth whorl of the shell), at first as weak vertical wrinkles, most pronounced below the sutures and gradually increasing in strength. On the fifth whorl appear a few weak spiral engraved lines, which gradually increase in numbers and strength, the decussation being distinct from the sixth whorl on. In young shells the nepionic shell and first post-nepionic whorl are shiny, the succeeding whorls dull, owing to the criss-cross or weave-type ("cancellate") microsculpture of the periostracum. The apex, at first colorless, gradually turns horn-color and eventually roseate (on shells 50 to 60 mm. long and over).

Although fully adult *A. albopicta* average smaller than *A. reticulata* of the same age and the same number of whorls, some shells of both species are about the same size. *A. albopicta* is, however, more slender and lighter, usually with more convex whorls; the coarse sculpture, although of the same type, is finer and more regular, and lacks the peculiar puckering which covers the welts in *reticulata*.

*A. albopicta* seems to be particularly prone to produce scalariform or subscalariform abnormalities, which emphasize the convexity of the whorls (Pl. 24, fig. 4). The deformity usually starts abruptly on the

fourth, fifth or sixth whorl, probably due to some injury. The new growth begins suddenly some distance below the suture of the fore-going area and some distance inside the aperture, thus producing at the suture a deep niche with a wide triangular opening. In most cases the new abnormal whorls are merely more strongly convex, with very deep sutures; in one shell they are in addition strongly shouldered below the suture, which is deeply and narrowly grooved. Of seven such abnormal shells seen, the largest is 96 mm. long, of 7 whorls; the smallest, 61 mm., of 6 whorls.

*Specimens Examined.* KENYA COLONY: Diani Beach, P. O. Ukunda, south of Mombasa (F. X. Williams.-M.C.Z.; U.S.N.M.); Tiwi Beach, 4 miles N. of Diani Beach (F. X. Williams.-M.C.Z.; U.S.N.M.); Malindi (A. Loveridge.-M.C.Z.).—TANGANYIKA TERRITORY: Siga Caves near Tanga (A. Loveridge.-M.C.Z.).

*Measurements of Adult Shells*

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
176 mm.	81	77	43	10		Diani Beach
168	80	73	43	10		" "
166	70.5	76.5	37	9 $\frac{1}{3}$		" "
166	70.5	74	39	9 $\frac{1}{2}$		" "
155	66	70	39	9 $\frac{1}{3}$		" "
147	67	73.5	37	9		Tiwi Beach
145	70.5	68	38	8 $\frac{1}{2}$		Diani Beach
141	65	68	34	8 $\frac{1}{2}$		Malindi
141	62.5	67	34	9		Tiwi Beach
132.5	60	61	34	8 $\frac{1}{2}$		Diani Beach
129.5	56	59	32.5	8 $\frac{1}{3}$		" "
120	51.5	54	28	8 $\frac{1}{2}$		" "
118	55	60	31	8 $\frac{1}{3}$		" "
116	51	55	28	8		" "
113	50	52.5	29	7 $\frac{3}{4}$		Siga Caves
110	51	51	28.5	8		Diani Beach
104	47	50.5	26.5	8		" "
97	44	43.5	26	7 $\frac{3}{4}$		" "

ACHATINA (LISSACHATINA) RETICULATA Pfeiffer

Pl. 9, fig. 4; Pl. 16, fig. 2; Pl. 63, fig. 4;

Pl. 66, fig. 1; Pl. 67, fig. 1; Pl. 71, fig. 4

*Achatina reticulata* Pfeiffer, 1845 (October), Proc. Zool. Soc. London, (for 1845), p. 74 (Africa); 1848, Monogr. Helic. Viv., 2, p. 252. Reeve, 1849, Conch. Icon., 5, *Achatina*, Pl. 2, fig. 9 (type, from Cuming Collection).

Deshayes, 1851, in Férussac, *Hist. Nat. Moll. Terr. Fluv.*, **2**, pt. 2, p. 160, and *Expl. of Plates*, p. 19 (Africa); *Atlas*, Pl. 129 (2 views of one shell. Plate published without name by Deshayes after Férussac's death, presumably in 1851). Pfeiffer, 1853, *Monogr. Helic. Viv.*, **3**, p. 487. H. and A. Adams, 1855, *Gen. Rec. Moll.*, **2**, p. 132. Dunker, 1857, in Pfeiffer, *Novit. Conchol.*, **1**, p. 98 (first definite record from Id. of Zanzibar). Pfeiffer, 1859, *Monogr. Helic. Viv.*, **4**, p. 603; 1860, *Syst. Conch.-Cab.*, **1**, Abt. 13, pt. 1, p. 326; Pl. 27, fig. 1 (specimen from Zanzibar, not the type). v. Martens, 1860, in Albers, *Die Heliceen*, 2d Ed., p. 202. A. D. Brown, 1861, *Cat. Shells Coll.*, p. 56. Bielz, 1865, *Verzeichn. Moll. Conch.-Samml.*, 3d Ed., p. 23. Pfeiffer, 1868, *Monogr. Helic. Viv.*, **6**, p. 217. Haines, 1868, *Cat. Terr. Shells Coll.*, p. 68. Paetel, 1869, *Moll. Syst. Cat.*, p. 80; 1873, *Cat. Conch.-Samml.*, p. 99. Fridrici, 1874, *Bull. Soc. Hist. Nat. Metz*, **13**, p. 184. Pfeiffer, 1876, *Monogr. Helic. Viv.*, **8**, p. 275. Roeters van Lennep, 1876, *Cat. Coll. Shells van Lennep*, p. 53. G. R. Batalha, 1878, *Cat. Coll. Conchyl. F. R. Batalha*, p. 1. G. Nevill, 1879, *Hand List Moll. Indian Mus.*, **1**, (1878), p. 145. Gibbons, 1879, *Jl. of Conch.*, **2**, p. 143 (Tanganyika Territory: Lindi Bay). Kobelt, 1880, *Illustriertes Conchylienbuch*, **2**, p. 262. Grasset, 1884, *Index Test. Viv. Coll.*, p. 199. Ancey, 1885, *Bull. Soc. Mal. France*, **2**, p. 139 (Tanganyika Territory: Lindi River, dextral shells and one sinistral). Rethaan Macaré, 1888, *Cat. Coll. Coq. Mme. Rethaan Macaré*, p. 23. Martorell y Peña, 1888, *Catálogo Colección Conchol. Museo Martorell, Barcelona*, p. 56. Bourguignat, 1889, *Moll. Afr. Equat.*, p. 79. Paetel, 1889, *Cat. Conch.-Samml.*, 4th Ed., **2**, p. 240. v. Martens, 1897, *Deutsch-Ost-Afrika*, **4**, *Beschalte Weichth.*, p. 81 (Id. of Zanzibar: Jambiani); 1897, *Arch. f. Naturgesch.*, **63**, pt. 1, p. 54. Boucard, 1901, *Cat. Coll. Coq. Terr.*, p. 49. Pilsbry, 1904, *Man. of Conch.*, (2), **17**, p. 34; Pl. 35, fig. 15 (after Pfeiffer, 1860). Ancey, 1906, *Bull. Scient. France Belgique*, **40**, p. 190 (sinistral). Julia E. Rogers, 1908, *The Shell Book*, p. 275. Kobelt, 1910, *Abh. Senckenberg. Naturf. Ges.*, **32**, p. 66. Dautzenberg, 1914, *Bull. Soc. Zool. France*, **39**, p. 57 (sinistral). Coen, 1945, *Catalogo Gasteropodi Polmonati Coll. Coen*, p. 42.

*Achatina* (*Archachatina*) *reticulata* Albers, 1850, *Die Heliceen*, pp. 190 and 192 (first more definite locality as "Coast of East Africa").

*Achatina* (*Achatinus*) *reticulata* Pfeiffer, 1856, *Malak. Blätt.*, **2**, (1855), p. 168; 1879, *Nomencl. Helic. Viv.*, p. 265. Römer, 1891, *Jahrb. Nassau. Ver. Naturk.*, **44**, p. 123.

Original description of *Achatina reticulata* Pfeiffer (1845): "Achat. testa oblongo-acuta, solida, ponderosa, longitudinaliter confertim plicata, sulcis concentricis profunde reticulata, albida, castaneo-marmorata et maculata; spira elongata, acuta, superne minute granulata; sutura subcrenulata; anfractibus 8 parum convexis, ultimo 3/7 longitudinalinis subaequante; columella crassa, alba, arcuata, abrupte truncata; apertura utrinque attenuata, oblongo-ovali. Long. 160, diam. 70 mill." The type, from the Cuming Collection, figured by

Reeve (1849), should be at the British Museum, although I did not see it there in 1933. Fortunately the species is easily recognized, particularly from the original figure (copied in my Pl. 67, fig. 1), which is slightly smaller than Pfeiffer's measurements, being only 155 mm. long, 68 mm. wide, with the aperture 70 by 35 mm.; but the earliest whorls appear to be lost. The shell figured later (1860) by Pfeiffer was somewhat larger, being 167 mm. long, 73 mm. wide, with the aperture 80 by 41 mm. Both were exceeded by Deshayes' example (1851), which was 188 mm. long, 83 mm. wide, with the aperture 90 by 45 mm.

*A. reticulata*, the most handsome of the Achatinidae, is the second largest of the living land snails. It exceeds slightly *A. achatina* in total length, but is less bulky, the body-whorl being comparatively narrow. Adult shell of 8 to nearly 10 whorls, averaging about 160 mm. in length and 75 mm. in greatest width, very elongate oval, with the greatest width at the lower third, the upper two-thirds forming a regular, slender cone which includes both the spire and the upper portion of the body-whorl. Shell thick, opaque, solid, and rather heavy. Spire with moderately convex whorls and narrowly impressed sutures; early whorls forming a bluntly pointed apex when preserved, usually broken off in the adult. Body-whorl occupying about two-thirds of the total length of the shell, very evenly convex and only slightly more so than penultimate whorl. Aperture long and moderately wide, usually much less than half the total length of the shell, semi-elliptical, with very evenly curved outer margin. Inside white with a slight bluish tinge. Outer lip simple, thick or very thick. Parietal wall with a thick porcellaneous, white deposit. Columella long, thick, white, as a rule moderately concave, sometimes nearly straight, strongly truncate close to the base of the aperture. Nepionic  $2\frac{1}{3}$  whorls (Pl. 71, fig. 4) smooth; next appear fine vertical growth-wrinkles, cut by a few superficial spiral engraved lines; from the fourth whorl on, the decussation is well-marked and is coarse and visible to the naked eye from the sixth on. On the body-whorl it is extremely rough and covers the entire surface fairly uniformly from suture to base; it consists of vertical welts, unequal in length, either simple or bifurcate, in regular, closely-set spiral rows, separated by deeply cut spiral lines at irregular intervals; in addition the welts show a fine, moderately deep, but dense puckering or puncturation visible only with a handlens. On the early whorls this microsculpture is also present, but more like impressed "weave" of cloth and is usually worn off in part. Growth-folds coarser below the sutures and set off there by a deep impressed line on the body-whorl and part of the penultimate whorl. *A. reticulata* is the most coarsely sculptured of all the Achatinidae. Nepionic and first post-



nepionic whorls dirty-yellowish, sometimes with a slight roseate tinge; remainder of shell with white or yellowish-white ground color and bold mahogany-brown to reddish-brown vertical markings; on the first post-nepionic whorls they are broad, straight or wavy streaks; from the fifth whorl on they are more irregular, either narrow or broad streaks or very deeply jagged at the edges or resolved into many, irregularly scattered, transverse blotches or small spots. The periostracum is completely lost in adult shells; in younger examples it is pale yellowish to golden-yellow and very thin.

*A. reticulata* is oviparous. Some eggs were deposited by live snails shipped from Zanzibar and kept at the M.C.Z. in Cambridge during the summer of 1948. At first they were pale saffron-yellow, but this color faded rapidly to a dirty yellowish-white. They are broadly and regularly ellipsoid in shape, 8 to 9 mm. long and 6.5 to 7.5 mm. in diameter.

*Specimens Examined.* Several without precise locality (Leid.M.; U.S.N.M.; Terv.M.; Ac.N.S.Phila.; A.M.N.H.).—ZANZIBAR ID.: without more precise locality (M.C.Z.; Ac.N.S.Phila.; A.M.N.H.; Amst.M.; Brus.M.; Brit.M.); Jambiani (Berl.M.); Chwaka Bay (F. X. Williams.—M.C.Z.; U.S.N.M.), abundant in the coral-limestone area of the East Coast of the Island.—TANGANYIKA TERRITORY: Mbanja Airfield near Lindi (A. Loveridge.—M.C.Z.).

#### Measurements of Adult Shells

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
208 mm.	94	98.5	52	9 $\frac{2}{3}$		Mbanja
198	87.5	89	47.5	9 $\frac{1}{3}$		"
192	83	90	42	9 $\frac{1}{2}$		Chwaka Bay
188	80	81	41	9 $\frac{1}{2}$		"
183	83	92	43	9 $\frac{1}{2}$		Mbanja
180	75	82.5	42	9		"
176	80	81	40	8 $\frac{1}{3}$		Chwaka Bay
172	73	76.5	38	8 $\frac{1}{2}$		"
170	83	87	40	8 $\frac{1}{2}$		"
167	81	77	42	8 $\frac{1}{2}$		"
161	74	79.5	35	8 $\frac{1}{2}$		"
155	66	70	35	8 $\frac{1}{2}$		"
155	73	75	38	8 $\frac{1}{2}$		"
155	66.5	71	33.5	8		Jambiani
147	71	74	38	8 $\frac{1}{2}$		Chwaka Bay
143	60	67	31	8 $\frac{1}{2}$		"
138	64	68	33	8		"
131	60	61	30	8		"
128	60	61.5	32	8		"

An abnormal umbilicate example from Chwaka Bay is shown in my Pl. 63, fig. 4.

#### 5. Subgenus **EUAETHIOPINA**, new name

*Euaethiops* Clench and Archer, 1930, Occas. Papers Boston Soc. Nat. Hist., **5**, p. 295. Monotypic for *Euaethiops loveridgei* Clench and Archer, 1930. Not of Hampson, 1926.

Shell elongate-oval, with high spire. Aperture less than half the height of the shell, narrowed above in the full-grown shell, the upper part of the body-whorl being flattened, extended forward and descending behind the outer lip. Peristome fairly thick and slightly flaring below, very oblique in profile. Columella only weakly truncate at base. Summit narrowly but bluntly conical. Nepionic whorls not granulose, smooth or with very weak vertical wrinkles. The anatomy, originally described by Clench and Archer and recently revised by Dr. A. Mead, shows no essential departure from that of *Achatina*, proper.

Subgenotype: *Euaethiops loveridgei* Clench and Archer, 1930. No other species is known. *Euaethiops obtusa* Connolly, 1931, Ann. Mag. Nat. Hist., (10), **8**, p. 314 (Uganda: Mt. Elgon, in North Bugishu District, 7,000 to 9,000 ft.), Pl. 12, figs. 10 (type) and 11-12 (paratypes), is a species of *Archachatina* of my new subgenus *Tholachatina*.

The holotype of *Achatina (Euaethiopina) loveridgei* (Clench and Archer) is shown in my Pl. 3, fig. 2.

#### 6. Subgenus **LEPTOCALINA** Bequaert and Clench

*Leptocala* sect. *Leptocalina* Bequaert and Clench, 1934, Rev. Zool. Bot. Afric., **26**, pt. 1, p. 117 (for *Achatina specularis* Morelet and *A. wildemani* Dautzenberg). Type by present designation: *Achatina specularis* Morelet, 1866.

*Leptocalina* is an annectant group between the subgenera *Pintoa* and *Leptocallista*, agreeing in general shape with both of them. It has the smooth nepionic whorls of *Leptocallista*; but the remainder of the adult shell shows at least traces of sculpture and is rather dull or moderately shiny, not highly polished or glossy. It was originally defined as follows: "Shell with very fine, irregular growth-striae and more or less wrinkled or finely crenulate below the suture; no spiral engraved lines. Columella simple." The species here included are relatively small (40 mm. or less in length), with short aperture and the shape of *Limicolaria*. There are no microscopic engraved lines.

Bequaert and Clench at first included in *Leptocalina* only *A. specularis* and *A. wildemani*, the latter being now regarded as a mere color race of the former. I now propose to extend the group to several similar species from Angola and the Belgian Congo, as listed below. In all specimens I have seen of these species the nepionic whorls were smooth; but, as newly hatched snails were not available, the early whorls may have lost the sculpture. Some of the species may therefore have to be transferred later to *Pintoa*. Moreover it should be noted that the early whorls are sometimes irregularly pitted through corrosion of the periostracum; this should not be mistaken for a true granulation caused by decussation, such as is present in *Pintoa*.

1. *A. brooksi* Bequaert and Clench, 1934.
2. *A. colubrina* Morelet, 1866.
3. *A. dewittei* Bequaert and Clench, 1934.
4. *A. specularis* Morelet, 1866; with subsp. *wildemani* Dautzenberg, 1908.
5. *A. sylvatica* Putzeys, 1898 (Synonym: *Achatina putzeysi* Dautzenberg and Germain, 1914); with "mut." *unicolor* Pilsbry, 1919.
6. *A. thermalis* Bequaert and Clench, 1936.
7. *A. zebriolata* Morelet, 1866.

### 7. Subgenus LEPTOCALLISTA Pilsbry

*Achatina* subg. *Leptocala* sect. *Leptocallista* Pilsbry, 1904, Man. of Conch., (2), 17, pp. 73 and 75 (for *Achatina raffrayi* Jousseume and *Stenogyra grandidieriana* Bourguignat).<sup>1</sup> Type by designation of Bequaert and Clench, 1934, Rev. Zool. Bot. Afric., 24, pt. 3, p. 273; *Stenogyra grandidieriana* Bourguignat, 1889.

*Leptocallista* agrees with *Leptocala* in having the post-nepionic as well as the nepionic whorls devoid of all trace of decussate sculpture, the entire shell being extremely smooth and glossy. It differs, however, in the absence of microscopic spiral engraved lines. In addition the base of the columella is somewhat flaring at the truncation. The few known species are restricted to East Africa.

1. *A. ariel* Preston, 1910.
2. *A. grandidieriana* (Bourguignat, 1889) (Synonym: *Achatina nitida* v. Martens, 1894).
3. *A. arthuri*, new name, for *Leptocala loveridgei* Bequaert and Clench, 1934; not *Achatina (Euaethiopina) loveridgei* (Clench and Archer, 1930).
4. *A. raffrayi* Jousseume, 1883. The generic allocation of this species is somewhat open to question.

<sup>1</sup> Kobelt (1910) credits the name *Leptocallista* by error to Bourguignat.

8. Subgenus **LEPTOCALA** Ancey

- Petitia* Jousseume, 1884, Bull. Soc. Zool. France, **9**, p. 171 (for *Petitia petitia* Jousseume and *Achatina raffrayi* Jousseume). Type by present designation: *Petitia petitia* Jousseume, 1884 = *Achatina mollicella* subsp. *petitia*. Not of Chitty, 1857.
- Leptocala* Ancey, 1888, Bull. Soc. Mal. France, **5**, p. 70, footnote (new name for *Petitia* Jousseume, 1884; to include *Achatina mollicella* Morelet and *A. pulchella* v. Martens). Type by designation of Ancey, 1898, The Nautilus, **12**, p. 92: *Achatina mollicella* Morelet, 1860.
- Achatina* subg. *Leptocola* Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 66. Misspelling of *Leptocala* Ancey, with same type. Not *Leptocola* Gerstaecker, 1883.

Jousseume's definition of *Leptocala* (under the name *Petitia*) is as follows (translated from the French): "This new genus may be characterized by saying that the shell is shaped like *Limicolaria*, but has the columellar truncation of *Urceus* (*Achatina* Lam.). The two species I have of the genus have a very thin shell and show over the surface longitudinal flammules darker than the ground color; the surface is glossy and shiny; the spire consists of 7 whorls; the embryonic nucleus is very voluminous." While the nepionic whorls are completely smooth and the post-nepionic whorls are also devoid of decussate or coarser sculpture, the surface is, however, densely covered with excessively fine, microscopic, slightly wavy, spiral engraved lines. The columella is simple at the basal truncation. The summit is bluntly conical and not in the least dome-shaped. The egg is no larger than usual in *Achatina* (5 by 4 mm. in *A. mollicella* subsp. *petitia*, according to d'Ailly). The only known species, restricted to Cameroon and Gaboon, is small (40 mm. or less in length), with relatively short aperture, thin, elongate oval.

1. *A. mollicella* Morelet, 1860; with subsp. *petitia* (Jousseume, 1884) (Synonyms: *Achatina pulchella* v. Martens, 1876, not of Spix and Wagner, 1827, nor of Pfeiffer, 1857; *Achatina smithii* G. B. Sowerby, 1890, not of Craven, 1881; *Achatina sowerbyi* E. A. Smith, 1890); and subsp. *zenkeri* (Bequaert and Clench, 1934). Pl. 58, fig. 5.

Genus **ARCHACHATINA** Albers

The Achatininae here gathered in *Archachatina* share only one feature differentiating them in every case from the species retained in *Achatina*. This is the wide, bulbous or dome-shaped summit of the shell, consisting of the nepionic (or embryonic) whorls produced by the snail before the egg hatches. This peculiarity is believed to be of

generic value, since it is correlated with the production by the snail of unusually large eggs, as compared with those of species of *Achatina* of approximately the same size. Possibly the anatomy may eventually disclose some additional feature of generic value; but, as this has been studied thus far for only four species, it would seem premature to draw general conclusions in this connection.

*Archachatina* has been used thus far almost universally for species restricted to West Africa, where they occur from Sierra Leone to the Belgian Congo. I propose to extend its limits here to include also several species of East and South Africa, where they are found from Abyssinia to the Cape Province. It should be noted, however, that as known at present the East and West African areas are not contiguous. The genus is not represented throughout a wide intervening area, which stretches from North to South across the Sudan, Uganda, the Belgian Congo, and the interior of South Central Africa.

All species included in the genus, on the basis of the dome-shaped apex and large egg, have the nepionic whorls decussately granulose. A further division of the genus must therefore be based on other characters of the shell. In an earlier paper Bequaert and Clench (1936, *Rev. Zool. Bot. Afric.*, 29, pt. 1, pp. 73-96) arranged the West African forms in three subgenera.<sup>1</sup> I now propose to add a fourth subgenus for the East and South African species.

### 1. Subgenus ARCHACHATINA, proper

*Achatina* section *Archachatina* Albers, 1850, *Die Heliceen*, p. 189 (for several species). Type by designation of Pilsbry, 1904, *Man. of Conch.*, (2), 17, p. 104: *Bulimus bicarinatus* Bruguière, 1792 = *Achatina sinistrorsa* Pfeiffer, 1848, one of the species originally included. As pointed out to me by Dr. H. A. Rehder (*in litt.*), Herrmannsen (1852) does not appear to have designated the type validly, as Bequaert and Clench (1936) believed.

Shell broadly oval, normally sinistral, large (110 to 150 mm. in length when full-grown, for  $6\frac{1}{2}$  to 7 whorls), roughened by fairly strong axial striae and a few more prominent folds or welts, sometimes weakly and bluntly carinate at the periphery and below the suture. Outer lip unexpanded, thin, sharp. Columella strongly sinuous, very obliquely truncate. Nepionic shell bulbous, bluntly pointed, with fine and rather regular granulation, often worn in older shells. On the post-nepionic whorls the axial or vertical striae are cut at irregular intervals

<sup>1</sup> The authors had overlooked an earlier name introduced by Pilsbry (1919) for one of the new subgenera. Owing to the failure to see proof, their paper also contained some disturbing misspellings. These errors were corrected in 1938 (*The Nautilus*, 52, p. 26).

by fine spiral engraved lines, which become fainter or disappear on the body-whorl. The only known species, restricted to Prince's Island, San Thome, and the neighboring Islet of Rolas, all in the Gulf of Guinea, is *Archachatina* (*Archachatina*) *bicarinata* (Bruguière), of which *Achatina sinistrorsa* Pfeiffer, 1848, and *Achatina sinistrorsa* var. *carnea* Pfeiffer, 1867, are synonyms.

## 2. Subgenus CALACHATINA Pilsbry

*Archachatina* subg. *Calachatina* Pilsbry, 1919, *The Nautilus*, **32**, p. 99, footnote

3. Type by original designation: *Achatina marginata* Swainson, 1821.

*Archachatina* subg. *Megachatina* Bequaert and Clench, 1936, *Rev. Zool. Bot. Afric.*, **29**, pt. 1, p. 76. Type by original designation: *Achatina marginata* Swainson, 1821.

*Archachatina* subg. *Magachatina* Bequaert and Clench, 1936, *Rev. Zool. Bot. Afric.*, **29**, pt. 1, p. 78 (misspelling of *Megachatina*, with same type).

Pilsbry originally proposed *Calachatina* for "the dextral continental species, which have the surface smoothish and even", intending to include all species of *Archachatina* of the Manual of Conchology, with the exception of *A. bicarinata* (Bruguière). The subgenus is more restricted here, comprising only the species with the following characters. Full-grown shell medium-sized to large (80 to 180 mm. long), broadly oval or elongate oval, of  $5\frac{1}{2}$  to 7 whorls, normally dextral, thick and often heavy. Surface fairly even; nepionic whorls of newly hatched shells finely granulose; later whorls either decussately sculptured or nearly smooth, sometimes with peculiar microsculpture. Outer lip of old shells more or less thickened, the edge flaring or expanded outwardly. Columella wide, more or less sinuous, strongly and obliquely truncate.

1. *A. degneri* Bequaert and Clench, 1936. See below.

2. *A. gaboonensis* Pilsbry, 1933. Although smaller and thinner than the other members of the subgenus, this species nevertheless forms when fully adult a thickened and slightly expanded outer lip. It seems related to *A. marginata*, although obviously transitional to subgenus *Megachatinaopsis*.

3. *A. marginata* (Swainson, 1821). See below.

4. *A. rhodostoma* (Philippi, 1849). See below.

5. *A. ventricosa* (Gould, 1850). See below.

### ARCHACHATINA (CALACHATINA) MARGINATA (Swainson)

Two main features distinguish the several variations of *A. marginata* from the related members of the genus. The first is the subsutural,

usually strongly marked engraved line, separated from the suture by a narrow depressed area covered with irregular, low, vertical folds, the suture itself being straight or very slightly wavy, not crenulate. The engraved line starts on the fourth or fifth whorl and is often deep and prominent, particularly on the body-whorl; but occasionally it is weak or almost lacking, especially in subsp. *eduardi* Pilsbry. The second feature is a peculiar microsculpture of the body-whorl, only visible with the proper magnification. It consists of numerous extremely fine, close-set, criss-cross or anastomosing lines, making the surface of the periostracum look as if it had been pressed with a very finely woven cloth. This "weave" type of microsculpture is more pronounced in some forms or races than in others. It is particularly conspicuous when the periostracum is well developed and preserved, as is more common in some of the Cameroon races, such as subsp. *egregia*. In old shells, even when taken alive, the microsculpture is sometimes almost completely worn off, but traces of it may generally be detected in a few spots. The nepionic whorls, when well preserved, as in newly hatched or very young shells, are densely covered with regular spiral and vertical rows of minute granulations, which become coarser on the first post-nepionic whorls (Pl. 76, fig. 4). The granulation, due to the decussation of close-set vertical growth-striae by evenly spaced spiral engraved lines, gradually disappears on the penultimate whorl and is almost wanting on the body-whorl, except sometimes below the suture. The growth-striae are, moreover, very weak on the body-whorl, which appears nearly smooth to the naked eye.

*Synopsis of Subspecies.* While most other species of *Archachatina* have a limited distribution, *A. marginata* covers a very wide territory, extending at least from Dahomey to the Lower and Middle Belgian Congo, and possibly in French Equatorial Africa to the Gribingui River (about 7° N., 19° W.). As a result it has produced several intraspecific variations, sometimes well segregated geographically, but more often overlapping, yet well worthy of varietal or subspecific names. These races are defined primarily by color peculiarities, in some cases also by the average size or the general shape. All of them have retained the characteristic microsculpture. As they frequently occur in the same territory with specimens of the typical race, although perhaps in a different type of environment, it is not surprising that connecting examples occur in some localities.

A. Shell fairly uniformly marked with numerous chestnut-brown or pale brown vertical streaks, stripes, zigzag lines, or blotches on a straw-yellow background.

a. Large and broad, up to 176 mm. long. Columella, outer lip and parietal wall white or bluish-white. Apex pale colored or roseate. Typical *marginata*.

b. Large and broad, shaped like the typical form, up to 170 mm. long. Outer lip white or bluish-white. Columella and parietal wall more or less extensively apricot-yellow. Apex yellowish. Subsp. *ovum*.

c. Medium-sized to fairly large, but usually more slender and with narrower body-whorl than the typical form, up to 135 mm. long. Outer lip white or bluish-white. Columella and parietal wall more or less extensively vinaceous-red. Apex usually, but not always reddish. Subsp. *suturalis*.

d. Small and unusually slender for the species, up to 110 mm. long, with relatively long and narrow aperture. Columella, parietal wall and outer lip white or bluish-white. Apex usually pale colored. Subsp. *eduardi*.

B. Lower half of body-whorl, or of earlier whorls in immature shells, mostly very dark chestnut-brown, except for a narrow, well-defined straw-yellow zone at the base around the columella; remainder of shell (above the periphery) marked as in the typical form. Medium-sized and moderately broad, up to 110 mm. long.

e. Columella, parietal wall and broad inner margin of outer lip vinaceous-red. Apex vinaceous-red. Subsp. *egregiella*.

f. Columella and parietal wall vinaceous-red. Inner margin of outer lip bluish-white or darkened. Apex yellowish or slightly roseate. Subsp. *egregia*.

g. Columella, parietal wall and inner margin of outer lip bluish-white. Apex pale colored or slightly roseate. Subsp. *clenchi*.

C. Shell mostly or uniformly straw-yellow or olive-yellow, without or with mere traces of darker markings.

h. Large and broad, shaped like the typical form, up to 136 mm. long. Columella, parietal wall and outer lip white or bluish-white. Apex pale colored. Subsp. *icterica*.

i. Large and broad, shaped like the typical form, up to 105 mm. long. Outer lip white or bluish-white. Apex, columella and parietal wall partly or mostly rose or vinaceous-red. Subsp. *grevillei*.

j. Small and relatively narrow, about 80 mm. long. Columella, parietal wall and outer lip white or bluish-white. Apex pale colored. Subsp. *candefacta*.

#### a. Typical A. MARGINATA

Pl. 9, fig. 3; Pl. 59, fig. 1; Pl. 64, fig. 1; Pl. 67, fig. 2; Pl. 68, fig. 1; Pl. 71, fig. 3; Pl. 75, fig. 2; Pl. 76, figs. 3-4; Pl. 80, fig. 4

[*Buccinum parvum integrum*, etc., Gualtieri, 1742, Index Test. Conch., Pl. 45, lower fig. B only; with letterpress].<sup>1</sup>

<sup>1</sup> Bequaert and Clench (1936, p. 79) included in the synonymy of *A. marginata* also Gualtieri's upper fig. B, as well as Pl. 71, figs. 1-3 and 7-9 of Seba (1758). A more careful study of these figures has now led me to refer them to *Achatina achatina* (Linné).



[The Heirs of G. W. Knorr, 1768, Vergnügen der Augen und des Gemüths, **3**, second printing of the Plates of the 1st Edition, Pl. 3\*\*, fig. 1 (Plate marked "ex Museo Schadeloockiano"; not the accompanying text which describes *Archachatina knorrii*, shown on the first printing of the same Plate 3\*\*); 1768, Délices des Yeux et de l'Esprit, **3**, second printing of Pl. 3\*\*, fig. 1 (as above); 1772, Verlostiging der Oogen en van den Geest, (Amsterdam), **3**, p. 86 (new text, not a translation from the original German or French); Pl. 3\*\*, fig. 1 (same Plate as above)].<sup>1</sup>

[? J. S. Schröter, 1782, Mus. Gottwaldiani Test., Pl. 35, fig. 220 (very poor figure)].

*Achatina marginata* Swainson, 1821, Zoolog. Illustr., Conchology, **1**, Pl. 30 ("Coast of Guinea"). Gray, 1825, Ann. of Philosophy, (N.S.), **9**, p. 414. Jay, 1839, Cat. Shells Coll., 3d Ed., p. 58. Swainson, 1840, Treatise on Malacology, p. 170, fig. 23. Pfeiffer, 1841, Symbolae Hist. Helic., **1**, p. 28. Catlow and Reeve, 1845, Conchologist's Nomenclator, p. 165. Gray, 1847, Proc. Zool. Soc. London, (for 1847), p. 177. Pfeiffer, 1848, Monogr. Helic. Viv., **2**, p. 249 (in part). Mörch, 1852, Cat. Conch. Yoldi, **1**, p. 20. Pfeiffer, 1853, Monogr. Helic. Viv., **3**, p. 482. H. and A. Adams, 1855, Gen. Rec. Moll., **2**, p. 132. Shuttleworth, 1856, Notitiae Malacologicae, **1**, p. 33 (young shell). Morelet, 1858, Séries Conchyl., **1**, p. 19 (Gaboon). Pfeiffer, 1859, Monogr. Helic. Viv., **4**, p. 600; 1860, Syst. Conch.-Cab., **1**, Abt. 13, pt. 1, p. 328; Pl. 29, fig. 1 (specimen). A. D. Brown, 1861, Cat. Shells Coll., p. 55. Mörch, 1863, Cat. Conchyl. Lassen, p. 4. Marrat, 1865, Cat. Coll. Dennison, p. 30. Bielz, 1865, Verzeichn. Moll. Conch.-Samml., 3d Ed., p. 23. Morelet, 1867, Voy. Welwitsch, Moll. Terr. Fluv., (1868), p. 65 (Southern Nigeria: Banks of the Niger). v. Martens, 1868, Malak. Blätt., **15**, p. 137. Haines, 1868, Cat. Terr. Shells Coll., p. 68. Pfeiffer, 1868, Monogr. Helic. Viv., **6**, p. 212. Paetel, 1869, Moll. Syst. Cat., p. 80; 1873, Cat. Conch.-Samml., p. 99. Dohrn, 1873, Malak. Blätt., **21**, p. 80. Roeters van Lennep, 1876, Cat. Coll. Shells van Lennep, p. 53. Pfeiffer, 1877, Monogr. Helic. Viv., **8**, p. 272. G. R. Batalha, 1878, Cat. Coll. Conchyl. F. R. Batalha, p. 2. G. Nevill, 1879, Hand List Moll. Indian Mus., **1**, (1878), p. 145. v. Martens, 1882, Jahrb. D. Mal. Ges., **9**, p. 245 (French Congo: mouth of the Quillu [=Kwilu] River on the Loango Coast). Grasset, 1884, Index Test. Viv. Coll., p. 199. Reyes y Prosper, 1886, An. Soc. Españ. Hist. Nat., **15**, p. 340 (Spanish Guinea: Ellobey Id.). Martorell y Peña, 1888, Catálogo Colección Conchol. Museo Martorell, Barcelona, p. 56. v. Martens, 1888, Sitzungsber. Ges. Naturf. Fr. Berlin, p. 148 (Cameroon: Barombi. Egg). Vignon, 1888, Bull. Soc. Mal. France, **5**, p. 68 (Gaboon). Paetel, 1889, Cat. Conch.-Samml., 4th Ed., **2**, p. 240. v. Martens, 1891, Sitzungsber. Ges. Naturf. Fr. Berlin, pp. 30 and 33. d'Ailly, 1896, Bih. Svenska Vet.-Ak. Handl., **22**, Afd. 4, No. 2, pp. 61 and 69, fig. (Cameroon: Massaka in Batanga District; Mekango; Etome; Ndian; part of these

<sup>1</sup> See my remarks on Knorr's work in the discussion following the bibliography.

- specimens only.<sup>1</sup> Radula; oviposition). Boucard, 1901, Cat. Coll. Coquilles Terr., p. 49. O. Boettger, 1905, *Nachrichtsbl. D. Mal. Ges.*, **37**, p. 165 (Cameroon: Rombone; Kurume on Bali Road; Kan on Bali Road; Mukonje Farm; Kokobuma. Egg; epiphragm). Germain, 1905, *Bull. Mus. Hist. Nat. Paris*, **11**, p. 250 (French Equatorial Africa: banks of the Gribingui River); 1907, *Arch. Zool. Gén. Expér.*, (4), **6**, pt. 4, p. 128. E. Smith, 1908, *Proc. Mal. Soc. London*, **8**, pt. 1, p. 2 (living specimen from Southern Nigeria: Ibadan, 100 miles inland). Germain, 1908, in A. Chevalier, *L'Afrique Centrale Française*, p. 487. Hidalgo, 1910, *Mem. Soc. Españ. Hist. Nat.*, **1**, No. 29, p. 508 (Spanish Guinea). Talbot, 1912, *In the Shadow of the Bush*, p. 473 (Southern Nigeria: Oban District). Tessmann, 1913, *Die Pangwe*, **2**, pp. 135 and 190 (Spanish Guinea). Spence, 1925, *Jl. of Conch.*, **17**, pt. 8, p. 248 (Cameroon: Mohive near Victoria; Isongo; Misse Uele near Tiko); 1928, *Op. cit.*, **18**, pt. 7, p. 213 (Cameroon: Ferme Suisse, 10° 7' E.; 3° 35' N.). W. P. Lowe, 1932, *The Trail That is Always New*, (London), p. 132 (Southern Nigeria: Lagos; feeding on dead rat); 1943, *The Ibis*, **85**, p. 101 (feeding on dead bird).
- Cochlitoma marginata* G. B. Sowerby, 1825, *Cat. Shells Earl Tankerville*, p. 38. Standen, 1917, *Jl. of Conch.*, **15**, pt. 6, p. 161 (egg; oviposition).
- Helix (Cochlitoma) marginata* Rang, 1831, *Ann. Sci. Nat.*, **24**, p. 33 (in part: the description, but possibly only Axim, in the Gold Coast, of the localities mentioned).
- Achatina (Achatina) marginata* Beck, 1837, *Index Moll.*, pt. 1, p. 75. v. Martens, 1860, in Albers, *Die Heliceen*, 2d Ed., p. 201 (in part: not the shell with reddish apex). Semper, 1874, *Reisen Arch. Philippinen*, pt. 2, *Wiss. Res.*, **3**, fasc. 2, p. 144 (animal; anatomy; radula; jaw).
- Oncaea marginata* Gistel (or Gistl), 1848, *Naturgesch. d. Thierreichs*, p. 168; Pl. 5, fig. 29.
- Achatina (Archachatina) marginata* Albers, 1850, *Die Heliceen*, p. 190. Germain, 1911, *Bull. Mus. Hist. Nat. Paris*, **17**, p. 224; 1912, *Ann. Inst. Océanogr. Monaco*, **5**, pt. 3, p. 123 (Dahomey: Abomey; Porto Novo); figs. 3A-B, on p. 124 (young shells); 1916, *Ann. Mus. Civ. Genova*, **47**, p. 244 (Fernando Po: Bahia de San Carlos. Gaboon: Fernand Vaz); 1917, *Bull. Mus. Hist. Nat. Paris*, **23**, p. 511 (Dahomey: Igbin). Dautzenberg, 1921, *Rev. Zool. Afric.*, **9**, pp. 92 and 96 (Ivory Coast: Assinie; this locality may have been due to erroneous labelling). Bofill and de Aguilar-Amat, 1924, *Trab. Mus. Cienc. Nat. Barcelona*, **10**, pt. 2, p. 6 (Spanish Guinea: Itime, Río Mayani). Germain, 1926, *C. R. Congr. Soc. Savantes*, (1925), *Sciences*, p. 493.
- Achatina (Achatinus) marginata* Pfeiffer, 1856, *Malak. Blätt.*, **2**, (1855), p. 167; 1879, *Nomencl. Helic. Viv.*, p. 264. Römer, 1891, *Jahrb. Nassau. Ver. Naturk.*, **44**, p. 123.
- Archachatina marginata* Pilsbry, 1904, *Man. of Conch.*, (2), **17**, p. 109 (Gaboon. Dahomey); Pl. 24, figs. 22 (young shell) and 23 (adult specimen); Pl. 25,

<sup>1</sup> d'Ailly examined from Cameroon 12 shells of the nominate race of *A. marginata* and over 70 of subsp. *suturalis* (his var. *gracilior*); but he did not state how they were divided among the localities listed.

fig. 26 (adult shell); 1905, *Op. cit.*, (2), **17**, pp. ix, fig. 1 (radula, after d'Ailly), and xiv (animal, anatomy, jaw, radula). Nobre, 1909, Bull. Soc. Portugaise Sc. Nat., **3**, Suppl. 2, p. 91. Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 66. C. R. Boettger, 1927, *Op. cit.*, **39**, pt. 4, p. 355 (Belgian Congo: Duma). Lamy, 1929, Jl. de Conchyl., **73**, p. 202 (egg). C. R. Boettger, 1932, Sitzungsber. Ges. Naturf. Fr. Berlin, p. 303 (in part. Gaboon: shells from mouth of Monda River, north of Libreville, only);<sup>1</sup> 1934, *Op. cit.*, (for 1933), p. 447 (Gaboon: mouth of Monda River). Haas, 1935, Arch. f. Molluskenk., **67**, pt. 3, p. 108 (introduced with bananas at Frankfurt a. Main, Germany; erroneously stated to have come from Jamaica, but actually from Cameroon). Darteville, 1936, Rev. Zool. Bot. Afric., **29**, p. 8 (Coast of Gaboon. Also one dead shell from Belgian Congo: Kifuenda near Banana); 1936, *Op. cit.*, **29**, Bull. Cercle Zoologique Congolais, **13**, pt. 1, p. (4) (Belgian Congo: Nouvelle Anvers). Bequaert and Clench, 1937, The Nautilus, **51**, p. 34. C. R. Boettger, 1938, Sitzungsber. Ges. Naturf. Fr. Berlin, (for 1937), p. 314 (live specimens, introduced from Cameroon, found on a city dump near Berlin, Germany); 1938, *Op. cit.*, (for 1938), p. 83. Coen, 1945, Catalogo Gasteropodi Polmonati Coll. Coen, p. 43. C. R. Boettger, 1947, Arch. f. Molluskenk., **76**, pts. 1-3, pp. 66 and 67.

*Archachatina (Megachatina) marginata* Bequaert and Clench, 1936, Rev. Zool. Bot. Afric., **29**, pt. 1, pp. 76 and 79 (Cameroon: Yaunde; Sakbayeme; Sangmelima. Fernando Po. Gaboon. Southern Nigeria: Old Calabar. Dahomey).

*Archachatina (Calachatina) marginata* C. R. Boettger, 1940, Sitzungsber. Ges. Naturf. Fr. Berlin, p. 233 (Cameroon: Ndongo near Likomba).

*Helix (Cochlitoma) amphora* Férussac, 1821, Tabl. Syst. Moll., Tabl. Limaçons, pp. 54 (or 50) (*nomen nudum*) and 74 (or 70) (with *A. marginata* Swainson as a variety).

*Achatina amphora* Catlow and Reeve, 1845, Conchologist's Nomenclator, p. 163.

*Archachatina marginata* var. *amphora* Pilsbry, 1904, Man. of Conch., (2), **17**, p. 110; Pl. 25, fig. 26 (specimen) (says this name might be used for the largest shells of the species, if these were separated as a variety).

*Achatina schweinfurthi* var. *foureaui* Germain, 1905, Bull. Mus. Hist. Nat. Paris, **11**, p. 251 (French Sudan: Sabakaufi in Damergu Country), fig. 1 (type); 1907, Arch. Zool. Gén. Expér., (4), **6**, pt. 4, p. 128; 1908, in A. Chevalier, L'Afrique Centrale Française, p. 488, fig. 87.

*Achatina (Archachatina) marginata* var. *fourneaui* Germain, 1908, Nouv. Arch. Miss. Sci. Litt., (3), **16**, p. 158 (with very brief description. Gaboon: banks of the Mawisch or Marwisch River); 1911, Bull. Mus. Hist. Nat. Paris, **17**, p. 224, fig. 50 (type). Dautzenberg, 1921, Rev. Zool. Afric., **9**, p. 95.

*Archachatina (Megachatina) marginata* var. *fourneaui* Bequaert and Clench, 1936, Rev. Zool. Bot. Afric., **29**, pt. 1, p. 84.

*Achatina (Archachatina) marginata* var. *fourneauxi* "Germain" Dautzenberg, 1921, Rev. Zool. Afric., **9**, p. 95 (as a synonym of var. *foureaui*. I cannot find that Germain ever used the spelling *fourneauxi* in print).

<sup>1</sup> The specimens from Lambarene were *Archachatina gaboonensis* var. *lambarenensis* Pilsbry.

- Archachatina (Megachatinoops) gaboonensis* var. *aequatorialis* Bequaert and Clench, 1936, Rev. Zool. Bot. Afric., **29**, pt. 1, p. 90 (Belgian Congo: Kunungu near Bolobo, holotype; Stanleyville, paratype); Pl. 1, fig. 4 (paratype); Pl. 2, fig. 14 (holotype).
- Archachatina aequatorialis* Darteville, 1939, Rev. Zool. Bot. Afric., **33**, Bull. Cercle Zool. Congolais, **16**, pt. 1, p. (23) (Belgian Congo: Yahuma, 1° 15' N., 23° E.).
- ? *Achatina paivana* Vignon, 1888, Bull. Soc. Mal. France, **5**, p. 71 (Ivory Coast: Grand Bassam. According to Ancey, *Op. cit.*, p. 71, footnote, Vignon's shell was *A. marginata*, in which case the locality was most probably erroneous). Not of Morelet, 1866.
- Achatina intuslalescens* "Paiva" Nobre, 1909, Bull. Soc. Portugaise Sc. Nat., **3**, Suppl. 2, p. 91 ("Guinea"; as a synonym of *A. marginata*).

Original description of *A. marginata* Swainson (1821): "A. testa ovato-oblonga, strigis inaequalibus ferrugineis; spira ad apicem obtusa, 5-voluta; sutura depressa linea sulcata marginali. Shell ovate-oblong, with irregular ferruginous stripes; spire obtuse at the tip, of 5 volutions; the suture depressed, with a marginal indented line." Additional remarks: "Spire of 5 whorls, the last or terminal one [at apex] very small and flattened; the apex obtuse; the suture depressed, as if flattened on the shell, and margined by 1 or sometimes 2 indented lines, parallel, and at the top of each whorl. In the colour of its mouth varying in sometimes having a tinge of rose-colour at the base and top of the spire, but the mouth is more generally white. The body-whorl is more or less ventricose; the outer lip is a little reflected, and the whole shell when full grown, much thicker and heavier than any of the other species. The epidermis is yellowish-brown, beneath which the shell is nearly white, beautifully marked with broad remote stripes of chestnut, with others more slender (and sometimes broken into spots) between." Of the three references given, only the one to Gualtieri (1742) refers correctly to typical *A. marginata*. Swainson's description was clearly based on two color forms; but his excellent figure shows the form without pink at the apex and with columella and parietal wall white, which I herewith designate as the nominate race of the species. This figure, copied in my Pl. 9, fig. 3, shows on a slant a shell not fully grown, with the outer lip scarcely expanded, smaller than average for the species. It is 104 mm. in length, 55 mm. in greatest width, with the aperture 59 by 29 mm. The surface shows no trace of decussate, spiral or granulose sculpture. The figured type appears to be lost.

*A. marginata* var. *fourneaui* was at first (1908) introduced with a few descriptive words: "a very fine variety with thin shell." A full description was published in 1911 (translated from the French): "Shell globular-ventricose, widened basally; spire only a little raised,

of  $5\frac{1}{2}$  convex, rapidly increasing whorls separated by almost horizontal and distinctly marginate sutures; last whorl [=body-whorl] very large, ventricose-globular, widened basally; columella curved, scarcely twisted, strongly truncate; aperture pyriform, very acute at upper end, broadly convex below and outwardly. Length 95 mm.; greatest diameter, 62 mm.; lesser diameter, 50 mm.; height of aperture, 61 mm.; diameter of aperture, 33 mm. Shell thin, light, translucent; first whorls reddish, the remaining having on a greenish-yellow background longitudinal [=axial or vertical] narrow, flame-like streaks of dark chestnut-brown narrowly bordered with reddish; these flame-like, not zigzag-shaped streaks extend to the mouth. The first whorls of the spire are almost smooth (longitudinal striae very fine, scarcely oblique); the others show longitudinal, slightly oblique, somewhat wavy striae, very distinctly wrinkled near the sutures and cut, near the sutures, by spiral striae producing a decussate appearance. Aperture inside pale Russian blue, somewhat shiny; parietal callus of the same color; columella whitish." The figure shows a decidedly immature shell, which accounts for the few whorls. The locality was first spelled "Mawisch River" (1908); later "Marvisch River" (1911). I have been unable to locate it on any map. The type of *fourneaui* could not be found at the Paris Museum in 1933. The original drawing of the type is copied in my Pl. 76, fig. 3. Spence's (1928) *A. marginata* var. *fourneaui*, from Southern Nigeria, said to be "a small, thin form," appears to have been *A. marginata eduardi* Pilsbry.

Germain (1905) described his *A. schweinfurthi* var. *foureaui* as follows (translated from the French): "Transitional between *Achatina schweinfurthi* and *A. marginata*. Compared with typical *schweinfurthi*, the var. *foureaui* differs in the spire, the first whorls of which are proportionately less raised; in the aperture being wider at the base and more broadly convex toward the outer margin; in the more twisted columella (the columella duplicates almost exactly that of *A. marginata*); finally in the smaller size. This variety cannot be referred to *Achatina zanzibarica* Bourguignat, although it has about the same dimensions. It differs from this in the much more twisted columella (in *A. zanzibarica* the columella is even less twisted than in *A. schweinfurthi*), but especially in the aperture being much more widened at the base, as shown in the figure. Length 177 mm. [evidently an error for 107 mm., as the figure, said to be two-thirds natural size, indicates]; greatest width, 58 mm.; length of aperture, 63 mm.; width of aperture, 36 mm." *A. schweinfurthi* v. Martens is a true *Achatina*, and the var. *foureaui* is clearly in no way related to it. From the photograph in my Pl. 80, fig. 4, as well as from the original figure, copied in my Pl. 75, fig. 2, *foureaui* is a fully adult specimen of the nominate form of *A.*

*marginata*, with expanded outer lip. The record cannot, however, be used as evidence that the species now occurs alive in the Damergu country, which is in the semi-desertic section of the French Sudan (about 15° N., 9° W.). Most probably the specimen had been carried in dead condition to the locality by natives. A study of the type at the Paris Museum in 1933 had already led me to the conclusion that *fourcaui* was typical *marginata*.

Copy of the original description of *A. gaboonensis* var. *aequatorialis*: "In general outline, shape of spire and type of sculpture, similar to typical *gaboonensis* and its var. *lambarenensis*, but differing in the type of color markings. The first two and a half whorls isabelline; the next half whorl reddish-brown passing rather abruptly into axial streaks of dark chestnut-brown overlying a ground color of dull orange-yellow; starting on the third whorl and continuing to the aperture, there are numerous chestnut-brown flecks disposed irregularly over the entire surface, but most prominent in the yellow intervals between the chestnut streaks; the individual flecks are approximately 1.5 by 1 mm. in size; the aperture and columella are pale whitish-blue." The holotype is 92.5 mm. long, 55 mm. wide, of 6 whorls, the aperture 57.5 by 30 mm.; the corresponding measurements of the paratype are 120.5 mm., 68.5 mm., aperture 70.5 by 37 mm., of 6¼ whorls. A more careful study of the holotype and paratype shows that they are immature *A. marginata* of the nominate form; they have the characteristic microsculpture of that species, which is entirely lacking in *A. gaboonensis*. Both types are shown in my Pl. 64, fig. 1, and Pl. 67, fig. 2.

Of the early figures which I refer to *A. marginata*, Gualtieri's (1742) lower fig. B of Pl. 45, copied somewhat reduced in my Pl. 68, fig. 1, seems to show the nominate race. The accompanying text reads: "Buccinum parvum, integrum, ore obliquo, ventricosum, striatum striis per longitudinem aequaliter percurrentibus, albidum, fulvidis, et vinosis maculis undatim depictum, et variegatum." Unfortunately it does not mention the color of the columella nor of the aperture inside, and moreover covers also the upper fig. B, which represents *Achatina achatina* (Linné). In the original, lower fig. B is 182 mm. long, 108 mm. wide, with the aperture 117 by 55 mm. The number of whorls cannot be determined, as the earlier ones were overlooked by the draughtsman. It exceeds the largest specimen now known of the species and I strongly suspect that it was drawn over-size.

Knorr's well-known pictorial work has a complicated history, which it would be a task in itself to try to unravel. The following few remarks are, however, essential to clear up the misunderstanding that may arise concerning Pl. 3\*\*, fig. 1. The first edition of the book, in

six parts, each with its own pagination of the text and each with 30 Plates colored by hand, appeared from 1757 to 1773. It was issued with a German or with a French text in separate copies. The German text was written by P. E. S. Müller of Erlangen. I have not been able to find who made the French translation, which is fairly literal. Only the first part was published by G. W. Knorr himself, the other parts being issued after his death by his Heirs. In all German or French copies known of this first edition the text and pagination are identical and there appears to have been only one printing of the text. In parts 1, 2, 4, 5, and 6 the Plates are also identical in all copies of both languages, so far as I know. Of part 3 there were, however, two different printings of the Plates, for both the French and German texts. Some of the Plates show different species in the two printings; in others the species are the same, but redrawn or engraved anew, as they are often in a slightly different position. As I have not seen the matter referred to in print, I am unable to offer an explanation.<sup>1</sup> Of the first edition there exists also a Dutch translation, or rather adaptation, the Dutch text resembling only vaguely or not at all the original German or French issues, and also carrying a different pagination. The pagination runs continuously through parts 1 to 3 (pp. 1-118) and again through parts 4 to 6 (pp. 1-118), the last part concluding with a Register of 24 unnumbered pages. Each part has the original number of 30 Plates, identical with the German and French issues, but those of part 3 are of the second printing.<sup>2</sup>

According to Boehmer (1786, *Bibliotheca Scriptorum Historiae Naturalis, Zoolog.*, 2, p. 444), an entirely new German edition of Knorr's work was started later with a corrected text, the first part appearing in 1776 (revised text by P. E. S. Müller), the second in 1784 (revised text by Meuschen). The pagination was continuous through these two parts (pp. 1-240). I have not seen this second edition. I do not know whether it was ever completed nor whether part 3 was issued. No corresponding French text appears to have been published.

Coming now to Pl. 3\*\*, fig. 1 of part 3, in the first printing this unquestionably represents *Archachatina knorrii* (Jonas), from the back, as may be seen from my copy in Pl. 39, fig. 2. It also agrees with the accompanying text, which I reproduce in my discussion of *A. knorrii*.

<sup>1</sup> So far as known, in every German or French copy of part 3, the Plates are either all of the first or all of the second printing. I regard as of the first printing the Plates showing shells which agree with the corresponding descriptions in the text. These descriptions often disagree with the shells shown in the second printing.

<sup>2</sup> The library of the M.C.Z. has two French copies of the first edition, each with a different printing of the Plates for part 3. The U.S.N.M. library has a German and a French copy, both with the second printing of the Plates for part 3. The Ac.N.S.Phila. has a German copy with the first printing for the Plates of part 3. The Department of Mollusks of the M.C.Z. was recently given a Dutch copy by Mr. Richard Foster.

In the second printing, however, Pl. 3\*\*, fig. 1, copied in my Pl. 71, fig. 3, is not *A. knorrii* at all, but a small example of *A. marginata*, 117 mm. long, 68 mm. wide. As it is shown from the back, the color of the columella is unknown; but as the summit is painted yellow, the shell presumably was of the nominate race.

*A. marginata* appears to be mainly a terrestrial snail. In Cameroon, R. Rohde (quoted by O. Boettger, 1905) found it estivating underground during the drier months, having closed the aperture with a solid, calcareous, white epiphragm. According to P. A. Talbot (1912), when the crawling snail is disturbed it produces a peculiar "screaming" noise by rapidly retracting into the shell. This species does not cause any appreciable damage to native crops; on the contrary, it is considered as an economic asset among many native West African tribes who include it in their diet. The solid, capacious and rather handsome shells lend themselves to many household purposes so that very large, usually badly worn specimens may be rather easily obtained in native villages.

Although d'Ailly (1896) claimed, but not from personal observation, that the snail oviposits on trees, in the forks of the branches close to the main trunk, he did not describe the egg. Correlated with the sizeable embryonic (or nepionic) shell, the egg is large. It was described by v. Martens (1888), O. Boettger (1905), Standen (1917) and Lamy (1929). O. Boettger says that it measures 20 to 20.5 mm. in length and 14 to 14.5 mm. in width in the nominate race of the species. The eggs which Standen described, from Fernando Po, were oblong oval, yellowish-white, 19 by 14.5 mm.; according to the collector they had been deposited on the ground at the foot of trees.

The newly hatched shell is 15 to 15.5 mm. long, 12 to 12.5 mm. in greatest width and consists of about  $3\frac{1}{2}$  whorls. A little less than the first whorl is smooth; then appear fine, vertical, slightly curved, oblique wrinkles, cut by many closely-set, fine, transverse engraved lines, producing regular spiral rows of granules, which increase gradually in size. The terminal embryonic shell is obtusely carinate at the periphery, below which it is at first smooth and shiny, later dull and covered with the "weave" criss-cross microsculpture I have described for the adult shell. The base of the columella is obliquely truncate and provided with a distinct, deep umbilical slit only partly covered by the reflexed outer edge, as was first pointed out by Shuttleworth (1856). The umbilicus closes rapidly in the post-nepionic stage, as I can find no trace of it in a shell only 23 mm. long.

*Specimens Examined.* Several in various museums (M.C.Z.; U.S.-N.M.; Amst.M.; A.M.N.H.; Ac.N.S.Phila.; etc.) merely labelled "Africa" or "West Africa."—DAHOMÉY: without precise locality



(M.C.Z.; Ac.N.S.Phila.). — NORTHERN NIGERIA: Egbe, south of Niger R. (Miss Clark.—U.S.N.M.). — SOUTHERN NIGERIA: Ado near Lagos (A.S. Pearse.—U.S.N.M.); Calabar (Brus.M.); Old Calabar (U.S.N.M.). — FERNANDO PO: (M.C.Z.). — CAMEROON: Sakbayeme near Edea (G. Schwab.—M.C.Z.); Yaunde (Ac.N.S.Phila.; M.C.Z.); Lolodorf (E. D. Horner.—M.C.Z.); Ngon near Ebolowa (Miss E. M. Daniels.—M.C.Z.); Kribi (Leid.M.); Bitye (Terv.M.); Metet (K.D. Grissett.—M.C.Z.); Sangmelima (M.C.Z.). — SPANISH GUINEA: Corisco Id. (A.M.N.H.; M.C.Z.); mouth of Benito River (M.C.Z.). — FRENCH CONGO: Gaboon (Terv.M.; Ac.N.S.Phila.; U.S.N.M.; M.C.Z.) — BELGIAN CONGO: Luvituku (Terv.M.); Lower Congo (Weyns.—Terv.M.); Kisala, Mayumbe (H. Schouteden.—M.C.Z.; Terv.M.); Duma on the Ubangi River (A. Schubotz.—Frankf.M.); Stanleyville, paratype of *A. gaboonensis* var. *aequatorialis* (J. Ghesquière.—M.C.Z. No. 103894); Kunungu near Bolobo, holotype of *aequatorialis* (Terv.—M.).—A very large, dead and much weathered specimen was picked up by Dr. W. Mann somewhere in Liberia; most probably it had been imported from Fernando Po or Cameroon by some native. No living specimens of *A. marginata* have been ever seen in Liberia.

There is at present no trustworthy evidence that true *A. marginata*, or any of its several races, have ever been found alive west of Dahomey. The older records by Rang (1831) for Liberia and the Ivory Coast, repeated by Pfeiffer (1848), were doubtless based on *A. ventricosa*, which was only recognized several years later as a distinct species. Rang's description, however, fits true *marginata* well and may have been based mainly on the specimen he cites from Axim on the Gold Coast. It is uncertain, nevertheless, whether *A. marginata* actually lives at present on the Gold Coast; even though v. Martens later (1860) described his var. *gracilior* (= *eduardi* Pilsbry) also from Axim. Vignon's (1888) supposed *A. paivana*, from Grand Bassam, which Ancy stated was *A. marginata*, if actually found alive there, may have been *A. ventricosa*; more probably it was from the Gaboon, where Vignon did most of his collecting. Dautzenberg's (1921) record from Assinie, although included in my bibliography of *marginata*, is open to question. No doubt dead specimens of *marginata* are often carried about by natives far from their true habitat, as large examples of this species lend themselves well to various domestic uses. This may account for their being found in native villages outside the true range of the species. The unusually large specimen found by Dr. W. Mann in Liberia was probably brought there from Fernando Po by a returning laborer. The possibility must also be considered that this snail may be transported to new territory as young or eggs. Live immature examples were introduced from Cameroon into Germany on at least

two occasions. Moreover, C. R. Boettger (1938) reported that in August, 1937, two live young *A. marginata*, respectively 24.5 and 24.2 mm. long, were found in the open on a city dump at Berlin-Blankenfelde. These importations were due to transport with bananas.

*Measurements of Adult Shells*

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
176 mm.	100	104	54	7½		"Liberia" (?)
150	81.5	87	44	7½		Sakbayeme
145	97	98	53	7½		"West Africa"
141	84	86	47	7½		Gaboon
141	88	87.5	47	7½		Corisco
140.5	77.5	79.5	42	7½		Egbe
137.5	83	83	44	7½		Sangmelima
137	88	85	49	7½		"West Africa"
136	87	87.5	46	7½		Gaboon
135.5	80	85	42	7½		Corisco
133	79	83	46	7¼		"West Africa"
130	81	77	47	7		Gaboon
127.5	73	73	39	7		"West Africa"
120	70.5	71	36	7		Sakbayeme
115	77	72	41	7		Corisco
114.5	70	71.5	38	7		"West Africa"
109	62	66	35	7		Old Calabar
102.5	63	63.5	35	6½		"West Africa"
102.5	58	58	30	6½		Gaboon
90	55	54	30.5	6		"
85.5	50	50	26	6		"West Africa"

The nominate race of *A. marginata* averages nearly 130 mm. in length and 80 mm. in greatest width.

b. *A. MARGINATA OVUM* (Pfeiffer)

Pl. 11, fig. 3; Pl. 70, fig. 1

*Achatina ovum* Pfeiffer, 1858, Malak. Blätt., **5**, p. 238 (no locality); 1860, Novit. Conch., **2**, p. 154; Pl. 40, figs. 3-4 (2 views of type; name misspelled "*orum*" on Plate); 1868, Monogr. Helic. Viv., **6**, p. 215; 1876, *Op. cit.*, **8**, p. 274. Paetel, 1889, Cat. Conch.-Samml., 4th Ed., **2**, p. 240.

*Achatina (Achatinus) ovum* Pfeiffer, 1879, Nomencl. Helic. Viv., p. 265.

*Archachatina ovum* Pilsbry, 1904, Man. of Conch., (2), **17**, p. 111; Pl. 24, figs. 20-21 (after Pfeiffer). Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 66.

*Archachatina (Megachatina) ovum* Bequaert and Clench, 1936, Rev. Zool. Bot. Afric., **29**, pt. 1, p. 92.

Original description of *A. ovum*: "T. ovata, tenuis, laevigata, fulvo-lutea, strigis angustis rufis, saepe maculosis interruptis picta; spira conica, sursum carnea, obtusa; sutura late marginata; anfr. 6 convexiusculi, superi sub lente minute granulati, ultimus spiram paulo superans, ventrosus; columella aurantiaco-carnea, arcuato-torta, basi vix truncata; apertura ampla, parum obliqua, late angulato-ovalis, intus concolor, submargaritacea; perist. simplex, tenue. Long. 65, diam. 35 mill. Ap. 38 mill. longa, medio 22 lata." This description is repeated in 1860, the additional German and French text being merely literal translations of the Latin diagnosis. The type, from the Cuming Collection, is now at the British Museum, where I saw it in 1933. It was then recognized as an immature specimen of a form of *A. marginata*, but the color of the columella, described as "orange flesh-colored" by Pfeiffer, was not noted at the time. This is, moreover, not shown in Pfeiffer's fig. 3, copied in my Pl. 11, fig. 3. At my request, Mr. T. Pain has recently examined the type once more. He reports that it "appears to have faint traces of very pale orange on the columella." In the material I have seen the orange color characteristic of this subspecies is always much less marked in immature than in full-grown shells.

Subsp. *ovum* is in fully adult specimens similar to the nominate race in size, general outline and shape of aperture, as well as in sculpture, having also the characteristic "weave" microsculpture. The coloration is the same, except for the columella which is more or less apricot-yellow, this color often extending upward over much of the glazed area of the parietal wall; a narrow outer zone of both parietal wall and columella remains bluish-white. The summit of the spire (first three whorls) also is usually suffused with yellow or orange-yellow.

*Specimens Examined.* SOUTHERN NIGERIA: Lagos, many specimens (A. Mead; Philip Souza.-M.C.Z.) and one immature shell from an old collection (M.C.Z.); Oloki Meji, Ibadan (J. C. Bridwell.-Bish.M.; M.C.Z.).

*Measurements of Adult Shells*

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
169 mm.	110	94	55	7½		Oloki Meji
163	96	96	53	7½		Lagos
162	94.5	94	53	7½		"
156	81.5	87	47	7½		"
150	85.5	85.5	48	7½		"
121.5	68.5	68	37	7		"
117.5	85.5	68	36	7		"
105	59	61	33	6½		"

Dr. A. Mead reports elsewhere on the anatomy of this race, which he studied on shells bought in the native market at Lagos, where the snail is commonly eaten.

c. *A. MARGINATA SUTURALIS* Philippi

Pl. 20, fig. 3; Pl. 62, fig. 5; Pl. 65, fig. 2; Pl. 72, fig. 3

- [Lister, 1688, Synopsis Method. Conchyl. Liber Quartus, Pl. 579, fig. 34].  
 [Klein, 1753, Tentamen Method. Ostracologicae, p. 47 ("Urceus spec. 6"); Pl. 3, fig. 60 (a poor copy of Lister's Pl. 579, fig. 34)].  
 [Petiver, 1764, Gazophylacium, 1, p. (10) of 6th Explanation of Plates; Pl. 152, fig. 11 (a poor copy of Lister's Pl. 579, fig. 34)].  
*Bulla achatina* Huddesford, 1770, in Lister, Hist. Conch., New Edition, Pl. 579, fig. 34; and Index, 2, p. 38. Not of Linné, 1758.  
*Bulla achatina* var. *marginata* Donovan, 1826 (May 1), Naturalist's Repository, 5, Pl. 149 (2 views of one shell; with letterpress; no locality). Not *Achatina marginata* Swainson, 1821.  
*Achatina marginata* Reeve, 1849, Conch. Icon., 5, *Achatina*, Pl. 4, fig. 14 (West Africa).  
*Achatina suturalis* Philippi, 1849, Abb. Besch. Conch., 3, pt. 5, p. 29 (p. 7 of *Achatina*); Pl. 2 (of *Achatina*), fig. 1 (no locality). Bourguignat, 1889, Moll. Afr. Equat., p. 78.  
*Archachatina (Magachatina) marginata* var. *suturalis* Bequaert and Clench, 1936, Rev. Zool. Bot. Afric., 29, pt. 1, p. 81 (Southern Nigeria: Calabar; Lagos. Dahomey: Whydah. Cameroon: Ndian; Etome; Mukonje Farm; Moliwe Plantation near Victoria).  
*Achatina cumingii* Shuttleworth, 1852, Mitth. Naturf. Ges. Bern, Nos. 248-249, p. 201 (West Coast of Africa). Pfeiffer, 1853, Monogr. Helic. Viv., 3, p. 482. H. and A. Adams, 1855, Gen. Rec. Moll., 2, p. 132. Pfeiffer, 1859, Monogr. Helic. Viv., 4, p. 601; 1868, *Op. cit.*, 6, p. 214. Haines, 1868, Cat. Terr. Shells Coll., p. 67 (Gaboon). Pfeiffer, 1876, Monogr. Helic. Viv., 8, p. 274.  
*Achatina (Achatinus) cumingii* Pfeiffer, 1879, Nomencl. Helic. Viv., p. 265.  
*Archachatina cumingii* Pilsbry, 1904, Man. of Conch., (2), 17, p. 112. Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., 32, p. 66.  
*Achatina marginata* var. *gracilior* d'Ailly, 1896, Bih. Svenska Vet.-Akad. Handl., 22, Afd. 4, No. 2, p. 61 (in part: some of the localities listed for *A. marginata* for Cameroon, but not separated from the others). O. Boettger, 1905, Nachrichtsbl. D. Mal. Ges., 37, p. 165 (Cameroon: Mukonje Farm; Johann-Albrechtshöhe near Kumba; Bakundu; Bibundi; village of Mundo on Lower Mungo River; Bakundu Kaki; Ekilliwindi; Mbanda or Mambanda; "Randgebirge" of the Interior. Egg). Spence, 1928, Jl. of Conch., 18, pt. 7, p. 213 (Southern Nigeria: Okaki, 6° 20' E.; 5° 5' N.). Not *Achatina gracilior* C. B. Adams, 1850, nor *A. m.* var. *gracilior* v. Martens, 1860.

- Archachatina marginata* var. *gracilior* Pilsbry, 1904, Man. of Conch., (2), **17**, p. 111 (description after d'Ailly, 1896; no specimen).
- Achatina* (*Archachatina*) *marginata* var. *gracilior* Germain, 1916, Ann. Mus. Civ. Genova, **47**, p. 246 (Cameroon: Buea, 800 to 1200 m. Fernando Po: Punta Frailes); Pl. 6, fig. 14 (young shell from Punta Frailes); Pl. 7, fig. 9 (adult from Punta Frailes); Pl. 10, fig. 14 (apex of young shell enlarged); 1917, Bull. Mus. Hist. Nat. Paris, **23**, p. 512 (Dahomey: Igbin). Dautzenberg, 1921, Rev. Zool. Afric., **9**, p. 94. Germain, 1926, C. R. Congrès Soc. Savantes, (1925), Sciences, p. 493.
- Archachatina marginata* var. *subsuturalis* Pilsbry, 1904, Man. of Conch., (2), **17**, p. 111 (new name for *A. suturalis* Philippi, 1849); Pl. 25, fig. 25 (after Philippi). Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 66.
- Achatina marginata* var. *subsuturalis* Hidalgo, 1910, Mem. Soc. Españ. Hist. Nat., **1**, No. 29, p. 508 (Spanish Guinea: Cabo San Juan).
- Achatina* (*Archachatina*) *marginata* var. *subsuturalis* Bofill and de Aguilar-Amat, 1924, Trab. Mus. Cienc. Nat. Barcelona, **10**, pt. 2, p. 7 (Fernando Po: Santa Isabel).

As Dautzenberg seems to have recognized first (1921), Lister's Pl. 579, fig. 34, copied in my Pl. 72, fig. 3, was drawn not from a specimen of the nominate race of *A. marginata*, but from subsp. *suturalis*. Lister's brief description leaves no doubt about this: "Cochlea ventricosior, fasciis ex nigro purpurascens, ad tergum certe undatis, ipsa columella purpurascens." The figure is too broad for *A. purpurea*, too smooth for *A. ventricosa*, and with too narrow an aperture for *A. degneri*. It was copied, but very crudely, by Klein and Petiver.

Original description of *A. suturalis* Philippi (1849): "A. testa ovato-conica, crassiuscula, in anfractibus superioribus tenuissime decussato-granulata, in ultimis laevissima, sub epidermide fulvo-lutea ad apicem purpurea, deinde alba, strigis crebris angustis, undulatis castaneis ornata; spira conica, acutiusecula; sutura marginata, haud crenulata; anfractibus septem, parum convexis, ultimo spiram longe superante; columella callosa, purpurea, breviter et abrupte truncata; apertura ovato-oblonga intus alba, labro intus nigricante, recto, in parte basali arcuato. Long. 42''' [=91.5 mm.]; lat. 26''' [=56.5 mm.]" The following additional notes are translated from the German: "As appears from the foregoing diagnosis, *A. suturalis* differs from the very similar *A. zebra* in the red apex, the marginate and not crenulated suture, the longer body-whorl as compared to the spire, and the red columella. My shell has 7 whorls, the upper 4, which form the rounded apex, being finely reticulate granulate and red. With whorl 4 appear the dark brown markings and the impressed line, which marginates the suture, devoid of crenulations. The lower whorls are white, with crowded, wavy, longitudinal dark brown streaks, occasionally broken

up into dots. These later whorls are all slightly convex and much higher in proportion to the width than in *A. zebra*, this being particularly true of the body-whorl, which is one and one-half times as long as the spire. The shape of the aperture is not peculiar, but the columella is shorter than in *A. zebra*, broader and more strongly curved, bright red as in *A. perdix*. *A. suturalis* differs from *A. perdix* very decidedly in the more obtuse red apex, the entirely smooth terminal whorls, the different proportion of the whorls, the coloration, etc." The present location of the type is unknown. To judge from the figure, copied in my Pl. 65, fig. 2, it was an immature-shell. The name *suturalis* need not be changed. The earlier *Achatina suturalis* Pfeiffer (1848) is not a true or primary homonym, but merely a new combination for *Polyphemus suturalis* Pfeiffer (1839), a shell not now placed in *Archachatina* nor in the family Achatinidae.

Reeve's (1849) Pl. 4, fig. 14, shows a fully adult *suturalis*, with reddish summit and columella, 118 mm. long, 72 mm. wide, with the aperture 65 by 38 mm. It is about average size for this race.

Original description of *Achatina cumingii* Shuttleworth (1852): "Testa ovato-oblonga, solida, striata, lineis punctatis obsolete decussata, sub epidermide flavido-albida strigis latis fuscis vel nigro-castaneis in anfractu ultimo basi confluentibus ornata; spira ovata, apice obtusa, rosea; anfr. 6, convexiusculi, ultimus fere  $\frac{5}{8}$  longitudinis aequans, vix inflatus; sutura marginata; columella arcuata, basi roseo-tincta, oblique truncata; apertura semiovalis, intus margaritacea; perist. simplex, rectum, subincrassatum, marginibus callo nitido albido junctis. Long. 77; Diam. 40 mill.: Apert. 40 mill. longa, 26 lata. Specimina 2 examinavi. Affinis *Ach. suturali* Phil. (*A. marginata* var. columella rosea auct.) sed gracilior, columella magis arcuata et testa multo minus inflata distincta." The two cotypes, none of which has ever been figured, should be at the Bern Museum. There seems to be no difficulty in recognizing from the description that *cumingii* was based on an immature, hence more slender *A. marginata suturalis*.

*A. marginata* var. *gracilior* v. Martens (1860), renamed *Archachatina marginata* var. *eduardi* by Pilsbry (1909), has been generally regarded thus far as a form with red columella, following d'Ailly's interpretation of v. Martens' account. As shown below, it was rather a small, slender race with whitish columella. Most of the specimens later referred to *gracilior* appear, however, to have been *A. marginata suturalis* (Philippi). d'Ailly's (1896) account of *marginata* and var. *gracilior* is not very clear. He says at first: "The second form, which seems to be the one cited by v. Martens as a variety (Monatsber., 1876), = var. *gracilior* v. Martens (Albers, Hel., 1860), is without violaceous color.

...<sup>1</sup> But on the same page below he states: "All the specimens belonging to the variety have the columella colored either deep carminrose or reddish-yellow, even to almost golden-tinged." From this it would seem that some of the shells at any rate, included by d'Ailly under var. *gracilior* were *suturalis*, although he did not separate their localities from those of typical *marginata* with a whitish columella. Pilsbry's (1904) description of *gracilior* was not based on specimens, but apparently on d'Ailly's account, since he emphasizes "the columella intense rose or reddish golden". O. Boettger (1905) also followed d'Ailly's interpretation, for he says (p. 166) that a pale unicolorous shell from Bibundi has a beautifully fleshy-red apex and columella and "is therefore var. *gracilior* v. Martens."<sup>2</sup> Germain's specimens of *gracilior* (1916 and 1917) were likewise *A. m. suturalis*, since the reddish columella is clearly mentioned in his discussions. As for Spence's (1928) *gracilior*, which he merely says to be "a richly coloured form", it is difficult to decide what it may have been, although the probability is for *suturalis*. Possibly some of the shells called *gracilior* by Germain and Spence were *A. papyracea* (= *adelinae*).

Donovan's (1826) two figures of *Bulla achatina* var. *marginata*, one of which is reproduced in my Pl. 62, fig. 5, although somewhat distorted, are nevertheless recognizable. The larger of the two shows the shell in front view, with the reddish apex and columella of subsp. *suturalis*, which are also mentioned in the brief accompanying description (English text only copied): "Shell ovate-oblong, ventricose, tip rosy, fulvous with longitudinal chestnut-coloured waves: pillar lip violet purple: lip within white."

According to O. Boettger's (1905) measurements, the egg of subsp. *suturalis* is slightly smaller than that of the nominate race, being 17.5 to 18 mm. long and 13 to 13.5 mm. wide. One egg which I found in a dead *suturalis* from Mukonje Farm, was 18 mm. long, 13.5 mm. wide.

*Specimens Examined.* "West Africa" (U.S.N.M.). — DAHOMEY: Whydah (Brus.M.). — SOUTHERN NIGERIA: Old Calabar (M.C.Z.); Lagos (A. R. Mead.-M.C.Z.; Hamb.M.). — CAMEROON: Edea (G. Schwab.-M.C.Z.); Ndian (Y. Sjöstedt.-Stockh.M.; M.C.Z.); Etome (P. Dusén.-Stockh.M.; M.C.Z.); Moliwe Plantation near Victoria (Berl.M.; M.C.Z.); Mukonje Farm (R. Rohde.-Frankf.M.; M.C.Z.). — FRENCH CONGO: Gaboon (A.M.N.H.; M.C.Z.).

Subsp. *suturalis* is also known definitely from Spanish Guinea and Fernando Po.

<sup>1</sup>"manque de la couleur violette," in the French original. In this quotation I have inserted the years so that the reader may trace the references in my bibliographies. It should be noted that the variety described and figured by v. Martens in 1876 appears to be *A. marginata egrégia* Dautzenberg, not *A. marginata suturalis*.

<sup>2</sup>"also zur var. *gracilior* v. Mts. gehörig," in the German original. This Bibundi shell was, however, *A. marginata grevillei* (Pfeiffer).

*Measurements of Adult Shells*

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
134.5 mm.	82.5	78	45	7		Lagos
130	78	78	43	7		"West Africa"
127	71	80.5	39	6½		Ndian
115.5	71	70.5	40	6½		Lagos
114	66	67	34	7		Old Calabar
108	55	57	30	6⅓		Gaboon
106	59	59	32	6½		Lagos
105	59	62	30.5	6½		Old Calabar
101.5	59.5	57.5	33.5	6½		" "
90	50	54.5	28.5	6		Etome
72.5	41.5	39	22.5	6		Old Calabar

It may be seen that subsp. *suturalis* is on the average smaller than the nominate race, being usually about 110 mm. long and 60 mm. wide. Immature shells of this race are often more slender and lighter than nominate *marginata* of about the same age; but these differences tend to disappear with age.

## d. A. MARGINATA EDUARDI Pilsbry

## Pl. 55, fig. 1

*Achatina marginata* var. *gracilior* v. Martens, 1860, in Albers, Die Heliceen, 2d Ed., pp. 201 and 203 ("Axim in Südafrika"; Axim is in the Gold Coast). Paetel, 1889, Cat. Conch.-Samml., 4th Ed., 2, p. 240. Not *Achatina gracilior* C. B. Adams, 1850.

*Archachatina marginata* var. *gracilior* Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., 32, p. 66.

*Achatina modestior* O. Boettger, 1905 (November 1), Nachrichtsbl. D. Malak. Ges., 37, p. 167 (Cameroon: in part: only the variety from Bibundi; not the holotype from Mukonje Farm); Pl. 7, fig. 3 (variety from Bibundi). Bequaert and Clench, 1938, The Nautilus, 52, p. 27 (Cameroon: Bibundi, paratypes; Moliwe Plantation near Victoria).

*Archachatina marginata* var. *eduardi* Pilsbry, 1909, Man. of Conch., (2), 20, p. 113 (new name for *A. marginata* var. *gracilior* v. Martens, 1860).

*Achatina marginata* var. *fourneaui* Spence, 1928, Jl. of Conch., 18, pt. 7, p. 213 (Southern Nigeria: Ogobo). Not of Germain, 1908.

*Archachatina (Megachatina) adelinae* Bequaert and Clench, 1936, Rev. Zool. Bot. Afric., 19, pt. 1, p. 87 (in part: specimens from Cameroon: Bibundi and Moliwe Plantation). Not of Pilsbry, 1905.

v. Martens' (1860) description of his *A. marginata* var. *gracilior* is rather confused (translated here from the German): "Reeve, Con-



chol. Icon. fig. 14 figures this species [= *marginata*] also with red columella and red apex. The specimen in Albers' collection likewise has a reddish apex. The most essential differences [of *marginata*] remain the smooth surface, the blunt apex, the broader angle at the junction of the outer lip [with the parietal wall], and the slight thickening followed by an expansion of the outer lip. All these characters are also present in a second, smaller and much more slender example in Albers' collection, only 110 mm. long, 50 mm. in diameter, with the aperture 60 by 35 mm. A comparison of the upper whorl [= body-whorl] with that of usual *marginata*, as well as the expanded and slightly thickened margin of the mouth, preclude its being regarded as not full-grown. In accordance with the slender shape, the columella is also but weakly curved. I have therefore listed it above as var. *gracilior*." It should be noted that the color of the columella and apex of this slender specimen is not mentioned. v. Martens discusses three different specimens: (1) The shell figured by Reeve (1849), Pl. 4, fig. 14, which has a red columella and is *A. m. suturalis*. (2) A shell in Albers' collection, with a reddish apex, but of which he does not describe the columella. Possibly this was *A. m. suturalis*, although I have seen examples of the nominate race of *marginata* with a decidedly pink summit. (3) A second shell in Albers' collection, of which he does not describe the color of the apex and columella, but which he says was smaller and more slender than Albers' first shell. To this second shell only he gave the name var. *gracilior*. The intervening sentence, about the essential differences, merely enumerates what he regards as the most characteristic features common to all forms or races of the species *A. marginata*, regardless of the color of apex and columella. For this reason I assume that the "second shell" from Albers' collection was of the smaller, more slender race with whitish columella. The present whereabouts of this shell, the type of v. Martens' *gracilior*, is unknown. It was not found at the Berlin Museum in 1933, but might have been overlooked, perhaps because it was not properly labelled. Whether the type had actually been found alive at Axim is doubtful, since no other specimen of *eduardi* has been taken that far West for nearly a century.

As v. Martens' *gracilior* is a primary homonym of *Achatina gracilior* C. B. Adams (1850), it was renamed *eduardi* by Pilsbry (1909), a name here adopted for the small subspecies of *A. marginata* with whitish columella.

Most, if not all, of the shells later referred by d'Ailly (1896), O. Boettger (1905), Germain (1916; 1917), and Spence (1928) to *gracilior* were *A. marginata suturalis* (Philippi), as I have pointed out in the discussion of that race.

O. Boettger (1905) confused two species in his original account of *A. modestior*; but the main description and the figures of the holotype from Mukonje Farm (Pl. 7, figs. 1-2) were based on *Archachatina papyracea* (Reeve) (= *A. adelinae* Pilsbry), where *modestior* will be discussed. The variety from Bibundi, shown in his Pl. 5, fig. 3, as well as other "paratypes" from the same locality, which I have seen, were, however, *A. m. eduardi*. Of this form he says: "A single shell from Bibundi, probably a variety of it [= *A. modestior*], is rather peculiar by the striking, strongly S-shaped curved columella, the deeper suture and the color and pattern. It may be defined as follows: Differt a typo t. minore, strigis multo latioribus, magis obscuris, latioribus quam interstitia, simplicibus, nullo modo fulguratis sed interstitiis hic illic brunneo punctatis, in anfr. ultimo supra et infra medium subaequalibus, prope columellam superne profunde concavam et validissime tortam subiti evanidis; apert. intus pallide violacea; columella albida. Alt. 65, diam. max. 39 mm.; alt. apert. 36, lat. apert. 24 mm. I do not want to give this example a name as it almost looks like an abnormality, because of a repaired injured area at the suture of the fourth whorl and the unusual shape of the columella."

*Specimens Examined.* "West Africa" (M.C.Z.; U.S.N.M.). — CAMEROON: Moliwe Plantation near Victoria (v. Maltzan.—Berl.M.; M.C.Z.); Bibundi, paratypes of "*modestior*" (R. Rohde.—Frankf.M.; M.C.Z.). — FERNANDO PO: Bantabury Plantation (A. Green.—M.C.Z. ex Connolly Collection).

#### Measurements of Adult Shells

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
101.5 mm.	54	61.5	30	61½	6	"West Africa"
86.5	48.5	50	26	6	6	" "
86	50	52.5	29	6	6	Bibundi
84.5	49	49.5	27.5	6	6	Moliwe
80.5	48	46.5	27	6	6	" "

A shell at U.S.N.M. (No. 516847), labelled Assinie, Ivory Coast, appears to be a dwarfed *A. m. eduardi*. It is 66.5 mm. long, 37 mm. wide, of 5¾ whorls, with the aperture 38.5 by 21 mm. Though not quite full-grown, it is narrower than other *eduardi* of approximately the same age. It resembles somewhat the dwarf variety (paratype) of *modestior* of O. Boettger's Pl. 7, fig. 3. The locality Assinie is open to question, there being no other reliable record of any race of *marginata* from West of Dahomey. Mr. T. Pain recently sent me a similar shell, with strongly concave columella, equally slender, but larger though

immature, from Fernando Po, 76 mm. long, 40 mm. wide, of nearly 6 whorls, with the aperture 41.5 by 20.5 mm. Both shells have a bluish-white columella.

e. *A. MARGINATA EGREGIELLA* Bequaert and Clench

Pl. 62, fig. 1

*Archachatina (Magachatina) marginata* var. *egregiella* Bequaert and Clench, 1936, Rev. Zool. Bot. Afric., **29**, pt. 1, p. 83; Pl. 1, fig. 3 (Cameroon: Kribi).

Original description of *A. marginata* var. *egregiella* Bequaert and Clench (1936): "Agrees in general type of coloration with var. *egregia*, but the first three whorls are vinaceous-red like the columella and the outer lip is broadly margined inside with the same vinaceous color. In the single, probably immature type, the columella is nearly straight and the aperture is much narrower than in *egregia*. Length, 80 mm.; greatest width, 47.2 mm.;  $5\frac{1}{2}$  whorls."

This form is known thus far only from the holotype (M.C.Z. No. 73135), in which the aperture is 45.5 mm. long and 23.5 mm. wide.

f. *A. MARGINATA EGREGIA* (Dautzenberg)

Pl. 54, fig. 2; Pl. 71, fig. 2

*Achatina marginata* var. v. Martens, 1876, Monatsber. Ak. Wiss. Berlin, p. 257; Pl. 2, fig. 1 (animal. Cameroon: Victoria. The figure shows the lower half of the body-whorl entirely dark brown and the columella is said to be reddish).

*Achatina (Archachatina) marginata* var. *egregia* Dautzenberg, 1921, Rev. Zool. Afric., **9**, p. 95; Pl. 6, fig. 3 (Cameroon: Yaunde, at 750 m.).

*Archachatina (Magachatina) marginata* var. *egregia* Bequaert and Clench, 1936, Rev. Zool. Bot. Afric., **29**, pt. 1, p. 83 (Cameroon: Yaunde; Bitye; Lolo-dorf; Metet; Kribi in Pangwe District).

*Achatina marginata* var. *nigrofasciata* "Thiele" Tessmann, 1913, Die Pangwe, **2**, p. 270 (Cameroon: Pangwe District; without description). *Nomen nudum*.

Original description of *A. marginata* var. *egregia* Dautzenberg (1921) (translated from the French): "In shape this variety is close to typical *A. marginata*, but the whorls are more convex and the body-whorl is more swollen in the upper part. Its microscopic sculpture is finer, more distinctly granulose. The var. *egregia* is remarkable especially for its coloration; the columella is bright carmine-red and the early whorls are

reddish. The spire and the upper half of the body-whorl have dark-brown flammules on a white background covered with a golden-yellow periostracum. The lower half of the body-whorl is distinctly divided from the upper portion by a broad black band which descends to a short distance from the base, where it borders a white area surrounding the columella. In the var. *gracilior* [*A. marginata suturalis* Philippi], the columella is red and the summit of the spire reddish, as in var. *egregia*, but there is no dark band on the body-whorl and the longitudinal vertical brown flammules descend to the base. Some years ago, Mr. Chaper brought us from his journey to Assinie numerous *A. marginata* in which the lower half of the body-whorl is darker than the upper half, but this color is not very dark, does not hide the brown flammules that cross it and does not extend to the base of the shell." The type was presumably figured natural size, being then 96 mm. long, 58 mm. wide, with the aperture 59 by 33 mm. The original figure is copied in my Pl. 54, fig. 2. The type should have been in Dautzenberg's own collection and therefore should now be at the Brussels Museum; but I failed to see it in 1933.

The first mention of this striking color form was by v. Martens in 1876, but he did not name it. In 1913 Tessmann mentions a var. *nigrofasciata* "Thiele" from the southern Cameroon. Specimens thus labelled in Thiele's handwriting, were seen at the Berlin Museum in 1933 and referred to var. *egregia* by Bequaert and Clench (1936). These authors also noted that some shells of *egregia*, from Bitye, at the British Museum and elsewhere, bear a manuscript specific name (by Preston), meaning "festive."

Subsp. *egregia* is characterized by the broad dark chestnut-brown or nearly black transverse band which occupies most of the lower two-thirds of the body-whorl, beginning at the periphery and leaving only a narrow columellar area straw-colored. Upper part of body-whorl with relatively few chestnut wavy streaks or spots. Inner margin of columella vinaceous-red. Apex of spire pale yellowish or more or less roseate. Outer lip bluish-white inside over the paler, and darker bluish over the brown area.

An interesting variant of *egregia*, from Lolodorf, is fairly uniformly straw-yellow, with a few narrow, widely spaced pale brown vertical streaks on the penultimate and the upper part of the body-whorl; below the periphery the body-whorl is at first streaked like the upper part; but in the terminal half it has a fairly distinct, very pale brown, darkened band, sharply set off in the usual manner from the straw-yellow base. Apical four whorls roseate. Columella and most of parietal wall intensely violaceous-red. Inner edge of outer lip white. Shell seemingly full-grown, with slightly expanded outer lip, but small:

81 mm. long, 51 mm. wide, of 6 whorls, with the aperture 47.5 by 26 mm.

*Specimens Examined.* CAMEROON: without precise locality (Leid.-M.); Yaunde (Ac.N.S.Phila.); Bitye (Brit.M.); Lolodorf (A. I. Good.-Carn.M.; M.C.Z.; Ac.N.S.Phila.); Bipindi (M.C.Z.; M.U.Mich.); Ebolowa (E. D. Horner.-M.C.Z.); Ntem (Miss E. M. Daniels.-M.C.Z.); Efulen (M.C.Z.; M.U.Mich.; Ac.N.S.Phila.); Metet (A. I. Good.-Carn.M.; M.C.Z.; Brit.M.; Ac.N.S.Phila.); Pangwe District (G. Tessmann.-Berl.M.); Bafia, at edge of forest in North Central section (E. D. Horner.-M.C.Z.).

*Measurements of Adult Shells*

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
111 mm.	65	63	34.5	6 $\frac{1}{3}$	6	Metet
110	67	63.5	37	6 $\frac{1}{3}$	6	"
103	65	62	37	6	6	Yaunde
89	52	52	28	6	6	Lolodorf
84	50	49	26.5	6	6	"

Subsp. *egregia* evidently is smaller when full-grown than the nominate race of *A. marginata*. Dautzenberg's type was about average.

g. *A. MARGINATA CLENCHI*, new subspecies

Pl. 14, fig. 2

Agrees with *egregia* and *egregiella* in the color pattern, having the same broad blackish-brown band over the lower half of the last whorl, sharply divided from the straw-yellow base. The dark band is, however, most complete behind the outer lip, being elsewhere more or less interrupted by vertical pale yellow streaks. Summit pale colored or slightly roseate. Columella, parietal wall and inner edge of outer lip bluish-white, without any trace of violaceous. Most specimens seen are immature. The largest and more nearly adult, chosen as the holotype, has the dark band somewhat broken up in front. This form is mainly of interest as showing the evident connection of *egregia* and *egregiella* with subsp. *eduardi*. All four subspecies are similar in size and shape.

*Specimens Examined.* CAMEROON: Edea, holotype (G. Schwab.-M.C.Z. No. 167946) and 4 paratypes (G. Schwab.-M.C.Z. No. 153150); Sakbayeme, paratype (G. Schwab.-M.C.Z. No. 166380).

*Measurements of Holotype*

Length	Greatest		Aperture		Whorls	Edea
	Width	Length	Width	Length		
96.5 mm.	57	56	29		6½	

## h. A. MARGINATA GREVILLEI (Pfeiffer)

Pl. 81, fig. 5

*Achatina grevillei* Pfeiffer, 1860, Proc. Zool. Soc. London, (for 1860), p. 138 (Southern Nigeria: Old Calabar); 1861, Malak. Blätt., **8**, p. 78 (more complete description); 1868, Monogr. Helic. Viv., **6**, p. 213; 1876, *Op. cit.*, **8**, p. 274. Paetel, 1889, Cat. Conch.-Samml., 4th Ed., **2**, p. 239.

*Achatina (Achatinus) grevillei* Pfeiffer, 1879, Nomencl. Helic. Viv., p. 265.

*Archachatina grevillei* Pilsbry, 1904, Man. of Conch., (2), **17**, p. 112.

*Archachatina grevillei* Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 66.

*Archachatina (Magachatina) marginata* var. *grevillei* Bequaert and Clench, 1936, Rev. Zool. Bot. Afric., **29**, pt. 1, p. 81 (holotype and another specimen from Old Calabar).

*Achatina marginata*, albino variety, O. Boettger, 1905, Nachrichtsbl. D. Mal. Ges., **37**, p. 166 (in part. Cameroon: specimen from Bibundi, said to have the apex and columella colored as in *suturalis*; the other albino specimens from Johann-Albrechtshöhe and Mukonje Farm appear to have had a white columella and were therefore of subsp. *candefacta*).

Original description of *A. grevillei* Pfeiffer (1860): "T. ovato-oblonga, solida, striatula, sub epidermide tenui, fuscula olivaceo-lutescens; spira conica, obtusa; sutura crenulata, late impresso-marginata; anfr. 6-7, supremi minutissime decussati, ultimus spiram superans, sublaevigatus, peripharia obsolete angulatus; columella subtorta, purpurea, anguste truncata; apertura parum obliqua, angulato-ovalis, intus margaritaceo-albida; perist. tenue, expansiusculum, marginibus callo purpureo, sursum pallidiore, junctis, dextro repando. Long. 105, diam. 55 mill." In 1861 Pfeiffer added that the aperture is 66 mm. long and 36 mm. wide. In 1933 I saw the type, of the Cuming Collection, at the British Museum. It is now figured for the first time (Pl. 81, fig. 5). It is the albino form of *A. marginata* with violaceous parietal wall and columella. It should be noted, however, that the columella of the type is now only partly roseate to vinaceous-red. It is one of the smaller specimens of the species, but fully adult, as shown by the number of whorls and the expanded outer lip.

*Specimens Examined.* SOUTHERN NIGERIA: Old Calabar, holotype (Brit. M.) and a similarly colored shell (Berl. M.). — Also an additional example from "West Africa" at Brit.M.

i. *A. MARGINATA ICTERICA* Bequaert and Clench

Pl. 26, fig. 1; Pl. 75, fig. 1

*Archachatina (Magachatina) marginata* var. *icterica* Bequaert and Clench, 1936, Rev. Zool. Bot. Afric., 29, pt. 1, p. 81 (Gaboon).

This form was originally described from an immature shell, from the Gaboon (holotype, M.C.Z. No. 45526), as "uniformly straw-yellow, also at apex, without any indication of streaks or spots. The interior of the aperture and upper part of the columella are slightly bluish." The type was 89.5 mm. long, 58 mm. in greatest width, of  $5\frac{1}{2}$  whorls, the aperture 60 by 32.5 mm. I have since seen two fully adult specimens, with expanded outer lip, also labelled "Gaboon," likewise straw-yellow, including the apex; but one of them shows faint traces of very pale brown, wavy vertical streaks. In all the aperture inside, the inner edge of the outer lip, the columella and the parietal wall are nearly white or very slightly tinged with blue. I figure both the holotype and one of the adults.

*Measurements of Adult Shells*

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
136 mm.	89	86	47	7		Gaboon
127.5	86	81.5	45	7		"

j. *A. MARGINATA CANDEFACATA* Bequaert and Clench

Pl. 74, fig. 2; Pl. 77, fig. 3

*Archachatina (Megachatinops) adelinae* var. *candefacta* Bequaert and Clench, 1936, Rev. Zool. Bot. Afric., 19, pt. 1, p. 87 (Cameroon: Johann-Albrechtshöhe).

*Archachatina modestior* var. *candefacta* Bequaert and Clench, 1938, The Nautilus, 52, p. 27.

*Achatina marginata*, albino variety, O. Boettger, 1905, Nachrichtsbl. D. Mal. Ges., 37, p. 166 (in part. Cameroon: specimens from Johann-Albrechtshöhe near Kumba, one of this lot being the holotype of *candefacta*; possibly also specimens from the Mukonje Farm).

Original description: "Differs from typical *adelinae* in the complete absence of dark markings. First four whorls pale orange-yellow, the remainder of the shell unicolorous straw-yellow; inside of the aperture and columella pure white. Shape and sculpture as in the typical

form." The holotype (M.C.Z. No. 79972), is 76.8 mm. long, 43 mm. wide, of 6 whorls, the aperture 46.9 by 23 mm. This form was at first erroneously referred to *A. adelinæ*. Subsp. *candefacta* has the characteristic "weave" microsculpture of *marginata*, of which no trace is to be found in *papyracea* (= *adelinæ*).

In addition to the holotype, possibly not fully adult, the M.C.Z. now has also another specimen, apparently full-grown, but unfortunately labelled "West Africa" only. It exceeds the type but slightly in size. Subsp. *candefacta* is clearly a dwarfed *A. m. icterica*, but is in proportion slightly narrower than the latter.

*Measurements of Adult Shell*

Length	Greatest Width	Aperture Length	Aperture Width	Whorls	
84 mm.	49	48	32	6½	"West Africa"

ARCHACHATINA (CALACHATINA) VENTRICOSA (Gould)

a. Typical *A. VENTRICOSA*

Pl. 6, fig. 3; Pl. 8, fig. 2; Pl. 9, fig. 2; Pl. 10, fig. 3;  
Pl. 22, fig. 3; Pl. 23, fig. 3; Pl. 45, fig. 1; Pl. 73, figs. 1-2

*Helix* (*Cochlitoma*) *marginata* Rang, 1831, Ann. Sci. Nat., **24**, p. 33 (in part: specimens from Coast of Malaguette [=Liberia] and Ivory Coast; not the description). Not of Swainson, 1821.

*Achatina marginata* Pfeiffer, 1848, Monogr. Helic. Viv., **2**, p. 249 (in part: records from Coast of Malaguette and Ivory Coast). Not of Swainson, 1821.

*Achatina purpurea* Philippi, 1849, Abb. Besch. Conch., **3**, pt. 5, p. 30 (p. 8 of *Achatina*) (shell used for comparison with his *A. rhodostoma*). Not of Gmelin, 1790.

*Achatina ventricosa* Gould, 1850 (April), Proc. Boston Soc. Nat. Hist., **3**, p. 195 (Liberia, in the interior; although no precise locality was given, the specimens were part of a lot of shells collected in the Cape Palmas area by Dr. George A. Perkins); 1862, Otia Conchologica, p. 208. (Anonymous), 1875, 27th Ann. Rept. New York State Mus., (for 1873), p. 51 (Gould's type). Boucard, 1901, Cat. Coll. Coq. Terr., p. 50.

*Archachatina ventricosa* Pilsbry, 1905, Man. of Conch., (2), **17**, p. 113 (Ivory Coast: Taboo.<sup>1</sup> Liberia: Cape Palmas); Pl. 21, fig. 6 (full-grown specimen from Cape Palmas); Pl. 23, fig. 19 (immature specimen from Taboo). Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 67.

<sup>1</sup> The locality Taboo, now in the French colony of the Ivory Coast, is only some 30 miles East of Cape Palmas.



*Archachatina (Magachatina) ventricosa* Bequaert and Clench, 1936, Rev. Zool. Bot. Afric., 29, pt. 1, p. 85 (Liberia: Camp No. 3 on Du River; Paiata; Suah Koko; Bolahun; Cape Palmas. Ivory Coast: Taboo); Pl. 2, fig. 13 (specimen from Taboo at Ac.N.S.Phila.).

Gould's original description is as follows: "Testa magna, solida conico-ovata, ex corneo virescente, longitrorsum obscure flammulata, granoso-reticulata; spira conica, anfr.  $6\frac{1}{2}$  convexis, ultimo ventricoso, obtuse carinato; sutura subcrenulata; apertura rotundato-ovata  $\frac{3}{5}$  long. testae adequante; labro everso intus incrassato, submargine et columella nitide purpureis; columella valde arcuata. Long. 5 [=127 mm.]; lat.  $3\frac{1}{2}$  poll. [=89 mm.]; aperturae long. 3 [=76 mm.]; lat.  $1\frac{3}{4}$  poll. [=45 mm.]. Closely allied to *A. purpurea*, but the form is constantly more ventricose, and by comparing an extensive series, including the young, the difference is plainly not accidental. The color is more mixed with green and less conspicuously flammulated, and often flecked with triangular pale spots, and the aperture more of a blood red." I have seen the only definitely known type specimen now extant in the Gould Collection, as it was bought by the New York State Museum at Albany, New York, in 1863 (lot No. 187). This shell, at present on temporary loan at the M.C.Z., is here figured for the first time (Pl. 22, fig. 3). It is much smaller than Gould's measurements, being only 109 mm. long, 70 mm. in greatest width, of  $6\frac{1}{3}$  whorls, the aperture 65 by 37 mm. It is, moreover, immature and does not have the thickened and expanded outer lip mentioned in Gould's description. Nevertheless it is easily matched with some of the specimens I collected in Liberia. Gould evidently gave the measurements of the largest of his several specimens, which was in fact close to the record size of the species. He considered all his shells as cotypes, distributing them freely to other collectors and keeping only the smaller, immature one in his own collection. One of the larger shells at the M.C.Z., now merely labelled "West Africa", comes so close to Gould's original measurements that it might well have been the one he measured. Its history is unfortunately unknown.

When in perfect condition, the shell is a dirty, dark or light olivaceous-yellow, with the summit yellowish or roseate, sometimes with a spiral pale brown line at the periphery of the last whorl, and with vertical dark chestnut-brown streaks at irregular intervals, particularly on the early whorls; in addition it is often sparsely speckled with irregularly distributed dark spots. The periphery is often very obtusely carinate, particularly in immature shells. The nepionic whorls of young shells are densely covered with medium-sized granulations in regular spiral and vertical rows. On the post-nepionic whorls the

granulations become gradually coarser, but less regular, being developed even below the periphery on full-grown shells. On the body-whorl the sculpture is distinct to the eye without magnification and easily felt by touch. The color of aperture inside, columella and parietal wall in fresh adult shells varies from violaceous pink to salmon pink, but is often faded in part; the inner edge of the outer lip is violaceous-black and a narrow violaceous-black streak often borders the outer side of the parietal violaceous area. The last three whorls are deeply depressed and margined by a line below the suture. The shell is very broadly oval, with a long and swollen body-whorl, rather sharply set off from the short, narrow spire. The aperture, though broadly semi-elliptical to nearly semi-circular, is relatively longer for its width than in *A. purpurea*, which, moreover, in fully adult shells is decidedly narrower than *A. ventricosa*. The granulose sculpture of the nepionic whorls is almost always completely worn off in fully adult living snails. The smallest young shell seen, 23.5 mm. long, of  $3\frac{3}{4}$  whorls, has the early whorls granulose, except for the wrinkled first; it also has a deep, open umbilical slit.

Pfeiffer (1853, Monogr. Helic. Viv., 3, p. 484; 1859, *Op. cit.*, 4, p. 601; 1868, *Op. cit.*, 6, p. 213; 1876, *Op. cit.*, 8, p. 273; 1879, Nomencl. Helic. Viv., p. 265) treated *ventricosa* as a synonym of *A. rhodostoma*, at first doubtfully, later definitely. Pilsbry (1905) recognized it as distinct from both *rhodostoma* and *purpurea*. I have reached the same conclusion from a study of numerous specimens, mostly gathered by myself in several Liberian localities over a wide area. I cannot, however, attach much importance to the supposed difference in sculpture between *ventricosa* and *purpurea*. Moreover, it is sometimes difficult to decide whether a given specimen is a very large *purpurea* or an immature or dwarfed *ventricosa*.

*Specimens Examined.* SIERRA LEONE: Njala, Dasse Chiefdom, Moyamba District (T. S. Jones.—M.C.Z.). — LIBERIA: without more precise locality (M.C.Z.; U.S.N.M.); Harbel (Firestone Plantation) on the Du (or Dukwa) and Farmington Rivers; Suah Koko; Dobl Id.; Sanoyea; Paiata; Zuodumai; Jenne; Sodu; Degei; Zorzor; Popolahun; Bolahun; Kasia; Kailahun; Pandamai; Nyandamolahun; Bondualahun; Sardu Pascia; Vasala; Poyakamara (all collected by J. Bequaert.—M.C.Z.); Bolahun (E. Maass.—Hamb.M.); Ganta (G. W. Harley.—M.C.Z.); Cape Palmas (M.C.Z.; U.S.N.M.; Ac.N.S.Phila.). — IVORY COAST: Taboo (Ac.N.S.Phila.); Grand Bassam (M.C.Z.); Assinie (Chaper.—Terv.M.) — Also several merely labelled "West Africa" (M.C.Z.; Ac.N.S.Phila.).

*A. ventricosa* is known at present only from southeastern Sierra Leone (about  $12^{\circ} 10' W.$ ,  $8^{\circ} 5' N.$ ), Liberia, where it is one of the most

common snails, and the Lower Ivory Coast (as far East as 3° 15' W.). It is commonly eaten by the autochthonous Liberian natives. The egg is regularly ellipsoidal, 16 to 17 mm. long and 12 to 12.5 mm. wide.

*Measurements of Adult Shells*

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
128 mm.	81	80	44	6½		West Africa
126	86	74	47.5	6½		"
118.5	76	75	41.5	6½		Grand Bassam
115	78	69	44.5	6½		Cape Palmas
114	76	73	40	6¼		West Africa
110.5	68	69	40	6		Harbel
109	74	72	41	6		Degei
103	66	65	36	6		Cape Palmas
100.5	61.5	57	35	5½		West Africa
98.5	62	63	33	5½		Sardu Pascia
95	63	61	34	5½		Degei
92	60	59	33	5½		Vasala
88	57.5	51.5	29.5	5½		West Africa
85	57	56	31	5½		Cape Palmas

b. *A. VENTRICOSA SPECTACULUM* Pilsbry

Pl. 18, fig. 1; Pl. 25, fig. 3; Pl. 46, fig. 1; Pl. 49, fig. 1; Pl. 60, fig. 3; Pl. 61, fig. 5; Pl. 75, fig. 4

[The Heirs of G. W. Knorr, 1769, Vergnügen der Augen und des Gemüths, 4, p. 39; Pl. 24\*\*\*, fig. 1 (front view of a polished shell from the Schadeloock Collection); 1770, Délices des Yeux et de l'Esprit, 4, p. 44; Pl. 24\*\*\*, fig. 1; 1773, Verlosting der Oogen en van den Geest, 4, p. 24; Pl. 24\*\*\*, fig. 1].

*Bulla achatina* P. L. S. Müller, 1775, in Linné, Vollständ. Natursyst., 6, pt. 1, p. 414 (both description and citation of Knorr, Pl. 24\*\*\*, fig. 1, refer this to *A. ventricosa spectaculum*). Shaw and Nodder, 1800, Naturalist's Miscellany, 12, Pl. 438 (with date on Plate; error for Pl. 447; var. "with blue variegations and crimson mouth" and reference to Knorr, Pl. 24\*\*\*, fig. 1, of which Pl. 438 is a copy). Not of Linné, 1758.

*Achatina purpurea* Deshayes, 1851, in Férussac, Hist. Nat. Moll. Terr. Fluv., 2, pt. 2, p. 161 (in part), and Explanation of Plates, p. 17; Atlas, Pl. 123, figs. 1-2 (2 views of one shell; Plate published after Férussac's death, presumably in 1851); 1863, in Maillard, Notes Ile Réunion, 2d Ed., 2, Annex E, p. 90 (with reference to Férussac's Pl. 123, figs. 1-2; listed by error among the mollusks of Réunion). Not of Gmelin, 1790.

*Archachatina spectaculum* Pilsbry, 1933, Proc. U. S. Nat. Mus., 72, Art. 19,

p. 2 (holotype from "West Africa"; paratype from Gambia); Pl. 2, fig. 4 (holotype).

*Archachatina (Megachatinops) spectaculum* Bequaert and Clench, 1936, Rev. Zool. Bot. Afric., 29, pt. 1, p. 95.

Pl. 24\*\*\*, fig. 1 of the work published by Knorr's Heirs, after his death, shows a polished shell, which for shape and color could be either *A. degneri* or *A. ventricosa*. The accompanying text is meaningless and scarcely describes the figured shell. The oblique cross-lines of the figure may represent the decussate sculpture, distinct in *ventricosa*, very weak in *degneri*. Moreover, the narrow blackish inner edge of the outer lip and of the left margin of the parietal wall, shown in the figure, are frequent features of *ventricosa*, which I have not observed in any of the fairly many *degneri* seen. Knorr's figure, reproduced in my Pl. 61, fig. 5, is much too broad for *purpurea*. It is 117 mm. long, 75 mm. in greatest width, with the aperture 68 by 42 mm. In general shape it agrees best with what I here regard as subsp. *spectaculum*. Shaw and Nodder's Pl. 438 is so similar to Knorr's figure, that it is clearly a copy (see my Pl. 49, fig. 1).

Deshayes' Pl. 123, figs. 1-2 seem to be good representations of *specaculum* and agree closely with some of the specimens at M.C.Z. which I refer to this race. The shell is much too wide for true *purpurea*. It measures on the figures 98 mm. in length, 63 mm. in greatest width, with the aperture 55 by 30 mm. One of Deshayes' figures is copied in my Pl. 75, fig. 4.

Original description of *Archachatina spectaculum* Pilsbry (1933): "The solid, ovate-conic shell is between olive-ochre and honey-yellow, with straight, widely spaced, brown and light brownish-olive streaks, the spire whitish to pale brown with darker brown irregular streaks; apex whitish. The whorls are rather weakly convex, less so than in *A. purpurea* or *A. ventricosa*. Suture with a rather weakly defined margination. Surface closely granulose, the granules in spiral lines and superposed on the irregular axial wrinkles, a little weaker below the periphery; on the early whorls similar to those of *A. purpurea*. The aperture is ovate, pale vinaceous-pink within, somewhat darker within the lip edge. Columella and parietal callus vinaceous, with a darker outer edge. Measurements are as follows: Type: length, 105 mm. [an obvious misprint, the actual length of the type being 115 mm.]; diameter, 68.5 mm.; length of aperture, 72.2 mm.; number of whorls, 7. Paratype: length, 99 mm.; diameter, 61.7 mm.; length of aperture, 66.2 mm.; number of whorls,  $6\frac{1}{3}$ . The shape is about that of *A. rhodostoma* (Philippi), but it differs from that by the well-developed granulation of the last whorl, as in *A. purpurea* and *A. ventri-*

*cosa*, and by the longer aperture, over 68 per cent of the length of the shell, while in *rhodostoma* the aperture occupies about 57 per cent and in *A. rhodostoma splendida* about 69.6 per cent. In *A. spectaculum* the aperture is distinctly narrower than in *A. rhodostoma*, *purpurea*, or *ventricosa*. The parietal callus has a dusky edge, not a lighter edge as in *A. rhodostoma*, in this respect resembling *A. purpurea*. The interior in *A. spectaculum* is decidedly paler than in *A. purpurea* and *A. ventricosa*, and the whorls are much less convex than in those species." The proper placing of *A. spectaculum* among the purple-mouthed *Archachatina* has given considerable trouble. It was thought at first that it might be identical with what was later described as *A. degneri*. A careful study of holotype and paratype at U.S.N.M. has shown that this was not possible, since *A. degneri* shows only faint traces of decussation on the last whorls, particularly on the body-whorl, while these whorls are distinctly granulose in *spectaculum*. It was eventually recognized that *spectaculum* is very closely related to *A. ventricosa*. Some of the shells which I had previously called *ventricosa* were not separable from Pilsbry's types. As *A. ventricosa* is rather variable in size, shape and sculpture, *spectaculum* may well represent individual extreme variants of this species. Too few specimens with reliable localities are known, however, to reach a final conclusion at present; so that I provisionally retain *spectaculum* with subspecific status. It seems to differ from the nominate race of *ventricosa* only in being relatively more slender, with less convex body-whorl, more raised spire and the aperture higher in proportion to the width. It also has nearly one whorl more for the same size. It should be noted that neither of the types has the expanded outer lip of completely grown specimens; the paratype is more immature than the holotype, and also has the granulose sculpture less pronounced. The holotype is shown in Pl. 18, fig. 1, after a new photograph kindly made for this paper by the U.S.N.M. Measurements of more fully adult shells are given below and some of them are figured.

#### Measurements of Adult Shells

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
125.5 mm.	72	75.5	40	7 1/3		"West Africa"
115.5	67.5	67	37	7		Cape Palmas
110.5	66.5	60	35	7		Liberia
107	62.5	60.5	32	6 3/4		"
103.5	59.5	57.5	33	6 3/4		"
101	59	55.5	32	7		"

*Specimens Examined.* "West Africa," holotype (U.S.N.M. No. 406386) and several other shells (U.S.N.M.; M.C.Z.). "Gambia," paratype (U.S.N.M. No. 20222 [not 20220]), an extremely doubtful locality, as no other specimen of *Archachatina* has been reliably recorded from that section of West Africa. — LIBERIA: several without more precise locality (M.C.Z.); Cape Palmas (Ferrand.—M.C.Z.).

ARCHACHATINA (CALACHATINA) DEGNERI Bequaert and Clench

Pl. 18, fig. 3; Pl. 56, fig. 3; Pl. 69, fig. 2

- Achatina purpurea* Allen and Thompson, 1848, Narrative Expedition Niger in 1841, 2, p. 510 (Southern Nigeria: Nun River). Reeve, 1848, Conch. Icon., 5, *Achatina*, Pl. 4, fig. 15a (only). Shuttleworth, 1852, Mitth. Naturf. Ges. Bern, Nos. 248-249, p. 201 (specimens supposedly from Gaboon). v. Martens, 1886, Sitzungsber. Ges. Naturf. Fr. Berlin, p. 114 (Gold Coast: Abetifi). Not of Gmelin, 1790.
- Achatina rhodostoma* v. Martens, 1860, in Albers, Die Heliceen, 2d Ed., p. 203 (shell in Berlin Mus., 115 mm. long, 69 mm. wide, the aperture 69 by 44 mm.); 1893, Mitth. Deutsch. Schutzgeb., 6, pt. 3, p. 216 (Togo: Bismarckburg). Not of Philippi, 1849.
- Achatina* (*Archachatina*) *rhodostoma* Germain, 1912, Ann. Inst. Océanogr. Monaco, 5, pt. 3, p. 124 (Dahomey: Abomey). Not of Philippi, 1849.
- Archachatina rhodostoma splendida* C. R. Boettger, 1927, Abh. Senckenb. Naturf. Ges., 39, pt. 4, p. 355 (shell, later made the type of *degneri*, "supposedly from Duma, Belgian Congo," obviously a locality error). Not of Pilsbry, 1905.
- Achatina* (*Archachatina*) *rhodostoma* var. *splendida* Germain, 1912, Ann. Inst. Océanogr. Monaco, 5, pt. 3, p. 125, fig. 4 (Dahomey: Abomey). Not of Pilsbry, 1905.
- Achatina ventricosa* Spence, 1928, Jl. of Conch., 18, pt. 7, p. 213 (Gold Coast: Bunso Plantation, 10° 28' W., 6° 18' N.). Not of Gould, 1850.
- Archachatina* (*Magachatina*) *degneri* Bequaert and Clench, 1936, Rev. Zool. Bot. Afric., 29, pt. 1, p. 78 (shell supposedly from Duma, Belgian Congo, called *A. rhodostoma splendida* by C. R. Boettger in 1927); Pl. 1, fig. 1 (type).

I have not seen the shells called *purpurea* by Allen and Thompson (1848) and v. Martens (1866), *rhodostoma* by v. Martens (1860; 1893) and Germain (1912), and *ventricosa* by Spence (1928), listed in the foregoing synonymy. I have referred them to *degneri* on zoogeographical grounds, as these several species are not known at present with certainty to occur in the parts of West Africa from which these authors mentioned them.

As *A. degneri* is a common, large and conspicuously colored snail in the Gold Coast, where it is a usual article of the native diet, it was

no doubt known to some of the earlier malacologists and collectors. It seems to have been confused first with *A. purpurea* and later with other large *Archachatinae*, particularly *A. rhodostoma* and its var. *splendida*. Reeve's (1848) Pl. 4, fig. 15a unquestionably represents it, his specimen being about average size, 120 mm. long, 73 mm. in greatest width, the aperture 72 by 40 mm., and easily matched with some of the shells I obtained at Accra. Shuttleworth's (1852) supposed *purpurea*, with which he compared his *porphyrostoma*, was described as follows: "*A. purpurea*, ab auctoribus incomplete descripta et delineata, dimensionibus valde alienis gaudet. Specimina mea, ex Gabon missa, 117 mm. longa et 66 lata sunt. Apertura etiam 71 mill. longa et 48 lata: anfr. ultimus valde inflatus, peristoma etiam ut in *A. marginata* expanso-patulum. Specimina juvenilia (anfr. 5) 60 mill. longa et 48 lata: Apert. 37 mill. longa et 25 lata." These shells could only have been *degneri*, even though the species is not known to occur in Gaboon, so that the locality should be regarded as erroneous. *A. marginata*, which exists in Gaboon, is ruled out, first because Shuttleworth uses it for comparison; secondly because he mentions no difference in color from his *porphyrostoma*, so that his shells must have been extensively purplish inside the aperture, a character not found in any of the several forms of *marginata* with which I am acquainted. The dimensions given do not fit *A. rhodostoma*.

*A. degneri* was originally described as follows, from a single adult specimen: "Shell solid, subovate, imperforate and somewhat shiny. Color: first three and a half whorls uniformly light brownish-yellow; following two whorls barred with irregular reddish-brown axial streaks which overlie the light brownish-yellow ground color; the reddish-brown color bars continue to the aperture, but the ground color changes from brownish-yellow to a decided light greenish-brown. On the last two whorls there appear upon close inspection a series of faint grayish, very fine zigzag lines, arranged more or less axially. Entire interior area of aperture, columella and parietal callus a deep vinaceous-red (Ridgway's pomegranate purple); extreme inner edge of outer lip and outer margin of parietal callus grayish-purple. Whorls 7, convex, the last two impressed somewhat below the suture. Spire somewhat extended, produced at an angle of 60°. Body whorl about 77 per cent of the total shell. Aperture rounded-ovate, about 65 per cent of the length of the shell, widest below the middle. Palatal lip flaring, bell-like, slightly thickened. Columella rather wide and twisted within, nearly straight and rather abruptly and broadly truncate. Sculpture: first one and a half whorls minutely rugose, gradually merging into the distinct, but very fine, beaded, decussate sculpture of the next three and a half whorls; on the remaining whorls the

sculpture becomes irregular and the beading is only very faintly indicated; body whorl roughened somewhat by the coarse growth-lines."

The type of *A. degneri* (Pl. 69, fig. 2) was an unusually large specimen, moreover from an erroneous locality. The species was since collected alive in some numbers in the Gold Coast, so that it is possible to give some additional information which may help to recognize it. When fully adult, with well formed and expanded outer lip, the shell is similar in outline and shape of aperture and columella to the nominate race of *A. marginata* and even more so to *A. ventricosa*. The subsutural impressed line of *marginata* is often lacking in *degneri* and, if present (as in the holotype), it is rather weak and irregular. The periostracum of *degneri* lacks the regular criss-cross, cancellate ("weave-like") microsculpture of *marginata*; instead, when well preserved, it is microscopically and irregularly rugulose. The granulose decussation is more pronounced in *degneri* than in *marginata*, although of the same general type; but it is very much weaker than in *ventricosa* and *purpurea*, being barely visible to the naked eye on the body-whorl. In this respect *degneri* approaches *A. rhodostoma*, although the sculpture is even weaker in the latter. On the other hand the growth-striae of the body-whorl are usually coarser in *degneri* than in either *marginata* or *rhodostoma*. When full-grown, *rhodostoma* differs also from *degneri* in being more slender in outline, with much less ventricose body-whorl and a relatively narrower aperture. The immature stages of these two species can, however, be readily confused. I regard Germain's fig. 4 (1912) of a supposed *A. rhodostoma* var. *splendida* as a young *A. degneri*.

In the holotype, the columella, parietal wall, inner margin of outer lip (except for the narrow edge) and entire inside of the aperture to far back in the shell are a gorgeous deep vinaceous-red. This is true also of a few of the shells I collected in the Gold Coast. More often, however, the inside is reddish, in varying shades from orange-red to violaceous, only near the outer lip over a width of an inch or less. All transitions may be observed between these two extremes. Possibly the vinaceous color spreads inward from the outer lip with age and becomes also more intense as the adult snails grow older.

The smallest immature *degneri* seen, from Nsawam (Pl. 18, fig. 3), is 28.5 mm. long, 21 mm. wide, of about 4 whorls. The very first half nepionic whorl is finely wrinkled; the remainder are densely granulose, in fairly regular spiral rows, but much more weakly below the periphery of the fourth whorl. The columella has a broad and deep umbilical slit, but is strongly truncate at the base. At the next larger stage seen, 62 mm. long, of  $5\frac{1}{2}$  whorls, the columella shows no trace of a slit. In most adult shells the nepionic sculpture is fairly well preserved.



*Specimens Examined.* Holotype (Hamb.M.), labelled "Duma, Belgian Congo," certainly an erroneous locality; the shell having probably been obtained either in Togo or the Gold Coast. The collector, H. Schubotz, was a member of the Second German Central African Expedition of the Duke of Mecklenburg (1910-1911). This started from the West Coast of Africa, eventually travelling overland across Cameroon and French Equatorial Africa to the Ubangi River. Most probably the malacological collections were either incompletely labelled or had lost their labels before reaching Europe, and having been shipped from Duma were assumed to have been collected there. — GOLD COAST: Accra, many specimens, offered for sale in the native market; Bawaleshi near Accra; Suhum near Accra; Senchi on the Volta River; Nsawam (M.C.Z.—All collected by J. Bequaert, A. R. Mead, and V. Dethier. Several snails of these lots were dissected by Dr. Mead); St. George d'Elmira (Amst.M.). — DAHOMEY: Abomey (Brus.M.).

The holotype is the property of the Hamburg Museum and has now been returned there, having been in the custody of the M.C.Z. since 1935. It is unusually large, but some of the shells I obtained in Accra are only slightly smaller.

#### Measurements of Adult Shells

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
145 mm.	91	94	54	7		Holotype
137	82	83.5	47	6½		Accra
127.5	80.5	78.5	44	6½		Bawaleshi
120	72.5	75	42	6½		Accra
116.5	74	70	41	6½		Nsawam
114.5	71.5	68	41	6½		Suhum
107.5	65	64	37.5	6¼		Nsawam
101	63.5	64	36	6¼		"

In the Gold Coast *A. degneri* is a much appreciated article of the native diet, being considered superior in taste by the epicurians to *Achatina achatina*, which is also eaten there. It is nearly always found in the native markets and its gathering is strictly regulated by native tribal custom. The snail is mentioned by Dr. David Fairchild in his book "Exploring for Plants" (1930, p. 536), one of his photographs showing live snails offered for sale at Nsawam. In the London "Times Weekly Edition" of September 1, 1936, there appeared the following letter by one "W.G.G.C." relating to the "Snail Trade on the Gold Coast": "Many years ago I trekked into a village near the Western

Frontier and found it deserted, but for a very old couple. I learnt that the townspeople were prisoners of a former powerful Sefwi chief, upon whose land they had been caught poaching snails. Incidentally, this is the finest snailing country in the Colony, and a very large trade exists between it and Kumasi, the capital of Ashanti. The fee for a license to snail here was at one time £5, and a man could take away all that he could carry in one load, probably about £10 in value. It is usual to eat only the yearlings, the three-year-olds being the chief breeders." A more recent note on the subject in "The Field" (April 6, 1940, **175**, No. 4554, p. 546), by C. S. Cansdale, is entitled "Giant Forest Snails of the Gold Coast": "The giant forest snail forms one of the most important meat supplies of the Gold Coast forest country and the trade in dried snails reaches an annual value of thousands of pounds. The collection is carefully controlled by local rules concerning collecting areas, close seasons, etc., and these are rigidly enforced. Family parties set off into the dense forest and bring back loads of snails to their hunting camps or villages; the shells are broken and the snails impaled on long wooden skewers and smoked over wood fires. It is in this form that they are sold for soup making. The size of these two snails can be judged by the half a crown placed on the shell of one of them." Mr. Cansdale's accompanying photograph shows alive both species that are eaten in the Gold Coast: the left-hand snail is *Achatina achatina*, the right-hand one *Archachatina degneri*.

In Ashanti, where *Achatinae* seem to be particularly sought after, the Government issued in 1944 an Order regulating their collection. It empowered the Chief to prohibit or restrict the gathering of snails on land within his jurisdiction. Infringement of the Chief's orders was made liable to a fine of £5 or imprisonment for 2 months.<sup>1</sup>

#### ARCHACHATINA (CALACHATINA) RHODOSTOMA (Philippi)

Pl. 13, fig. 2; Pl. 22, fig. 2; Pl. 28, fig. 1;

Pl. 33, fig. 1; Pl. 73, fig. 3; Pl. 74, fig. 1

*Achatina purpurea* G. B. Sowerby, 1823 (March), Gen. Rec. Fossil Shells, pt. 14, *Achatina*, Pl., fig. 1 (with name on plate and in letterpress; no locality; shell 129 mm. long, 72 mm. in greatest width, the aperture 72 by 40 mm.). Reeve, 1842, Conch. System., **2**, p. 85; Pl. 176, fig. 1 (copy of Sowerby's fig.). Not of Gmelin, 1790.

*Achatina rhodostoma* Philippi, 1849 (April), Abb. Beschr. Conch., **3**, pt. 5, p. 29 (p. 7 of *Achatina*) (no locality); Pl. 2 (of *Achatina*), fig. 2. Pfeiffer,

<sup>1</sup> I am under obligation to the Colonial Secretary's Office at Accra and to Mr. M. A. Tazelaar, of University College, Achimote, Gold Coast, for a copy of this Government Regulation.

- 1849, Zeitschr. f. Malakoz., **6**, p. 92; 1853, Monogr. Helic. Viv., **3**, p. 484. H. and A. Adams, 1855, Gen. Rec. Moll., **2**, p. 132. Pfeiffer, 1857, Syst. Conch.-Cab., **1**, Abt. 13, pt. 1, p. 293; Pl. 23, fig. 3 (copy of Philippi's fig.). v. Martens, 1860, in Albers, Die Heliceen, 2d Ed., p. 201 (in part only). A. D. Brown, 1861, Cat. Shells Coll., p. 56 (Liberia: Cape Palmas). Bielz, 1865, Verzeichn. Moll. Conch.-Samml., 3d Ed., p. 23. Haines, 1868, Cat. Terr. Shells Coll., p. 68 (Liberia: Cape Palmas). Pfeiffer, 1868, Monogr. Helic. Viv., **6**, p. 213. Paetel, 1869, Moll. Syst. Cat., p. 80; 1873, Cat. Conch.-Samml., p. 99. Roeters van Lennep, 1876, Cat. Coll. Shells van Lennep, p. 53. Pfeiffer, 1877, Monogr. Helic. Viv., **8**, p. 273. Grasset, 1884, Index Test. Viv. Coll., p. 199. Rethaan Macaré, 1888, Cat. Coll. Coq. Mme. Rethaan Macaré, p. 23. Paetel, 1889, Cat. Conch.-Samml., 4th Ed., **2**, p. 240. Bourguignat, 1889, Moll. Afr. Equat., p. 77.
- Achatina* (*Archachatina*) *rhodostoma* Albers, 1850, Die Heliceen, p. 190.
- Achatina* (*Achatinus*) *rhodostoma* Pfeiffer, 1856, Malak. Blätt., **5**, (1855), p. 168; 1879, Nomencl. Helic. Viv., p. 265. Römer, 1891, Jahrb. Nassau. Ver. Naturk., **44**, p. 123.
- Archachatina rhodostoma* Pilsbry, 1905, Man. of Conch., (2), **17**, p. 115; Pl. 22, fig. 11 (after Philippi). Kobelt, 1910, Abh. Senckenb. Naturf. Ges., **32**, p. 67.
- Archachatina* (*Magachatina*) *rhodostoma* Bequaert and Clench, 1936, Rev. Zool. Bot. Afric., **29**, pt. 1, p. 84 (French Guinea: Kankan).
- Archachatina rhodostoma* var. *splendida* Pilsbry, 1905, Man. of Conch., (2), **17**, p. 116 ("West Africa"); Pl. 22, fig. 12 (holotype; refers to it also Reeve's Pl. 176, fig. 1 of 1842). Kobelt, 1910, Abh. Senckenb. Naturf. Ges., **32**, p. 67.
- Archachatina* (*Magachatina*) *rhodostoma* var. *splendida* Bequaert and Clench, 1936, Rev. Zool. Bot. Afric., **29**, pt. 1, p. 85; Pl. 2, fig. 12 (holotype.)

Original description of *A. rhodostoma* Philippi (1849): "A. testa oblongo-conica, crassiuscula, striata, sub epidermide fulvo-lutea albida, strigis crebris, rectis, rufis, longitudinalibus ornata; spira conica obtusiuscula; sutura parum crenulata, vix marginata; anfractibus  $6\frac{1}{2}$ , parum convexis, summis tenuissime decussato-granulatis, inferioribus laevissimis, ultimo spiram superante; columella valde arcuata, purpurea, basi oblique truncata; apertura ampla semiovali, in fundo lilacina, anterius purpurea; peristomate acuto, marginibus callo nitido purpurascente introrsum diffuso junctis. Alt.  $40''$  [= 87 mm.]; diam.  $23''$  [= 50 mm.]" The following additional remarks are translated from the German: "I had this species for a long time as *A. purpurea*, until I received a beautiful specimen of the latter from M. Petit de la Saussaye, and found it to differ greatly from the present shell. Apart from the size, which reaches  $4\frac{1}{2}$  inches [= 117.5 mm.] in *purpurea*, that species is much wider, more conical, more pointed, the sutures are strikingly marginate, which is scarcely indicated in *A. rhodostoma*;

finally the surface is distinctly and strongly granulose in *A. purpurea*, even on the body-whorl, not at all *obsolete decussata*. The color likewise differs somewhat. Lamarck describes *A. purpurea* as brownish-red, with spaced, oblique, zigzag rust-brown streaks, and the body-whorl beneath the yellow periostracum pale bluish-violet or grey, with occasional dark vertical streaks. Our *A. rhodostoma*, on the other hand, is ornamented with straight reddish-brown vertical streaks on a pale brownish-white background, the streaks very crowded on the body-whorl, where they cover much more of the surface than the ground-color." The present location of the type is unknown. The foregoing account, together with the original figure, copied in my Pl. 13, fig. 2, makes recognition not too difficult, although it is one of the rarer species in collections. Philippi compared it evidently, not with the true *A. purpurea* (Gmelin) as recognized in the present paper, but with *A. ventricosa* (Gould), which actually differs from *rhodostoma* in the characters he pointed out.

Pilsbry's var. *splendida* is in my opinion a fully adult specimen of *rhodostoma* with the outer lip thickened and expanded, Philippi's type being as yet immature. It was described as follows: "Acute ovate, thick and heavy. Whorls  $6\frac{1}{2}$ , the last two with a distinct sutural margin. Surface minutely, somewhat obsoletely granulose even on the last whorl; irregularly streaked with brown on a lighter ground, under a thin yellow cuticle, the spire marbled with white and angularly streaked with brown. Aperture bright pink inside, with a band of deeper salmon-pink near the edge, which is bordered with white. Columella similarly colored. The outer and basal margins of the lip are expanded. Length 117, diam. 70, length of aperture 70 mm." I have studied in Philadelphia the unique type, shown in my Pl. 28, fig. 1, from a photograph. The aperture is 38 mm. wide. The granulation of the body-whorl is much weaker than in *A. ventricosa* and *A. purpurea*. As recognized by Pilsbry, the same form was figured, as *A. purpurea*, by Sowerby (1823) and Reeve (1842), both figures being based on the same shell. Sowerby's original is copied in my Pl. 74, fig. 1. It shows the largest known example of the species, being 128.5 mm. long, 72 mm. wide, with the aperture 72 by 41 mm.

The true *A. rhodostoma* is rare in collections. Shells so called are more often *A. purpurea* or immature *A. ventricosa*. Although included in my bibliography, the shells recorded by A. D. Brown (1861), Bielz (1865), Haines (1868), Paetel (1869, 1873, 1889), Roeters van Lennep (1876), Grasset (1884), Rethaan Macaré (1888) and Römer (1891) may not all be correctly named. The reported locality Cape Palmas I cannot at present regard as reliable. There are thus far only three precise localities for the species. Popolahun, in northwestern Liberia

(8° 15' N., 10° 15' W.), Kankan, in French Guinea (10° 20' N., 9° W.), and Bouaké, in the Ivory Coast (about 7° 38' N., 5° W.). I was fortunate to collect at Popolahun a fair number of specimens in various stages of growth, which enabled me to recognize the true specific characters and also to connect the immature "*rhodostoma*" with the fully adult "*splendida*" stage.

*A. rhodostoma*, when fully adult, is most easily recognized among the purple-mouthed *Archachatinae* by the extremely weak decussate or granulose sculpture, which it shares only with *A. degneri*. On the body-whorl and over most of the penultimate whorl the granulations are small or even superficial, sometimes nearly lacking, being barely seen with the naked eye and not felt by touch. The granulation is perhaps even less pronounced in *A. degneri*, which however, has coarse growth-striae, while in *rhodostoma* the surface of the body-whorl is nearly even. In general shape *rhodostoma* is often relatively more slender, with a somewhat higher spire, than *degneri* and *ventricosa*. Some of the more slender *ventricosa* may approach it in shape, in which case the two must be separated solely on the basis of sculpture. At Popolahun I collected both species, but was unable to find truly transitional specimens. On the other hand, while immature and particularly very young *rhodostoma* are decidedly more slender than *ventricosa* or *degneri* of the same age, they are very similar in shape to some adult *A. purpurea*, a species which does not develop an expanded outer lip when full-grown. Young *rhodostoma* are more finely granulose than *purpurea* and the whorls are not so convex. *A. rhodostoma* may sometimes simulate small *A. marginata*, particularly if the inside is not fully colored or is faded; but the periostracum lacks the criss-cross microsculpture of that species, being instead minutely and irregularly rugulose.

#### Measurements of Adult Shells

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
120.5 mm.	72	71	37	6½		Popolahun
115	69	69	36	6½		"
102	62	56	33	6⅓		"West Africa"
101	62	63	35	6⅓		Popolahun
98	63	62.5	33.5	6		"
96.5	57	54	30.5	6⅓		"
91	53	52.5	28	6		"West Africa"
88	51.5	50.5	27.5	6		Popolahun

*Specimens Examined.* "West Africa," holotype of *A. rhodostoma* var. *splendida* (Ac.N.S.Phila., No. 3095), and some immature shells (Hamb.M.; Ac.N.S.Phila.; Leid.M.; Amst.M.; Berl.M.; Brit.M.; U.S.N.M.; M.C.Z.). — LIBERIA: without more precise locality (Brus. M.); Popolahun (J. Bequaert.-M.C.Z.). — FRENCH GUINEA: Kankan (Brus.M.; M.C.Z.). — IVORY COAST: Bouaké (R. Delattre.-M.C.Z.).

### 3. Subgenus MEGACHATINOPSIS Bequaert and Clench

*Archachatina* subg. *Megachatinopsis* Bequaert and Clench, 1936, Rev. Zool. Bot. Afric., **29**, pt. 1, p. 76. Type by original designation: *Achatina knorrii* Jonas, 1839.

*Archachatina* subg. *Megachatinops* Bequaert and Clench, 1936, Rev. Zool. Bot. Afric., **29**, pt. 1, p. 87 (misspelling of *Megachatinopsis*, with same type).

Full-grown shell medium-sized (50 to 120 mm. long), broadly ovate, elongate ovate, or spindle-shaped, of 5 to 7 whorls, normally dextral, often thin and light. Surface even; nepionic whorls of newly hatched snails finely granulose; later whorls either granulose, coarsely decussate or almost smooth. Outer lip always simple, the edge usually thin and sharp, not at all expanded.

1. *A. camerunensis* d'Ailly, 1896. See Pl. 53, fig. 4 (summit).
2. *A. knorrii* (Jonas, 1839). See below.
3. *A. papyracea* (Pfeiffer, 1845). See below.
4. *A. purpurca* (Gmelin, 1790). See below.
5. *A. siderata* (Reeve, 1849). See below.

#### ARCHACHATINA (MEGACHATINOPSIS) KNORRII (Jonas)

Pl. 37, figs. 1-2; Pl. 39, fig. 2; Pl. 40, fig. 1; Pl. 51, fig. 3; Pl. 53, fig. 1; Pl. 56, fig. 1; Pl. 76, fig. 1

[The Heirs of G. W. Knorr, 1768, Vergnügen der Augen und des Gemüths, **3**, p. 11; first printing of the Plates of the 1st Edition, Pl. 3\*\*, fig. 1 (Plate marked "ex Museo Breynianio"); 1768, Délices des Yeux et de l'Esprit, **3**, p. 11; first printing of Pl. 3\*\*, fig. 1 (as above)].

*Achatina knorrii* Jonas, 1839, Arch. f. Naturgesch., **5**, pt. 1, p. 345 (description of 2 shells; no locality; with reference to Knorr's Pl. 3\*\*, fig. 1). Catlow and Reeve, 1845, Conchologist's Nomenclator, p. 165. Pfeiffer, 1848, Monogr. Helic. Viv., **2**, p. 250; 1853, *Op. cit.*, **3**, p. 485 (West Africa. New description of shell in Hamburg Mus.). H. and A. Adams, 1855, Gen. Rec. Moll., **2**, p. 132. Pfeiffer, 1859, Monogr. Helic. Viv., **4**, p. 601. v. Martens, 1860, in Albers, Die Heliceen, 2d Ed., p. 201. Pfeiffer, 1865,

- Syst. Conch.-Cab., 1, Abt. 13, pt. 1, p. 365; Pl. 47, figs. 11–12 (specimen). Haines, 1868, Cat. Terr. Shells Coll., p. 67. Pfeiffer, 1868, Monogr. Helic. Viv., 6, p. 214; 1876, *Op. cit.*, 8, p. 274; 1877, *Op. cit.*, 8, p. 616. Dohrn, 1878, Jahrb. D. Mal. Ges., 5, p. 156 (Liberia). Grasset, 1884, Index Test. Viv. Coll., p. 199. Schepman, 1888, Notes Leyden Mus., 10, p. 247 (Liberia). Paetel, 1889, Cat. Conch.-Samml., 4th Ed., 2, p. 240. Büttikofer, 1890, Reisebilder aus Liberia, 2, pp. 454 and 481. Johnston, 1906, Liberia, 2, p. 861.
- Achatina* (*Archachatina*) *knorri* Albers, 1850, Die Heliceen, p. 190.
- Achatina* (*Achatinus*) *knorri* Pfeiffer, 1856, Malak. Blätt., 2, (1855), p. 168; 1879, Nomencl. Helic. Viv., p. 265.
- Achatina* (*Urceus*) *knorrii* Mörch, 1857, Cat. Conch. Suenson, p. 6.
- Serpaea knori* Bourguignat, 1889, Moll. Afr. Equat., p. 85.
- Archachatina knorrii* Pilsbry, 1905, Man. of Conch., (2), 17, p. 118; Pl. 20, figs. 1–3 (2 specimens). Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., 32, p. 66.
- Archachatina* (*Megachatinopsis*) *knorri* J. Bequaert and Clench, 1936, Rev. Zool. Bot. Afric., 29, pt. 1, pp. 76 (as type of subg. *Megachatinopsis*) and 91 (Liberia: Camp No. 3 on Du or Dukwa River [now Harbel Plantation]; Kakatown [Kakata]; Gbanga; Paiata; Vahun; Robertsport).
- Achatina prunum* Reeve, 1849, Conch. Icon., 5, *Achatina*, Pl. 4, fig. 13 (West Africa). H. and A. Adams, 1855, Gen. Rec. Moll., 2, p. 132. (Anonymous), 1875, 27th Ann. Rept. New York State Mus., (for 1873), p. 51 (specimen in Gould Coll.). Roeters van Lennep, 1876, Cat. Coll. Shells van Lennep, p. 54.

In Knorr's work, vol. 3 of which was published after Knorr's death by his Heirs, the following text (translated here from the German) describes Pl. 3\*\*, fig. 1, of the first German and French printings of part 3: "This thin buccinum with broad waves is the most ventricose of all. The first whorl [= body-whorl] is beautifully convex; its ground color is white, drenched with red like that of apple-flowers, over which descend broad chestnut-brown waves. The upper whorls [= spire] are beautifully red. The shell is thin, transparent and whitish inside, but in such a way that the brown waves show through somewhat. Some specimens are half a foot long; but there is also a small kind which measures only one or two inches." In the French copies, the text is a fairly exact translation from the German.<sup>1</sup> The figure, copied in my Pl. 39, fig. 2, is clearly based on the species later described by Jonas as *Achatina knorrii*. It shows, from the back, a shell deprived of the periostracum and probably polished, 83 mm. long and 47 mm. in greatest width, being one of the largest known of the species.

Jonas' original description of *A. knorrii* was as follows: "*A. testa*

<sup>1</sup> Some copies of part 3 of Knorr's work, both with the French and the German text, have plates of a second printing. In these, Pl. 3\*\*, fig. 1, represents *Archachatina marginata* (Swainson), not *A. knorrii*. The matter is discussed at some length under *A. marginata*.

ovata, ventricosa, decussata, superne intense rosea, inferne ex roseo albescente, flammis longitudinalibus fuscis inferne latioribus, ad basin confluentibus, ibique nigrescentibus eleganter picta; anfractibus senis convexis, duobus infimis infra suturam linea impressa circumdatis, ultimo spira longiore; spira conica, obtusa; apertura oblongo-ovata, intus alba, labro limbo fusco marginato; columella arcuata, callosa, nitida, alba. Longit. 2'' 11''' [German inches and lines=76 mm.]. Latit. 1'' 8''' [=43.5 mm.]. Aperturæ altitudo 1'' 10''' [=48 mm.]. Epidermis viridi-flava est." This description was based on two shells, whose present whereabouts is not known. Jonas' reference to Knorr's figure is to the first printing of the Plates of vol. 3. The shell described anew by Pfeiffer in 1853, from the Hamburg Museum, may have been one of Jonas' types, as the measurements agree fairly well. Pfeiffer's (1865) figures appear to be of another shell, however. Pilsbry's (1905) figures are excellent.

Original description of *A. prunum* Reeve (1849): "Achat. testâ ovata, tenui, ventricosiuscula, spira apicem versus obtusa, anfractibus quinque, infra suturas appressis, laeviusculis, apicem versus minutissime decussatis, columella arcuata, vix truncata; aureo-lutescente, castaneo latistrigata, superne purpureo-rosea. Shell ovate, thin, rather ventricose, obtuse towards the apex, whorls five in number, appressed beneath the sutures, somewhat smooth, very minutely decussated towards the apex, columella arched, but slightly truncated; pale golden-yellow, broadly streaked with chesnut, purple-rose towards the upper part. A striking species, distinguished by its obtuse growth and peculiar colouring. The last whorl is of a delicate golden-yellow, marked with dark chesnut streaks converging together at the base, whilst the upper whorls are of a purple-rose, indistinctly spotted at the sutures. The species may possibly have been taken for the young of *A. marginata*, but is certainly distinct." Although *prunum* was described from the Cuming Collection, I was unable to find the type at the British Museum in 1933. Possibly Cuming recognized later that it was *A. knorrii* and deleted Reeve's name from his collection. Fortunately there can be little doubt that it is a synonym of *knorrii*. Reeve's figure, copied in my Pl. 40, fig. 1, is 68 mm. long, 39 mm. wide, with the aperture 38 by 21 mm. Some of the *knorrii* I collected in Liberia agree well with it.

Adult *A. knorrii* is a medium-sized shell, rarely exceeding 80 mm. in length, broadly fusiform or spindle-shaped, light, thin but fairly solid, translucent, the darker pattern showing inside the aperture; elliptical in outline, widest at about mid-length. Spire short, scarcely narrower than the base, forming a very wide cone, ending in a broadly rounded, dome-shaped apex. Whorls  $5\frac{1}{4}$  to  $5\frac{1}{2}$ , moderately and



increasingly convex from the third on, with narrow, shallow sutures. Flattened subsutural area as a rule restricted to the body-whorl, narrow, set off by a weakly impressed line. Upper 3 whorls (including nepionic shell) forming a broad, hemispherical dome; first whorl much flattened; succeeding whorls gradually increasing in length and width. Body-whorl very long, about four-fifths of the total length of the shell in front view, fairly obese, slightly more convex than penultimate whorl. Aperture broadly semi-elliptical, longer than half, though shorter than two-thirds of the total length of the shell; outer margin evenly and moderately curved. Inside bluish-white, the inner edge with a broad, dark purplish-brown margin. Outer lip thin, sharp, not at all expanded nor flaring, scarcely or not produced forward in profile, not appreciably descending at the insertion on the body-whorl. Parietal wall with a very thin, bluish-white glaze. Columella very narrow, nearly straight or slightly concave, gradually narrowed below to the oblique truncation, which is placed close to the base of the outer lip; entirely bluish-white in all examples seen. Youngest shell seen (31 mm. long; 4 whorls) with the early 3 whorls densely and minutely granulose in spiral rows, except the first which has fine vertical wrinkles (Pl. 76, fig. 1). Granulose sculpture rapidly decreasing in strength from the fourth whorl on, faintly indicated or nearly wanting on the body-whorl, which to the naked eye appears smooth with many low growth-wrinkles; under the lens it shows a few, weak, more or less interrupted engraved lines, below as well as above the periphery and is in addition microscopically rugulose, but not "cancellate." Periostracum thin, readily lost, very pale straw-yellow, shiny; shell underneath it white, except on the spire which is dull purplish-red (sometimes faded to pink) as far as most of the penultimate whorl. Early whorls with only faint traces of vertical darker streaks, which become more pronounced on the penultimate whorl. Body-whorl, as a rule, boldly marked with broad, straight, wavy or zigzag, dark chestnut-brown streaks, fairly regularly spaced; streaks often extending separately from suture to base, sometimes confluent near the columella; or they may be narrow, interrupted, divided into fine, wavy lines, or broken up into blotches above the periphery, or some of them may stop abruptly at the periphery; in a few shells most of the lower half of the body-whorl chestnut-brown, irregularly jagged toward the periphery. In addition, the subsutural depressed area is ornamented with alternate yellowish and dark-brown blotches, some of the latter connected with vertical streaks, producing a peculiar tessellated design, more pronounced in some shells than in others. The tessellation occurs also on the spire, where it may be traced to the third whorl in young shells. The egg is as yet unknown.

*Specimens Examined.* LIBERIA: several without more precise locality (Ac.N.S.Phila.; U.S.N.M.; M.C.Z.; Amst.M.; Leid.M.; Berl.M.); Harbel (Firestone Plantation), on the Du or Dukwa River (J. Bequaert.-M.C.Z.); Kakata (J. Bequaert.-M.C.Z.); Paiata (or Pehata) (J. Bequaert.-M.C.Z.); Degei (J. Bequaert.-M.C.Z.); Gbanga (J. Bequaert.-M.C.Z.); Paynesville near Monrovia (J. Bequaert.-M.C.Z.); Lakrata (J. Bequaert.-M.C.Z.); Jenne (J. Bequaert.-M.C.Z.); Vahun (E. Maass.-Hamb.M.); Ganta (G. W. Harley.-M.C.Z.); Robertsport (J. Büttikofer.-Leid. M.).—Several collections also have specimens labelled merely "West Africa." I have seen some erroneously labelled "Niger" (Brus.M.) and "Prince's Island" (U.S.N.M.).

*A. knorrii* is known with certainty from Liberia only, where it is restricted to primary rain forest and appears to be fairly widely distributed, although there are as yet no records from the southeastern half of the country. It appears to be absent from the Cape Palmas region. It disappears where the primary rain forest is replaced by thickets of second-growth woody vegetation. As the virgin forest is now being rapidly destroyed, the species may well become extinct within the next half century. The snail is strictly terrestrial and lives so well hidden in the undergrowth and litter that it is rarely seen alive.

d'Ailly's (1896) records of *A. knorrii* from Cameroon were based on misidentifications of *A. papyracea* (Pfeiffer), which resembles it somewhat in shape and pattern. *A. knorrii* lacks, however, the more distinct granulation of the body-whorl of adult *papyracea*. I saw d'Ailly's specimens at the Stockholm Museum in 1933.

#### Measurements of Adult Shells

Length	Greatest		Aperture		Whorls	
	Width	Length	Width			
81.5 mm.	48.5	49	25	5½		"West Africa"
76	41	43.5	21.5	5½		" "
75	44	44	24	5½		Liberia
72.5	41	45.5	23	5½		Harbel
67.5	38	40	21	5½		"
65	37.5	38.5	20.5	5¼		Jenne
62.5	34.5	37	19	5¼		Ganta
59	35.5	36	21	5¼		"

Pfeiffer's first (1853) specimen was 80 mm. long, 42 mm. wide, of 5 whorls, with the aperture 50 by 26 mm. He figured a much smaller shell in 1865, only 58 mm. long, 32 mm. wide, with the aperture 35 by 15 mm.

## ARCHACHATINA (MEGACHATINOPSIS) SIDERATA (Reeve)

Pl. 41, fig. 3; Pl. 52, fig. 3; Pl. 61, fig. 2; Pl. 69, fig. 3

*Achatina sideratus* Reeve, 1849, Conch. Icon., **5**, *Achatina*, Pl. 12, fig. 38 (locality unknown).

*Achatina siderata* Pfeiffer, 1853, Monogr. Helic. Viv., **3**, p. 486. H. and A. Adams, 1855, Gen. Rec. Moll., **2**, p. 132. Pfeiffer, 1859, Monogr. Helic. Viv., **4**, p. 602. v. Martens, 1860, in Albers, Die Heliceen, 2d Ed., p. 201 (Liberia). A. D. Brown, 1861, Cat. Shells Coll., p. 56 (Liberia: Cape Palmas). Haines, 1868, Cat. Terr. Shells Coll., p. 68. Pfeiffer, 1868, Monogr. Helic. Viv., **6**, p. 216; 1876, *Op. cit.*, **8**, p. 274. Roeters van Lennep, 1876, Cat. Coll. Shells van Lennep, p. 51. Grasset, 1884, Index Test. Viv. Coll., p. 199. Paetel, 1889, Cat. Conch.-Samml., 4th Ed., **2**, p. 240. Ancey, 1902, Jl. de Conchyl., **50**, p. 280 (Liberia: Cape Palmas).

*Achatina (Achatinus) siderata* Pfeiffer, 1856, Malak. Blätt., **2**, (1855), p. 168; 1879, Nomencl. Helic. Viv., p. 265.

*Archachatina siderata* Pilsbry, 1905, Man. of Conch., (2), **17**, p. 117 (Liberia: Cape Palmas); Pl. 25, fig. 24 (after Reeve). Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 67.

*Archachatina (Megachatinops) siderata* Bequaert and Clench, 1936, Rev. Zool. Bot. Afric., **29**, pt. 1, p. 95 (Liberia: Cape Palmas; Bolahun).

*Achatina siderea* (Anonymous), 1875, 27th Ann. Rept. New York State Mus., (for 1873), p. 47 (specimen in Gould Collection).

Original description of *A. sideratus* Reeve (1849): "Achat. testa ovata, ventricosa, tenuicula, anfractibus quinque, creberrime minute granulatis, columella contorta; fusca, castaneo acute et subtiliter fulgurata, aperturæ fauce pallide caerulescente. Shell ovate, ventricose, rather thin, whorls five in number, very closely minutely granulated, columella twisted; brown, marked with fine sharply zigzag chestnut streaks, interior of the aperture faintly blue. This is apparently a shell of immature growth, but so peculiar in its colour and marking, that I venture to describe it as new. Of a warm brown silken hue, painted with fine sharply zigzag streaks somewhat broken, much more delicate and numerous towards the apex." The original figure, copied in my Pl. 41, fig. 3, is 55.5 mm. long, 32 mm. wide, with the aperture 33.5 by 17 mm. The type lot, seen at the British Museum in 1933, consists of 3 shells, including the one figured by Reeve, which may be selected as the lectotype. All three have a pale, whitish columella, which is true also of some 25 other examples I have seen of this species.

*A. siderata* is thinner and more fragile than *A. knorrii*, from which it is, moreover, separated by the slender, more regularly fusiform outline, the relatively broader and shorter spire, the shape of the

aperture and the sculpture. The aperture is half-pearshaped, being usually widest below the middle and somewhat flaring, while the edge extends forward in this area (in profile, Pl. 52, fig. 3); the terminal portion of the body-whorl is somewhat flattened or even slightly descending at the upper corner of the outer lip. All whorls are densely granulose, to near the outer lip; on the body-whorl the granulations are vertically elongate, rather than rounded, and extend over the base, though much weaker and more superficial below the periphery. The sculpture also differentiates *siderata* from *papyracea*, which in addition is not fusiform in outline, the spire being much narrower than the base.

*Specimens Examined.* "West Africa" (Hamb.M.; U.S.N.M.). — LIBERIA: without more precise locality (Brit.M.; Brus.M.; Berl.M.; A.M.N.H.; Ac.N.S.Phila.; M.C.Z.); Cape Palmas (Farrand.-M.C.Z.); Bolahun (E. Maass.-Hamb.M.; M.C.Z.). — The type lot at Brit.M. bears no locality.

*A. siderata* is restricted to Liberia, where it appears to be very rare and difficult to find. At any rate I was never able to obtain a specimen during my two West African journeys. Most shells in collections are small and immature.

#### Measurements of Adult Shells

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
71 mm.	39	44.5	21.5	5½		Liberia
65	33	39	19	5½		"
60	33	37	19	5		"
59	32.5	36.5	18.5	5		Cape Palmas
57.5	32.5	34	18	5		Bolahun
56.5	31.5	34.5	18	5		"
55.5	31	35.5	18	5		Liberia

#### ARCHACHATINA (MEGACHATINOPSIS) PAPYRACEA (Pfeiffer)

Pl. 5, fig. 1; Pl. 23, fig. 1; Pl. 60, fig. 1; Pl. 63, fig. 1;  
Pl. 70, fig. 2; Pl. 72, fig. 4; Pl. 74, fig. 3; Pl. 81, fig. 1.

*Achatina papyracea* Pfeiffer, 1845, Proc. Zool. Soc. London, (for 1845), p. 74 (Southern Nigeria: Nun River); 1848, Monogr. Helic. Viv., 2, p. 254. Reeve, 1849, Conch. Icon., 5, *Achatina*, Pl. 2, fig. 6 (type from Cuming Collection). Pfeiffer, 1853, Monogr. Helic. Viv., 3, p. 486. H. and A. Adams, 1855, Gen. Rec. Moll., 2, p. 132. Pfeiffer, 1859, Monogr. Helic. Viv., 4, p. 602; 1860, Syst. Conch.-Cab., 1, Abt. 13, pt. 1, p. 329; Pl. 28,

- figs. 8-9. Morelet, 1867, Voy. Welwitsch, Moll. Terr. Fluv., (1868), p. 66 (Southern Nigeria: banks of the Niger). Pfeiffer, 1868, Monogr. Helic. Viv., **6**, p. 215; 1876, *Op. cit.*, **8**, p. 274. Grasset, 1884, Index Test. Viv. Coll., p. 199. Paetel, 1889, Cat. Conch.-Samml., 4th Ed., **2**, p. 240.
- Achatina* (*Archachatina*) *papyracea* Albers, 1850, Die Heliceen, p. 190. Dautzenberg, 1921, Rev. Zool. Afric., **9**, pts. 1-2, p. 96.
- Achatina* (*Achatinus*) *papyracea* Pfeiffer, 1856, Malak. Blätt., **2**, (1855), p. 168; 1879, Nomencl. Helic. Viv., p. 265.
- Archachatina papyracea* Pilsbry, 1905, Man. of Conch., (2), **17**, p. 117; Pl. 44, fig. 1 (after Reeve); Pl. 23, figs. 17-18 (after Pfeiffer, 1860). Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 66.
- Archachatina* (*Megachatinops*) *papyracea* Bequaert and Clench, 1936, Rev. Zool. Bot. Afric., **29**, pt. 1, p. 92 (type and another specimen at British Museum).
- Achatina knorri* d'Ailly, 1896, Bih. Svenska Vet.-Akad. Handl., **22**, Afd. 4, No. 2, p. 63 (Cameroon: Etome; Bonge). Not of Jonas, 1839.
- Archachatina papyracea* var. *adelinae* Pilsbry, 1905 (March 1), Man. of Conch., (2), **17**, p. 118 ("West Africa"); Pl. 20, figs. 4 (paratype) and 5 (holotype); 1905 (December), The Nautilus, **19**, p. 96.
- Achatina* (*Archachatina*) *papyracea* var. *adelinae* Dautzenberg, 1921, Rev. Zool. Afric., **9**, p. 97 (Cameroon: Yaunde).
- Archachatina* (*Megachatinops*) *adelinae* Bequaert and Clench, 1936, Rev. Zool. Bot. Afric., **19**, pt. 1, p. 87 (in part: Cameroon: Yaunde; Kribi; Bakundu Kaki near Elephant Lake. Gaboon. "West Africa"); 1938, The Nautilus, **52**, p. 27 (corrected localities).
- Achatina modestior* O. Boettger, 1905 (November 1), Nachrichtsbl. D. Malak. Ges., **37**, p. 167 (Cameroon: Rombone; Bolo Kurume; Nongo madiba; Bakunbundo; Johann-Albrechtshöhe near Kumba; Monbanda or Mbanda; Mukonje Farm); Pl. 7, figs. 1-2 only (2 views of holotype from Mukonje Farm).
- Achatina gracilior* Pilsbry, 1905 (December), The Nautilus, **19**, p. 96 (error for *modestior* O. Boettger). Not of C. B. Adams, 1850, nor of v. Martens, 1860.
- Achatina aurora* Pfeiffer, 1855, Proc. Zool. Soc. London, (for 1854), p. 294 (supposedly from Natal); 1859, Monogr. Helic. Viv., **4**, p. 602; 1868, *Op. cit.*, **6**, p. 215; 1877, *Op. cit.*, **8**, p. 274. Paetel, 1889, Cat. Conch.-Samml., 4th Ed., **2**, p. 239. Connolly, 1912, Ann. South African Mus., **11**, pt. 3, p. 191; 1916, *Op. cit.*, **13**, pt. 5, p. 188.
- Achatina* (*Achatinus*) *aurora* Pfeiffer, 1856, Malak. Blätt., **5** (1855), p. 168; 1879, Nomencl. Helic. Viv., p. 265.
- Cochliotoma aurora* Pilsbry, 1904, Man. of Conch., (2), **17**, p. 102. Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 66.
- Archachatina* (*Megachatinops*) *aurora* Bequaert and Clench, 1936, Rev. Zool. Bot. Afric., **29**, pt. 1, p. 88 (type at Brit.M.).

Original description of *A. papyracea* Pfeiffer (1845): "Achat. testa ovato-oblonga, tenui, striis longitudinalibus et concentricis obsolete

decussata, diaphana, fulva, castaneo obsolete marmorata; spira conica, apice obtusa; sutura marginata; anfractibus  $5\frac{1}{2}$  vix convexiusculis, ultimo spiram vix superante; columella subrecta, basin aperturæ fere attingente, oblique truncata, linea purpurea ornata; apertura ovali, intus margaritacea. Long. 66, diam. 30 mill." The species was originally described from the Cuming Collection and the type should therefore presumably be at the British Museum. In 1853 Pfeiffer repeated his earlier description without change, merely adding that the aperture was 35 mm. long and 19 mm. wide. He also noted that he had a specimen in his own collection, presumably a cotype which he had retained from the Cuming lot. In 1860 the description is the same, but the measurements are translated in German inches: length,  $2\frac{3}{4}$  inches (=62 mm.); width,  $2\frac{1}{4}$  inches (an obvious error for  $1\frac{1}{4}$  inches=32.5 mm.). The figure accompanying the text in 1860 (Pl. 28, figs. 8-9) does not agree with the original measurements of 1845 and 1853, being 57 mm. long, 31 mm. wide, with the aperture 30 by 17.5 mm. In all probability it was drawn from the specimen (probably a cotype) in Pfeiffer's collection. This shell has the columella extensively reddish, except over the lower outer border, and is a good representation of some small or immature "*adelinae*" I have seen from Cameroon. In this connection it should be noted that Pfeiffer's original and later descriptions mention only that the columella has a purple line.

Reeve's figure of *papyracea* (1849), copied in my Pl. 23, fig. 1, shows a shell said to be from the Cuming Collection and agreeing closely with Pfeiffer's original measurements, being 68 mm. long, 37.5 mm. wide (Pfeiffer's original width of 30 mm. was clearly an oversight, probably for 36 mm.), with the aperture 36 by 20 mm. It shows no red on the columella. Moreover, in the letterpress to Pl. 2, Reeve gives a somewhat modified description of *papyracea* (English text only copied here): "Shell oblong-ovate, thin, whorls six in number, minutely decussately granulated, margined at the sutures, columella slightly twisted, but little truncated; light brown, clouded with darker brown, columella sometimes pinkish. A light, semi-transparent shell, of which the interior is slightly iridescent." The mention of the columella being "sometimes pinkish" no doubt was induced by the figure which shows the columella unicolorous bluish-white. The type lot at the British Museum, which I saw in 1933, comprises two shells, the larger of which was figured by Reeve; since its dimensions are practically those given in Pfeiffer's original description of 1845, there can be little doubt that this figured example is the true holotype. It seems strange therefore that Pfeiffer described the columella as streaked with purple, whereas Reeve's figure shows no trace of this.

Possibly the purple color was restricted to the extreme inner edge (as in some shells I have seen from Cameroon), so that it was not visible in a direct front view, and Reeve corrected the description from the figure, not from the shell. Unfortunately I failed to examine the types carefully enough for this peculiarity.

*A. aurora* Pfeiffer (1855) was known thus far only from the original description: "A. testa oblongo-ovata, solida, sublaevigata, fulvida, strigis sparsis, saturate castaneis variegata; spira conica, obtusa; sutura marginata; anfract. 6 convexiusculis, ultimo spiram subaequante; columella perarcuata, purpurea, basi late truncata; apertura parum obliqua, sinuato-ovali, intus lilaceo-rosea, nitida; perist. simplicem, fusco-limbato, marginibus callo roseo intrante junctis. Long. 59, diam. 28 mill." The type, figured for the first time in my Pl. 81, fig. 1, is at the British Museum, where I saw it in 1933. It is an immature, much worn, possibly beach-rolled shell, of a little over 5 whorls. As Connolly (1912) remarked, no shell even remotely resembling this specimen has ever been found since in South Africa. The locality "Natal" must be erroneous, unless the shell had been brought there in ballast. It may be fairly matched with immature specimens of *A. papyracea*, with which it agrees in the color of columella and parietal wall, while the faded markings are of the type found in that species. I do not hesitate in including it among the synonyms of *A. papyracea*. Pilsbry (1904) first suggested that it was a West African shell.

Original description of *A. papyracea* var. *adelinae* Pilsbry (1905): "The shell is shaped like *papyracea*, much more slender than *knorrii*. Early whorls roseate, the last two pale yellowish-green, sparsely ornamented with deep chestnut flames, very few of them reaching the suture above, widening downwards. No subsutural tessellation. Surface smooth and glossy, very weakly decussate. Aperture less than 0.6 the shell's length, the columella short, narrow, quite concave and crimson. Length 68, diam. 35, aperture 37 mm." I have studied the two types at Ac.N.S.Phila. The larger of the two, here selected as the lectotype, is shown in Pilsbry's Pl. 20, fig. 5. I publish a photograph of this shell (Pl. 74, fig. 3). I have seen a fair number of specimens from Cameroon, some of them nearly identical with the types of *adelinae*, others departing from them in various details. Their study, together with a consideration of Pfeiffer's original description and Reeve's and Pfeiffer's figures of *A. papyracea*, has led me to conclude that *adelinae* is to be considered as a synonym of *papyracea*. Three differences may be noted between Reeve's figure and most examples of "*adelinae*." The most important of these is the color of the columella. But, as noted above, Pfeiffer's original description states

that the columella was streaked with purple, the usual condition in *adelinae*. On the other hand, in the shells from Cameroon, the extent of "purple" or rather "pinkish" (as Reeve calls it) on the columella varies a great deal, even in a lot from one locality, being sometimes limited to a very narrow inner line. I have also seen Cameroon shells without any trace of it, although they are otherwise like "*adelinae*." In Reeve's figure the whorls above the body-whorl are all light purplish. In the Cameroon "*adelinae*" the early whorls are pinkish to a varying extent, sometimes even over part of the penultimate whorl (but not over the whole of this whorl in any shells I have seen). The darker, chestnut-brown markings are rather obscure, narrow and irregularly wavy throughout in Reeve's figure, whereas in most "*adelinae*" they are more conspicuous, much widened and often confluent at the base, extending above the periphery as narrowed flame-like streaks which rarely reach the suture; but some Cameroon shells, not otherwise separable from "*adelinae*," do not conform to this pattern, approaching more *papyracea* as figured by Reeve.

Original description of *A. modestior* O. Boettger (1905) (German text translated): "Differt ab *A. knorri* Jon. spira graciliore, anfr. ultimo 4/7 altitudinis testae aequante, flammulis infrasuturalibus in illa crebris et distinctissimis hic tenuibus et evanidis vel subnullis, apert. multo minus alta, spiram vix superante. — T. modica, fusiformi-ovata, tenuiuscula, sub epidermide decidua, opaca, lutescente pallide straminea vel cornea, oleo nitens, versus apicem intense rosea, ab anfr. tertio flammis distantibus angustis, initio rectis, tum elegantissime fulguratis, obscure castaneis picta, flammis infra medium anfr. ultimi latis, aut versus basin confluentibus aut basi plene nigricante; spira elate conica lateribus vix convexiusculis; apex sat acutatus. Anfr. 6 sat convexiusculi, distincte striatis, lineis spiralibus impressis subtiliter decussati, sutura submarginata et distinctius striata disjuncti, ultimus ventriosior, basi spiraliter non striatus, 4/7 altitudinis testae subaequans. Apert. obliqua, truncato-ovalis, superne flammis albis perlucentibus picta, basi livide caerulescens, intus margaritacea; perist. simplex, acutum, nigrolimbatum, marginibus callo tenui pelucido caerulescente junctis; columella angusta, subverticalis, leviter protracta, albida et oblique intuenti saepe rosea vel purpurea, basi oblique truncata. Alt. 66-67, diam. max. 36½ mm.; alt. apert. 36-39, lat. apert. 22-24 mm. — Eggs: Alt. 15-15½, diam. max. 11-12 mm. This as yet unrecognized species resembles *A. knorri* Jonas of Liberia, but is undoubtedly specifically distinct. The spire is higher, the whorls are somewhat flatter, the body-whorl shorter and less swollen. Color and markings are similar, yet different in many particulars. Only the upper three whorls are fleshy-red, the remainder of the shell cor-



neous or straw-yellow, not bright yellowish-white; the dark hooked streaks below the suture, which are so numerous in *A. knorri*, are lacking or indicated only by faint dots or small streaks; the large flame-like markings on the middle whorls are vertical and are not oblique from right to left. On the other hand, the strong flame-like pattern of the last two whorls has the same character, except for the almost complete absence of flame-like spots at the sutures. The body-whorl has 10 to 12 such flame-like elongate markings. The columella has often a purple-red margin, which is always wanting in the true *A. knorri* Jonas. An example of the latter in my collection, from Liberia, has the length 68, the diameter  $38\frac{1}{2}$  mm., the length of the aperture  $44\frac{1}{2}$ , the width of the aperture 22 mm., the proportion of length of aperture to length of shell being then 1 : 1.53 (in Pfeiffer 1 : 1.60). *A. modestior* on the contrary has the proportion 1 : 1.77. It is always separated with certainty from *A. marginata* Swainson, which lives mixed with it, by the smaller size, the thinner shell, the slender shape and the bright color and markings." In 1933 I examined several specimens of the type series at the Senckenberg Museum in Frankfurt, including the shell from Mukonje Farm figured by the author on Pl. 7, figs. 1-2; this shell was selected as the lectotype. One of the original figures is copied in my Pl. 60, fig. 1. It should be noted that this figured lectotype is larger than the measurements given in the description, being 78 mm. long, 43 mm. wide, with the aperture 44 by 24 mm. This specimen is not separable from Pilsbry's *A. adelinae*, as Pilsbry recognized later. Pilsbry's name has several months priority; but both names should now be regarded as synonyms of *A. papyracea*. However, some of O. Boettger's paratypes of *modestior*, particularly the shell he figured as a variety from Bibundi (Pl. 7, fig. 3), were of a different species and are referred in the present paper to *A. marginata eduardi* Pilsbry.

The adult shell of *A. papyracea* is medium-sized, less than 100 mm. in length, broadly ovate-oblong, light, thin but fairly solid, translucent, the darker pattern showing in the aperture; widest usually a little below mid-length, or at lower third. Spire much raised, considerably narrower than base, forming a wide cone, ending in a broadly rounded, dome-shaped apex. Whorls 6 to  $6\frac{1}{2}$ , moderately and increasingly convex from the third on, with narrow, shallow sutures. Flattened subsutural area often starting on the fourth whorl, but most pronounced on the body-whorl, varying in width, set off more or less by an impressed line, sometimes wanting. Upper 3 whorls (including nepionic shell) forming a hemispherical dome, the first scarcely flattened; next whorls gradually increasing in length and width. Body-whorl very long, about three-fourths of the total length of the shell

in front view, moderately obese, often little more convex than penultimate whorl. Aperture rather narrow, about half the total length of the shell or slightly longer, semi-elliptical; outer margin evenly and moderately curved. Inside bluish-white, also along the inner edge. Outer lip thin, sharp, not at all expanded nor flaring. Parietal wall with a very thin, bluish-white glaze, sometimes partly vinaceous-red below, toward the columella. Columella very narrow, more or less concave or somewhat twisted, gradually narrowed below to the oblique truncation, which is placed much above the base of the aperture; usually with a vinaceous-red inner edge, varying greatly in extent, but rarely covering the entire columella; in a few shells from Cameroon, not differing otherwise from those with reddish columella, this is entirely bluish-white; but whether this was true in life remains to be determined. In the youngest shell seen, 18 mm. long, of  $3\frac{1}{2}$  whorls (Pl. 5, fig. 1), most of the nepionic whorls densely covered with minute granulations in spiral rows, except the first which is very finely vertically wrinkled. Granulation about the same or a little stronger on the next whorls, as far as the first half of the fourth, but never visible to the naked eye; beyond this decreasing rapidly in strength. Penultimate and body-whorl of full-grown shells appearing smooth, but under the lens with superficial granulations, which extend also below the periphery to near the columella; sculpture more distinct below the sutures, where there are several spiral rows of minute granulations. Periostracum thin, shiny, pale straw-yellow, usually well preserved, except on the early whorls. First three or four whorls (rarely more) pink to pale vinaceous-red, with rather faint darker vertical streaks from the latter part of the third on. Succeeding whorls with chestnut-brown, usually very bold, vertical streaks, extremely variable in shape, width and length, as a rule fairly evenly spaced and slightly wavy; sometimes broken up into spots. Below the periphery the streaks tend to be broader and to unite at the base in the columellar region; the transition between the narrower and broader portions may be gradual, the streaks ending flame-like at or more often some distance below the suture; sometimes the streaks widen abruptly at the periphery or only a few of them extend above it; occasionally they combine below the periphery, most of the lower half of the body-whorl being chestnut-brown (somewhat as in *A. marginata egregia*). In very young shells (18 mm. or less in length), the columella has a narrow open slit, but is distinctly truncate at the base; the slit is no longer present in a shell 28 mm. long. The egg is as yet unknown.

*Specimens Examined.* Several from "West Africa" (Ac.N.S.Phila., No. 185105, lectotype and paratype of *adclinae*; A.M.N.H.; M.C.Z.).—CAMEROON: Yaunde (M.C.Z.; Mich.M.; Ac.N.S.Phila.; Brus.M.);

Lolodorf (E. D. Horner.-M.C.Z.); Etome (P. Dusén.-Stockh.M.; M.C.Z.); Edea (G. Schwab.-M.C.Z.); Bakundu Kaki near Elephant Lake (R. Rohde.-Hamb.M.; M.C.Z.); Tyange near Kribi (E. D. Horner.-M.C.Z.); Kribi (Leid.M.).

The species was originally described from the "Nun River," with which was meant no doubt the Nun Entrance of the Niger, in Southern Nigeria (4° 21' N.; 6° 4' E., some 200 miles to the west of Mt. Cameroon); otherwise it is known with certainty only from Cameroon. The M.C.Z. has a shell from an old collection labelled "Gaboon," which I regard as a very doubtful locality.

*Measurements of Adult Shells*

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
79 mm.	43	45.5	23.5	6½		Yaunde
78.5	43.5	45.5	23.5	6⅓		"
77	40.5	42	22	6⅓		Lolodorf
76	39.5	41	22	6⅓		Yaunde
71	35	36.5	20	6		Lolodorf
69	38.5	39	21	6		"
67	39	38	21.5	6		Kribi
65	33.5	35.5	18.5	6		Lolodorf

ARCHACHATINA (MEGACHATINOPSIS) PURPUREA (Gmelin)

Pl. 4, fig. 1; Pl. 6, fig. 2; Pl. 8, fig. 3; Pl. 11, fig. 1; Pl. 24, fig. 1; Pl. 25, fig. 2; Pl. 39, fig. 4; Pl. 58, fig. 1; Pl. 61, fig. 1; Pl. 62, fig. 4; Pl. 64, fig. 3; Pl. 68, fig. 2; Pl. 72, figs. 1-2.

[Lister, 1688, Synopsis Method. Conchyl. Liber Quartus, Pl. 581, fig. 35 (shell in front view, 85 mm. long, 52 mm. in greatest width, the aperture 45 by 27 mm.).]

[*Bulla purpurea*, etc. Chemnitz, 1786, Syst. Conch.-Cab., 9, pt. 2, p. 25; Pl. 118, figs. 1017-1018 (supposedly from the Gold Coast; descriptions and figures of 2 specimens). Not binominal.]

[*Bulla purpurea* Gmelin, 1790, in Linné, Syst. Nat., 13th Ed., 1, pt. 6, p. 3433 ("in Africae campis"; with description and a reference to Chemnitz, Pl. 118, figs. 1017-1018, to which figures the name is herewith restricted). Schreibers, 1793, Versuch Conchylienkenntniss, 1, p. 90. Turton, 1806, in Linné, System of Nature, Animal Kingdom, 4, p. 357. Dillwyn, 1817, Descr. Cat. Recent Shells, 1, p. 495. Wood, 1818 (and 1825), Index Testaceologicus, p. 89; Pl. 18, fig. 54. Mawe, 1823, Linnaean Syst. Conch., p. 102. Wood, 1856, Index Testaceologicus, Hanley Ed., p. 95; Pl. 18, fig. 54.]

- Ampulla purpurea* Röding, 1798, Museum Boltenianum, **2**, p. 110 (with reference to Chemnitz, Pl. 118, figs. 1017–1018); 1819, *Op. cit.*, 2d Ed. (by J. Noodt), p. 78.
- Helix* (*Cochlitoma*, *Achatina*) *purpurea* Férussac, 1821, Tabl. Syst. Moll., Tabl. Limaçons, p. 49 (or 53) (with *Bulla purpurea* Gmelin and *Bulmus purpurascens* Bruguière as synonyms; and with reference to Chemnitz, Pl. 118, figs. 1017–1018).
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- Achatina (Cochlitoma) purpurea* Menke, 1830, Synopsis Method. Moll., 2d Ed., p. 28.
- Agathina purpurea* Deshayes, 1831, Dict. Class. Hist. Nat., **17**, p. 122 (Explanation of Pl. 87, fig. 1, of Atlas).
- Helix (Cochlitoma) purpurea* Rang, 1831, Ann. Sci. Nat., **24**, p. 27 (in part: Coast of Malaguette [=Liberia], particularly at the Mesurado [=Monrovia], Sestre and Sino Rivers. Animal and egg).
- Achatina (Achatina) purpurea* Beck, 1837, Index Moll., pt. 1, p. 75. v. Martens, 1860, in Albers, Die Heliceen, 2d Ed., p. 208 (Malaguette [=Liberia]).
- Bulimus (Achatina) purpurea* Anton, 1839, Verzeichn. Conch. Samml., p. 44.
- Oncaea purpurea* Gistel (or Gistl), 1848, Naturgesch. d. Thierreichs, p. 168; Pl. 5, fig. 26.
- Achatina (Archachatina) purpurea* Albers, 1850, Die Heliceen, p. 190.
- Achatina (Achatinus) purpurea* Pfeiffer, 1856, Malak. Blätt., **2**, (1855), p. 168; 1879, Nomencl. Helic. Viv., p. 265. Römer, 1891, Jahrb. Nassau. Ver. Naturk., **44**, p. 123.
- Achatina (Urceus) purpurea* Mörch, 1857, Cat. Conch. Suenson, p. 6.
- Archachatina purpurea* Pilsbry, 1905, Man. of Conch., (2), **17**, p. 114 (Liberia: Cape Palmas); Pl. 21, figs. 6-7 (2 specimens). Kobelt, Abh. Senckenberg. Naturf. Ges., **32**, p. 66. Standen, 1917, Jl. of Conch., **15**, pt. 6, p. 161 (egg). Lamy, 1929, Jl. de Conchyl., **73**, p. 202 (egg).
- Archachatina (Megachatinops) purpurea* Bequaert and Clench, 1936, Rev. Zool. Bot. Afric., **29**, pt. 1, p. 93 (in part: some of the references only. Liberia: Monrovia; Cape Palmas).
- Bulimius purpurascens* Bruguière, 1792, Encyclop. Méthod., Vers, **1**, pt. 2, p. 360 (no locality; description of a shell; references to Lister, Pl. 581, fig. 35, and to Chemnitz, Pl. 118, figs. 1017-1018, only).
- Achatina erythrostoma* Swainson, 1822, Cat. Shells Coll. Mrs. Bligh, pp. 44 and 51 (no description); Appendix, p. 14 (no locality; with description and reference to *Bulla purpurea* Chemnitz, Pl. 118, figs. 1017-1018, and to *Bulimus purpurascens* Bruguière).
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- Achatina (Achatinus) porphyrostoma* Pfeiffer, 1879, Nomencl. Helic. Viv., p. 265.
- Archachatina porphyrostoma* Pilsbry, 1905, Man. of Conch., (2), **17**, p. 115. Kobelt, 1910, Abh. Senckenberg. Naturf. Ges., **32**, p. 66.

- Archachatina* (*Megachatinops*) *porphyrostoma* Bequaert and Clench, 1936, Rev. Zool. Bot. Afric., **29**, pt. 1, p. 93.
- Achatina viridescens* Ancey, 1888, Bull. Soc. Mal. France, **5**, p. 69, footnote (Liberia: Monrovia).

The first recognizable figure of what might be called the "least purple-mouthed agate snail" is that of Lister (1688; reproduced in my Pl. 11, fig. 1), as Lamarck (1822) correctly indicated; it shows both the coarse sculpture and the outline characteristic of the species. Gmelin (1790) based his *Bulla purpurea* on two figures by Chemnitz (1786) and one figure in Knorr's (1769; 1770) work. The description, seemingly made not from a specimen but from the figures, is as follows: "B. testa ventricosa rugosa longitudinaliter strigosa intus purpurea; columella truncata, apertura ovata labro acuminato: limbo intus nigerrimo." Chemnitz's two figures (copied in my Pl. 24, fig. 1, and Pl. 72, fig. 2), cited first by Gmelin, are herewith selected as typical for *A. purpurea*, since they agree well with some of the specimens of what has been more generally regarded as this species, particularly by Pilsbry, the first reviser of the group. Fig. 1017 shows a shell from the back, 70 mm. long and 45 mm. in greatest width, with the olivaceous periostracum and the coarse decussation well preserved. Fig. 1018, on the other hand, is a front view of a shell, 74 mm. long, 48 mm. in greatest width, with the aperture 43 by 23 mm. This shell had been, in Chemnitz's own words, "well polished and somewhat ground,"<sup>1</sup> which explains the different color and the smoothness. Although Chemnitz states that he received his specimens from a ship's surgeon who brought them from the Gold Coast, no true *purpurea* are known with certainty at present from the restricted section of West Africa now called the Gold Coast. Either the term was used more loosely in the early days or the shells were obtained farther West in the course of a journey to the Gold Coast, where the main Danish trading posts were located at that time. Chemnitz's specimens have not been traced, although they may yet be in some collection.

Lister's and Chemnitz's figures are readily matched with Liberian specimens of *purpurea* (compare Pl. 8, fig. 3). However, Knorr's Pl. 24\*\*\*, fig. 1 (reproduced in my Pl. 61, fig. 5), also cited by Gmelin for his *Bulla purpurea*, represents in my opinion a very different species. I discuss this figure under *A. ventricosa spectaculum* Pilsbry, as well as the figure referred to *purpurea* by Deshayes (1851, in Férussac).

*Bulimus purpurascens* was described by Bruguière (1792) as follows (French text translated): "*Bulimus*, testa ovata ventricosa decussata, viridescente, fusco strigata, columella arcuata, apertura purpurascente.

<sup>1</sup> "mit ihrer wohlpolirten und etwas abgeschliffenen Schale."

This *Bulime* differs from the *Bulime perdrix* [= *Achatina achatina* Linné] only in the following characters. 1. The shell is always smaller than in the other, consisting of 6 whorls only; the entire surface covered with a dense network of fine and closely set crossing striae, which make it slightly granulose. 2. The lower whorl of the spire [body-whorl] bears on the middle of its convexity [at the periphery] a perfectly smooth transverse band on which are seen but a few longitudinal striae even weaker here than elsewhere. 3. The aperture is similar to that of the *Bulime perdrix*, as well for the two lips as for the general shape and the oblique truncation of the columella, but both its margins and the bottom of the cavity [aperture inside] are purple, only with the difference that the color of the outer walls [outer lip] is slightly less intense than that of the left side [parietal wall and columella]. 4. The shell is greenish outside and marked at intervals with a number of brown longitudinal [vertical] zones marking the several additions by growth. The apex is very obtuse and the last three whorls [apical whorls] are flesh-color. It is also to be noted that the rim of the right lip [outer lip] is very thin and bears inside a brown transparent zone, which Chemnitz described as black in his shell." Unfortunately no measurements are given and the type appears to be lost. Bruguière cites figures by Lister (Pl. 581, fig. 35) and by Chemnitz (Pl. 118, figs. 1017-1018), which, in my opinion, represent true *A. purpurea* Gmelin, as well as by Knorr (Pl. 24\*\*\*, fig. 1), the latter here referred to a form of *A. ventricosa*. Nevertheless *A. purpurascens* may safely be synonymized with *A. purpurea*, since the description agrees well with this species. Moreover, two early French authors, Férussac (1821) and Lamarck (1822), treated *purpurascens* as a synonym of *purpurea*. They may have been acquainted with Bruguière's type, although they do not say so.

*Achatina erythrostoma* Swainson (1822) was clearly intended to be a substitute name for *purpurea* and *purpurascens*, although it was accompanied by the following description: "A. testa ob-ovata, subtilissime cancellata, epidermide olivaceo-flava; spira obtusa; apertura labioque interiore rubris, margine fusca. Shell obovate, with very fine cancellated striae, epidermis yellowish-olive; spire obtuse; aperture and inner lip red; the margin brown." The description is vague, but contains nothing that could not be applied to what is here called *purpurea*. Unfortunately no measurements were given. I have been unable to discover what became of the type.

Since Gmelin's time the trivial name *purpurea* has no doubt been applied sometimes to other purple- or pink-mouthed species of *Archachatina*, such as *A. ventricosa* (Gould), *A. rhodostoma* (Philippi), and *A. degneri* Bequaert and Clench. Except in the few cases where the

shells were figured or preserved to this day, it seems impossible to decide what was actually recorded under the name. For this reason I have included most published references to *purpurea* in my bibliography of this species. Rang's (1831) *purpurea* was a mixture of that species, *ventricosa* and possibly *rhodostoma*, or perhaps even *degneri*. The only size he gives is that of his largest shells (150 to 190 mm.), which exceeds by far that of any true *purpurea* I have seen. Reeve's (1848) Pl. 4, fig. 15a, appears to represent *A. degneri*, where I have listed it, not *A. ventricosa* as Pilsbry suggested with doubt. Pilsbry recognized his *A. rhodostoma* var. *splendida* in Reeve's (1842) Pl. 176, fig. 1. Philippi (1849) compared his *A. rhodostoma* with a supposed *purpurea*, which seems to have been *A. ventricosa*.

Shuttleworth (1852) first noticed that more than one species was being confused under *purpurea*. Unfortunately he redescribed small, slender specimens of true *purpurea* as his new *A. porphyrostoma*, as shown by his description, one of the best ever written of the species: "Testa ovato-oblonga, solidiuscula, striata, lineisque granulosis spirali-bus crebris decussata, olivacea, strigis maculisque fuscis marmorata; spira ovato-conoidea, obtusa, purpureo-rosea; anfr. 6, convexiusculi, ultimus vix inflatus, 3/5 longitudinis aequans; sutura impresse margi-nata, crenulata; columella arcuata, purpurea, basi oblique truncata; apertura mediocris, semiovalis, intus lilacina; perist. acutum, simplex, marginibus callo tenuissimo nitido purpurascente introrsum effuso junctis. Long. 60; Diam. 32 mill. Apert. 32 longa, 20 lata." His unfigured types should be at the Bern Museum. My Pl. 68, fig. 2 shows a specimen agreeing well with his description. The supposed *A. purpurea*, with which Shuttleworth compared his *porphyrostoma*, were *A. degneri*, as I have shown under that species.

*A. viridescens* Ancey was briefly described as follows (translated from the French): "Smaller, more granulose [than *A. purpurea*, sup-posedly], with the body-whorl shorter and much more ventricose; mouth smaller, peristome less expanded, usually marked with a darker streak, inside of a deeper purplish, the periostracum constantly glaucous greenish." No measurements were given. I have seen two of Ancey's cotypes, one at the Tervuren Museum, the other now at the Brussels Museum. They do not differ in sculpture, shape, color or size from typical *purpurea*. One is 87.5 mm. long, 53 mm. in greatest width, of 6 whorls, with the aperture 50 by 31 mm. (Brus.M.), and is shown in my Pl. 6, fig. 2. Ancey evidently compared his *viridescens* with *A. ventricosa*, which occurs in the same general area and which he mistook for the true *purpurea*.

Connolly (1928) mentions an interesting variation of *purpurea* with a plain yellow shell, from Kaiyima, Sierra Leone.



Standen (1917) states that the eggs of *A. purpurea* are very large, 18 by 12.25 mm., yellowish-white. Those I saw from Cape Palmas were smaller, 14.5 to 15.5 mm. long and 10.4 to 10.6 mm. wide, regularly elliptical. Standen's eggs may have been those of *A. ventricosa* or *A. degneri*.

What I regard as true *A. purpurea* agrees with Pilsbry's (1905) interpretation of the species, as shown by his description and figures. Shell medium-sized, not reaching 100 mm., lengthened ovate-oblong, solid, opaque, widest at about lower third. Spire much raised, considerably narrower than the base, forming a wide cone, ending in a broadly rounded, dome-shaped apex. Whorls 6 to  $6\frac{3}{4}$ , markedly and increasingly convex from the third on, with narrow, moderately deep sutures. Flattened subsutural area of body-whorl broad, set off by a deeply impressed line, which starts on the penultimate whorl. Upper 3 whorls (including nepionic shell) forming a hemispherical dome, the first whorl flattened; following whorls gradually increasing in length and width. Body-whorl long, obese, more convex than penultimate whorl, from two-thirds to three-fourths of the total length of the shell in front view. Aperture short, wide, nearly semi-circular, slightly over half the total length of the shell; outer margin strongly but evenly curved. Inside varying from pale vinaceous-red to dark purple, usually with a broad blackish purple inner edge. Outer lip thin, sharp, neither expanded nor flaring even in the largest shell seen, very slightly produced forward in profile, not descending at the insertion on the body-whorl. Parietal wall with a purplish-red glaze. Columella purplish-red, broad, sharply truncate close to the base of the aperture. Purple area of parietal wall and columella often with a narrow, darker purplish-brown outer edge on the body-whorl. Youngest shell seen, 18.5 mm. long, of  $3\frac{1}{2}$  whorls (Pl. 4, fig. 1), with nepionic whorls densely granulose in regular spiral, but rather ill-defined vertical rows, except the first whorl, which is very finely, vertically wrinkled; early sculpture usually worn off in part or entirely on adult shells. Granulations covering the whole of the following whorls, gradually coarser, easily seen with the naked eye on the body-whorl, where they extend to the edge of the outer lip and to the base of the columella, though weaker and more superficial below the periphery; on the body-whorl they also tend to be lengthened into short, somewhat curved, vertical welts. Periostacum thin, dull, pale olivaceous-yellow, usually lost on the early whorls, which are then pinkish to light vinaceous-red and marked with rather faint darker red vertical streaks. Penultimate and body-whorl of adult shells with nearly straight, narrow, dark-brown vertical streaks or lines, irregularly spaced and varying greatly in numbers, and in addition with a scattering of dark dots or blotches. In very young shells

the columella has an open slit, though it is distinctly truncate; the slit closes before the shell reaches 23 mm. in length.

*Specimens Examined.* Several from "West Africa" (Ac.N.S.Phila.; U.S.N.M.; M.C.Z.). — LIBERIA: without more precise locality (Leid.M.; Amst.M.; M.C.Z.; U.S.N.M.; Brit.M.); Monrovia (J. Bequaert.—M.C.Z.; Brus.M., including cotype of *A. viridescens*; Terv.M.; Leid.M.; Hamb.M.); Cape Palmas (U.S.N.M.; M.C.Z.; Ac.N.S.Phila.; A.M.N.H.). — SIERRA LEONE: Mano Bonjeima, Manoba Krim Chiefdom (T. S. Jones.—M.C.Z.); Dama, S. E. of Pujehun (T. S. Jones.—M.C.Z.); Kale, Mesi Krim Chiefdom (T. S. Jones.—M.C.Z.); Mosente on Lake Kwarko, Kwarko Krim Chiefdom (T. S. Jones.—M.C.Z.); these localities are all in the southeastern coastal area, between Sherbro Id. and the Mano River.

True *A. purpurea* is known with certainty only from the coastal areas of Sierra Leone, Liberia and the Ivory Coast. During my two visits to Liberia, I never observed it in the interior of the country, although it is quite common in the city of Monrovia. Many so-called *purpurea* in collections are misidentified; but some contain true *purpurea* with erroneous localities, such as "Gaboon."

#### Measurements of Adult Shells

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
89.5 mm.	51	50	28	6 $\frac{3}{4}$		Cape Palmas
88.5	51	51	30	6 $\frac{3}{4}$		Liberia
88	52	48.5	27	6 $\frac{3}{4}$		Monrovia
87.5	53	50	31	6		Monrovia; cotype of <i>viridescens</i>
84	49	48	26	6 $\frac{1}{2}$		Liberia
82	47.5	47	26	6 $\frac{1}{2}$		"West Africa"
77	45	43	25	6 $\frac{1}{3}$		Liberia
74	39.5	36.5	21.5	6		Cape Palmas
73	40	40	21	6 $\frac{1}{3}$		"West Africa"
66.5	37	35	20	6		Cape Palmas

#### 4. Subgenus THOLACHATINA, new

J. Thiele (1933, Sitzungsber. Ges. Naturf. Fr. Berlin, p. 296) first recognized that Achatininae with the conchological characters of the West African *Archachatina* were also found in East Africa. In the present paper I transfer to that genus, but in a distinct subgenus, the majority of the South African and several of the East African species

thus far included in *Achatina* or *Cochlitoma*. These species all have the broad dome-shaped or bulbous nepionic whorls, correlated with the production of unusually large eggs, both features being characteristic of *Archachatina*. As in the West African species, the nepionic whorls are densely granulose upon hatching and this sculpture is often well preserved in adult shells, though occasionally worn off. The other shell characters are mostly those of the subgenus *Megachatinopsis*, the outer lip in particular being simple, either with a sharp or a more or less thickened edge, but never flaring nor expanded. The distinctive features of the subgenus are the more elongate shape and the slender, more narrowly conical spire. In the subgenotype, the body-whorl is relatively broad, contrasting with the attenuate spire. The majority of the species, however, are narrow and slender throughout, being similar in appearance to *Limicolariopsis*, which has likewise a broad, dome-shaped nepionic shell. They differ, moreover, from the latter in the distinctly truncate columella. The sculpture varies greatly on the post-nepionic whorls, some species (such as the subgenotype) being coarsely granulose or decussate over the entire adult shell, others (such as *ustulata*) nearly smooth on the body-whorl. In one species (*vestita*) the sculpture is concealed by a thick periostracum, which is raised into many soft vertical ridges. The shells are small to medium-sized (40 to 135 mm. in length) and consist of many whorls for the size (5 to 7 in the smaller forms, as many as 8 to 9 in the larger ones, in the adult), shorter and more tightly coiled than in most West African species of the genus.

Subgenotype: *Achatina zebra* var. *granulata* Krauss, 1848 = *Achatina granulata* Pfeiffer, 1854. I have chosen this species as the type because it is likely to be in most collections. It is the largest member of the group.

I include at present in *Tholachatina* the following species of which I have seen specimens. No attempt is made, however, to revise them critically. Their number will no doubt be somewhat reduced eventually. Three species are here described as new; the anatomy of one of these has been studied by Dr. Mead.

1. *A. burnupi* (E. A. Smith, 1890).
2. *A. churchilliana* (Melvill and Ponsonby, 1895).
3. *A. cinnamomea* (Melvill and Ponsonby, 1894).
4. *A. dacostana* (Preston, 1909).
5. *A. dimidiata* (E. A. Smith, 1878). With subsp. *schenecki* (v. Martens, 1889).
6. *A. drakensbergensis* (Melvill and Ponsonby, 1897).
7. *A. granulata* (Krauss, 1848). Pl. 62, fig. 2 (summit).
8. *A. livingstonei* (Melvill and Ponsonby, 1897).

9. *A. machachensis* (E. A. Smith, 1902).
10. *A. meari* J. Bequaert, 1950. See below.
11. *A. neumanni* Thiele, 1933.
12. *A. obtusa* (Connolly, 1931).
13. *A. osborni* (Pilsbry, 1919). With subsp. *afromontana* (Bequaert and Clench, 1934).
14. *A. pentheri* (Sturany, 1898). With subsp. *subcylindrica* (Preston, 1909).
15. *A. sandgroundi* J. Bequaert, 1950. See below.
16. *A. semidecussata* (Pfeiffer, 1846).
17. *A. semigranosa* (Pfeiffer, 1861).
18. *A. simplex* (E. A. Smith, 1878). With subsp. *crawfordi* (Morelet, 1889) (Synonyms: *A. oedigyra* Melvill and Ponsonby, 1894; *A. zebrula* v. Martens, 1900).
19. *A. stefaninii* (Connolly, 1925).
20. *A. transvaalensis* (E. A. Smith, 1878).
21. *A. ustulata* (Lamarck, 1822) (Synonym: *A. rhabdota* Melvill and Ponsonby, 1898).
22. *A. vestita* (Pfeiffer, 1855).
23. *A. weberi* J. Bequaert, 1950. See below.
24. *A. zuluensis* (Connolly, 1939).

*Bulimus* subgenus *Omphalostyla* Schlüter (1838, Kurzgefasstes Syst. Verz. Conchyliensamml., p. 7; with brief description) was monotypic for *Bulimus ustulatus* Menke, 1830. Unfortunately it does not seem possible to accept this name for my new subgenus of South and East African *Archachatinae*. Menke's *Bulimus ustulatus* was introduced without a description, but with a doubtful reference to *Achatina ustulata* Lamarck, which I here include in *Tholachatina*. Since Menke grouped it with *Bulimus kambeul*, most probably his specimen of *ustulatus* was a *Limicolaria*, as P. Fischer surmised (1892, JI. de Conchyl., 40, p. 210). Schlüter does not group *Omphalostyla* with the species of *Bulimus* to which he attributes a truncate columella. His description, "Spindelrand perpendicular eingerollt," fits species of *Limicolaria*, but not *Achatininae* with a truncate columella.

#### ARCHACHATINA (THOLACHATINA) SANDGROUNDI, new species

Pl. 2, fig. 3; Pl. 6, fig. 4; Pl. 20, fig. 4; Pl. 57, fig. 3

Adult shell small, slender, subulate or narrowly clavate, widest at lower third, the upper part of the body-whorl and the spire forming one broad cone with very blunt apex; imperforate, thin but fairly solid, translucent, showing the markings somewhat within the aperture,

dull when fresh. Whorls 7, slightly convex, separated by narrow, weakly impressed sutures, those of the apex forming a broad, nearly hemispherical dome; the first flattened or even depressed, remainder gradually increasing in length and width. Body-whorl long and narrow, about 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, much less than half the total length of the shell, with evenly curved, semi-elliptical outer margin. Inside white. Outer lip thin, sharp. Parietal wall with a very thin, white callus. Columella white, long and narrow, fairly strongly but evenly concave, obliquely truncate a short distance from the base. First whorl worn in all examples seen (probably at least in part granulose); second and third with distinct, granulose decussation; on the fourth the granulations turn into vertically elongate welts; from the fifth on the transverse engraved lines gradually weaken, being very superficial over the terminal half (above the periphery) of the body-whorl; below the periphery the body-whorl has only faint growth-striae, but the transition at the periphery is very gradual; growth-striae coarse below the finely and superficially crenulate sutures. Periostracum, when preserved, very thin, dull, pale yellowish. Apical three whorls dull reddish-yellow; remainder of shell straw-yellow with reddish-brown or chestnut vertical streaks, straight, oblique or more or less wavy, usually narrowed toward the upper sutures, occasionally broken up, increasing in size toward the body-whorl.

*A. sandgroundi* has the shape of a *Limicolariopsis*, from which it is readily differentiated by the truncate columella. It is most closely related to *Archachatina ustulata* (Lamareck) and *Archachatina pentheri* (Sturany), both of which are larger for the same number of whorls. *A. ustulata* is also broader, with the summit not so broadly flattened dome-like, with less concave columella, and with the decussate sculpture weaker, the body-whorl of full-grown shells being almost smooth. *A. pentheri* has about the shape of *sandgroundi*, but the whorls are more convex and the sculpture is coarser, the decussation being strong over the entire upper half of the body-whorl of the largest example seen (70 mm.; of 7 whorls).

This new species was determined as *Achatina vassei* Germain by one malacologist and is found under that name in some collections. The true *vassei*, the type of which I saw at the Paris Museum in 1933, is, however, in no way related. It is a thin shell, with acuminate, narrow apex, allied to *Achatina craveni* E. A. Smith, and apparently of the subgenus *Lissachatina* in the genus *Achatina*.

*Specimens Examined.* SOUTHERN RHODESIA: Mt. Selinda, Chirinda Forest, holotype (M.C.Z. No. 82445) and four paratypes (M.C.Z. No. 94745); collected by Dr. J. Sandground.

*Measurements of Adult Shells*

Length	Greatest		Aperture		Whorls	
	Width	Length	Width			
58.5 mm.	23	24.5	13	7		Paratype
57.5	22.5	24	11.5	7		Holotype
57	23.5	25.5	11.5	7		Paratype
56.5	24	26	13	7		"
55.5	22	24	11.5	6½		"

## ARCHACHATINA (THOLACHATINA) MEADI, new species

Pl. 23, fig. 5; Pl. 77, fig. 1

Adult shell small, elongate-ovate, widest below mid-length, the spire forming a broad, short cone ending in a bluntly rounded apex; imperforate, thin but fairly solid, translucent, showing the markings very distinctly within the aperture, dull. Whorls 6½ to 7, decidedly and increasingly convex from the fifth on, separated by narrow, deeply impressed sutures; first very slightly raised; upper three (including the nepionic shell) forming a moderately wide bulbous apex; remainder increasing rather rapidly in width and length. Body-whorl long and narrow, about two-thirds of the total length of the shell in front view, slightly more convex than penultimate whorl. Aperture long, moderately wide, about half the total length of the shell, with strongly but evenly curved, semi-elliptical outer margin. Inside white. Outer lip thin, sharp. Parietal wall scarcely glazed, without callus, the markings being as distinct there as elsewhere. Columella white, long and very narrow, nearly straight but somewhat oblique, distinctly and obliquely truncate very close to the base. In a young shell (Pl. 77, fig. 1) 41 mm. long, of 5 whorls, nepionic whorls densely and finely granulose, except for the nearly smooth earliest third of the first whorl; nepionic sculpture preserved in all adult shells seen. Post-nepionic whorls coarsely decussate and at first granulose; from the fifth whorl on with short, vertical welts, gradually increasing in strength; body-whorl with strong sculpture over the upper half, much more weakly decussate below the periphery to close to the base. On 5th to 7th whorls, growth-striae becoming coarse folds below the sutures, crenulating them superficially. Periostracum very thin, pale yellowish, dull, well preserved in all specimens seen. Apical 2 whorls (nepionic shell) unicolorous, dirty pale yellowish; remainder of shell straw-yellow, with many reddish-brown or chestnut markings, in the shape of narrow, oblique or wavy streaks on the earlier whorls; from the fifth on streaks mostly broken up irregularly into spots or blotches; below periphery

of body-whorl, streaks more complete, with jagged edges and usually connected with a fairly broad chestnut-brown circum-columellar area.

*A. meadi* is most nearly related to the South African *Archachatina semidecussata* (Pfeiffer), *Archachatina drakensbergensis* (Melvill and Ponsonby), and *Archachatina semigranosa* (Pfeiffer), with which it agrees in the outline of the shell and the bulbous shape of the apex. It is, however, smaller for the same number of whorls, with more convex whorls, which increase more rapidly in length. The decussation is less developed than in *A. semidecussata*, finer and more regular than in *A. semigranosa*, and decidedly stronger (particularly on the body-whorl) than in *A. drakensbergensis*.

*Specimens Examined.* TANGANYIKA TERRITORY: Ngosi Volcano in the Rungwe Mountains, holotype (M.C.Z. No. 182903) and 3 adult and 1 immature paratypes (M.C.Z. No. 81351); collected by Mr. A. Loveridge.

One of the paratypes was dissected by Dr. A. Mead from preserved material.

#### Measurements of Adult Shells

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
63 mm.	29.5	32.5	17	6½	6½	Paratype
62.5	30	31	18	7	7	Holotype
62	26	31	14	6½	6½	Paratype
60.5	28	32	16	6⅓	6⅓	"

#### ARCEACHATINA (THOLACHATINA) WEBERI, new species

Pl. 8, fig. 1; Pl. 10, figs. 1 and 4; Pl. 20, fig. 1

Adult shell small, elongate-ovate but rather obese, widest below mid-length, the spire forming a very short, broad cone ending in a bluntly rounded apex; imperforate, moderately thick, solid, slightly translucent, dull. Whorls 6, decidedly and increasingly convex from the fourth on, separated by narrow, deeply impressed sutures; first flattened; upper three (including the nepionic shell) forming a broad, nearly hemispherical dome; remaining gradually increasing in length and width. Body-whorl long, fairly obese, about two-thirds of the total length of the shell in front view, decidedly more convex than penultimate whorl. Aperture semi-elliptical, short and wide, at most half the total length of the shell (usually somewhat less) with strongly but evenly curved outer margin. Inside white. Outer lip thin, sharp. Parietal wall with a slight, glazed, white callus. Columella white,

very narrow, nearly straight or slightly twisted, gradually narrowed over the basal third into a very weak, oblique truncation, ending close to the base of the outer lip. In a young shell, 13 mm. long, of 3 whorls (Pl. 10, fig. 1), nepionic whorls densely and finely granulose, except for the nearly smooth, or slightly wrinkled, earliest third of the first whorl; nepionic sculpture preserved in all adult shells seen, persisting even after weathering. Post-nepionic whorls coarsely decussate and in some examples (including the holotype) almost uniformly granulose; in some of the paratypes the granulations are more lengthened and welt-like on the upper half of the body-whorl; they become very weak or obsolete on the lower half of the body-whorl, which instead shows numerous, fine, somewhat wavy spiral engraved lines. On the 4th to 6th whorls, growth-striae coarser below the sutures; body-whorl often with a deep impressed line setting off a very narrow, irregularly crenulate, subsutural area. Periostracum very thin, pale straw-yellow, dull, readily worn off. Apical 3 whorls unicolorous, pale reddish-brown; remainder of shell yellowish with many fairly broad, straight, wavy or zigzag, reddish-brown streaks, narrowed toward the sutures, occasionally anastomosing. One paratype has the dark streaks very pale reddish and another is unicolorous straw-yellow.

*A. weberi* is related to the three species of *Archachatina* described thus far from Northeastern Africa: *A. stefaninii* (Connolly), *A. obtusa* (Connolly), and *A. neumanni* Thiele. It differs from all of these in the extremely weak, sometimes nearly rudimentary truncation of the columella. *A. stefaninii* and *A. neumanni* are also very different in shape. *A. obtusa* is similar in outline, but the aperture has a different shape, the thickened outer lip being somewhat shouldered before ending almost at a right angle on the parietal wall. The spire and particularly the dome-shaped summit are decidedly narrower in *A. weberi* than in *A. obtusa*.

Owing to the poorly developed truncation of the columella, one might be tempted to place *A. weberi* in *Limicoliariopsis* (of which it has the shape) rather than in *Archachatina*. The relationship of *weberi* to *obtusa* (in which the columella is decidedly truncate) is so evident that I cannot but place both species in the same subgeneric division of *Archachatina*.

*Specimens Examined.* ANGLO-EGYPTIAN SUDAN: Imatong Mountains, 4° 15' to 4° 30' N., 32° 30' E., holotype (from below Lomuleng, 7400 ft.; J. G. Myers Collector.—M.C.Z. No. 182901); and 10 paratypes (6 immature), 6200 to 8700 ft. (N. A. Weber Collector.—M.C.Z. No. 182902). According to Dr. Weber this snail lives in the mossy rain forest and the *Podocarpus* stands.



*Measurements of Adult Shells*

Length	Greatest		Aperture		Whorls	
	Width	Length	Width	Length		
52.5 mm.	28	26.5	14	6	6	Paratype
51	25	23.5	13	6	6	Holotype
49.5	26	24.5	12	6	6	Paratype
47	22.5	22.5	11.5	6	6	"
46	22.5	21	12	6	6	"



# INDEX<sup>1</sup>

- Acahina* 11  
*Achantina* 10  
*Achathina* 9  
*Achatina* 6, **7**, 8, **9**, 10, 11, 12, 14, 16, 21, 34, 48, 49, 53, 70, 71, 73, 74, 86, 138, 139, 147, 201, 203  
 achatina, *Achatina* 9, 10, 12, 13, 14, 15, **16**, 17, 18, 19, **20**, 22, 25, 27, 28, 29, 31, 32, 33, 34, 35, 38, 39, 48, 53, 71, 90, 134, 142, 175, 176, 197; Pl. 3, fig. 1; Pl. 4, fig. 3; Pl. 8, fig. 4; Pl. 11, fig. 2; Pl. 13, fig. 4; Pl. 14, fig. 4; Pl. 16, fig. 4; Pl. 39, fig. 3  
 achatina, *Ampulla* 29, 31  
 achatina, *Bulla* 9, 10, 11, 20, 21, 22, 23, 24, 25, 31, 54, 154, 169  
 achatina, *Cochlitoma* 22  
 achatina, *Helix* 22, 29  
 achatinae, *Wandolleckia* 19, 23  
*Achatinia* 11  
*Achatinus* 10, 104  
*achatinus*, *Bullimus* 21  
*achatinum*, *Buccinum* 21, 29, 34  
*Achatium* 9  
*acuta*, *Achatina* 14, 60, 61, 64, 67, 76, 81, 89, 118  
*acuta*, *Helix* 61, 65  
*adelinae*, *Achatina papyracea* var. 187  
*adelinae*, *Archachatina* 157, 158, 160, 165, 166, 187, 188, 190, 192  
*adelinae*, *Archachatina papyracea* var. 187, 189  
*aequatorialis*, *Archachatina* 146  
*aequatorialis*, *Archachatina gaboone* var. 146, 148, 151  
*afromontana*, *Archachatina osborni* 202  
*Agathina* 10, 11
- Agatina* 11  
*Aghatina* 10  
 albicans, *Achatina* 14, 49  
*albina*, *Achatina iostoma* form 43, 44, 45  
 albopicta, *Achatina* 49, 126 **127**, 128, 130, 131; Pl. 5, fig. 4; Pl. 12, fig. 3; Pl. 21, figs. 1 and 3; Pl. 24, fig. 4; Pl. 27, fig. 1; Pl. 40, fig. 2; Pl. 42, fig. 2; Pl. 43, fig. 2; Pl. 52, fig. 2; Pl. 58, fig. 2; Pl. 63, fig. 2; Pl. 65, fig. 1; Pl. 66, fig. 2; Pl. 67, fig. 3; Pl. 81, fig. 6  
*albopicta*, *Cochlitoma* 128  
 allisa, *Achatina* 12, 14, 49, **121**, 122, 123, 124, 126; Pl. 63, fig. 3  
*allisa*, *Achatina* 123  
*amphora*, *Achatina* 145  
*amphora*, *Archachatina marginata* var. 145  
*amphora*, *Helix* 145  
*Ampulla* 11  
*angulatum*, *Achatina panthera* monstr. 102, 104  
*antourtoirensis*, *Achatina* 112  
 antourtoirensis, *Achatina panthera* 99, 100, **112**, 113; Pl. 25, fig. 4; Pl. 79, fig. 1  
*anturturensis*, *Achatina* 112  
*Archachatina* 6, 9, 12, 17, 19, 21, 28, 38, 48, 63, **138**, **139**, 140, 141, 156, 171, 172, 197, 200, 201, 202, 206  
 arctespirata, *Achatina craveni* 50  
 ariel, *Achatina* 137  
**arthuri**, *Achatina* 137  
*aurora*, *Achatina* 187, 189  
*aurora*, *Archachatina* 187  
*aurora*, *Cochlitoma* 187  
*autourtoirensis*, *Achatina* 112

<sup>1</sup> Synonyms are printed in *italics*; new names proposed in this paper and main references in **bold face**.

- balteata, *Achatina* 12, 13, 14, **39**,  
 40, **41**, 42, 43, 44, 45, 46; Pl. 17,  
 figs. 1 and 3; Pl. 18, fig. 2; Pl. 41,  
 fig. 1; Pl. 71, fig. 1; Pl. 77, fig. 4  
 bandeirana, *Achatina* 12, 13, 39, 42,  
 46  
*bayaona*, *Achatina* 49  
*bayoli*, *Achatina* 31, 37  
 bayoli, *Achatina achatina* 16, 20,  
**37**, 38; Pl. 6, fig. 1; Pl. 9, fig. 1  
*bayoli*, *Archachatina* 37  
 bayoniana, *Achatina* 49  
*berevoensis*, *Achatina panthera* var.  
 104, 106, 107  
 bicarinata, *Archachatina* 140  
*bicarinatus*, *Bulimus* 139  
 bisculpta, *Achatina* 13  
 bloyeti, *Achatina* 49, 78, 88  
*bombarda*, *Ampulla* 22, 25  
*borbonica*, *Achatina* 61, 66  
*borbonica*, *Achatina mauritiana* var.  
 61  
*borbonica*, *Helix* 55  
 brooksi, *Achatina* 137  
 Buccinum 70  
 buchneri, *Achatina schweinfurthi* 13  
 Bulimus 202  
*Bulla* 9, 10  
 burnupi, *Archachatina* 201  
  
 Calachatina 140  
 camerunensis, *Archachatina* 180;  
 Pl. 53, fig. 4  
*canaliculatum*, *Achatina fulica* mon-  
 str. 63  
*canaliculatum*, *Achatina panthera*  
 monstr. 104  
*candefacta*, *Archachatina adelinae*  
 var. 165  
 candefacta, *Archachatina marginata*  
 142, **165**, 166; Pl. 74, fig. 2; Pl. 77,  
 fig. 3  
*candefacta*, *Archachatina modestior*  
 var. 165  
*capacior*, *Achatina bandeirana* 39, 46  
 capelloi, *Achatina* 47, 48, 49, 122  
*carnea*, *Achatina sinistrorsa* var. 140  
  
*castanea*, *Achatina* 66, 76, 77, 78  
 castanea, *Achatina fulica* 54, **76**, 78,  
 93; Pl. 7, fig. 3; Pl. 22, fig. 4; Pl.  
 54, fig. 3  
*chaperi*, *Achatina* 30, 32  
*chaperi*, *Achatina achatina* var. 30  
*Chersina* 10  
*chrysoderma*, *Achatina panthera* var.  
 62, 66, 67  
*chrysoleuca*, *Achatina* 89, 90, 91, 93,  
 94  
 churchilliana, *Archachatina* 201  
 cinnamomea, *Archachatina* 201  
**clenchi**, *Archachatina marginata*  
 142, **163**; Pl. 14, fig. 2  
*Cochlitoma* 9, 10, 12, 17, 123, 201  
 coloba, *Achatina fulica* 54, **78**; Pl.  
 27, fig. 3  
 colubrina, *Achatina* 47, 48, 137  
*compressum*, *Achatina panthera*  
 monstr. 104  
 connollyi, *Achatina* 50  
*contabulatum*, *Achatina panthera*  
 monstr. 104  
*couroupa*, *Achatina* 53, 61, 63, 66, 71  
*courouya*, *Achatina* 63  
 craveni, *Achatina* 50, 130, 203  
*crawfordi*, *Archachatina* 119  
 crawfordi, *Archachatina simplex* 202  
*cumingii*, *Achatina* 154, 156  
*cumingii*, *Archachatina* 154  
*cyanea*, *Achatina* 33, 34, 35  
  
 dacostana, *Archachatina* 201  
 dammarensis, *Achatina* 11, 13  
*daroliensis*, *Achatina* 89, 92, 93  
*degenerata*, *Achatina schinziana* var.  
 13  
 degneri, *Archachatina* 19, 140, 155,  
 170, 171, **172**, 173, 174, 175, 176,  
 179, 197, 198, 199; Pl. 18, fig. 3;  
 Pl. 56, fig. 3; Pl. 69, fig. 2  
 delorioli, *Achatina* 50, **122**, 123, 126;  
 Pl. 4, fig. 4  
**depravata**, *Achatina achatina* 20,  
**29**, 35, 36; Pl. 2, fig. 1  
 dewittei, *Achatina* 137

- dimidiata*, *Achatina* 46  
 dimidiata, *Archachatina* 201  
 dohrmiana, *Achatina* 11, 12, 13, 39  
 drakensbergensis, *Archachatina* 201, 205  
  
*eburnoides*, *Achatina* 103  
 eduardi, *Archachatina marginata* 142, 147, 151, 156, **158**, 159, 160, 163, 191; Pl. 55, fig. 1  
 egregia, *Achatina marginata* var. 161  
 egregia, *Archachatina marginata* 141, 142, 157, **161**, 162, 163, 192; Pl. 54, fig. 2; Pl. 71, fig. 2  
 egregiella, *Archachatina marginata* 142, **161**, 163; Pl. 62, fig. 1  
 elegans, *Achatina achatina* 10, 15, 16, 19, 20, **29**, 30, 31, 32, 34; Pl. 12, fig. 1; Pl. 14, fig. 1; Pl. 15, fig. 1  
 elegans, *Achatium* 10, 29  
 elongata, *Achatina lactea* var. 95  
 erlangeri, *Achatina* 89, 91, 92, 93, 94  
 erythrostoma, *Achatina* 195, 197  
*Euachatina* 11  
**Euaethiopia** 136  
*Euaethiops* 9, 136  
 eugraptia, *Achatina pfeifferi* 48  
  
*fasciata*, *Agathina* 62  
*fatalis*, *Achatina* 49  
*flammea*, *Ampulla* 22, 25  
*flammea*, *Bulla* 22  
*foureaui*, *Achatina schweinfurthi* var. 145, 147, 148  
*fourneaui*, *Achatina marginata* var. 145, 146, 147, 158  
*foureaui*, *Archachatina marginata* var. 145  
*fourneauxi*, *Achatina marginata* var. 145  
*fulgurata*, *Achatina* 14  
 fulgurata, *Achatina zebra* 13, 14  
 fulica, *Achatina* 8, 10, 14, 33, 34, 35, 49, **50**, 51, 52, 53, **54**, 55, 59, 63, 64, 65, 66, 67, 68, 70, 71, 72, 73, 74, 75, 76, 77, 78, 82, 84, 85, 86, 92, 94, 97, 99, 100, 103, 105, 108, 112, 113, 118; Pl. 7, fig. 1; Pl. 16, fig. 3; Pl. 19, fig. 3; Pl. 20, fig. 2; Pl. 21, fig. 2; Pl. 22, fig. 1; Pl. 23, fig. 4; Pl. 24, fig. 2; Pl. 25, fig. 1; Pl. 26, fig. 2; Pl. 27, fig. 2; Pl. 28, fig. 2; Pl. 29, figs. 1-2; Pl. 30, fig. 2; Pl. 31, figs. 1-2; Pl. 32, figs. 1-2; Pl. 33, fig. 2; Pl. 34, fig. 2; Pl. 35, fig. 1; Pl. 36, figs. 1-2; Pl. 37, fig. 4; Pl. 38, fig. 3  
*fulica*, *Achatina* 80, 95  
*fulica*, *Agathina* 60  
*fulica*, *Cochlitoma* 59  
*fulica*, *Helix* 55, 59  
*fulminea*, *Achatina* 11  
*fulva*, *Achatina* 24, 33, 41, 61, 62, 65, 66, 81, 104, 105  
*fulva*, *Helix* 60  
*fulvescens*, *Achatina* 33, 61  
*fulvus*, *Bulimus* 33, 34, 35, 41, 62, 65, 104  
  
 gaboonensis, *Archachatina* 140, 145, 146, 148, 151  
*Geodes* 11  
 glaucina, *Achatina* 50  
 glutinosa, *Achatina* 14, 50  
*gracilior*, *Achatina* 154, 158, 159, 187  
*gracilior*, *Achatina marginata* var. 144, 151, 154, 155, 156, 157, 158, 159, 162  
*gracilior*, *Archachatina marginata* var. 155, 158  
*gracilis*, *Achatina sennaariensis* var. 30  
*gracilis*, *Achatina variegata* var. 30, 31, 32  
 grandidieriana, *Achatina* 137  
*grandidieriana*, *Stenogyra* 137  
*granulata*, *Achatina* 201  
*granulata*, *Achatina zebra* var. 201  
 granulata, *Archachatina* 201; Pl. 62, fig. 2  
*grevillei*, *Achatina* 164  
*grevillei*, *Archachatina* 164

- grevillei, *Archachatina marginata*  
 142, 157, **164**; Pl. 81, fig. 5  
*greyi*, *Achatina* 13, 15  
*gruveli*, *Achatina* 39
- Halia** 11  
*hamillei*, *Achatina* 14, 36, 37, 52, 53,  
 79, 81, 91  
*hamillei*, *Achatina fulica* 37, 51, 54,  
 63, 67, 68, **79**, 82, 83, 84, 85, 86,  
 88, 91, 93, 94, 100, 108, 112, 118;  
 Pl. 15, fig. 2; Pl. 19, figs. 2 and 4;  
 Pl. 40, fig. 3; Pl. 42, fig. 1; Pl. 43,  
 fig. 1; Pl. 45, fig. 2; Pl. 46, fig. 2;  
 Pl. 47, figs. 1 and 3; Pl. 48, fig. 1;  
 Pl. 49, fig. 2; Pl. 50, figs. 1-2; Pl.  
 55, fig. 3; Pl. 78, figs. 2-3; Pl. 79,  
 fig. 2; Pl. 80, figs. 1-3 and 5  
*hammillei*, *Achatina* 79  
*Helix* 10  
*hessei*, *Achatina* 39  
*hortensiae*, *Achatina* 11, 12, 13  
*hylaetae*, *Achatina osborni* 40
- icterica*, *Archachatina marginata*  
 142, **165**, 166; Pl. 26, fig. 1; Pl.  
 75, fig. 1  
*ihotelleri*, *Achatina* 114  
*immaculata*, *Achatina* 14, 50, 100  
*immaculata*, *Helix* 14  
*inaequalis*, *Achatina* 16  
*indotata*, *Achatina* 13, 15, 16  
*infracusca*, *Achatina* 46  
*infracusca*, *Achatina balteata* 39,  
 40, **46**, 47; Pl. 44, fig. 1; Pl. 51,  
 figs. 1-2  
*intusalescens*, *Achatina* 146  
*iostoma*, *Achatina* 12, 13, 39, 40, 43,  
 44  
*iredalei*, *Achatina* 50, 122, **123**, 124,  
 125, 126, 130; Pl. 13, fig. 3; Pl. 14,  
 fig. 3; Pl. 57, fig. 2; Pl. 60, fig. 2;  
 Pl. 61, figs. 3-4; Pl. 64, fig. 2; Pl.  
 65, fig. 3; Pl. 77, fig. 2  
*iwensi*, *Achatina* 48  
*acobi*, *Achatina* 50
- johnstoni*, *Achatina* 50  
*kafuensis*, *Achatina morelli* var. 50  
*kambeul*, *Ampulla* 55  
*kambeul*, *Bulimus* 55, 202  
*kambeul*, *Limicolaria* 55  
*kilimae*, *Achatina* 50, 141, 116  
*kirkii*, *Achatina* 50  
*knori*, *Achatina* 11  
*knori*, *Serpaea* 181  
*knorri*, *Achatina* 181, 187, 190, 191  
*knorrii*, *Achatina* 11, 12, 38, 180, 181  
*knorrii*, *Archachatina* 143, 149, 150,  
**180**, 181, 182, 184, 185; Pl. 37,  
 figs. 1-2; Pl. 39, fig. 2; Pl. 40,  
 fig. 1; Pl. 51, fig. 3; Pl. 53, fig. 1;  
 Pl. 56, fig. 1; Pl. 76, fig. 1  
*kraussii*, *Achatina zebra* 13
- lactea*, *Achatina* 50, 89, **94**, 95, 96,  
 97, 98; Pl. 24, fig. 3; Pl. 48, fig. 2  
*lacteae*, *Ampulla* 22, 25  
*lamarcki*, *Achatina* 109  
*lamarckiana*, *Achatina* 103, 109  
*lamarckiana*, *Achatina panthera* 100  
 108, **109**, 110, 112; Pl. 35, figs.  
 2-3; Pl. 38, fig. 1; Pl. 55, fig. 2;  
 Pl. 76, fig. 2  
*lamarckiana*, *Achatina* 109  
*lambarenensis*, *Archachatina gaboon-*  
*ensis* var. 145, 148  
*lanceolata*, *Achatina rhodesiaca* var.  
 50  
*layardi*, *Achatina* 50, 100  
*layardi*, *Achatina* 104  
*lechaptoisi*, *Achatina* 104, 106  
*lencostyla*, *Achatina panthera* var. 63  
*Leptocala* 9, 136, 137, **138**  
*Leptocalina* 48, **136**, 137  
*Leptocallista* 136, **137**  
*Leptocola* 138  
*letourneuxi*, *Achatina* 80, 82, 84, 85  
*leucopasa*, *Achatina rhodesiaca* var.  
 50  
*leucostyla*, *Achatina* 81, 108  
*leucostyla*, *Achatina panthera* var.  
 63, 81, 82, 84, 87

- levior*, *Achatina schweinfurthi rhodacme* mut. 13  
*lhotelleriei*, *Achatina* 114  
*lhotellerii*, *Achatina* 114, 115, 121  
*lhotellerii*, *Achatina zanzibarica* var. 114  
*Limicolaria* 11, 21, 48, 49, 119, 136, 138, 202  
*Limicolariopsis* 203, 206  
*linterae*, *Achatina zebra* 13  
**Lissachatina** 9, 48, 49, 50, 203  
*livingstonei*, *Archachatina* 201  
*lorioli*, *Achatina* 122  
*loveridgei*, *Achatina* 136; Pl. 3, fig. 2  
*loveridgei*, *Euaethiops* 136, 137  
*loveridgei*, *Leptocala* 137  
  
*machachensis*, *Archachatina* 202  
*macrostoma*, *Achatina zebra* var. 61  
*maculata*, *Achatina* 61, 65, 66  
*madaziniana*, *Achatina* 114, 117, 118, 121  
*Magachatina* 140  
*marginata*, *Achatina* 11, 27, 140, 143, 144, 145, 146, 154, 156, 159, 164, 165, 166  
*marginata*, *Archachatina* 19, 21, 25, 27, 140, 141, 142, 144, 145, 146, 147, 148, 150, 151, 153, 155, 157, 158, 159, 161, 162, 163, 164, 166, 173, 174, 179, 181, 182, 191; Pl. 9, fig. 3; Pl. 59, fig. 1; Pl. 64, fig. 1; Pl. 67, fig. 2; Pl. 68, fig. 1; Pl. 71, fig. 3; Pl. 75, fig. 2; Pl. 76, figs. 3-4; Pl. 80, fig. 4  
*marginata*, *Bulla achatina* var. 154, 157  
*marginata*, *Cochlitoma* 144  
*marginata*, *Helix* 144, 166  
*marginata*, *Oncaea* 144  
*mariei*, *Achatina* 14, 50  
*marioni*, *Achatina* 95, 96, 97, 98  
*mauriciansa*, *Achatina* 60  
*mauritaniana*, *Achatina* 60, 62, 63, 64, 65, 66  
**meadi**, *Archachatina* 202, 204, 205; Pl. 23, fig. 5; Pl. 77, fig. 1  
  
*Megachatina* 140  
*Megachatino*ps 180  
*Megachatinopsis*, 140, 180, 181, 201  
*milne-edwardsi*, *Achatina* 80  
*milne-edwardsiana*, *Achatina* 80, 83, 84, 88  
*minima*, *Achatina* 30  
*minima*, *Achatina achatina* var. 15, 30, 31, 32  
*minor*, *Achatina panthera* var. 30, 109, 110  
*minor*, *Achatina variegata* var. 30, 31, 38  
*modestior*, *Achatina* 158, 160, 187, 190, 191  
*mollicella*, *Achatina* 138; Pl. 58, fig. 5  
*monetaria*, *Achatina* 42, 43  
*monochromatica*, *Achatina* 33  
*monochromatica*, *Achatina achatina* 16, 20, 33, 34, 35, 65; Pl. 10, fig. 2; Pl. 13, fig. 1; Pl. 19, fig. 1; Pl. 75, fig. 3  
*monstrosa*, *Achatina fulica* var. 62  
*morrelli*, *Achatina* 49, 122  
*mossambica*, *Achatina* 104, 105, 106, 108  
*mossambica*, *Achatina panthera* var. 104  
  
*naegelei*, *Achatina zanzibarica* var. 114, 117, 121  
*nasimoyensis*, *Achatina* 83  
*nasimoyensis*, *Achatina panthera* var. 80, 83  
*natalensis*, *Achatina* 13, 15, 16  
*neumanni*, *Achatina panthera* var. 81, 84  
*neumanni*, *Archachatina* 202, 206  
*nigrofasciata*, *Achatina marginata* var. 161, 162  
*nitida*, *Achatina* 137  
  
*obesa*, *Achatina* 11, 12, 15  
*obesa*, *Achatina zebra* 13, 15  
*obtusa*, *Archachatina* 202, 206  
*obtusa*, *Euaethiops* 136

- occidentalis*, *Achatina* 13, 15  
*oedigyra*, *Achatina* 202  
 okapia, *Achatina schweinfurthi* 13  
*Omphalostyla* 202  
*Oncaea* 10, 11  
*osborni*, *Achatina* 40  
*osborni*, *Archachatina* 202  
*ovata*, *Achatina* 50  
*ovum*, *Achatina* 152, 153  
*ovum*, *Archachatina* 152  
*ovum*, *Archachatina marginata* 142,  
 152, 153; Pl. 11, fig. 3; Pl. 70,  
 fig. 1  
  
*paivaeana*, *Achatina* 13  
*paivana*, *Achatina* 146, 151  
*Pandanus* 73  
*panthera*, *Achatina* 10, 50, 51, 59,  
 67, 68, 70, 71, 84, 85, 86, 97, 98,  
 99, 100, 101, 103, 104, 105, 106,  
 107, 108, 110, 111, 112, 113; Pl. 5,  
 fig. 3; Pl. 34, fig. 1; Pl. 38, fig. 2;  
 Pl. 56, fig. 2; Pl. 57, fig. 1; Pl. 58,  
 fig. 3  
*panthera*, *Achatina* 62, 79, 80, 81, 82,  
 83, 109  
*panthera*, *Helix* 101, 104  
*pantherina*, *Achatina* 80, 103  
*papyracea*, *Achatina* 38, 42, 186, 187  
*papyracea*, *Archachatina* 157, 160,  
 166, 180, 184, 186, 187, 188, 189,  
 190, 191; Pl. 5, fig. 1; Pl. 23, fig. 1;  
 Pl. 60, fig. 1; Pl. 63, fig. 1; Pl. 70,  
 fig. 2; Pl. 72, fig. 4; Pl. 74, fig. 3;  
 Pl. 81, fig. 1  
*Parachatina* 11, 12  
*parthenia*, *Achatina* 48  
*passargei*, *Achatina schinziana* 13  
*penestes*, *Achatina* 48  
*pentheri*, *Archachatina* 202, 203  
*perdix*, *Achatina* 11, 23, 26, 29, 103,  
 156  
*perdix*, *Bulimus* 24  
*perdrix*, *Achatina* 24  
*petersi*, *Achatina* 14, 50, 91  
*Petitia* 9, 138  
*petitia*, *Achatina mollicella* 138; Pl.  
 58, fig. 4  
  
*petitia*, *Petitia* 138  
*pfeifferi*, *Achatina* 47, 48; Pl. 23,  
 fig. 2  
*pilsbryi*, *Achatina* 128, 129  
*Pintoa* 47, 48, 49, 136, 137  
*pintoi*, *Achatina* 11  
*Podocarpus* 206  
*polychroa*, *Achatina* 47, 48  
*ponderosa*, *Achatina fulica* var. 95  
*porphyrostoma*, *Achatina* 173, 195,  
 198  
*porphyrostoma*, *Archachatina* 195,  
 196  
*priamus*, *Achatina* 11  
*prunum*, *Achatina* 181, 182  
*pulchella*, *Achatina* 138  
*purpurascens*, *Bulimus* 194, 195,  
 196, 197  
*purpurea*, *Achatina* 11, 166, 169, 172,  
 176, 177, 178, 194, 195  
*purpurea*, *Agathina* 195  
*purpurea*, *Ampulla* 194  
*purpurea*, *Archachatina* 155, 168,  
 170, 171, 173, 174, 177, 178, 179,  
 180, 193, 195, 196, 197, 198, 199,  
 200; Pl. 4, fig. 1; Pl. 6, fig. 2;  
 Pl. 8, fig. 3; Pl. 11, fig. 1; Pl. 24,  
 fig. 1; Pl. 25, fig. 2; Pl. 39, fig. 4;  
 Pl. 58, fig. 1; Pl. 61, fig. 1; Pl. 62,  
 fig. 4; Pl. 64, fig. 3; Pl. 68, fig. 2;  
 Pl. 72, figs. 1-2.  
*purpurea*, *Bulimus* 195  
*purpurea*, *Bulla* 193, 195, 196  
*purpurea*, *Cochlitoma* 195  
*purpurea*, *Helix* 194, 195  
*purpurea*, *Oncaea* 195  
*putzeysi*, *Achatina* 137  
  
*raffrayi*, *Achatina* 137  
*randabeli*, *Achatina craveni* 50  
*rediviva*, *Achatina* 62, 67  
*reticulata*, *Achatina* 50, 96, 129,  
 130, 131, 132, 133, 134, 135; Pl. 9,  
 fig. 4; Pl. 16, fig. 2; Pl. 63, fig. 4;  
 Pl. 66, fig. 1; Pl. 67, fig. 1; Pl. 71,  
 fig. 4  
*retzii*, *Achatina* 49



- rhabdota*, *Achatina* 202  
*rhodacme*, *Achatina schweinfurthi* 13  
*rhodesiaca*, *Achatina capelloi* 50  
*rhodostemma*, *Achatina schweinfurthi*  
*rhodacme* mut. 13  
*rhodostoma*, *Achatina* 166, 172, 176,  
 177  
*rhodostoma*, *Archachatina* 140, 168,  
 171, 173, 174, **176**, 177, 179, 197,  
 198; Pl. 13, fig. 2; Pl. 22, fig. 2;  
 Pl. 28, fig. 1; Pl. 33, fig. 1; Pl.  
 73, fig. 3; Pl. 74, fig. 1  
*rodatzii*, *Achatina* 88, 89  
*rodatzii*, *Achatina fulica* 54, **88**, 90,  
 91, 92, 93, 94, 97; Pl. 3, fig. 3;  
 Pl. 11, fig. 4; Pl. 30, fig. 1; Pl. 44,  
 fig. 2; Pl. 52, fig. 1; Pl. 53, figs.  
 2-3; Pl. 54, fig. 1  
*rollei*, *Achatina kilimae* var. 114, 116  
*rosaxis*, *Achatina weynsi* mut. 13  
**roseolabiata**, *Achatina achatina*  
 20, **28**; Pl. 1, fig. 1; Pl. 12, fig. 2  
*rugosa*, *Achatina* 12, 40, 43  
  
**sandgroundi**, *Archachatina* **202**,  
 203; Pl. 2, fig. 3; Pl. 6, fig. 4; Pl.  
 20, fig. 4; Pl. 57, fig. 3  
*scaevola*, *Achatina* 13  
*scalaroides*, *Achatina fulica* var. 62  
*scalaris*, *Achatina fulica* monstr. 63  
*schencki*, *Archachatina dimidiata*  
 201  
*schinziana*, *Achatina* 13  
*schoutedeni*, *Achatina* 50  
*schweinfurthi*, *Achatina* 13, 115,  
 145, 147  
*semidecussata*, *Achatina* 47, 48  
*semidecussata*, *Archachatina* 202,  
 205  
*semifusca*, *Achatina schweinfurthi*  
 13  
*semigranosa*, *Archachatina* 202, 205  
*semisculpta*, *Achatina* 48  
*Serpaea* 11, 12  
*siderata*, *Achatina* 38, 185  
*siderata*, *Archachatina* 180, **185**,  
 186; Pl. 41, fig. 3; Pl. 52, fig. 3;  
 Pl. 61, fig. 2; Pl. 69, fig. 3  
*siderea*, *Achatina* 185  
*simplex*, *Archachatina* 202  
*sinistrorsa*, *Achatina* 139, 140  
*sinistrorsa*, *Achatina mauritiana* var.  
 62  
*sinistrorsa*, *Achatina panthera* var.  
 103  
*sinistrorsum*, *Achatina fulica* monstr.  
 62  
*sinistrorsum*, *Achatina panthera*  
 monstr. 104  
*sinistrosa*, *Achatina mauritiana* var.  
 62  
*smithii*, *Achatina* 13  
*smithii*, *Achatina* 138  
*solida*, *Achatina fulica* var. 95, 97  
*sowerbyi*, *Achatina* 138  
*spectaculum*, *Archachatina* 169, 170,  
 171  
*spectaculum*, *Archachatina ventri-*  
*cosa* **169**, 170, 196; Pl. 18, fig. 1;  
 Pl. 25, fig. 3; Pl. 46, fig. 1; Pl. 49,  
 fig. 1; Pl. 60, fig. 3; Pl. 61, fig. 5;  
 Pl. 75, fig. 4  
*specularis*, *Achatina* 136, 137  
*spekei*, *Achatina* 50, 122, 126; Pl.  
 62, fig. 3; Pl. 81, figs. 2 and 3  
*splendida*, *Achatina rhodostoma* var.  
 172  
*splendida*, *Archachatina rhodostoma*  
 171, 172, 173, 174, 177, 178, 179,  
 180, 198  
*stefaninii*, *Archachatina* 202, 206  
*studleyi*, *Achatina* 13, 15  
*stuhlmanni*, *Achatina* 12, 13, 40  
*subcylindrica*, *Archachatina pen-*  
*theri* 202  
*subsuturalis*, *Achatina marginata*  
 var. 155  
*subsuturalis*, *Archachatina marginata*  
 var. 155  
*subunicolor*, *Achatina albopicta* var.  
 128, 129  
*suturalis*, *Achatina* 154, 155, 156  
*suturalis*, *Archachatina marginata*  
 25, 142, 144, **154**, 155, 156, 157,

- 159, 162; Pl. 20, fig. 3; Pl. 62, fig. 5; Pl. 65, fig. 2; Pl. 72, fig. 3  
*suturalis*, *Polyphemus* 156  
*sylvatica*, *Achatina* 137
- tavaresiana, *Achatina* 13, 15  
 thermalis, *Achatina* 137  
**Tholachatina** 48, 200, 201, 202  
*thomsoni*, *Achatina* 11, 12, 50, 126  
*tiara*, *Achatina* 39  
*tigrina*, *Achatina zebra* 13, 15, 16;  
 Pl. 81, fig. 4  
*tincta*, *Achatina* 13, 15, 64  
*tincta*, *Achatina* 30  
*togoensis*, *Achatina* 36  
*togoensis*, *Achatina achatina* 16, 20,  
 36; Pl. 2, fig. 2; Pl. 5, fig. 2; Pl. 7,  
 fig. 2; Pl. 39, fig. 1  
*tracheia*, *Achatina* 13  
*transvaalensis*, *Archachatina* 202  
*Tripachatina* 48
- umbilicata*, *Achatina fulica* var. 62,  
 104  
*umbilicatum*, *Achatina fulica* monstr. 62  
*umbilicatum*, *Achatina panthera*  
 monstr. 104  
*unicolor*, *Achatina* 33  
*unicolor*, *Achatina sylvatica* mut. 137  
*unicolor*, *Achatina variegata* var. 33  
*Urceus* 11, 21, 138  
*usambarensis*, *Achatina* 113, 114,  
 116, 120  
*usambarica*, *Achatina* 114  
*ustulata*, *Achatina* 202  
*ustulata*, *Archachatina* 202, 203  
*ustulatus*, *Bulimus* 202
- varicosa*, *Achatina* 11, 13  
*variegata*, *Achatina* 11, 22, 23, 25,  
 30, 31, 33, 38, 90  
*vassei*, *Achatina* 50, 203  
*ventricosa*, *Achatina* 166, 172  
*ventricosa*, *Archachatina* 19, 140,  
 151, 155, 166, 167, 168, 170, 171,  
 174, 178, 179, 197, 198, 199; Pl.  
 6, fig. 3; Pl. 8, fig. 2; Pl. 9, fig. 2;  
 Pl. 10, fig. 3; Pl. 22, fig. 3; Pl. 23,  
 fig. 3; Pl. 45, fig. 1; Pl. 73, figs.  
 1-2  
*vestita*, *Archachatina* 123, 202  
*vidaleti*, *Achatina balteata* var. 43, 44  
*vignioniana*, *Achatina* 48; Pl. 17,  
 fig. 2; Pl. 69, fig. 1  
*virginea*, *Bulla* 10  
*virgulata*, *Achatina craveni* 50  
*viridescens*, *Achatina* 196, 198, 200
- Wandolleckia 19, 23  
**weberi**, *Archachatina* 202, 205, 206;  
 Pl. 8, fig. 1; Pl. 10, figs. 1 and 4;  
 Pl. 20, fig. 1  
*welwitschi*, *Achatina* 11, 12, 13, 16  
*weynsi*, *Achatina* 13  
*wildemani*, *Achatina* 136, 137  
*wildemani*, *Achatina specularis* 137
- yalaensis*, *Achatina* 50
- zanzibarensis*, *Leptocala* 114  
*zanzibarica*, *Achatina* 50, 113, 114,  
 115, 116, 117, 118, 119, 121, 125,  
 126, 130, 147; Pl. 1, fig. 2; Pl. 4,  
 fig. 2; Pl. 16, fig. 1; Pl. 36, fig. 3;  
 Pl. 37, figs. 3 and 5; Pl. 41, fig. 2;  
 Pl. 47, fig. 2; Pl. 59, fig. 2; Pl. 73,  
 fig. 4; Pl. 77, fig. 5; Pl. 78, fig. 1;  
 Pl. 79, figs. 3-4  
*zebra*, *Achatina* 10, 12, 13, 14, 15,  
 17, 33, 55, 103, 155, 156  
*zebra*, *Achatina* 24, 103  
*zebra*, *Achatinus* 10  
*zebra*, *Ampulla* 11  
*zebra*, *Buccinum* 11  
*zebra*, *Bulimus* 10, 17, 24, 54, 55, 103  
*zebra*, *Helix* 10  
*zebrina*, *Achatina* 50, 66, 77, 93  
*zebrina*, *Helix* 76  
*zebriola*, *Achatina* 47  
*zebriolata*, *Achatina* 47, 48, 137  
*zebroides*, *Achatina zebra* 13  
*zebrula*, *Achatina* 202  
*zenkeri*, *Achatina mollicella* 138  
*zuluensis*, *Archachatina* 202

PLATES

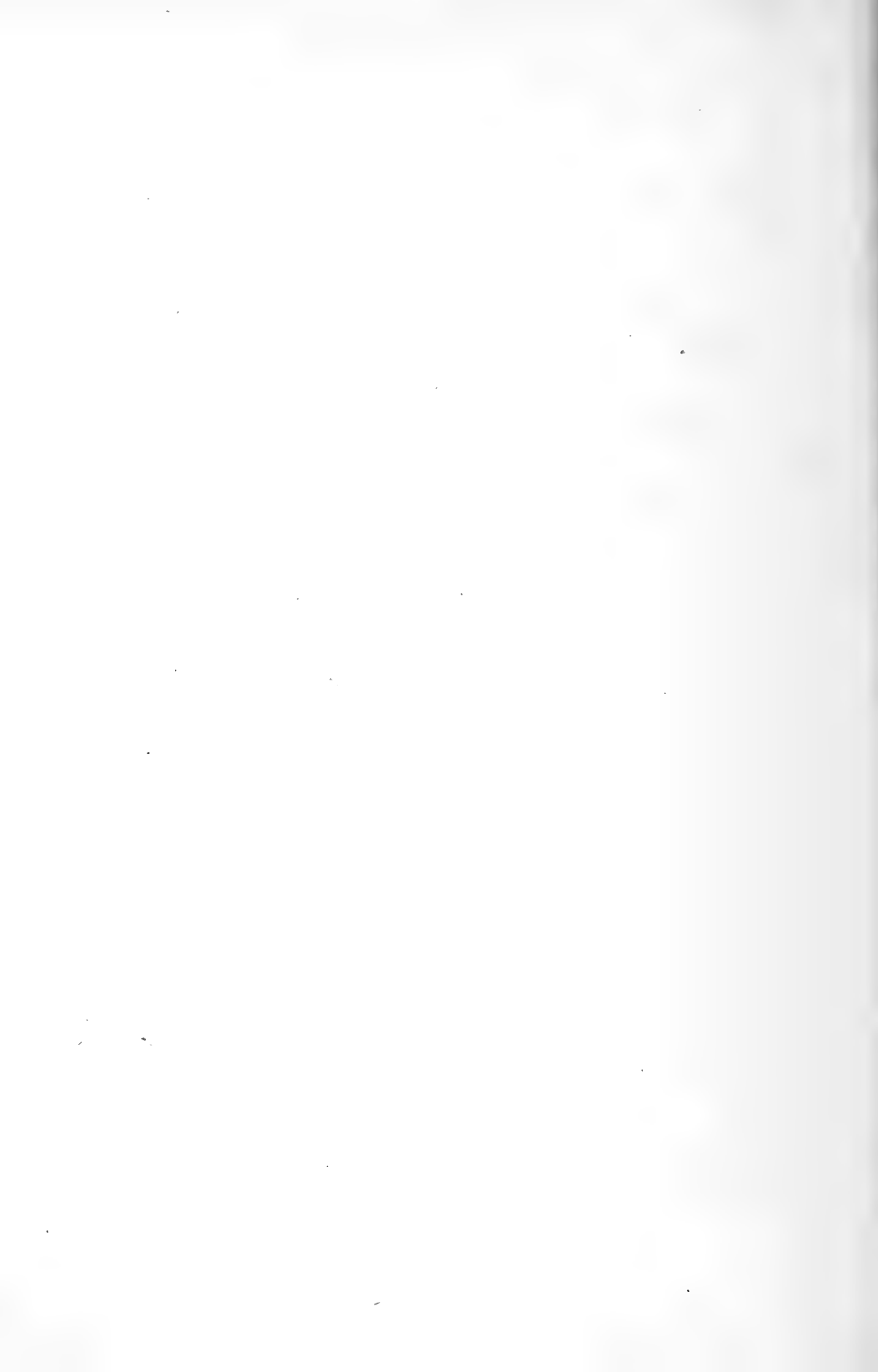


PLATE 1

PLATE 1

Fig. 1. *Achatina achatina roseolabiata* J. Bequaert. Bolahun. Holotype, M.C.Z. No. 163513. Slightly reduced; length, 181 mm.

Fig. 2. *Achatina zanzibarica* Bourguignat. Copy of original figure of *A. zanzibarica* var. *naegelei* C. R. Boettger. Same size.







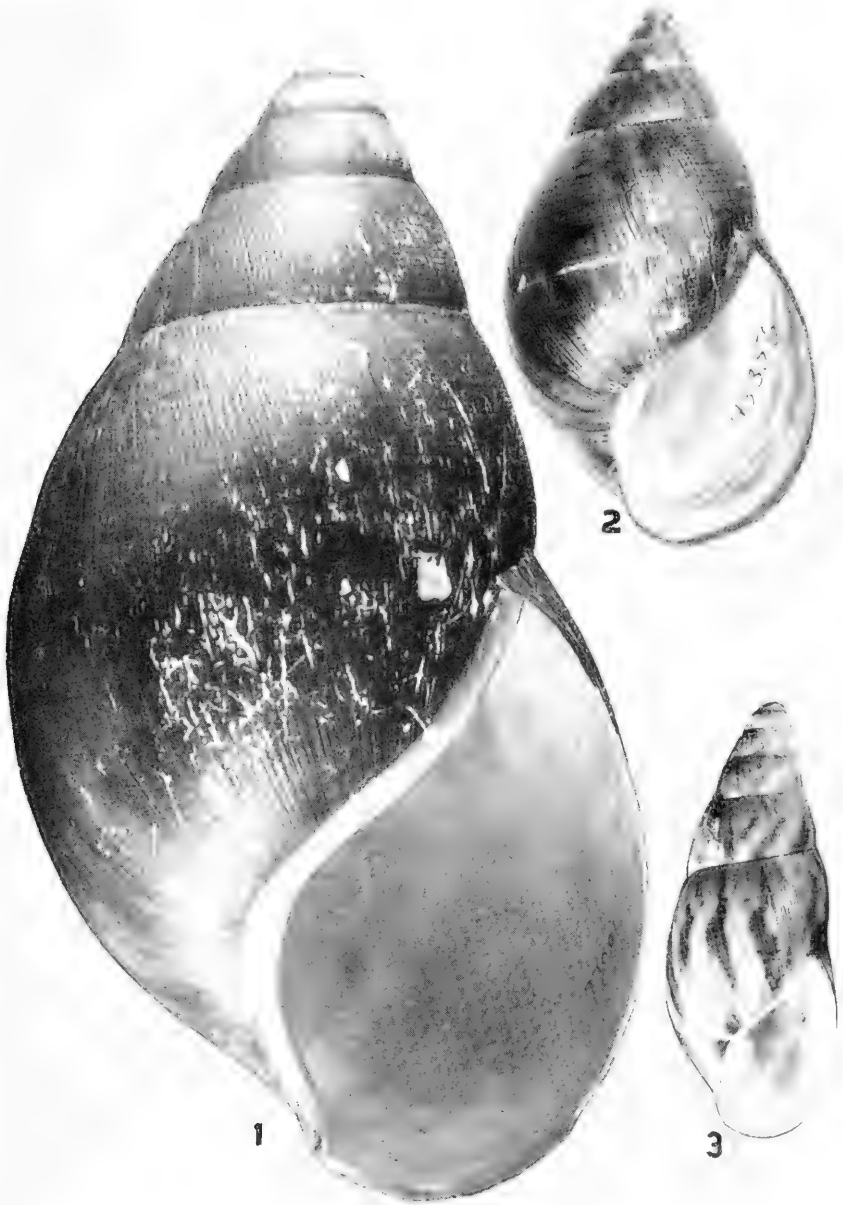
PLATE 2

PLATE 2

Fig. 1. *Achatina achatina depravata* J. Bequaert. Harbel. Holotype, M.C.Z. No. 77001. Slightly reduced; length, 177 mm.

Fig. 2. *Achatina achatina togoënsis* Bequaert and Clench. Bismarckburg. Paratype, Berlin M. No. 43356. Natural size.

Fig. 3. *Archachatina sandgroundi* J. Bequaert. Mt. Selinda. Paratype, M.C.Z. No. 94745. Natural size.





**PLATE 3**

PLATE 3

Fig. 1. *Achatina achatina achatina* (Linné). Copy of Gualtieri's (1742) Pl. 45, upper fig. B. Slightly reduced; original 178 mm. long.

Fig. 2. *Achatina (Euaethiopina) loveridgei* (Clench and Archer). Bagilo. Holotype, M.C.Z. No. 58934. Natural size.

Fig. 3. *Achatina fulica rodatzi* Dunker. Copy of figure of type of *A. daroliensis* Kobelt. Same size.



1



2



3





PLATE 4

PLATE 4

Fig. 1. *Archachatina purpurea* (Gmelin). Cape Palmas. M.C.Z. No. 45529.  
Young shell, X 2.

Fig. 2. *Achatina zanzibarica* Bourguignat. Magotto. M.C.Z. No. 100507.  
Natural size.

Fig. 3. *Achatina achatina achatina* (Linné). Copy of Seba's (1758) Pl. 71,  
fig. 3. Same size, reversed.

Fig. 4. *Achatina delorioli* Bonnet. Copy of figure of type. Same size.

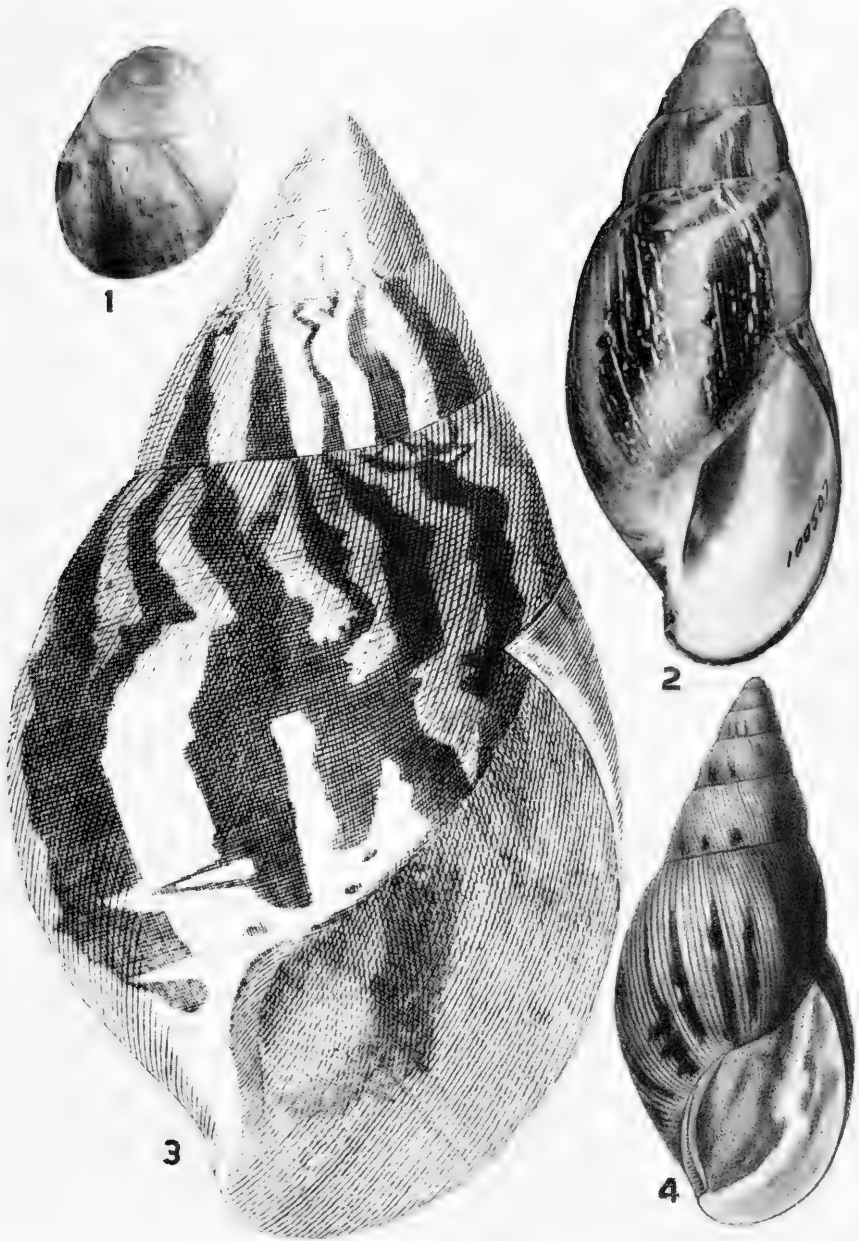




PLATE 5

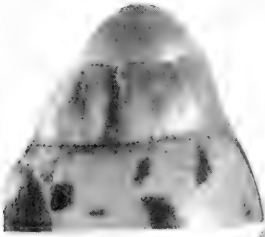
PLATE 5

Fig. 1. *Archachatina papyracea* (Reeve). Yaunde. M.C.Z. No. 139532. Summit of young shell, X 2.

Fig. 2. *Achatina achatina togoënsis* Bequaert and Clench. Bismarckburg. Holotype, Berlin M. No. 47176. Natural size.

Fig. 3. *Achatina panthera panthera* (Férussac). Lectotype of *A. panthera* var. *berevoensis* Clench and Archer. Between Mahabo and Berevo. M.C.Z. No. 31078. Natural size.

Fig. 4. *Achatina albopicta* E. A. Smith. Diani Beach, M.C.Z. No. 167391. Young shell, natural size.



1



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4





PLATE 6

PLATE 6

Fig. 1. *Achatina achatina bayoli* Morelet. Assinie. M.C.Z. No. 40904. Natural size.

Fig. 2. *Archachatina purpurea* (Gmelin). Monrovia. Cotype of *A. viridescens* Ancy. Natural size. Courtesy of Brussels Museum.

Fig. 3. *Archachatina ventricosa ventricosa* (Gould). Liberia. M.C.Z. Natural size.

Fig. 4. *Archachatina sandgroundi* J. Bequaert. Mt. Selinda. Holotype, M.C.Z. No. 82445. Natural size.

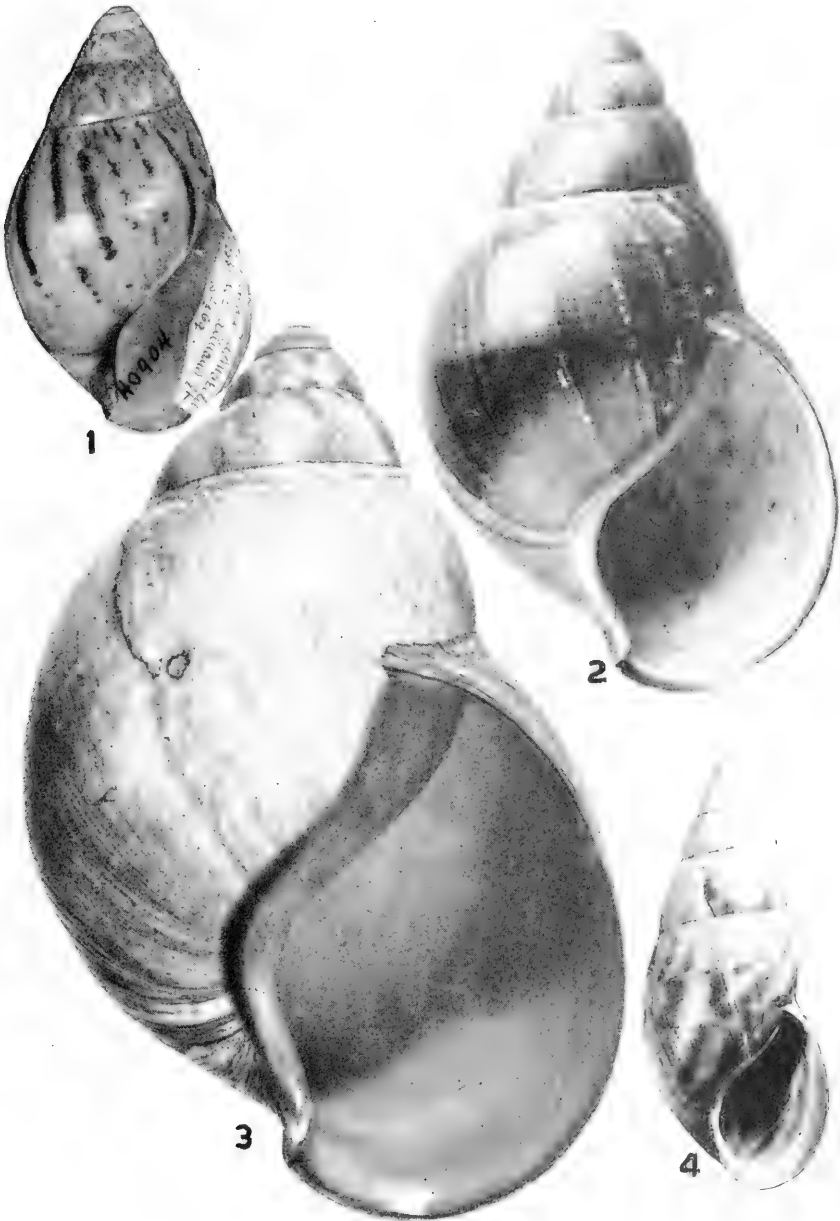




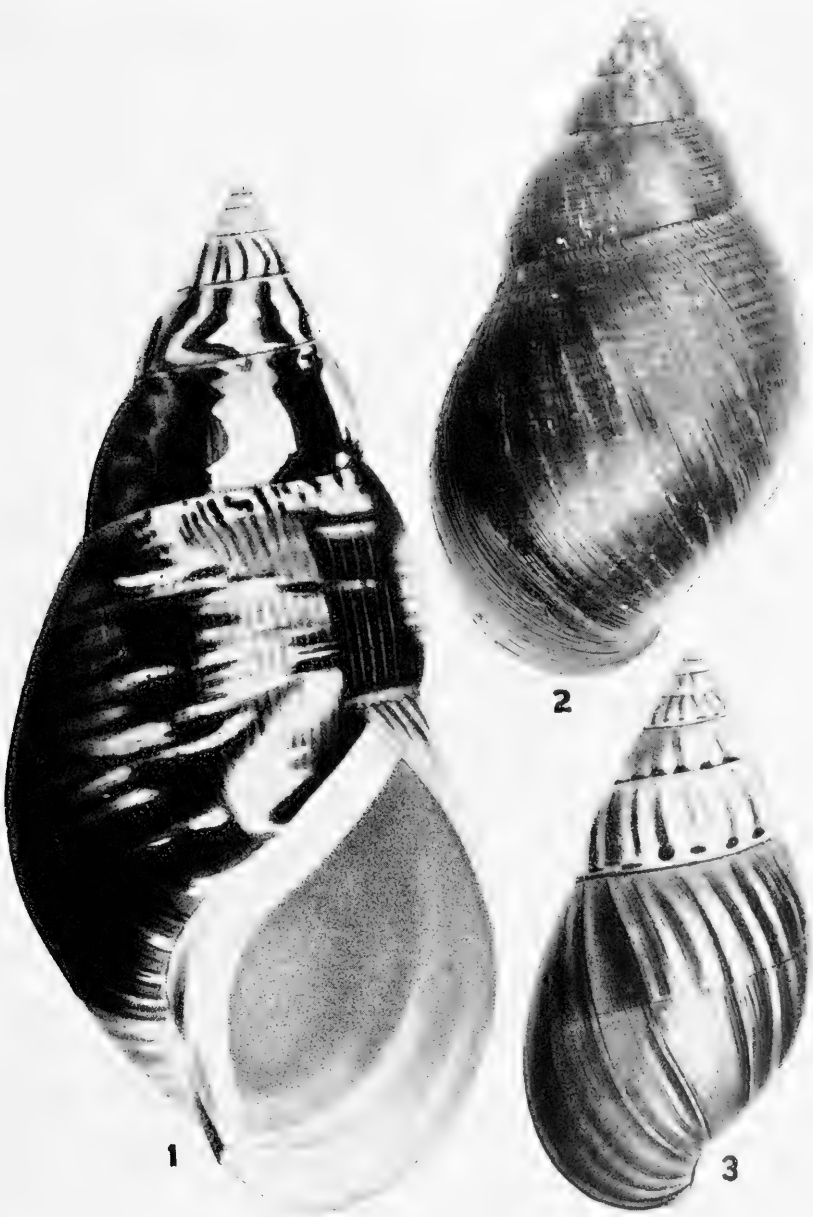
PLATE 7

PLATE 7

Fig. 1. *Achatina fulica fulica* Bowdich. Copy of Férussac's (1832) Pl. 124A, left fig. 2 ("*Helix acuta*"). Slightly larger than original, which is 120 mm. long.

Fig. 2. *Achatina achatina togoënsis* Bequaert and Clench. Bismarekburg. Paratype, M.C.Z. No. 98688. Natural size.

Fig. 3. *Achatina fulica castanea* Lamarck. Copy of Férussac's (1823) Pl. 125, fig. 4 ("*Helix zebrina*"). Original 76 mm. long.



1

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3





PLATE 8

PLATE 8

Fig. 1. *Archachatina weberi* J. Bequaert. Imatong Mts. Paratype, M.C.Z. No. 182902. Natural size.

Fig. 2. *Archachatina ventricosa ventricosa* (Gould). West Africa. M.C.Z. Natural size.

Fig. 3. *Archachatina purpurea* (Gmelin). Liberia. M.C.Z. No. 27089. Natural size.

Fig. 4. *Achatina achatina achatina* (Linné). Copy of d'Argenville's (1742) Pl. 13, fig. E. Same size.

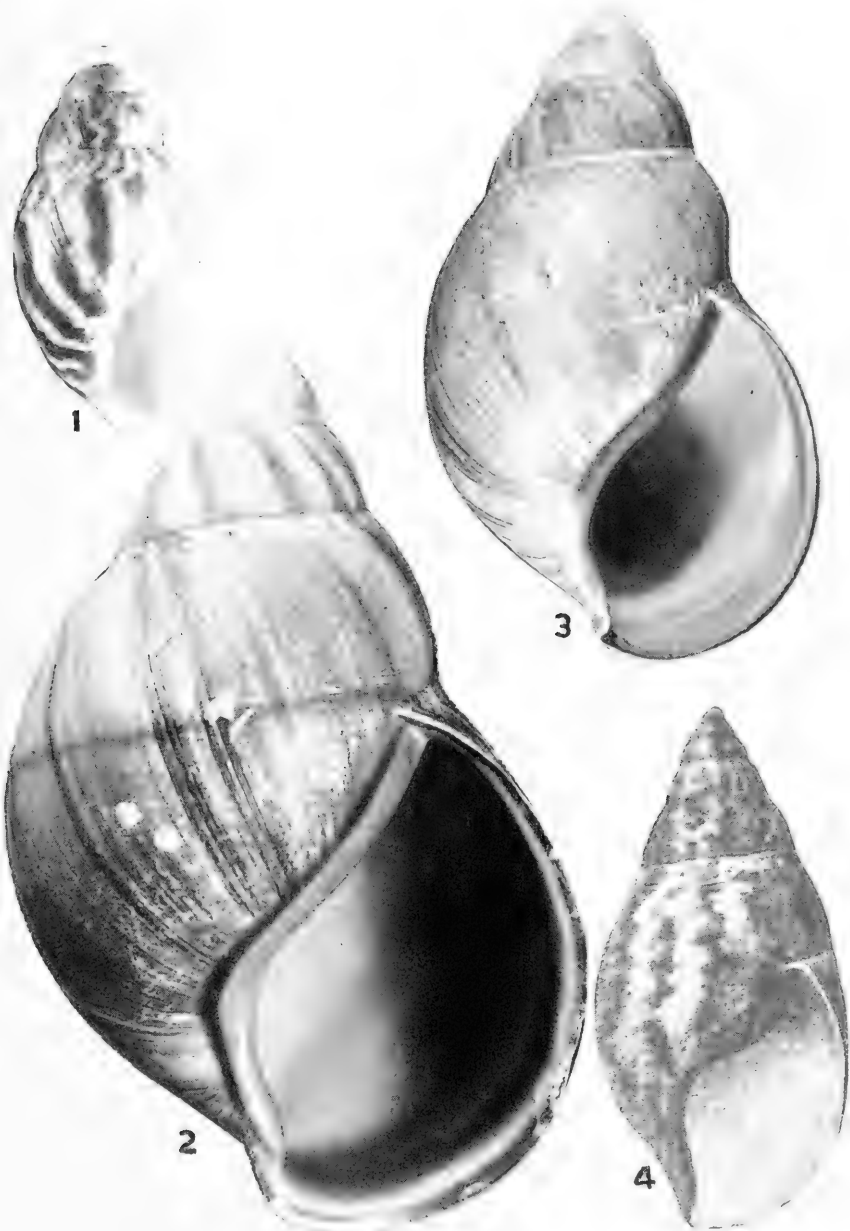




PLATE 9

PLATE 9

- Fig. 1. *Achatina achatina bayoli* Morelet. Copy of figure of type. Same size.  
Fig. 2. *Archachatina ventricosa ventricosa* (Gould). West Africa. M.C.Z.  
Natural size.  
Fig. 3. *Archachatina marginata marginata* (Swainson). Copy of figure of  
type. Same size.  
Fig. 4. *Achatina reticulata* Pfeiffer. Chwaka Bay. M.C.Z. No. 167407.  
Young shell. Natural size.







PLATE 10

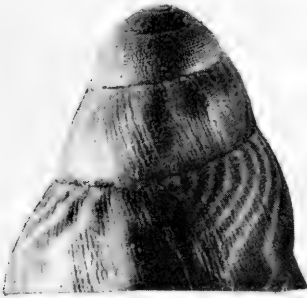
PLATE 10

Fig. 1. *Archachatina weberi* J. Bequaert. Imatong Mts. Paratype, M.C.Z. No. 182902. Summit, X 2.

Fig. 2. *Achatina achatina monochromatica* Pilsbry. M.C.Z. No. 97934. Natural size.

Fig. 3. *Archachatina ventricosa ventricosa* (Gould). West Africa. M.C.Z. Natural size.

Fig. 4. *Archachatina weberi* J. Bequaert. Imatong Mts. Holotype, M.C.Z. No. 182901. Natural size.



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PLATE 11

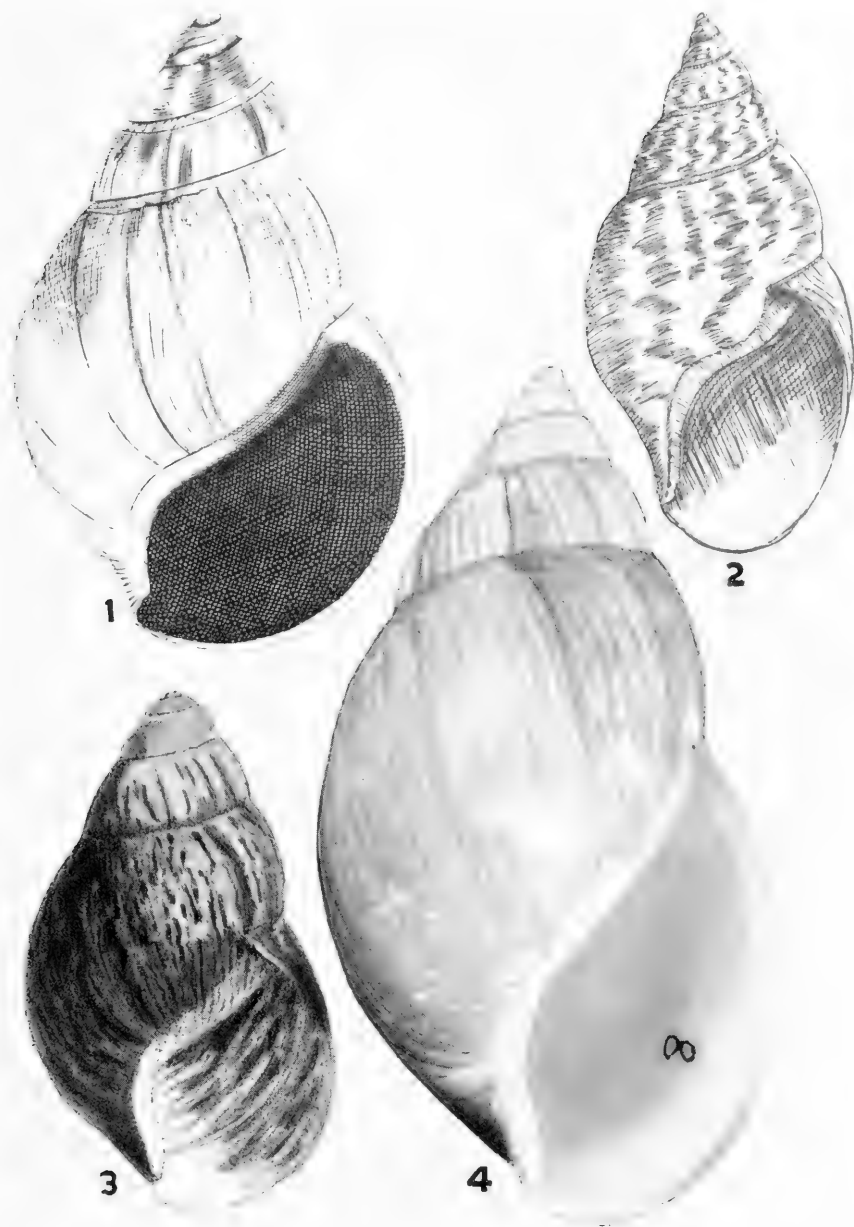
PLATE 11

Fig. 1. *Archachatina purpurea* (Gmelin). Copy of Lister's (1688) Pl. 581, fig. 35. Same size.

Fig. 2. *Achatina achatina achatina* (Linné). Copy of Fabius Columna's (1616) Pl. on p. xvi, lower right hand fig. Same size.

Fig. 3. *Archachatina marginata ovum* (Pfeiffer). Copy of figure of type. Same size.

Fig. 4. *Achatina fulica rodatzki* Dunker. Zanzibar Id. M.C.Z. No. 167406. Dissected specimen. Natural size.







**PLATE 12**

PLATE 12

Fig. 1. *Achatina achatina elegans* (Link). Copy of Chemnitz' (1786) Pl. 118, fig. 1013. Same size.

Fig. 2. *Achatina achatina roscolabiata* J. Bequaert. Copy of Shaw and Nodder's (1796) Pl. 248 ("*Bulla achatina*"). Same size.

Fig. 3. *Achatina albopicta* E. A. Smith. Diani Beach. M.C.Z. No. 167391. Natural size.





PLATE 13

PLATE 13

Fig. 1., *Achatina achatina monochromatica* Pilsbry. Brussels M. Natural size.

Fig. 2. *Archachatina rhodostoma* (Philippi). Copy of figure of type. Same size.

Fig. 3. *Achatina iredalei* Preston. Shimba Hills. Paratype, M.C.Z. No. 75563. Natural size.

Fig. 4. *Achatina achatina achatina* (Linné). Copy of Bonanno's (1684) fig. 192. Same size.

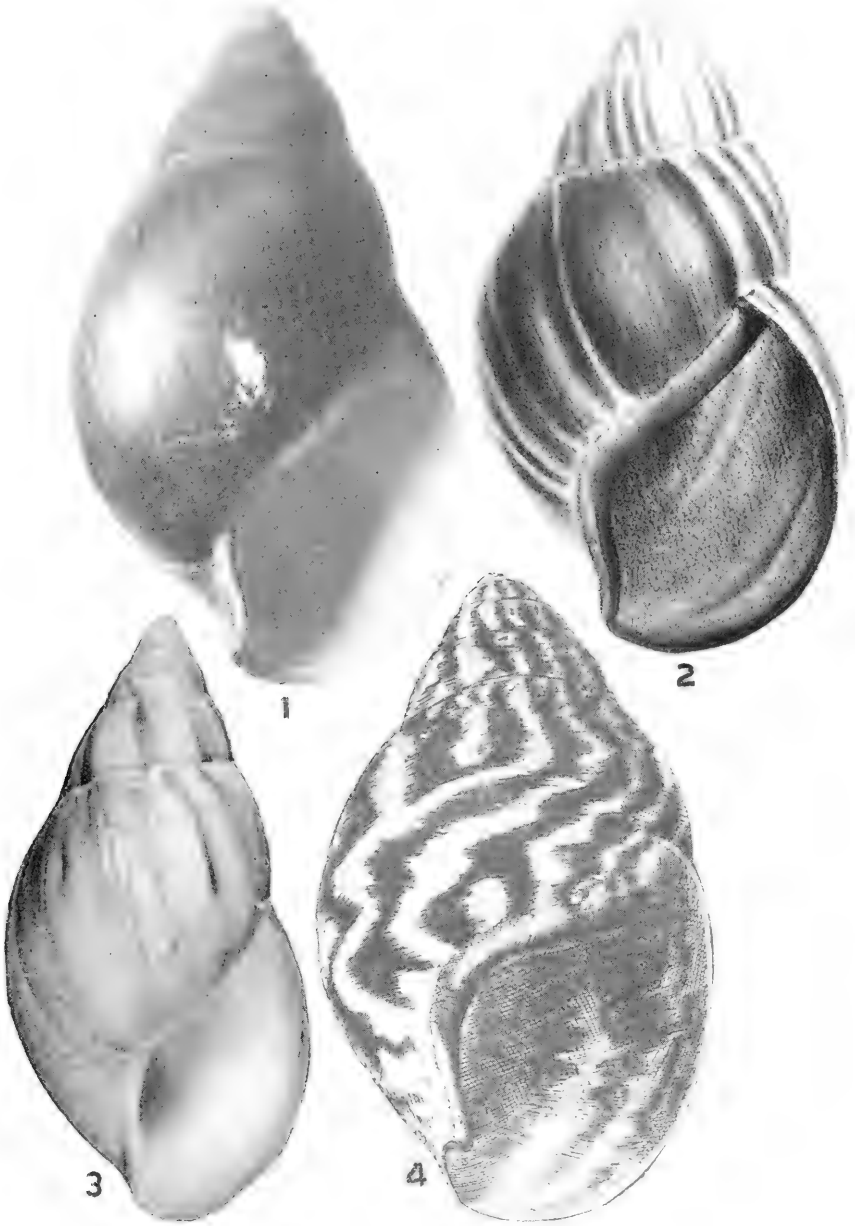






PLATE 14

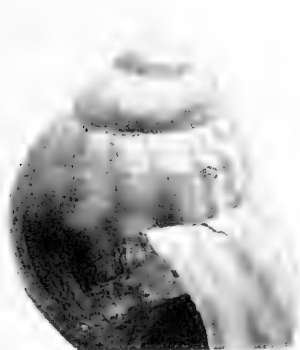
PLATE 14

Fig. 1. *Achatina achatina elegans* (Link). Copy of Chemnitz' (1786) Pl. 118, fig. 1012. Same size.

Fig. 2. *Archachatina marginata clenchi* J. Bequaert. Edea. Holotype, M.C.Z. No. 167946. Natural size.

Fig. 3. *Achatina iredalei* Preston. Copy of figure of type. Same size.

Fig. 4. *Achatina achatina achatina* (Linné). Harbel. M.C.Z. No. 163509. Young shell, X 3.



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PLATE 15

PLATE 15

Fig. 1. *Achatina achatina elegans* (Link). West Africa. M.C.Z. No. 626. Natural size.

Fig. 2. *Achatina fulica hamillei* Petit. Copy of figure of type of *A. panthera* var. *neumanni* v. Martens. Same size.







PLATE 16

PLATE 16

Fig. 1. *Achatina zanzibarica* Bourguignat. Copy of C. R. Boettger's (1913) figure of a cotype of *A. usambarensis* Rolle. Same size.

Fig. 2. *Achatina reticulata* Pfeiffer. Chwaka Bay. M.C.Z. No. 167407. Young shell. Natural size.

Fig. 3. *Achatina fulica fulica* Bowdich. Copy of Lister's (1688) Pl. 578, fig. 33. Same size.

Fig. 4. *Achatina achatina achatina* (Linné). Copy of Favanne's (1780) Pl. 65, fig. M5. Same size.

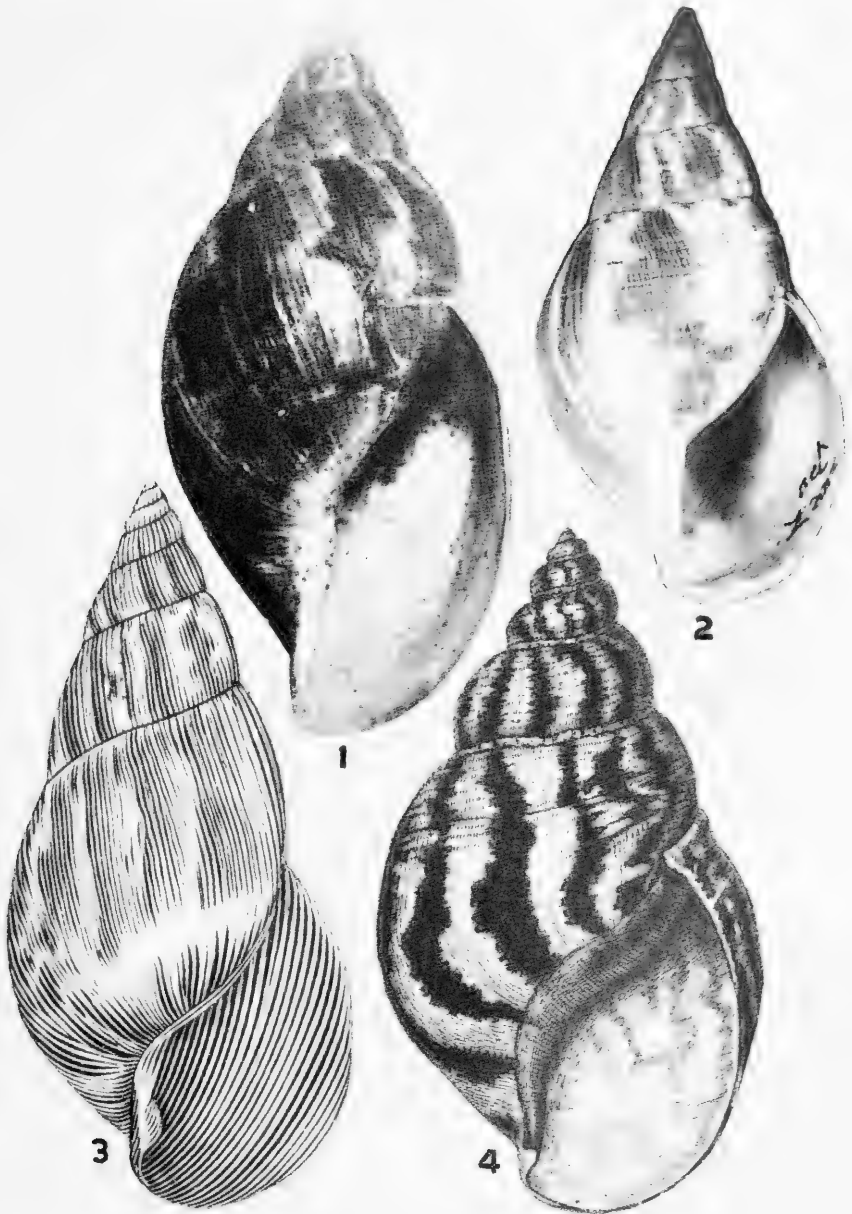




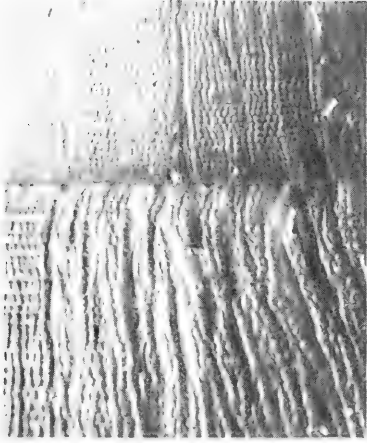
PLATE 17

PLATE 17

Fig. 1. *Achatina balteata balteata* Reeve. Part of penultimate and body-whorl of shell of fig. 3, to show sculpture. X 4.

Fig. 2. *Achatina (Tripachatina) vignoniana* Morelet. Copy of figure of type. Same size.

Fig. 3. *Achatina balteata balteata* Reeve. Ngayu. Am.M.N.H. Natural size.



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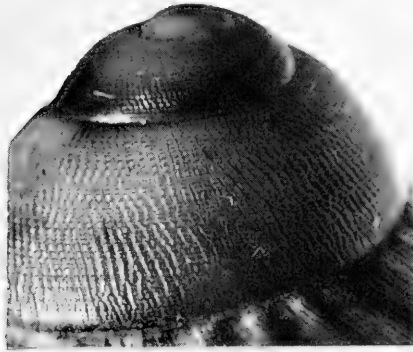
PLATE 18

PLATE 18

Fig. 1. *Archachatina ventricosa spectaculum* Pilsbry. Holotype. U.S.N.M. No. 406386. Natural size. Courtesy of U.S.N.M.

Fig. 2. *Achatina balteata balteata* Reeve. Copy of figure of type. Same size.

Fig. 3. *Archachatina degneri* Bequaert and Clench. Nsawam. M.C.Z. No. 163653. Young shell, X 7.



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PLATE 19

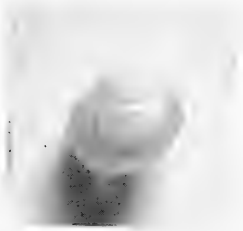
PLATE 19

Fig. 1. *Achatina achatina monochromatica* Pilsbry. Holotype, Ac.N.S.Phila. No. 78483. Natural size. Courtesy of Ac.N.S.Phila.

Fig. 2. *Achatina fulica hamillei* Petit. Copy of figure of type. Same size.

Fig. 3. *Achatina fulica fulica* Bowdich. Guam. M.C.Z. No. 180138. Young shell, one week old, X 3.

Fig. 4. *Achatina fulica hamillei* Petit. Mombasa. M.C.Z. No. 167394. Young shell removed from egg, X 3.



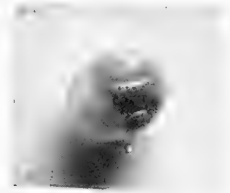
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PLATE 20

PLATE 20

Fig. 1. *Archachatina weberi* J. Bequaert. Imatong Mts. Paratype, M.C.Z. No. 182902. Natural size.

Fig. 2. *Achatina fulica fulica* Bowdich. Mauritius. Umbilicate abnormality. M.C.Z. No. 73734. Natural size.

Fig. 3. *Archachatina marginata suturalis* (Philippi). Lagos. M.C.Z. No. 143678. Natural size.

Fig. 4. *Archachatina sandgroundi* J. Bequaert. Mt. Selinda. Paratype, M.C.Z. No. 94745. Natural size.

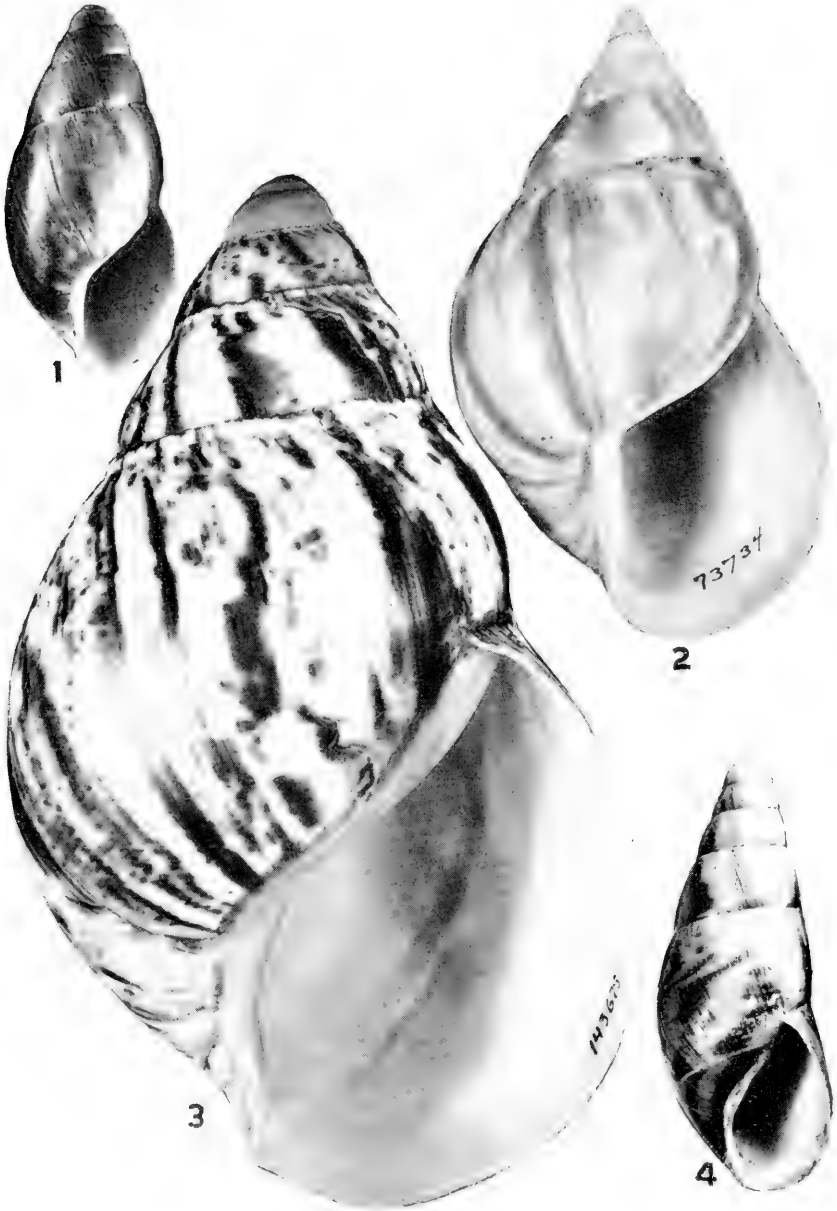




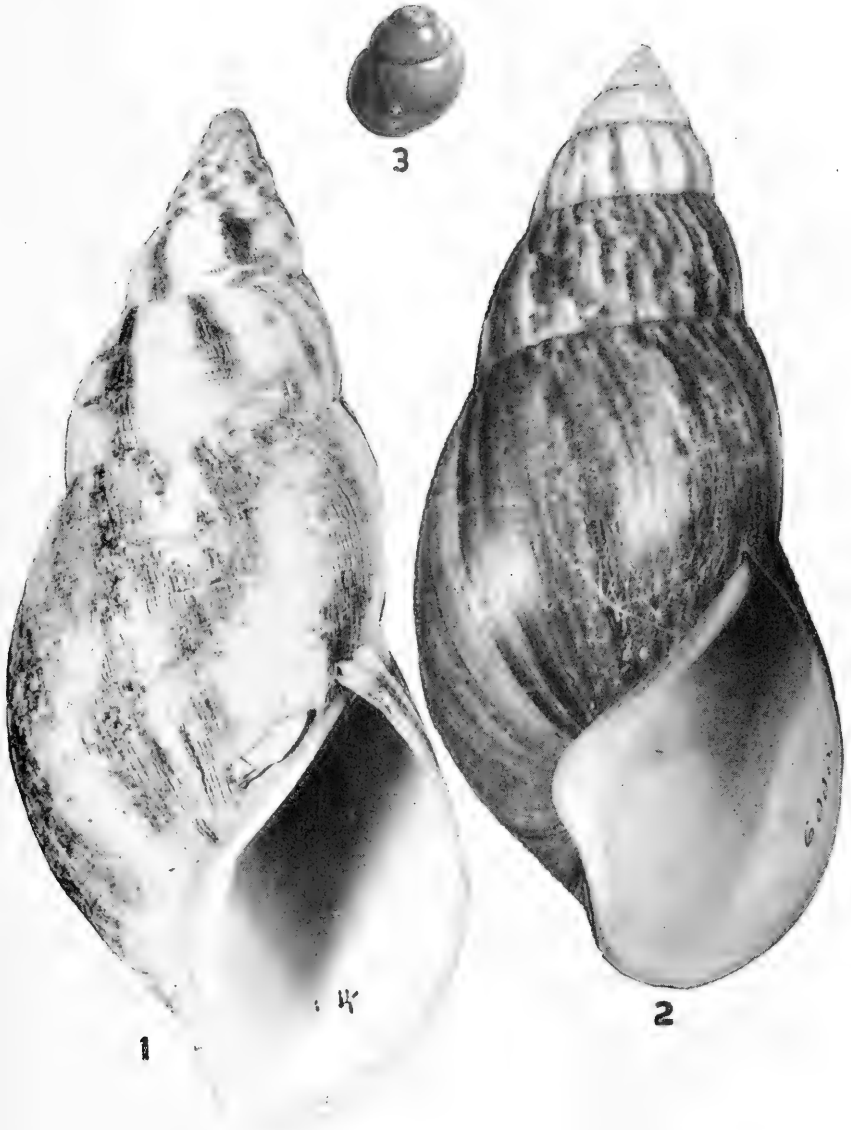
PLATE 21

PLATE 21

Fig. 1. *Achatina albopicta* E. A. Smith. Diani Beach. M.C.Z. No. 167391. Dissected specimen. Natural size.

Fig. 2. *Achatina fulica fulica* Bowdich. Ipoh, Perak. M.C.Z. No. 60001. Natural size.

Fig. 3. *Achatina albopicta* E. A. Smith. Diani Beach. M.C.Z. No. 167391. Young shell removed from egg, X 3.







**PLATE 22**

PLATE 22

Fig. 1. *Achatina fulica fulica* Bowdich. M.C.Z. Scalariform abnormality. Natural size.

Fig. 2. *Archachatina rhodostoma* (Philippi). West Africa. M.C.Z. Natural size.

Fig. 3. *Archachatina ventricosa ventricosa* (Gould). Type from Gould Collection. Liberia. Natural size.

Fig. 4. *Achatina fulica castanea* Lamarck. Copy of Férussac's (1823) Pl. 125, fig. 3. Same size.

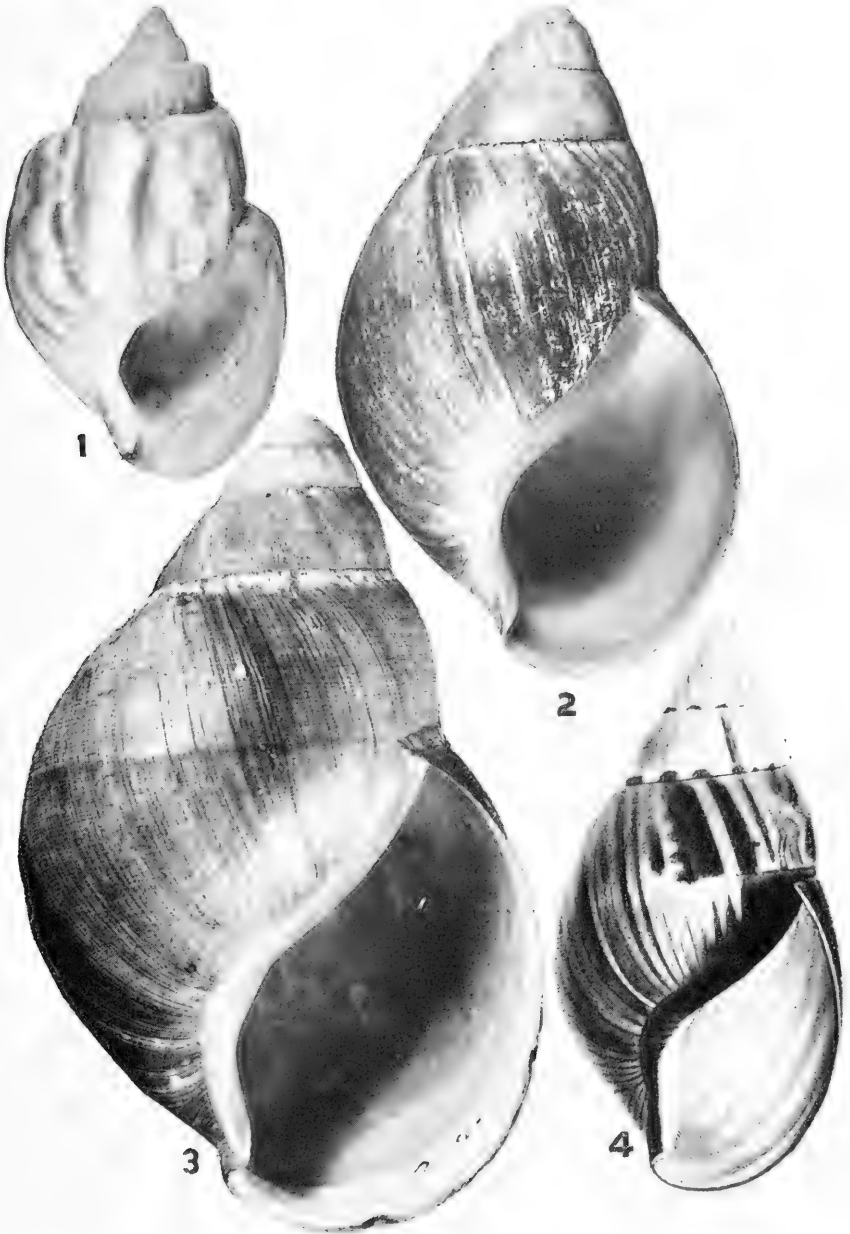




PLATE 23

PLATE 23

Fig. 1. *Archachatina papyracea* (Pfeiffer). Copy of Reeve's figure of type. Same size.

Fig. 2. *Achatina pfeifferi* Dunker. Angola. M.C.Z. No. 58845. Natural size.

Fig. 3. *Archachatina ventricosa ventricosa* (Gould). Cape Palmas. M.C.Z. No. 59312. Natural size.

Fig. 4. *Achatina fulica fulica* Bowdich. Ipoh, Perak. M.C.Z. No. 60001. Natural size.

Fig. 5. *Archachatina meadi* J. Bequaert. Ngosi. Holotype, M.C.Z. No. 182903. Natural size.

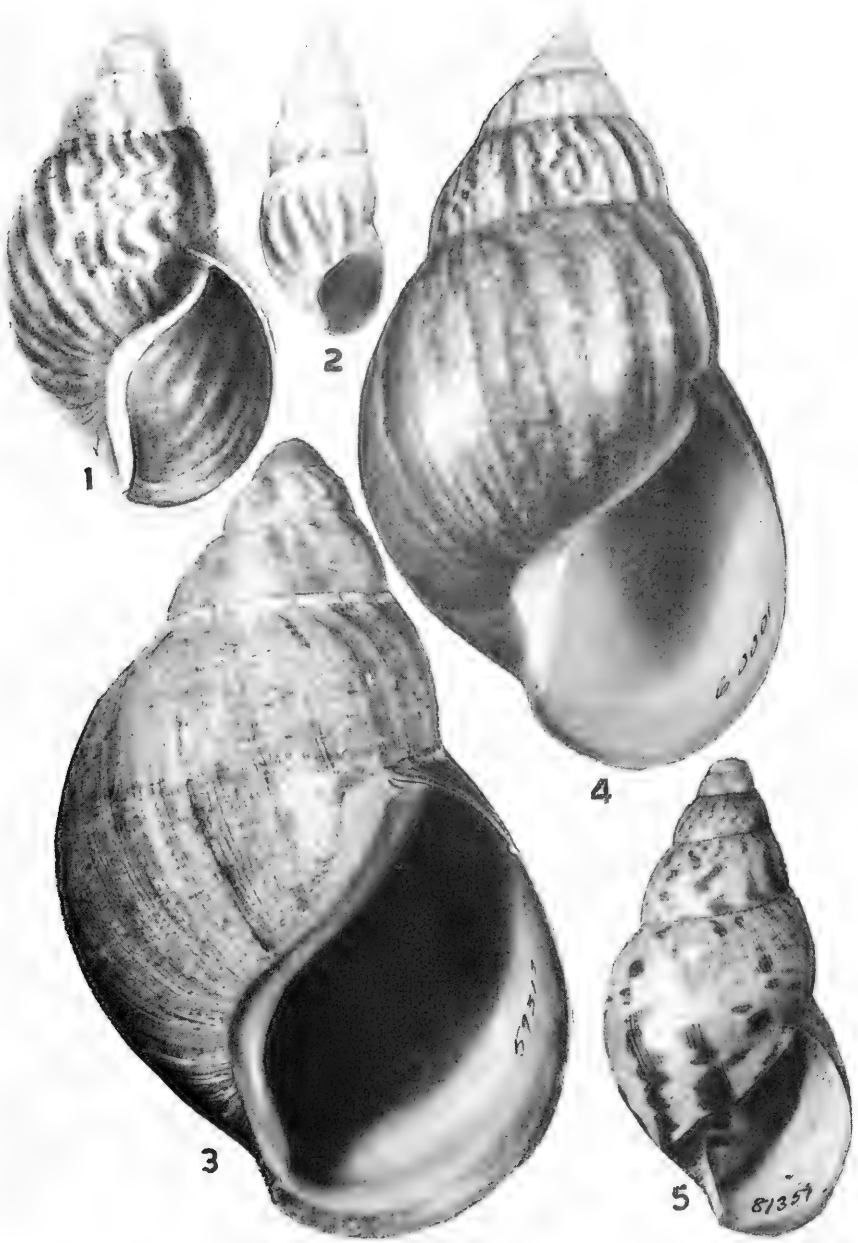






PLATE 24

PLATE 24

Fig. 1. *Archachatina purpurea* (Gmelin). Copy of Chemnitz' (1786) Pl. 118, fig. 1017. Same size.

Fig. 2. *Achatina fulica fulica* Bowdich. Copy of figure of type. Same size.

Fig. 3. *Achatina lactea* Reeve. "Zanzibar". M.C.Z. No. 151502. Natural size.

Fig. 4. *Achatina albopicta* E. A. Smith. Diani Beach. Scalariform abnormality. M.C.Z. No. 167392. Natural size.

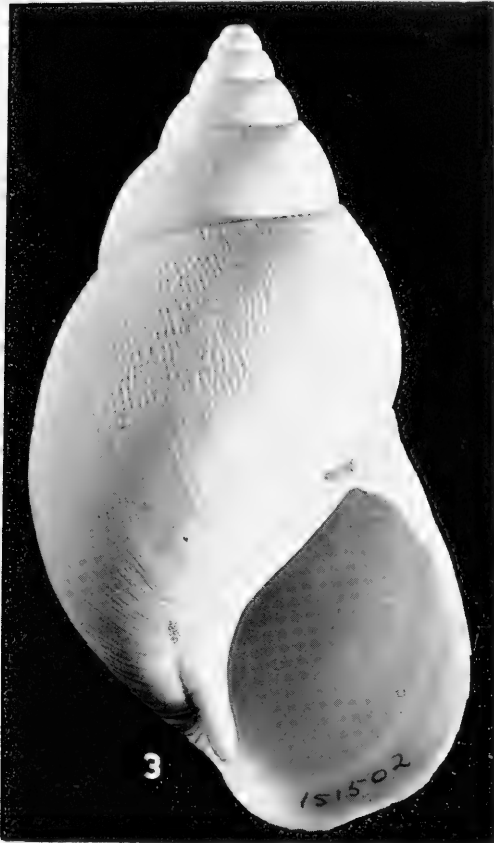
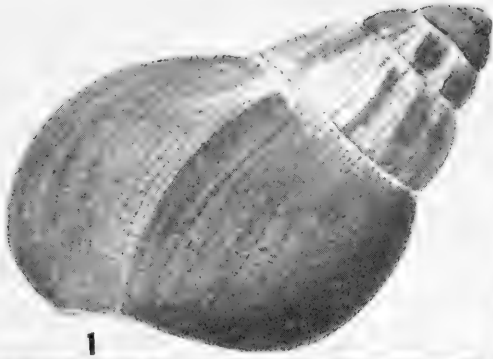




PLATE 25

PLATE 25

Fig. 1. *Achatina fulica fulica* Bowdich. Koror. M.C.Z. No. 166429.  
Natural size.

Fig. 2. *Archachatina purpurea* (Gmelin). Cape Palmas. M.C.Z. No. 45529.  
Natural size.

Fig. 3. *Archachatina ventricosa spectaculum* Pilsbry. Liberia. M.C.Z.  
Natural size.

Fig. 4. *Achatina panthera antourtourensis* Crosse. Copy of original (1879)  
figure of type. Same size:

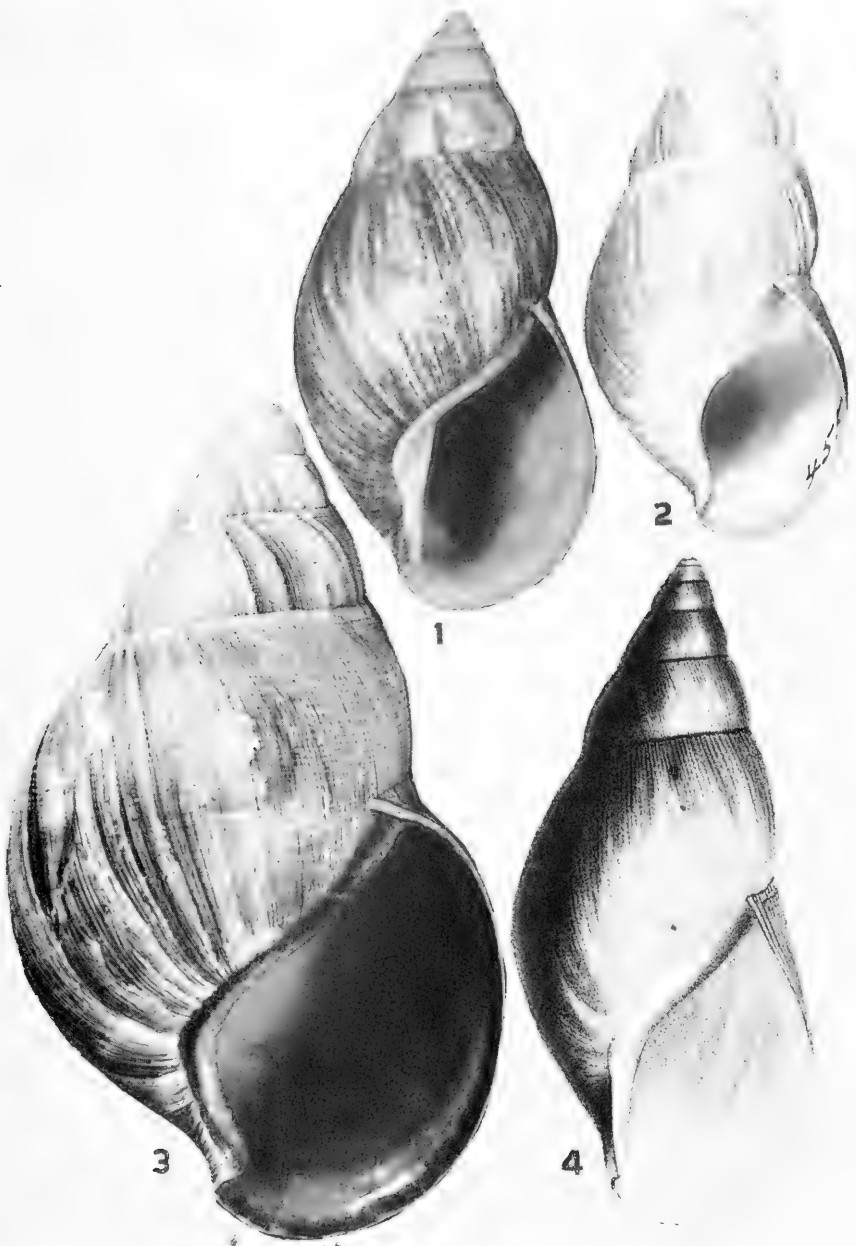






PLATE 26

PLATE 26

Fig. 1. *Archachatina marginata icterica* Bequaert and Clench. Gaboon. M.C.Z. Natural size.

Fig. 2. *Achatina fulica fulica* Bowdich. Saipan. M.C.Z. No. 167844. Natural size.

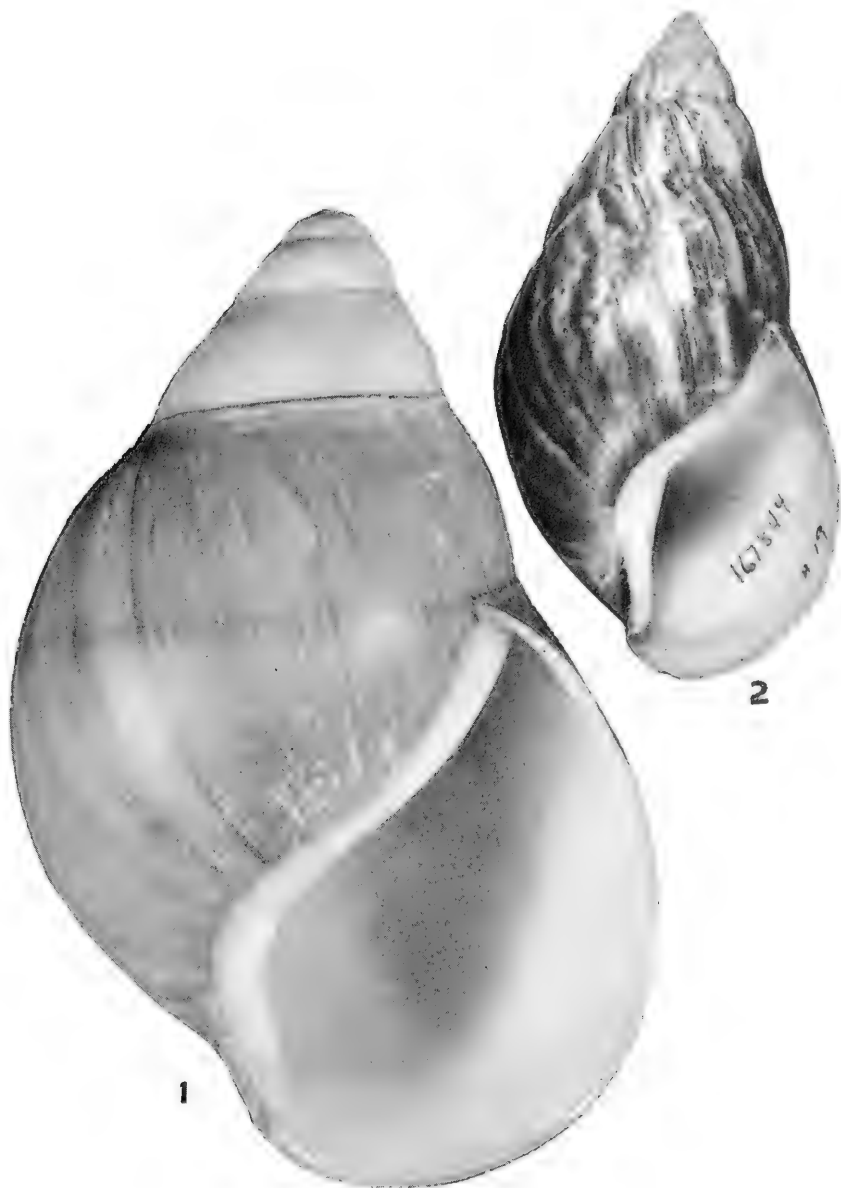




PLATE 27

PLATE 27

Fig. 1. *Achatina albopicta* E. A. Smith. Diani Beach. M.C.Z. No. 167391. Slightly reduced; length, 166 mm.

Fig. 2. *Achatina fulica fulica* Bowdich. Guam. M.C.Z. No. 180138. Natural size.

Fig. 3. *Achatina fulica coloba* Pilsbry. Cotype. Ac.N.S.Phila. No. 30266. Natural size. Courtesy of Ac.N.S.Phila.

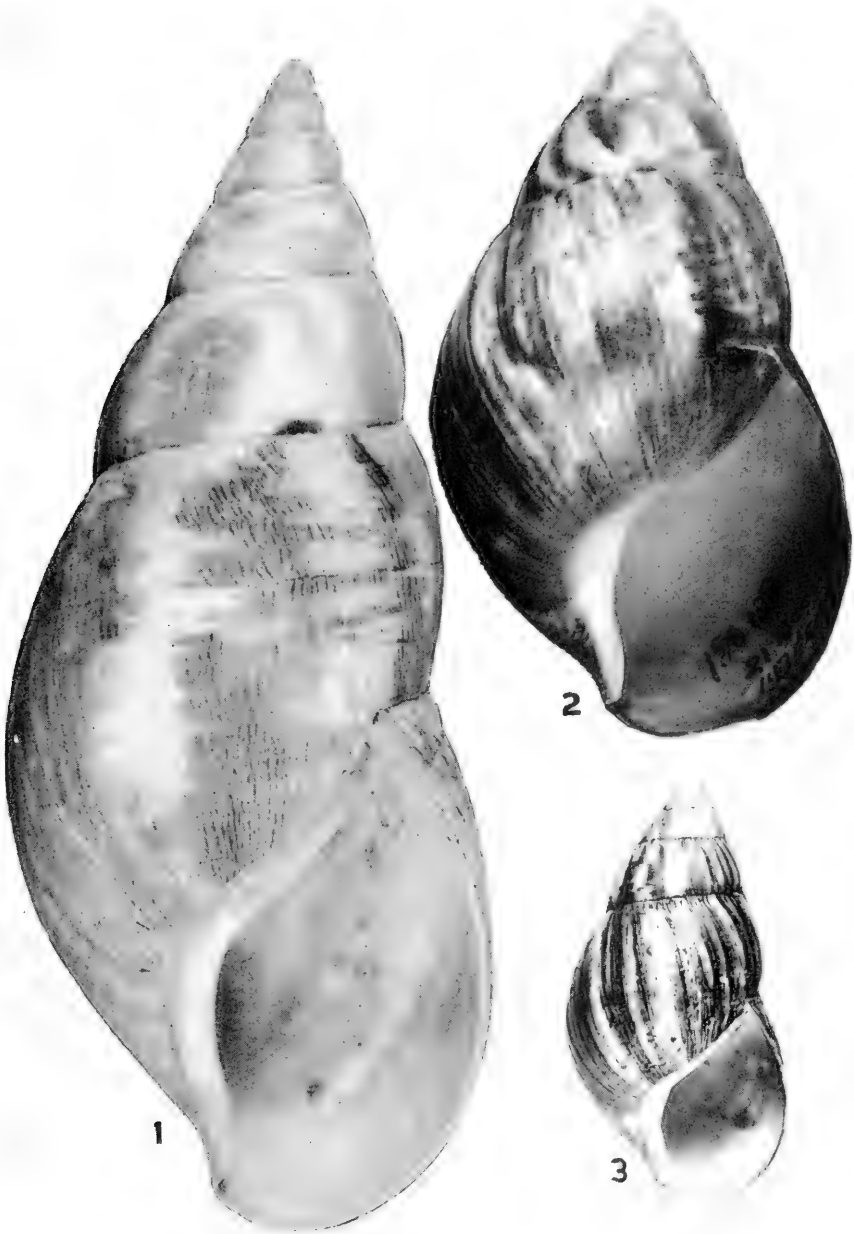






PLATE 28

PLATE 28

Fig. 1. *Archachatina rhodostoma* (Philippi). Holotype of *A. rhodostoma* var. *splendida* Pilsbry. Ac.N.S.Phila. No. 3095. Natural size. Courtesy of Ac.N.S.Phila.

Fig. 2. *Achatina fulica fulica* Bowdich. Singapore. M.C.Z. No. 145426. Natural size.

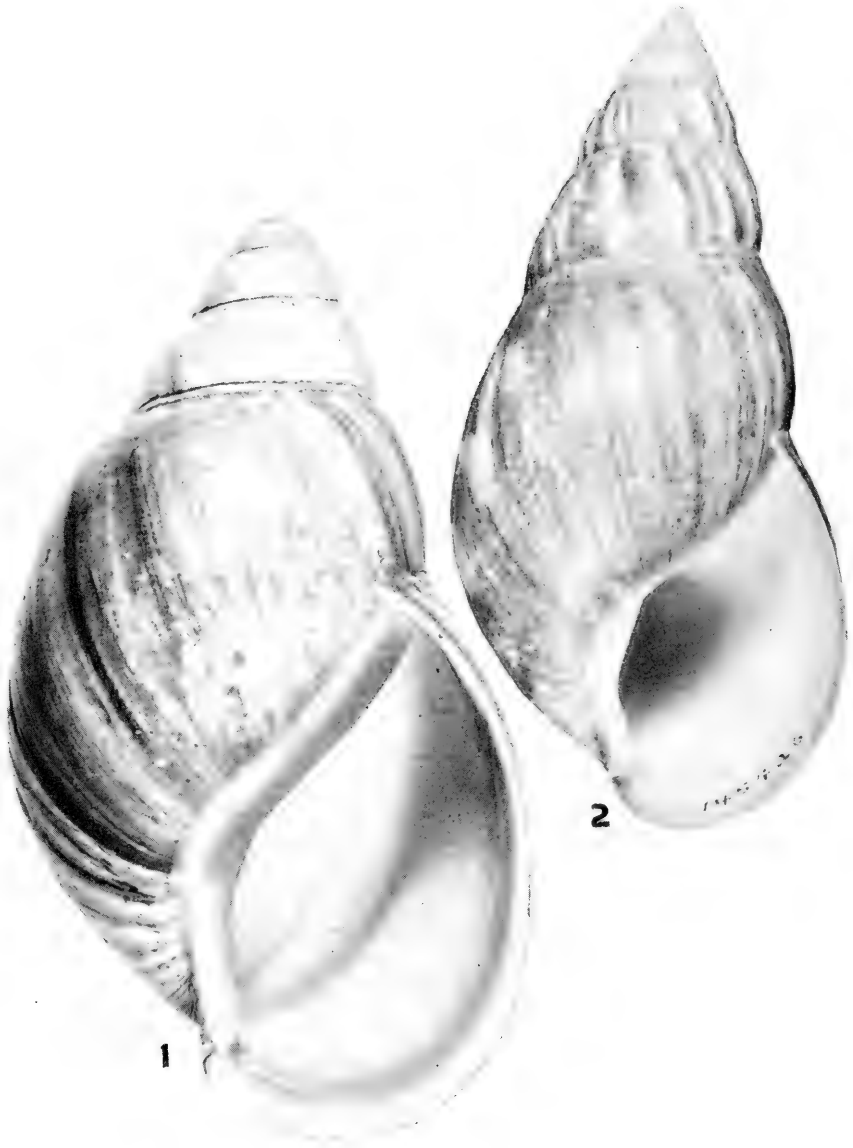


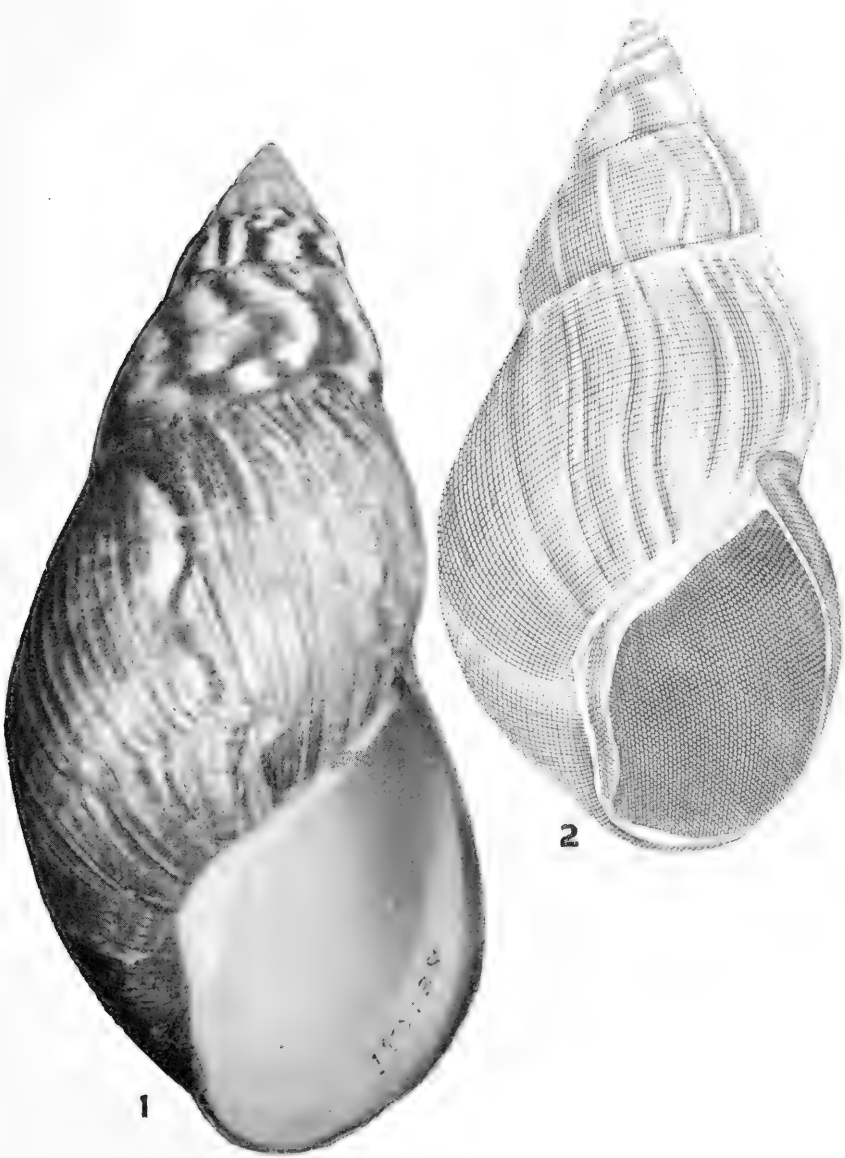


PLATE 29

PLATE 29

Fig. 1. *Achatina fulica fulica* Bowdich. Guam, M.C.Z. No. 180138.  
Natural size.

Fig. 2. *Achatina fulica fulica* Bowdich. Copy of Lister's (1688) Pl. 582,  
fig. 35a. Same size.



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PLATE 30

PLATE 30

Fig. 1. *Achatina fulica rodatzii* Dunker. Copy of one of the figures of the type. Same size.

Fig. 2. *Achatina fulica fulica* Bowdich. Copy of Seba's (1758) Pl. 71, fig. 5. Same size, reversed.

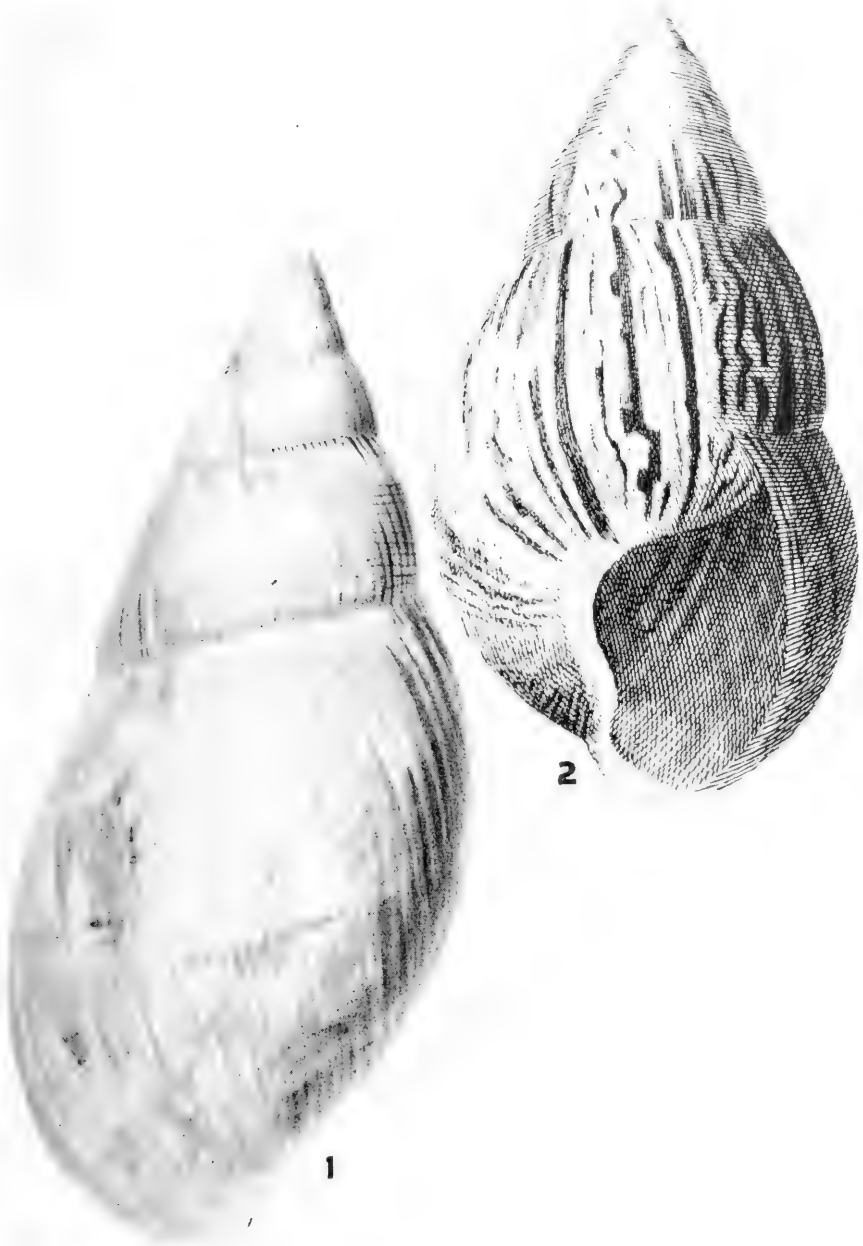




PLATE 31

PLATE 31

Figs. 1 and 2. *Achatina fulica fulica* Bowdich. Two cotypes of *A. panthera* var. *chrysoderma* Pilsbry. Ac.N.S.Phila. No. 4241. Nearly natural size. Courtesy of Ac.N.S.Phila.

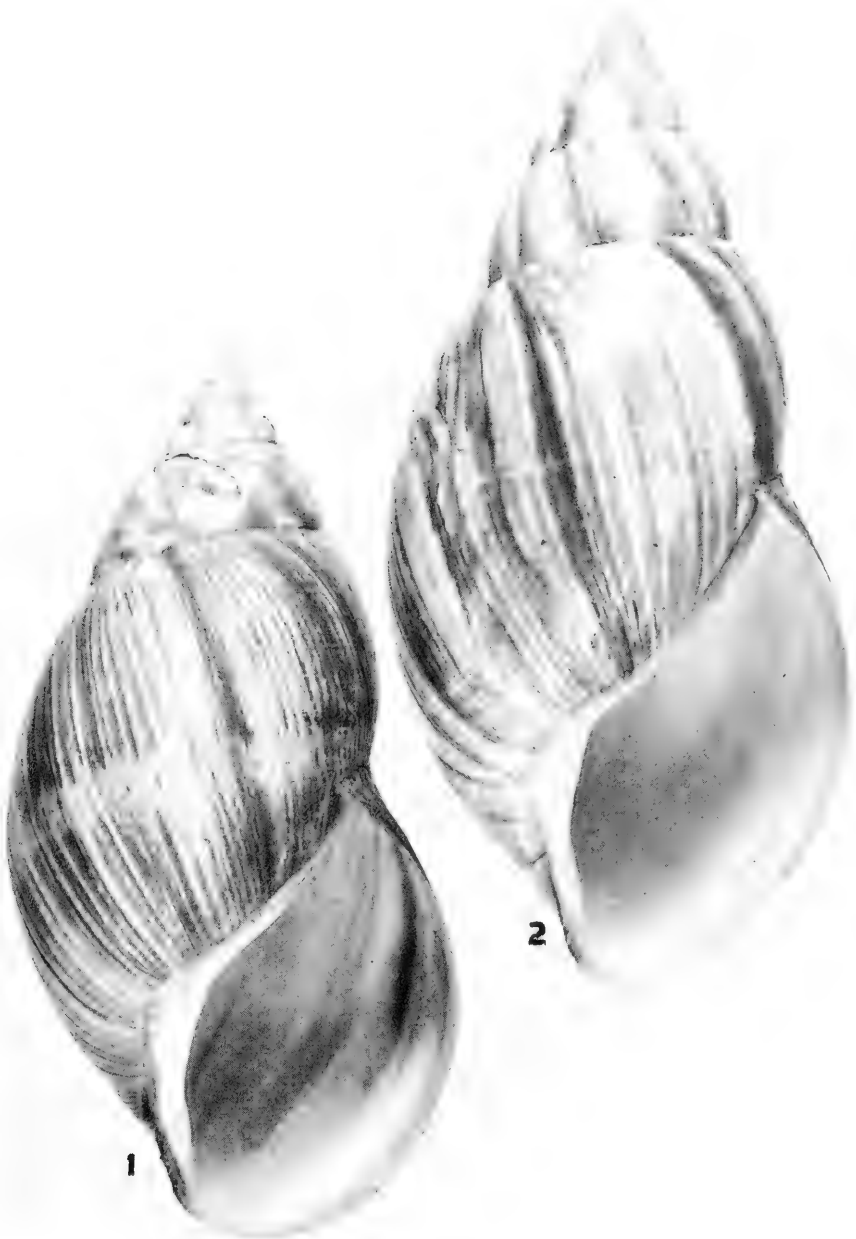






PLATE 32

PLATE 32

Fig. 1. *Achatina fulica fulica* Bowdich. Copy of Reeve's (1849) Pl. 3, fig. 10 ("*A. fulva*"). Same size.

Fig. 2. *Achatina fulica fulica* Bowdich. Copy of Deshayes' (1851) Pl. 124, fig. 1 ("*A. fulva*"). Slightly reduced; original 133 mm. long.



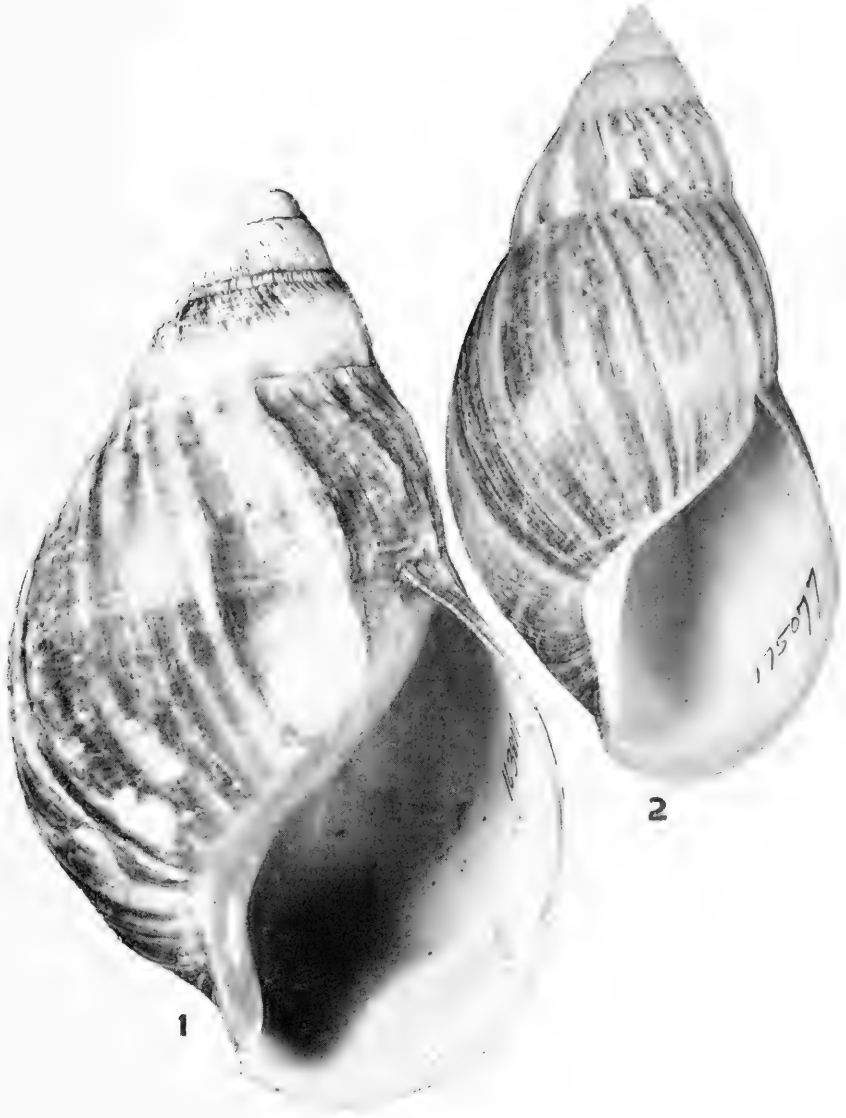


PLATE 33

PLATE 33

Fig. 1. *Archachatina rhodostoma* (Philippi). Popolahun. M.C.Z. No. 163877. Natural size.

Fig. 2. *Achatina fulica fulica* Bowdich. Manila. M.C.Z. No. 175077. Natural size.



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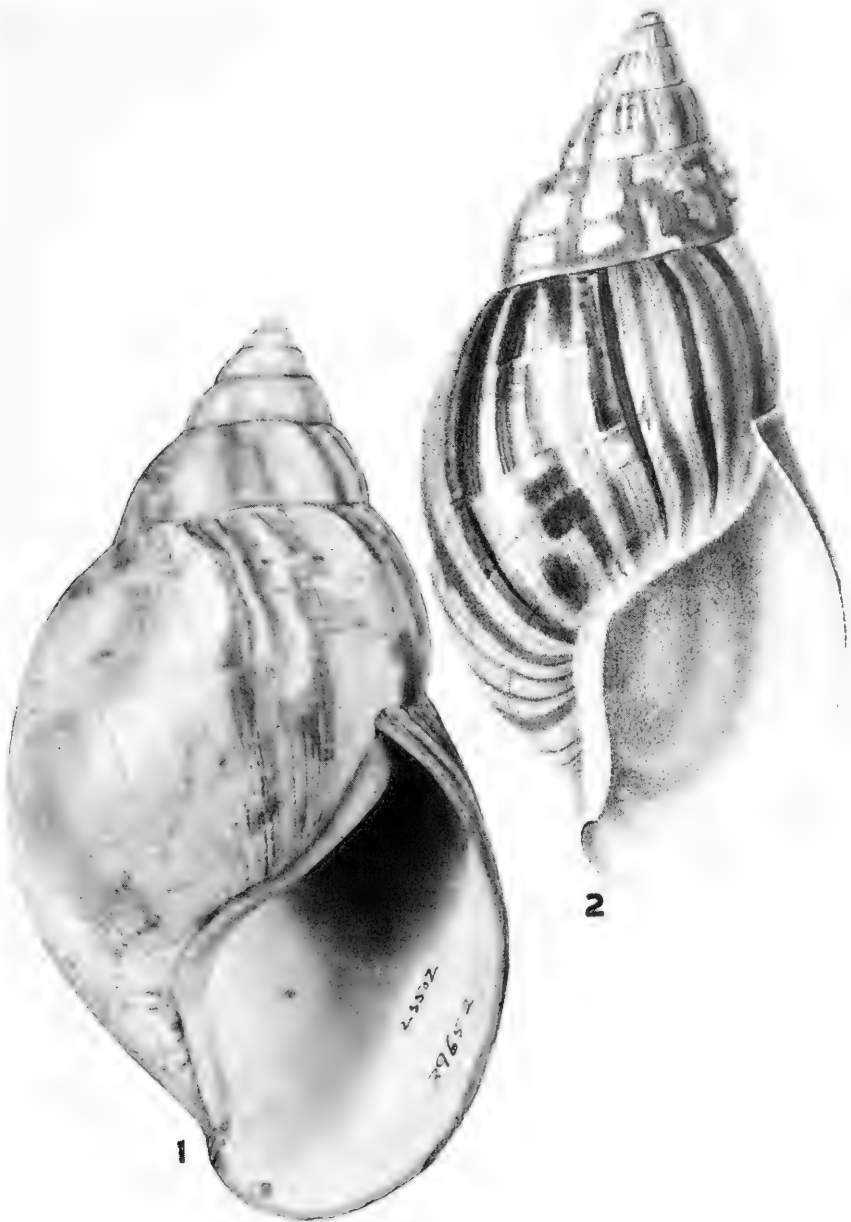


PLATE 34

PLATE 34

Fig. 1. *Achatina panthera panthera* (Férussac). Madagascar. M.C.Z. No. 39652. Natural size.

Fig. 2. *Achatina fulica fulica* Bowdich. Copy of figure of type of *A. couroupa* Lesson. Same size.





**PLATE 35**

PLATE 35

Fig. 1. *Achatina fulica fulica* Bowdich. Comoros. M.C.Z. No. 79134. Natural size.

Fig. 2. *Achatina panthera lamarckiana* Pfeiffer. Mauritius. M.C.Z. No. 79116. Dissected specimen. Natural size.

Fig. 3. *Achatina panthera lamarckiana* Pfeiffer. Madagascar. M.C.Z. No. 79115. Natural size.







PLATE 36

PLATE 36

Fig. 1. *Achatina fulica fulica* Bowdich. Koror. M.C.Z. No. 166429.  
Natural size.

Fig. 2. *Achatina fulica fulica* Bowdich. Oahu. M.C.Z. No. 180613.  
Natural size.

Fig. 3. *Achatina zanzibarica* Bourguignat. Amani. M.C.Z. No. 45554.  
Natural size.

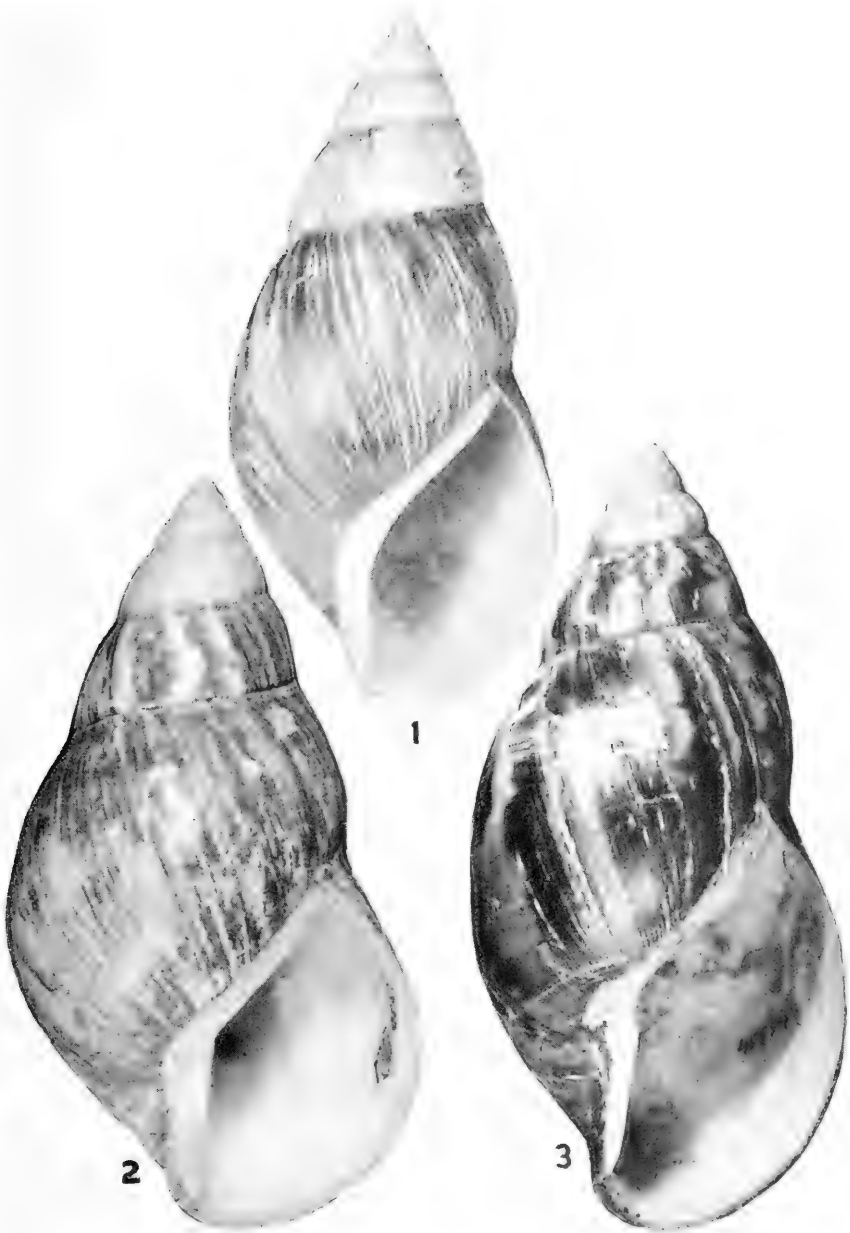




PLATE 37

PLATE 37

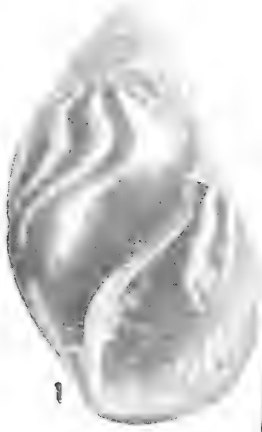
Fig. 1. *Archachatina knorrii* (Jonas). Paynesville. M.C.Z. No. 163660. Natural size.

Fig. 2. *Archachatina knorrii* (Jonas). Paiata. M.C.Z. No. 77009. Natural size.

Fig. 3. *Achatina zanzibarica* Bourguignat. Magrotto. M.C.Z. No. 100507. Natural size.

Fig. 4. *Achatina fulica fulica* Bowdich. Mauritius. M.C.Z. No. 79160. Natural size.

Fig. 5. *Achatina zanzibarica* Bourguignat. Lutindi. M.C.Z. No. 55904. Natural size.



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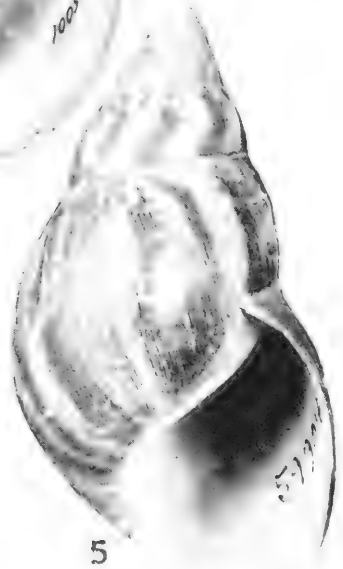
3



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PLATE 38

PLATE 38

Fig. 1. *Achatina panthera lamarckiana* Pfeiffer. Mauritius. M.C.Z. No. 79116. Natural size.

Fig. 2. *Achatina panthera panthera* (Férussac). Mauritius. Sinistral abnormality. M.C.Z. No. 73733. Natural size.

Fig. 3. *Achatina fulica fulica* Bowdich. Mauritius. M.C.Z. No. 79160. Natural size.





PLATE 39

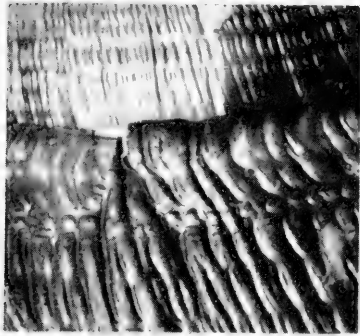
PLATE 39

Fig. 1. *Achatina achatina togoënsis* Bequaert and Clench. Part of penultimate and body-whorl of holotype, to show sculpture. X 4.

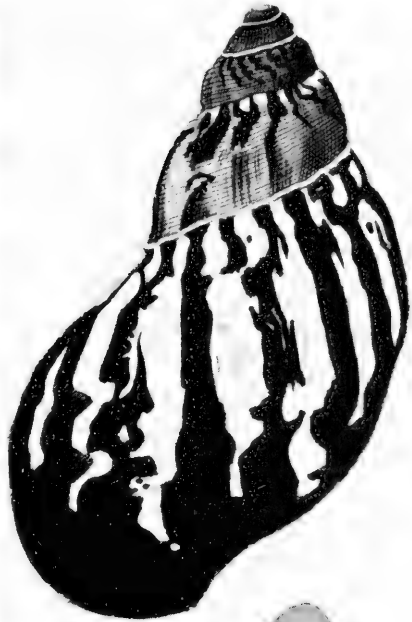
Fig. 2. *Archachatina knorrii* (Jonas). Copy of Knorr's (1768) Pl. 3\*\*, fig. 1, first printing. Same size.

Fig. 3. *Achatina achatina achatina* (Linné). Umbilicate abnormality. M.C.Z. Natural size.

Fig. 4. *Archachatina purpurea* (Gmelin). Liberia. M.C.Z. No. 27089. In profile. Natural size.



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PLATE 40

PLATE 40

Fig. 1. *Archachatina knorrii* (Jonas). Copy of figure of type of *A. prunum* Reeve. Same size.

Fig. 2. *Achatina albopicta* E. A. Smith. Diani Beach. M.C.Z. No. 167391. Natural size.

Fig. 3. *Achatina fulica hamillei* Petit. Copy of figure of paratype of *A. milne-edwardsiana* Révoil. Slightly reduced; original 190 mm. long.

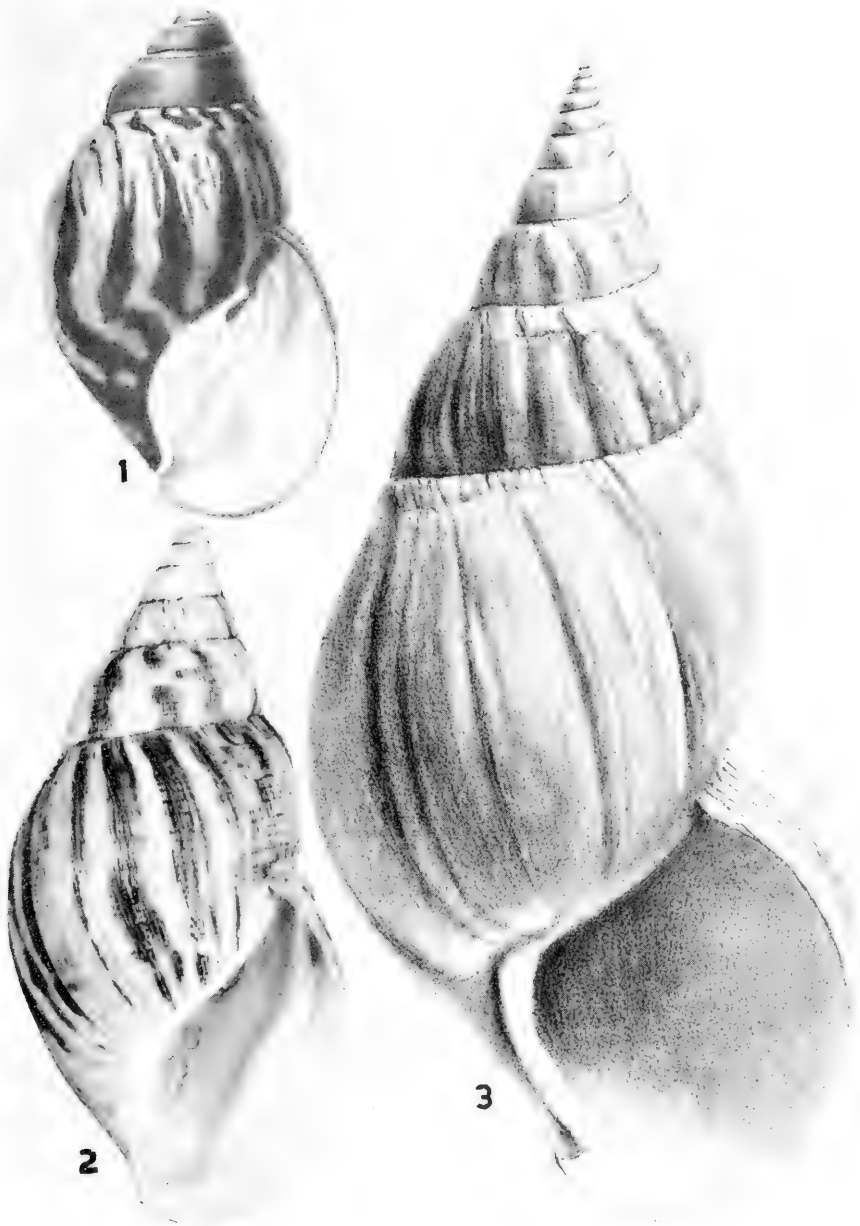




PLATE 41

PLATE 41

Fig. 1. *Achatina balteata balteata* Reeve. Copy of figure of type of *A. monetaria* Morelet. Same size.

Fig. 2. *Achatina zanzibarica* Bourguignat. Magrotto. M.C.Z. No. 100507. Natural size.

Fig. 3. *Archachatina siderata* (Reeve). Copy of figure of lectotype. Same size.

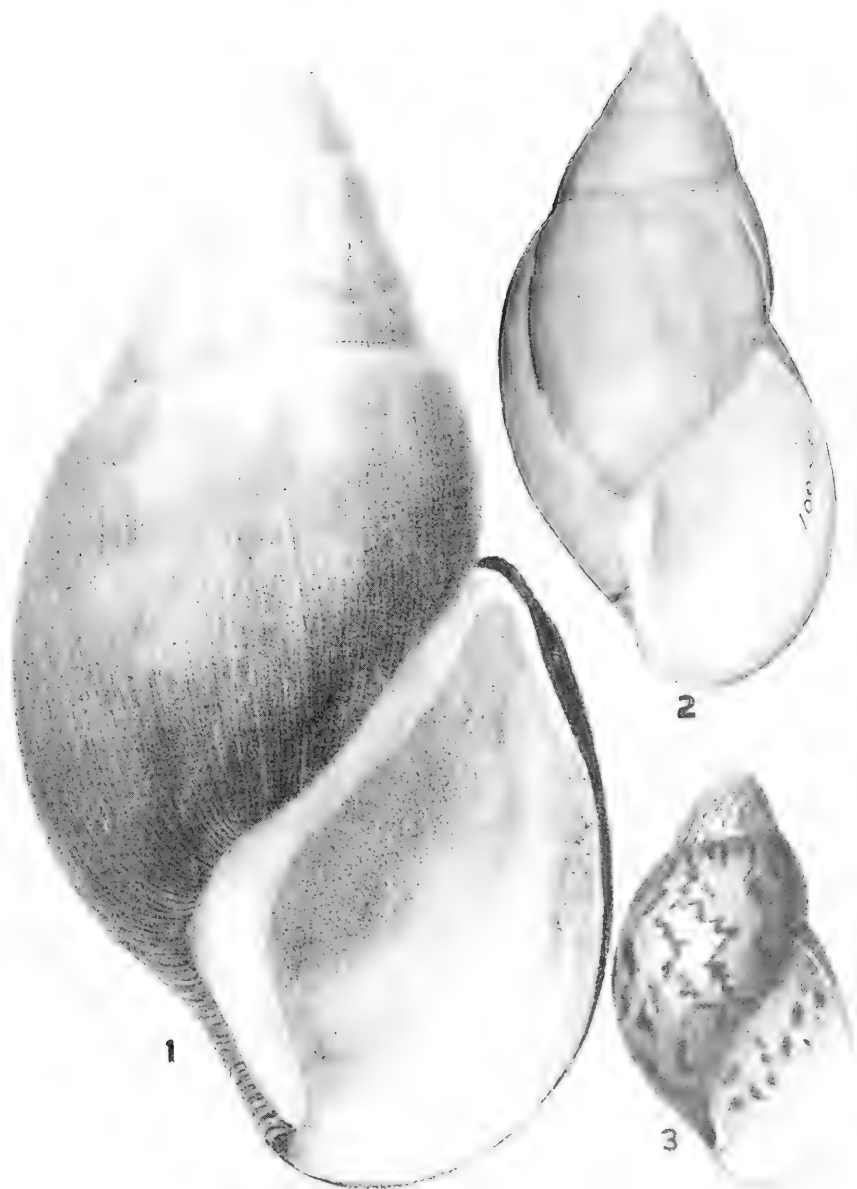






PLATE 42

PLATE 42

Fig. 1. *Achatina fulica hamillei* Petit. Mikindani. M.C.Z. No. 100509.  
Natural size.

Fig. 2. *Achatina albopicta* E. A. Smith. Diani Beach. M.C.Z. No. 167391.  
Natural size.

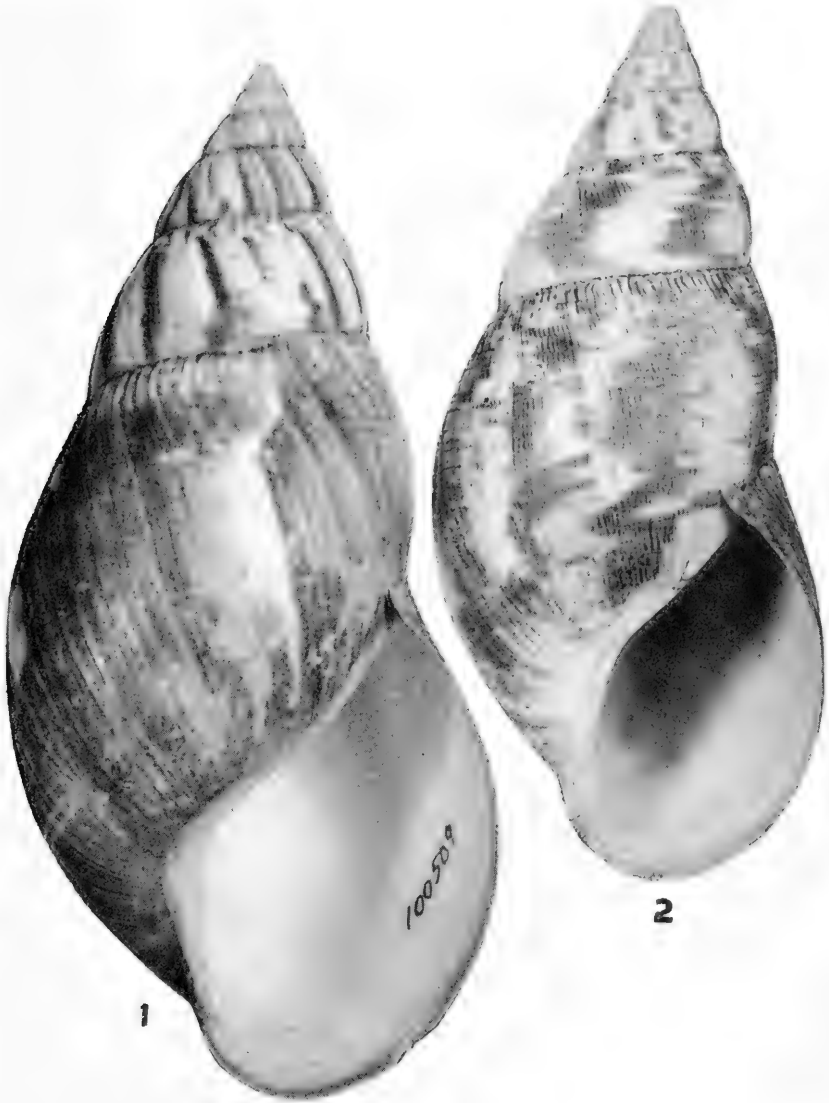




PLATE 43

PLATE 43

Fig. 1. *Achatina fulica hamillei* Petit. Mombasa. M.C.Z. No. 167394.  
Dissected specimen. Natural size.

Fig. 2. *Achatina albopicta* E. A. Smith. Diani Beach. M.C.Z. No. 167391.  
Natural size.







PLATE 44

PLATE 44

Fig. 1. *Achatina balteata infrafusca* v. Martens. Copy of figure of type. Same size.

Fig. 2. *Achatina fulica rodatzii* Dunker. Holotype of *A. chrysoleuca* Pilsbry. Ac.N.S.Phila. No. 68113. Nearly natural size. Courtesy of Ac.N.S.Phila.





PLATE 45

PLATE 45

Fig. 1. *Archachatina ventricosa ventricosa* (Gould). Harbel. M.C.Z. No. 163811. Natural size.

Fig. 2. *Achatina fulica hamillei* Petit. Mikindani. M.C.Z. No. 100509. Natural size.







PLATE 46

PLATE 46

Fig. 1. *Archachatina ventricosa spectaculum* Pilsbry. Cape Palmas. M.C.Z. No. 79204. Natural size.

Fig. 2. *Achatina fulica hamillei* Petit. Mikindani. M.C.Z. No. 100509. Natural size.

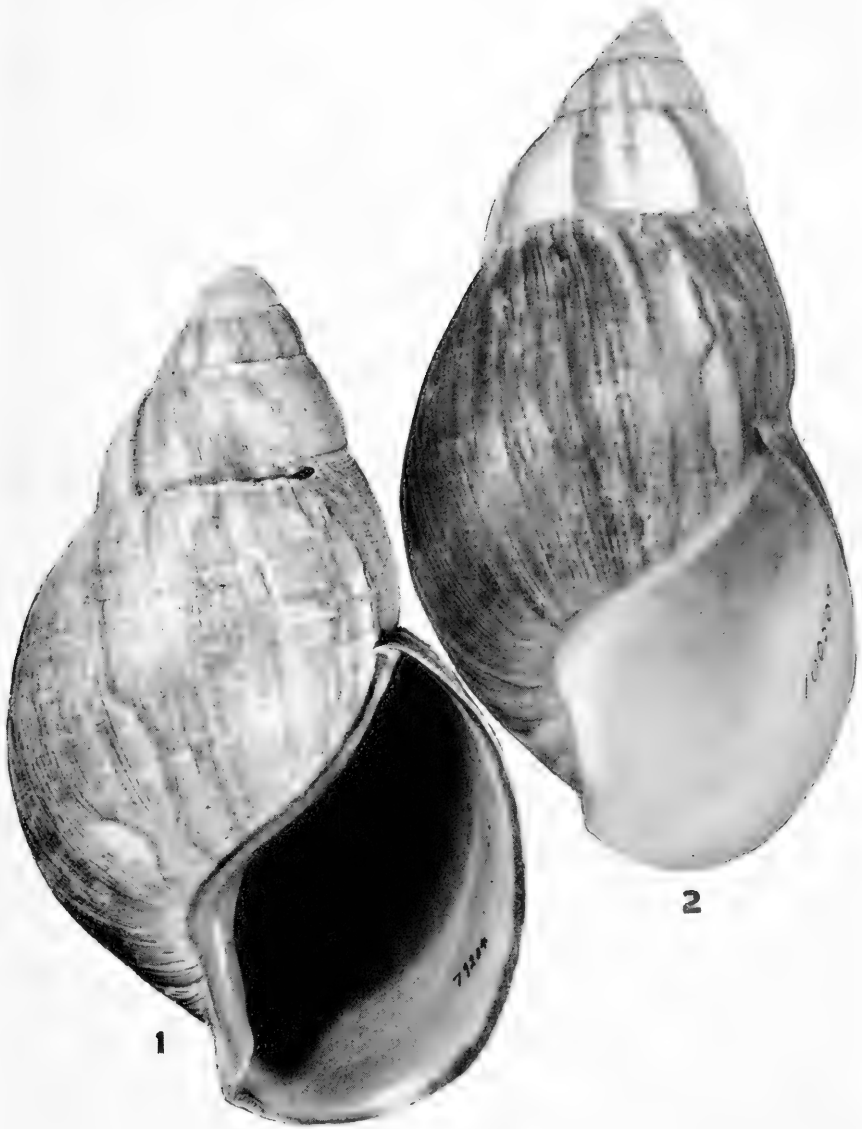




PLATE 47

PLATE 47

Fig. 1. *Achatina fulica hamillei* Petit. Largest cotype of *A. panthera* var. *leucostyla* Pilsbry. Ac.N.S.Phila. No. 81980. Nearly natural size. Courtesy of Ac.N.S.Phila.

Fig. 2. *Achatina zanzibarica* Bourguignat. Amani. M.C.Z. No. 167404. Natural size.

Fig. 3. *Achatina fulica hamillei* Petit. Zanzibar Id. M.C.Z. No. 167395. Diseased dwarfed shell. Natural size.





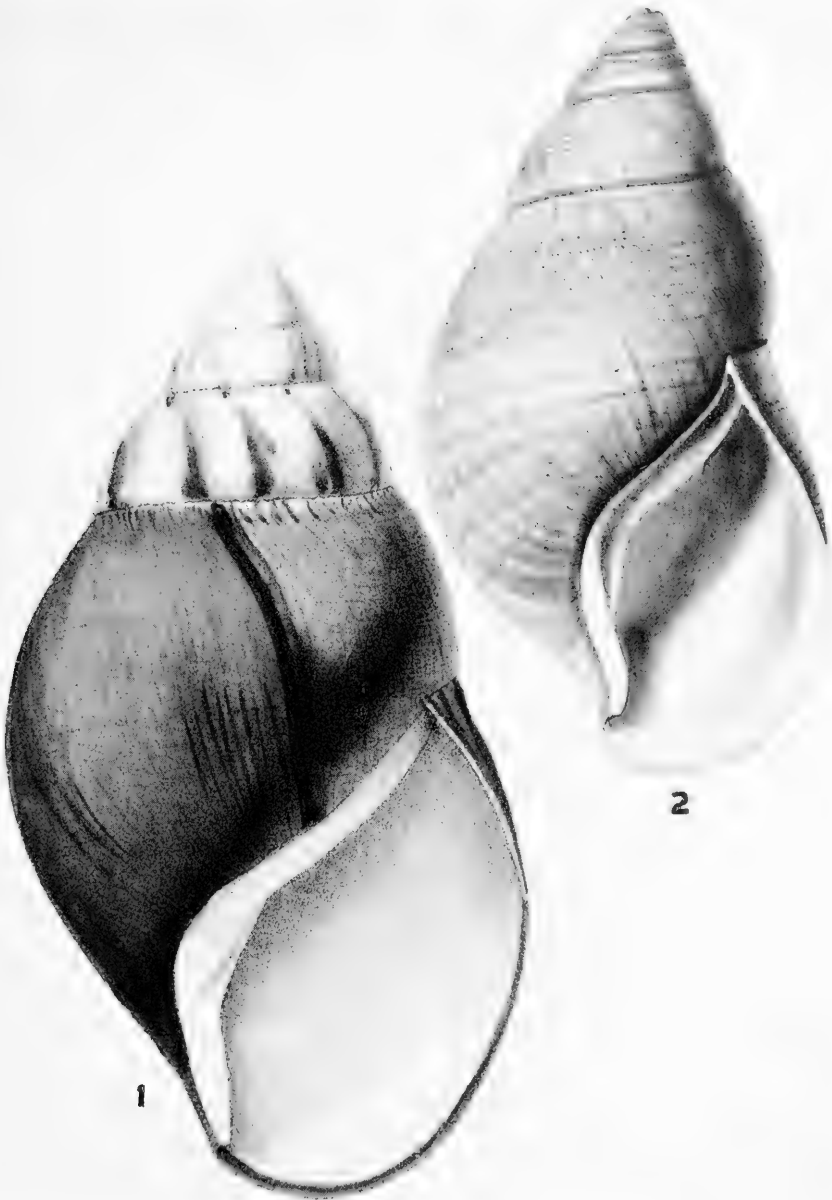


PLATE 48

PLATE 48

Fig. 1. *Achatina fulica hamillei* Petit. Copy of Smith's (1881) figure.  
Same size.

Fig. 2. *Achatina lactea* Reeve. Copy of Reeve's first (1842) figure of type.  
Same size.



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2



PLATE 49

PLATE 49

Fig. 1. *Archachatina ventricosa spectaculum* Pilsbry. Copy of Shaw and Nodder's (1800) Pl. 438 ("*Bulla achatina*"). Same size.

Fig. 2. *Achatina fulica hamillei* Petit. Mombasa. M.C.Z. No. 167394. Natural size.







PLATE 50

PLATE 50

Fig. 1. *Achatina fulica hamillei* Petit. Mombasa. M.C.Z. No. 167394.  
Natural size.

Fig. 2. *Achatina fulica hamillei* Petit. Magrotto. M.C.Z. No. 100499.  
Natural size.



1

2



PLATE 51

PLATE 51

Fig. 1. *Achatina balteata infrafusca* v. Martens. Gaboon. M.C.Z. No. 39653. Natural size.

Fig. 2. *Achatina balteata infrafusca* v. Martens. Gaboon. Umbilicate abnormality. M.C.Z. Natural size.

Fig. 3. *Archachatina knorrii* (Jonas). Kakata. M.C.Z. No. 77010. Natural size.







PLATE 52

PLATE 52

Fig. 1. *Achatina fulica rodatzki* Dunker. Copy of figure of type of *A. erlangeri* Kobelt. Same size.

Fig. 2. *Achatina albopicta* E. A. Smith. Diani Beach. M.C.Z. No. 167391. Natural size.

Fig. 3. *Archachatina siderata* (Reeve). Bolahun. M.C.Z. No. 106767. Natural size.

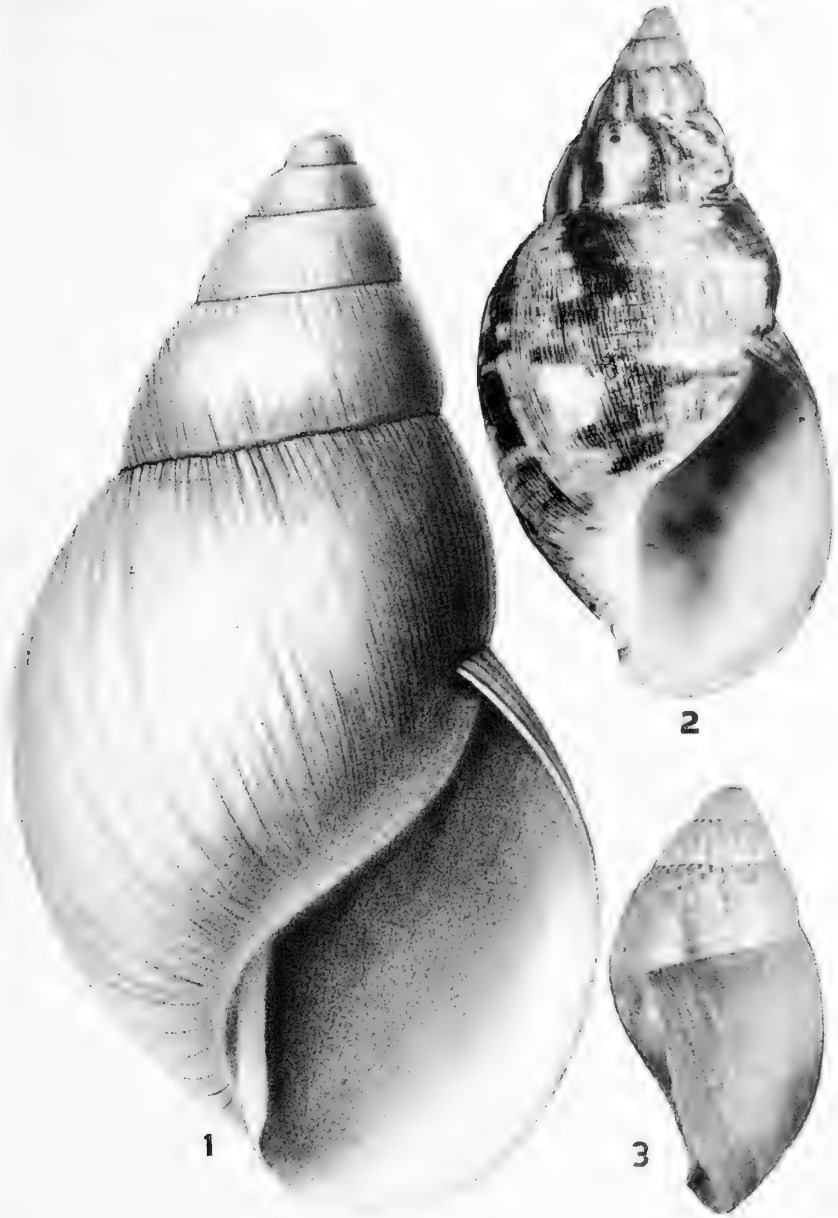




PLATE 53

PLATE 53

Fig. 1. *Archachatina knorrii* (Jonas). Harbel. M.C.Z. No. 163661. Young shell, X 2.

Fig. 2. *Achatina fulica rodatzi* Dunker. East Africa. M.C.Z. Umbilicate abnormality. Natural size.

Fig. 3. *Achatina fulica rodatzi* Dunker. Paratype of *A. erlangeri* Kobelt. Ganale. M.C.Z. No. 79982. Natural size.

Fig. 4. *Archachatina camerunensis* (d'Ailly). Lolodorf. M.C.Z. No. 65194. Young shell, X 2.



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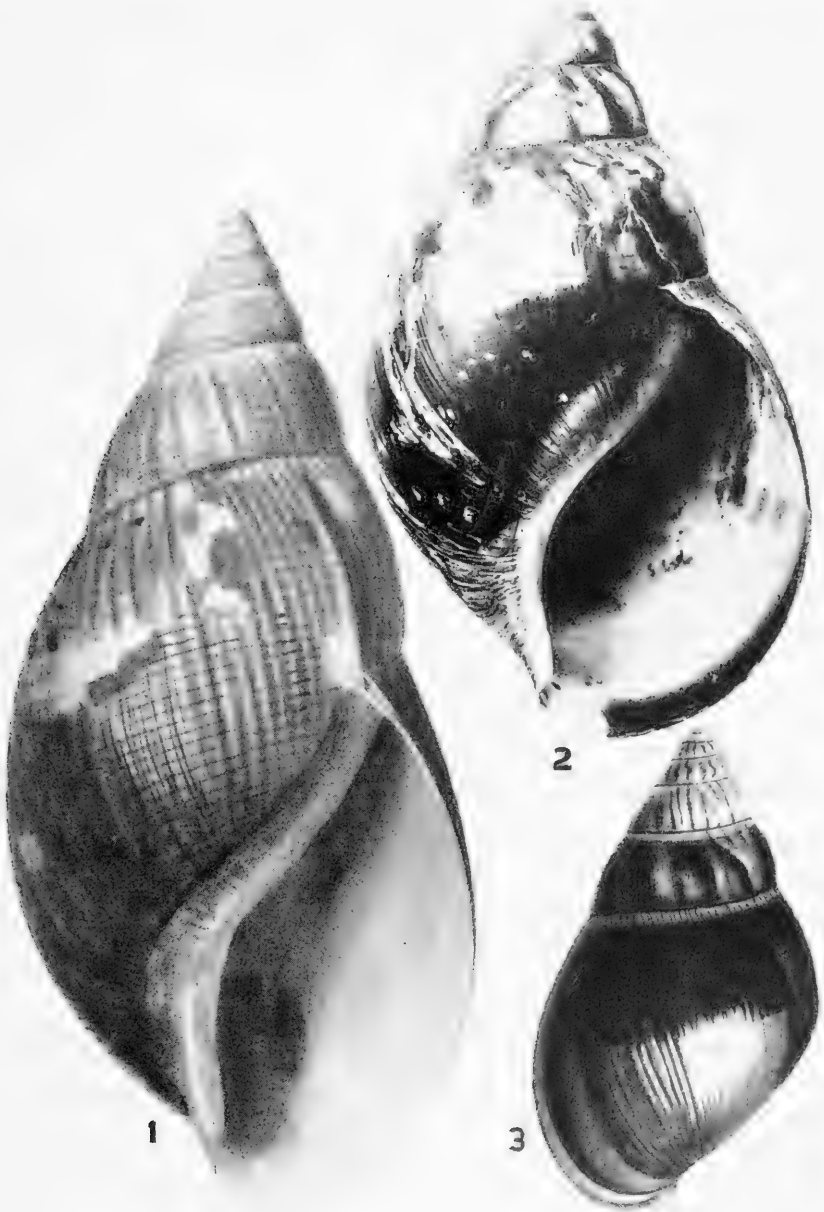
PLATE 54

PLATE 54

Fig. 1. *Achatina fulica rodatzi* Dunker. Copy of one of the figures of type. Same size.

Fig. 2. *Archachatina marginata egregia* (Dautzenberg). Copy of figure of type. Same size.

Fig. 3. *Achatina fulica castanea* Lamarck. Copy of Férussac's (1823) Pl. 125, fig. 5 ("*Helix zebrina*"). Same size.





**PLATE 55**

PLATE 55

Fig. 1. *Archachatina marginata eduardi* Pilsbry. Bibundi. M.C.Z. No. 79970. Natural size.

Fig. 2. *Achatina panthera lamarckiana* Pfeiffer. Madagascar. M.C.Z. No. 27082. Natural size.

Fig. 3. *Achatina fulica hamillei* Petit. Voi. M.C.Z. No. 106080. Transitional to *A. f. rodatzii*. Natural size.







PLATE 56

PLATE 56

Fig. 1. *Archachatina knorrii* (Jonas). West Africa. M.C.Z. Profile view. Natural size.

Fig. 2. *Achatina panthera panthera* (Férussac). M.C.Z. Scalariform abnormality. Natural size.

Fig. 3. *Archachatina degneri* Bequaert and Clench. Accra. M.C.Z. No. 163652. Natural size.





PLATE 57

PLATE 57

Fig. 1. *Achatina panthera panthera* (Férussac). Lumbo. M.C.Z. No. 53183. Natural size.

Fig. 2. *Achatina iredalei* Preston. Diani Beach. M.C.Z. No. 167403. Natural size.

Fig. 3. *Archachatina sandgroundi* J. Bequaert. Mt. Selinda. Paratype, M.C.Z. No. 94745. Natural size.







PLATE 58

PLATE 58

Fig. 1. *Archachatina purpurea* (Gmelin). Monrovia. M.C.Z. No. 77004. Natural size.

Fig. 2. *Achatina albopicta* E. A. Smith. Diani Beach. M.C.Z. No. 167403. Natural size.

Fig. 3. *Achatina panthera panthera* (Férussac). Copy of figure of type (1832, Pl. 126, fig. 1). Slightly reduced. Original 151 mm. long.

Fig. 4. *Achatina (Leptocala) mollicella petitia* (Jousseaume). Mts. of Molobo, Cameroon. M.C.Z. No. 124380. Natural size.

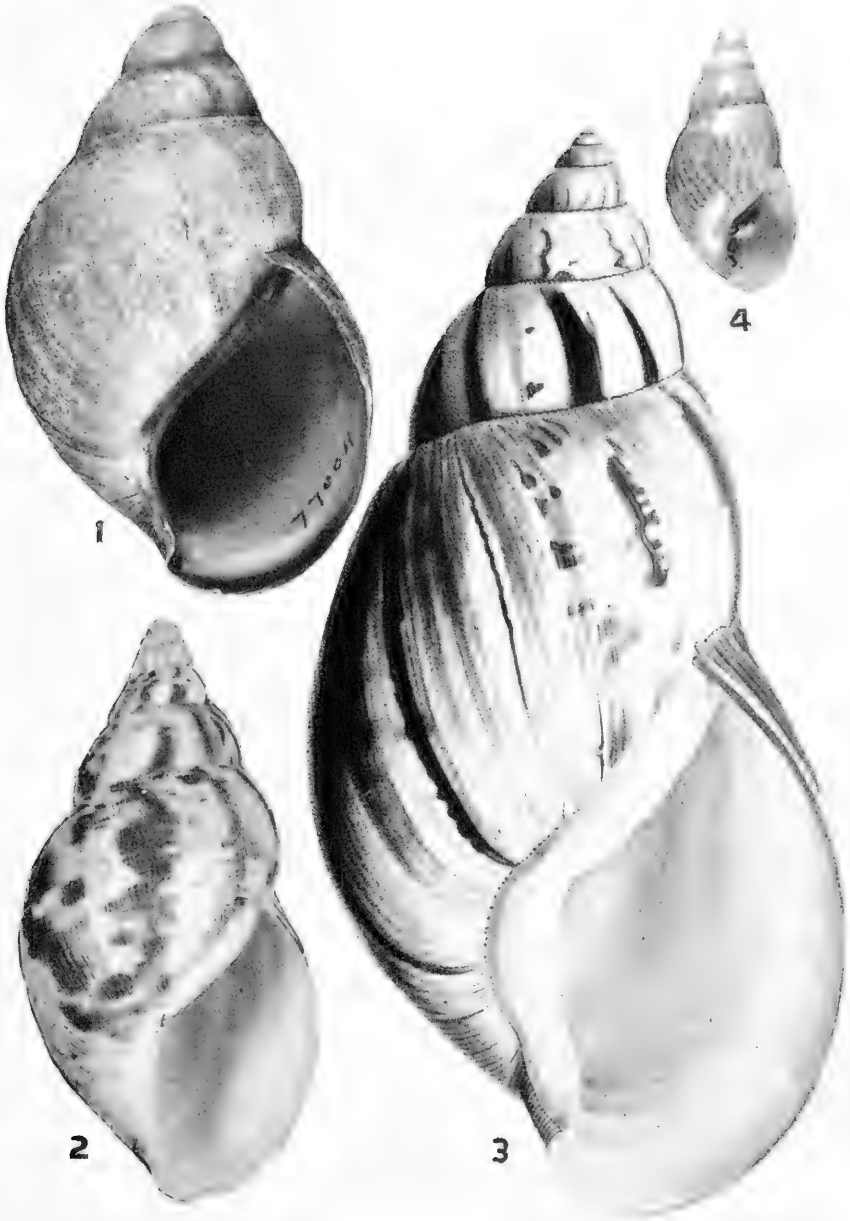




PLATE 59

PLATE 59

Fig. 1. *Archachatina marginata marginata* (Swainson). Corisco. M.C.Z. No. 181425. Natural size.

Fig. 2. *Achatina zanzibarica* Bourguignat. Copy of figure of type of *A. kilimae* var. *rollei* C. R. Boettger. Same size.



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2





PLATE 60

PLATE 60

Fig. 1. *Archachatina papyracea* (Pfeiffer). Copy of figure of holotype of *A. modestior* O. Boettger. Same size.

Fig. 2. *Achatina iredalei* Preston. Zanzibar Id. M.C.Z. No. 167400. Dissected specimen. Natural size.

Fig. 3. *Archachatina ventricosa spectaculum* Pilsbry. West Africa. M.C.Z. Natural size.

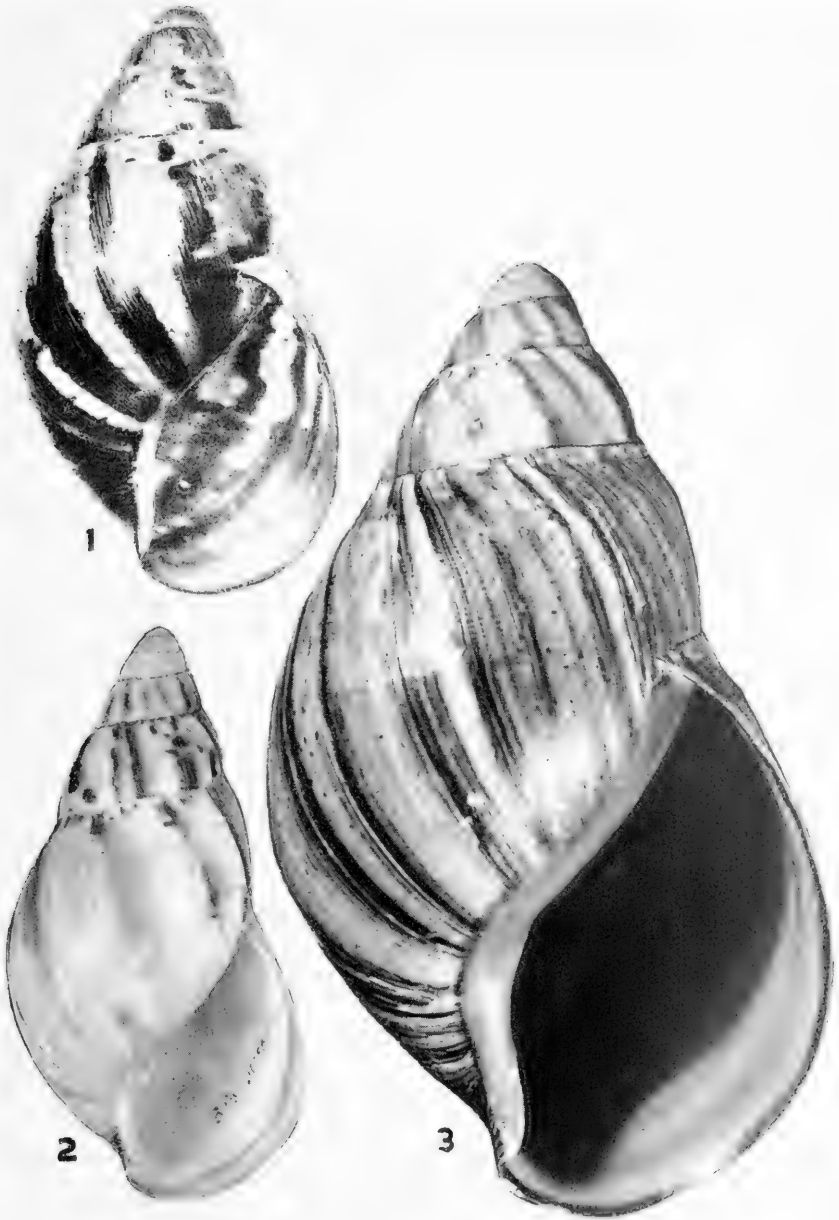




PLATE 61

PLATE 61

Fig. 1. *Archachatina purpurea* (Gmelin). Cape Palmas. M.C.Z. No. 45528. Natural size.

Fig. 2. *Archachatina siderata* (Reeve). Cape Palmas. M.C.Z. No. 79495. Young shell, X 2.

Fig. 3. *Achatina iredalei* Preston. Zanzibar Id. M.C.Z. No. 167400. Dissected specimen. Natural size.

Fig. 4. *Achatina iredalei* Preston. Diani Beach. M.C.Z. No. 167403. Natural size.

Fig. 5. *Archachatina ventricosa spectaculum* Pilsbry. Copy of Knorr's (1769) Pl. 24\*\*\*, fig. 1. Same size.

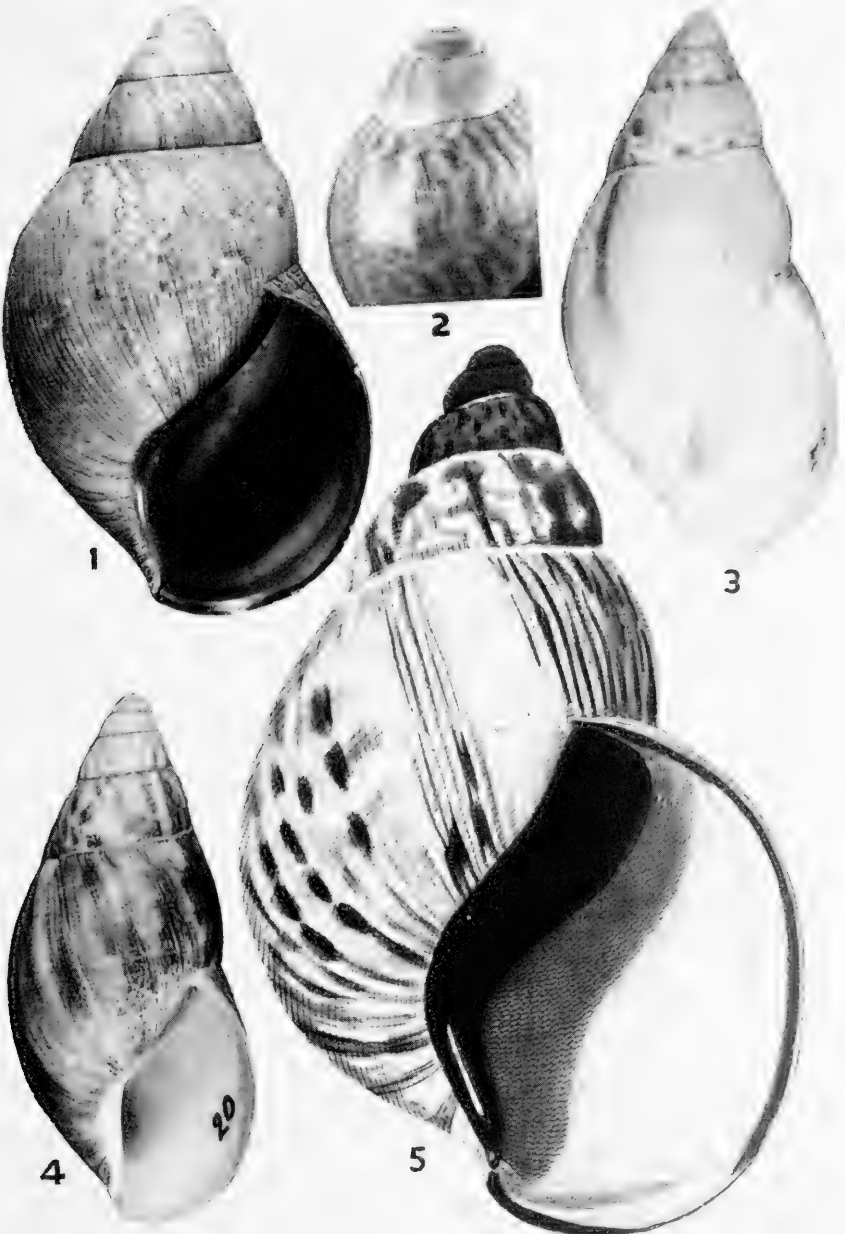






PLATE 62

PLATE 62

Fig. 1. *Archachatina marginata egregiella* Bequaert and Clench. Kribi. Holotype, M.C.Z. No. 73135. Natural size.

Fig. 2. *Archachatina granulata* (Pfeiffer). South Africa. Summit, X 2.

Fig. 3. *Achatina spekei* Dohrn. Copy of figure of type of *A. thomsoni* E. A. Smith. Same size.

Fig. 4. *Archachatina purpurea* (Gmelin). Cape Palmas. M.C.Z. No. 53487. Natural size.

Fig. 5. *Archachatina marginata suturalis* (Philippi). Copy of Donovan's (1826) Pl. 149 ("*A. marginata*"). Same size.





PLATE 63

PLATE 63

Fig. 1. *Archachatina papyracea* (Pfeiffer). Yaunde. M.C.Z. No. 139532. Natural size.

Fig. 2. *Achatina albopicta* E. A. Smith. Copy of figure of type of *A. pilsbryi* d'Ailly. Same size.

Fig. 3. *Achatina alisa* Reeve. Copy of figure of type. Same size.

Fig. 4. *Achatina reticulata* Pfeiffer, Chwaka Bay. Umbilicate abnormality. M.C.Z. No. 167407. Natural size.

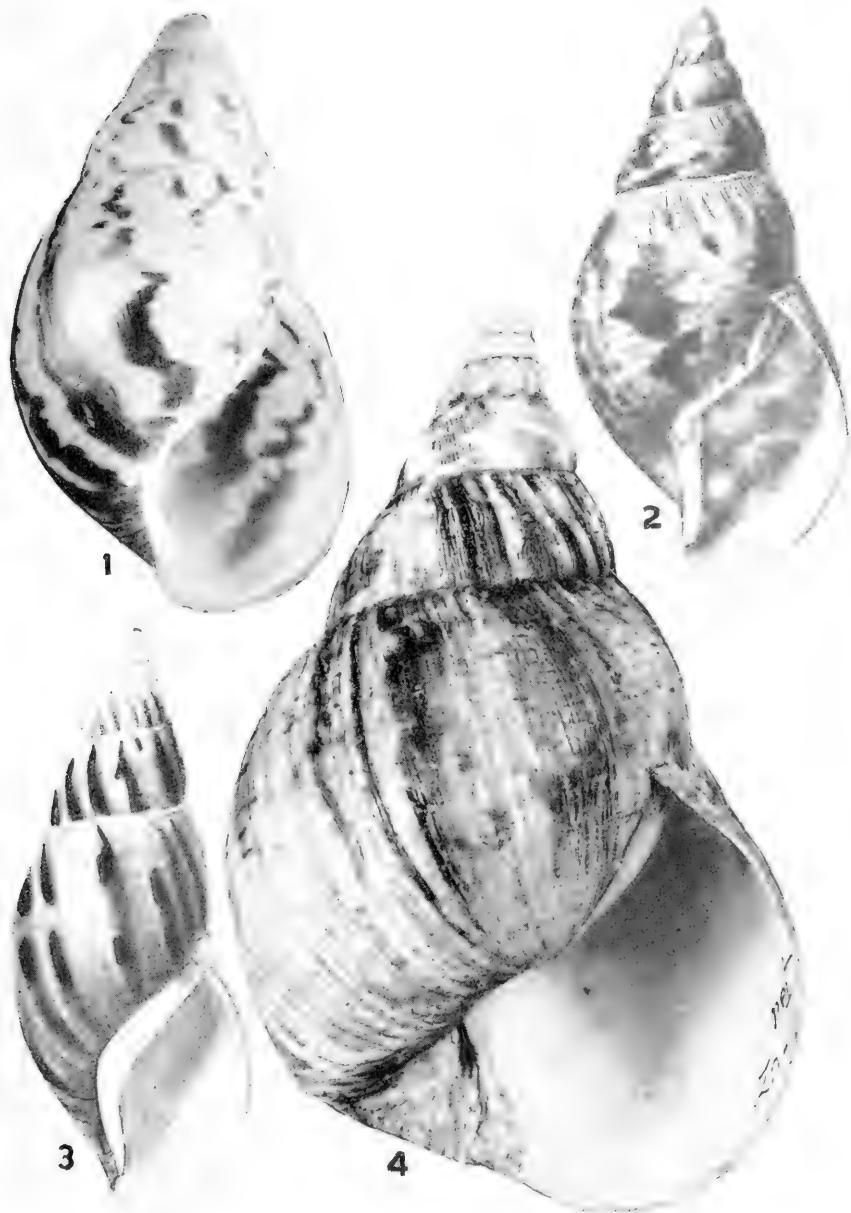






PLATE 64

PLATE 64

Fig. 1. *Archachatina marginata marginata* (Swainson). Stanleyville. Paratype of *A. gaboonensis* var. *aequatorialis* Bequaert and Clench. M.C.Z. No. 103894. Natural size.

Fig. 2. *Achatina iredalei* Preston. Diani Beach. M.C.Z. No. 167403. Natural size.

Fig. 3. *Archachatina purpurea* (Gmelin). Monrovia. M.C.Z. No. 77004. Natural size.

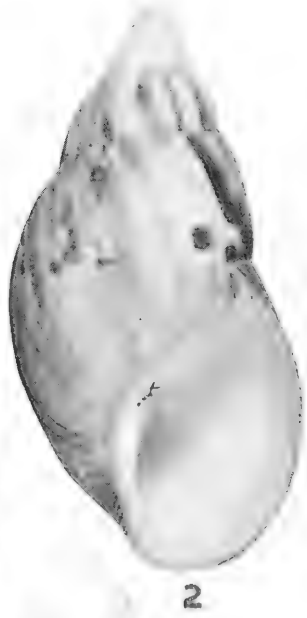




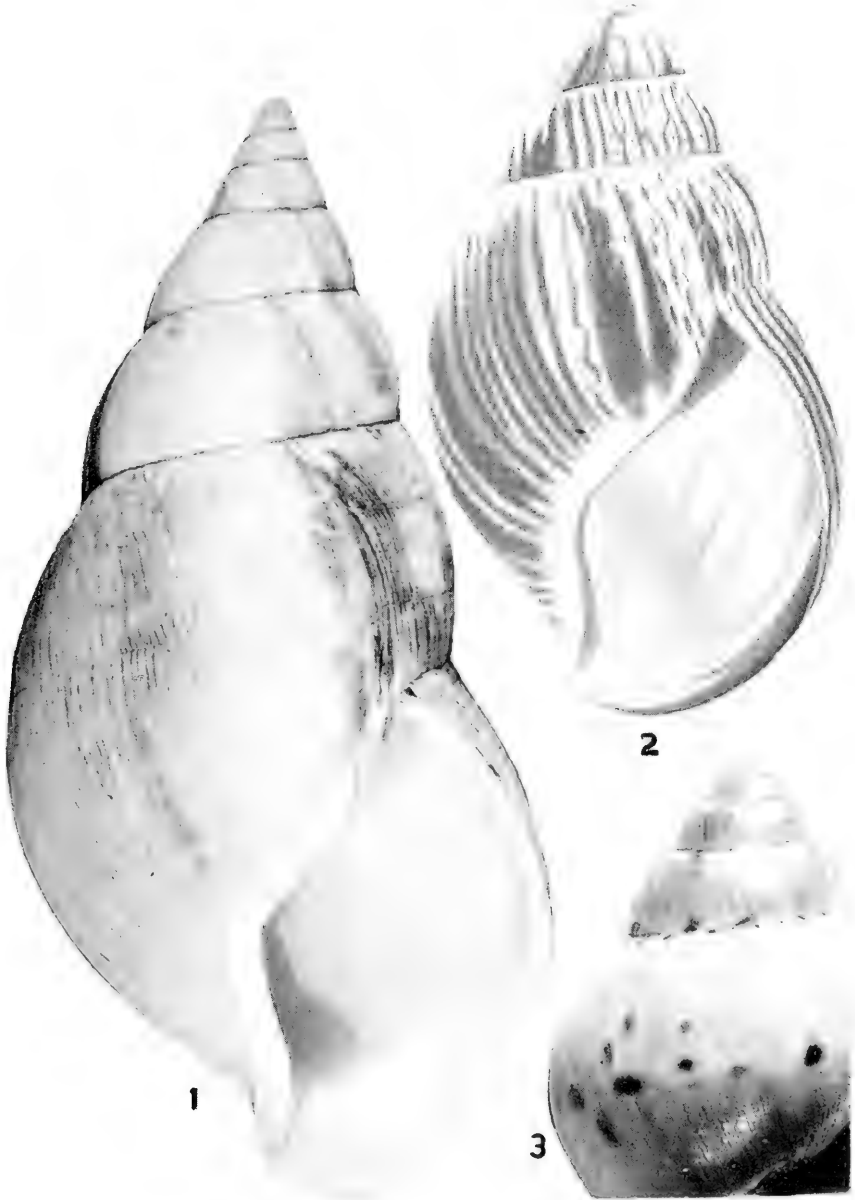
PLATE 65

PLATE 65

Fig. 1. *Achatina albopicta* E. A. Smith. Diani Beach. M.C.Z. No. 167403.  
Natural size.

Fig. 2. *Archachatina marginata suturalis* (Philippi). Copy of figure of type.  
Same size.

Fig. 3. *Achatina ircdalei* Preston. Zanzibar Id. M.C.Z. No. 167400.  
Young shell, X 3.



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PLATE 66

PLATE 66

Fig. 1. *Achatina reticulata* Pfeiffer. Chwaka Bay. M.C.Z. No. 167407.  
Dissected specimen. Natural size.

Fig. 2. *Achatina albopicta* E. A. Smith. Diani Beach. M.C.Z. No. 167403.  
Natural size.





PLATE 67

PLATE 67

Fig. 1. *Achatina reticulata* Pfeiffer. Copy of Reeve's (1849) figure of type. Same size.

Fig. 2. *Archachatina marginata marginata* (Swainson). Kunungu. Holotype of *A. gaboonensis* var. *aequatorialis* Bequaert and Clench. Tervuren Mus. Natural size.

Fig. 3. *Achatina albopicta* E. A. Smith. Diani Beach. M.C.Z. No. 167403. Natural size.



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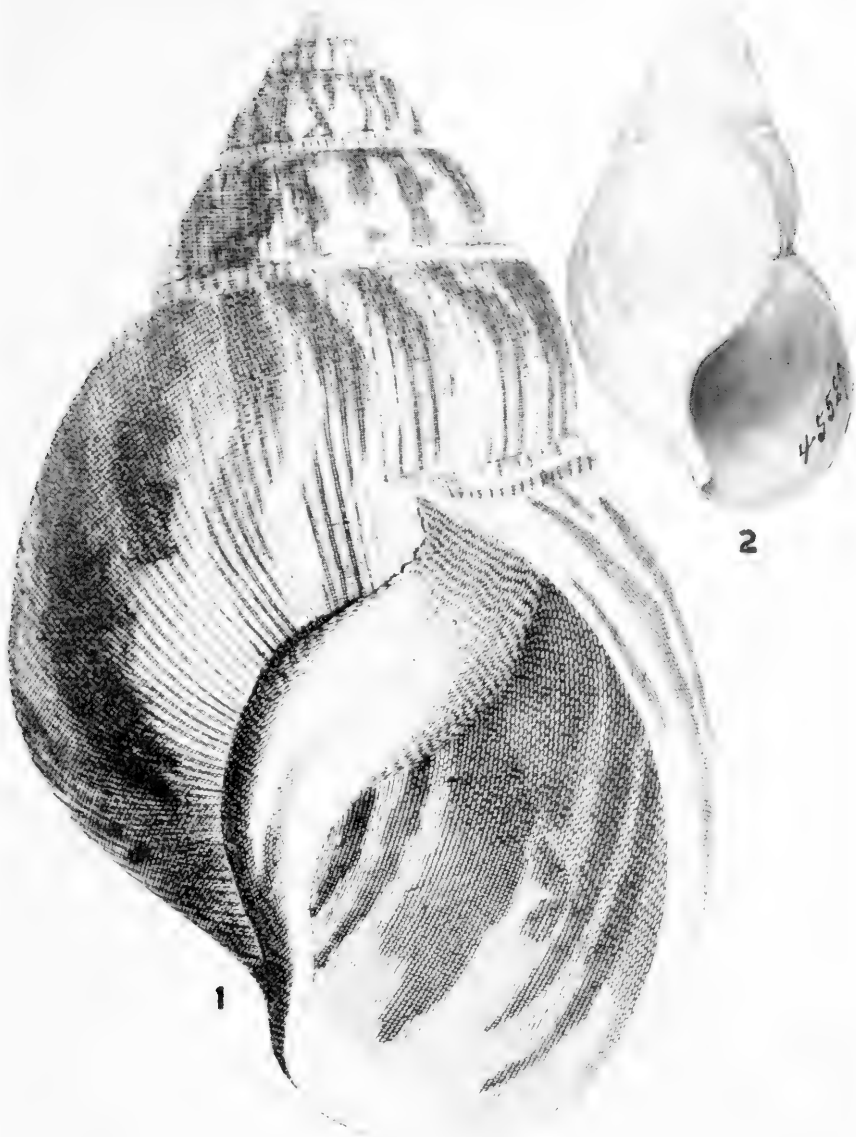


**PLATE 68**

PLATE 68

Fig. 1. *Archachatina marginata marginata* (Swainson). Copy of Gualtieri's (1742) Pl. 45, lower fig. B. Slightly reduced; original 182 mm. long.

Fig. 2. *Archachatina purpurea* (Gmelin). Cape Palmas. M.C.Z. No. 45529. Natural size.



1

2



PLATE 69

PLATE 69

Fig. 1. *Achatina (Tripachatina) vignoniana* Morelet. Gaboon. Immature shell. M.C.Z. No. 58817. Natural size.

Fig. 2. *Archachatina degneri* Bequaert and Clench. Holotype. Hamburg Mus. Natural size.

Fig. 3. *Archachatina siderata* (Reeve). Cape Palmas. M.C.Z. No. 79495. Natural size.



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PLATE 70

PLATE 70

Fig. 1. *Archachatina marginata ovum* (Pfeiffer). Lagos. M.C.Z. No. 167408.  
Natural size.

Fig. 2. *Archachatina papyracea* (Pfeiffer). Yaunde. M.C.Z. No. 139532.  
Natural size.



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2



PLATE 71

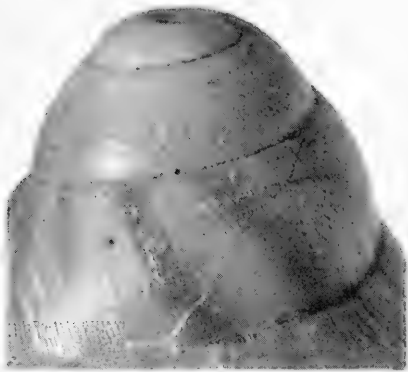
PLATE 71

Fig. 1. *Achatina balteata balteata* Reeve. Kribi. M.C.Z. No. 15800. Summit of young shell, X 10.

Fig. 2. *Archachatina marginata egregia* (Dautzenberg). Metet. M.C.Z. No. 59414. Natural size.

Fig. 3. *Archachatina marginata marginata* (Swainson). Copy of Knorr's (1768) Pl. 3\*\*, fig. 1, second printing. Same size.

Fig. 4. *Achatina reticulata* Pfeiffer. Chwaka Bay. M.C.Z. No. 167407. Young shell, X 3.



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4





PLATE 72

PLATE 72

- Fig. 1. *Archachatina purpurea* (Gmelin). Liberia. M.C.Z. Natural size.  
Fig. 2. *Archachatina purpurea* (Gmelin). Copy of Chemnitz' (1786) Pl. 118, fig. 1018. Same size.  
Fig. 3. *Archachatina marginata suturalis* (Philippi). Copy of Lister's (1688) Pl. 579, fig. 34. Same size.  
Fig. 4. *Archachatina papyracea* (Pfeiffer). Lolodorf. M.C.Z. No. 124357. Natural size.

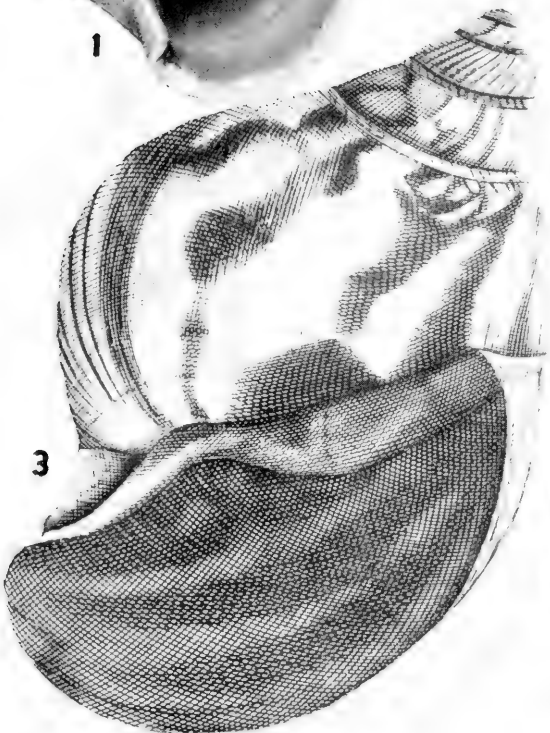




PLATE 73

PLATE 73

Fig. 1. *Archachatina ventricosa ventricosa* (Gould). Kasia. M.C.Z. No. 163807. Young shell, X 10.

Fig. 2. *Archachatina ventricosa ventricosa* (Gould). Grand Bassam. M.C.Z. No. 167410. Natural size.

Fig. 3. *Archachatina rhodostoma* (Philippi). Kankan. M.C.Z. No. 102334. Natural size.

Fig. 4. *Achatina zanzibarica* Bourguignat. Amani. M.C.Z. No. 45556. Young shell from uterus of snail, X 3.



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PLATE 74

PLATE 74

Fig. 1. *Archachatina rhodostoma* (Philippi). Copy of Sowerby's (1823) figure of "*A. purpurea*".

Fig. 2. *Archachatina marginata candefacta* Bequaert and Clench. "West Africa." M.C.Z. Natural size.

Fig. 3. *Archachatina papyracea* (Pfeiffer). "West Africa." Lectotype of *A. papyracea* var. *adelinae* Pilsbry. Ac.N.S.Phila. No. 185105. Natural size. Courtesy of Ac.N.S.Phila.

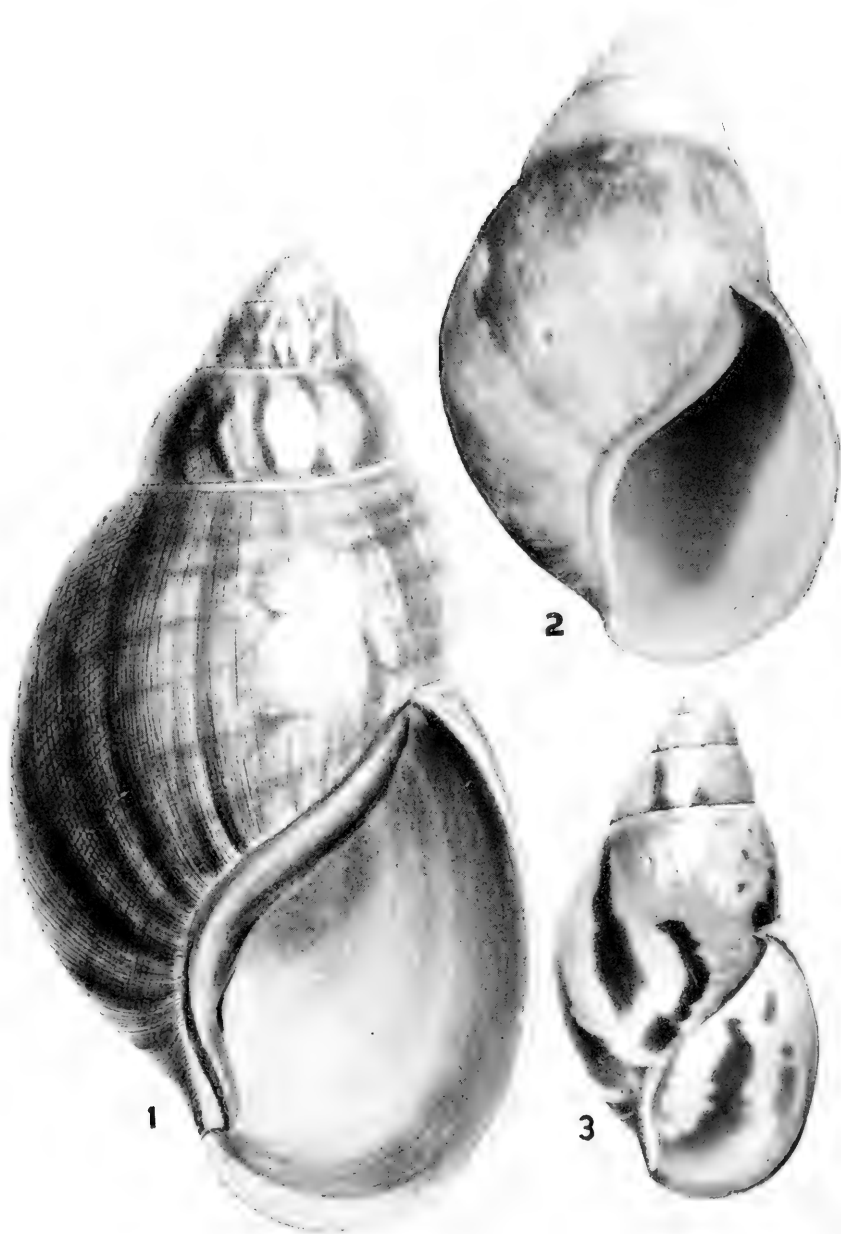




PLATE 75

PLATE 75

Fig. 1. *Archachatina marginata icterica* Bequaert and Clench. Gaboon. Holotype, M.C.Z. No. 45526. Natural size.

Fig. 2. *Archachatina marginata marginata* (Swainson). Copy of figure of type of *A. schweinfurthi* var. *fourcaui* Germain. Same size (X  $\frac{2}{3}$ ).

Fig. 3. *Achatina achatina monochromatica* Pilsbry. Copy of figure of type of *A. variegata* var. *unicolor* Deshayes. Same size.

Fig. 4. *Archachatina ventricosa spectaculum* Pilsbry. Copy of Deshayes' (1851) Pl. 123, fig. 1 ("*A. purpurea*"). Same size.







PLATE 76

PLATE 76

Fig. 1. *Archachatina knorrii* (Jonas). Ganta. M.C.Z. No. 63446. Young shell, X 2.

Fig. 2. *Achatina panthera lamarckiana* Pfeiffer. Copy of figure of type of *A. panthera* var. *minor* Deshayes. Same size.

Fig. 3. *Archachatina marginata marginata* (Swainson). Copy of figure of type of *A. marginata* var. *fourneaui* Germain. Same size.

Fig. 4. *Archachatina marginata marginata* (Swainson). Sakbayeme. M.C.Z. No. 50121. Summit of young shell, X 2.

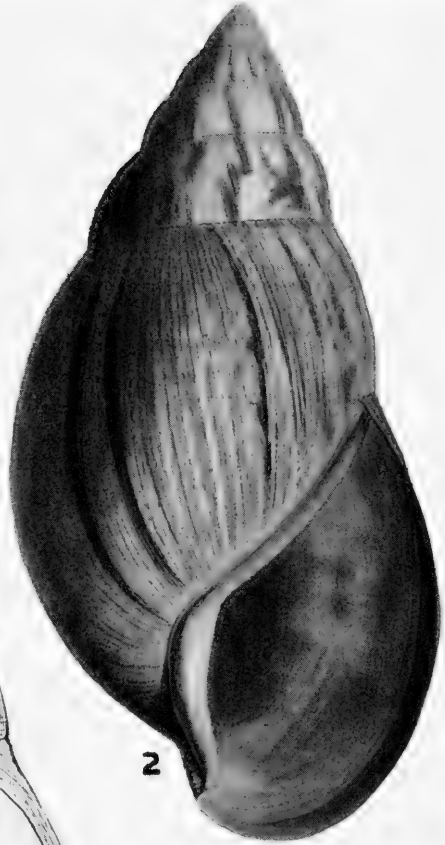




PLATE 77

PLATE 77

Fig. 1. *Archachatina meadi* J. Bequaert. Ngosi. Paratype, M.C.Z. No. 81351. Summit X 2.

Fig. 2. *Achatina iredalei* Preston. Zanzibar Id. M.C.Z. No. 167400. Abnormal shell. Natural size.

Fig. 3. *Archachatina marginata candefacta* Bequaert and Clench. Johann-Albrechtshöhe. Holotype, M.C.Z. No. 79972. Natural size.

Fig. 4. *Achatina balteata balteata* Reeve. Nongo Madiba. Paratype of *A. iostoma* form *albina* O. Boettger. M.C.Z. No. 79975. Natural size.

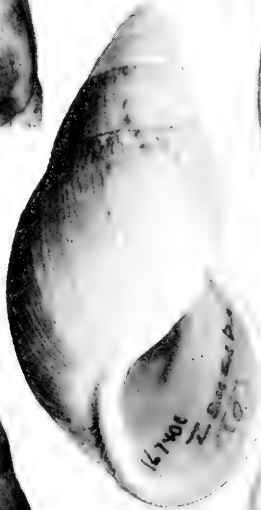
Fig. 5. *Achatina zanzibarica* Bourguignat. Madazini. Holotype of *A. madaziniana* Clench and Archer. M.C.Z. No. 53185. Natural size.



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5





PLATE 78

PLATE 78

Fig. 1. *Achatina zanzibarica* Bourguignat. Holotype of *A. lhotellerii* Bourguignat. Nasimoya. Natural size. Courtesy of Paris Mus.

Fig. 2. *Achatina fulica hamillei* Petit. Holotype. Natural size. Courtesy of Dr. E. Fischer-Piette.

Fig. 3. *Achatina fulica hamillei* Petit. Specimen from Guedi at Paris Mus., labelled *A. milne-edwardsiana* Révoil. Natural size. Courtesy of Paris Mus.





PLATE 79

PLATE 79

Fig. 1. *Achatina panthera antourlourensis* Crosse. Holotype. Nossi-Be. Natural size. Courtesy of Dr. E. Fischer-Piette.

Fig. 2. *Achatina fulica hamillei* Petit. Holotype of *A. panthera* var. *nasimoyensis* Bourguignat. Nasimoya. Natural size. Courtesy of Paris Mus.

Fig. 3. *Achatina zanzibarica* Bourguignat. Holotype. Nasimoya. Natural size. Courtesy of Paris Mus.

Fig. 4. *Achatina zanzibarica* Bourguignat. Amani. M.C.Z. No. 41847. Abnormal shell. Natural size.







PLATE 80

PLATE 80

Figs. 1-3. *Achatina fulica hamillei* Petit. Chwaka Bay. Immature shells. M.C.Z. No. 167396. Natural size.

Fig. 4. *Archachatina marginata* (Swainson). Holotype of *Achatina schweinfurthi* var. *foureaui* Germain. Natural size. Courtesy of Paris Mus.

Fig. 5. *Achatina fulica hamillei* Petit. Holotype of *A. letourneuxi* Bourguignat. Nasimoya. Natural size. Courtesy of Paris Mus.

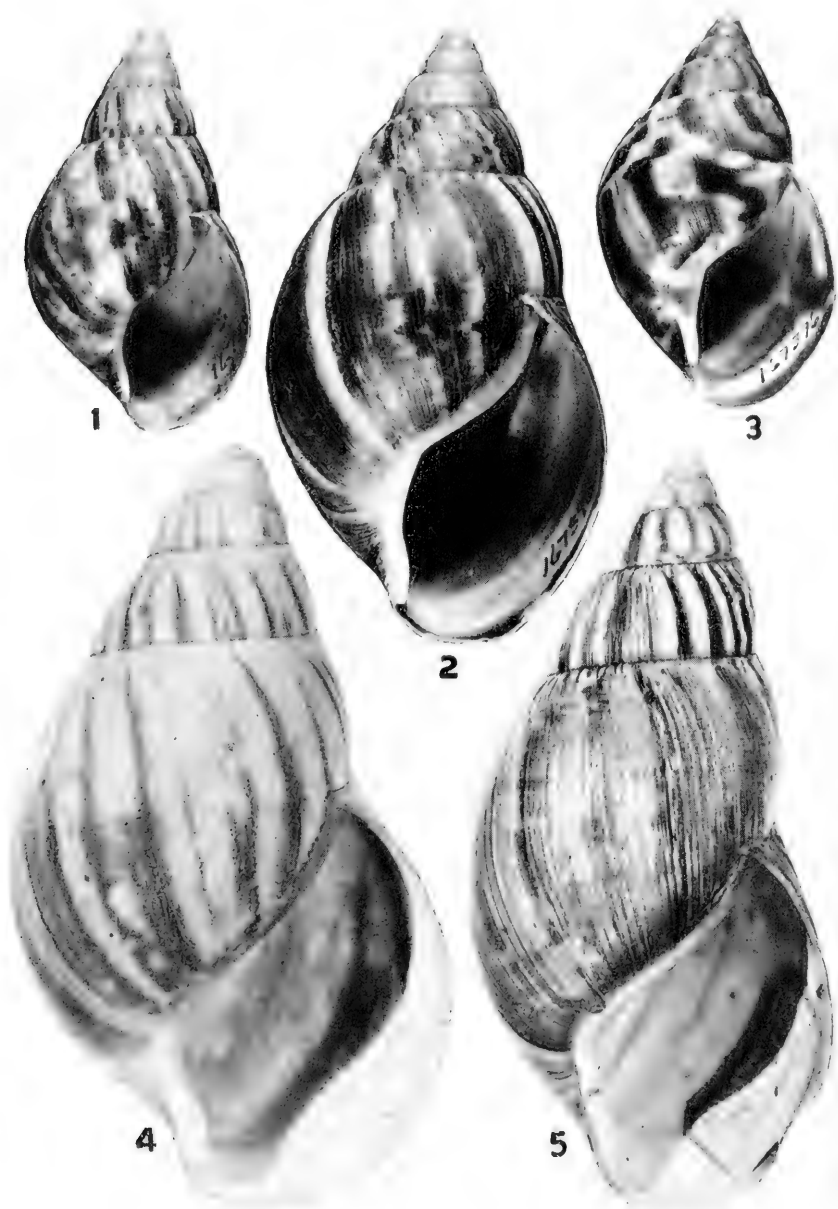




PLATE 81

PLATE 81

Fig. 1. *Archachatina papyracea* (Pfeiffer). Holotype of *Achatina aurora* Pfeiffer. Natural size.

Figs. 2-3. *Achatina spekei* Dohrn. Holotype (Fig. 3) and immature paratype. Natural size.

Fig. 4. *Achatina zebra tigrina* Beck. Holotype of *Achatina inaequalis* Pfeiffer. Natural size.

Fig. 5. *Archachatina marginata grevillei* (Pfeiffer). Holotype. Natural size.

Fig. 6. *Achatina albopicta* E. A. Smith. Holotype. Natural size.

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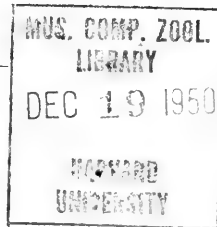


Bulletin of the Museum of Comparative Zoölogy

AT HARVARD COLLEGE

Vol. 105, No. 2

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COMPARATIVE GENITAL ANATOMY OF SOME  
AFRICAN ACHATINIDAE (PULMONATA)

BY ALBERT R. MEAD

WITH NINE PLATES

CAMBRIDGE, MASS., U. S. A.  
PRINTED FOR THE MUSEUM

December, 1950



No. 2. — *Comparative Genital Anatomy of Some African Achatinidae (Pulmonata)*<sup>1</sup>

BY ALBERT R. MEAD  
Department of Zoology  
University of Arizona

CONTENTS

	PAGE
Introduction . . . . .	220
Genital Anatomy . . . . .	224
<i>Achatina (Achatina) achatina</i> (Linné) . . . . .	224
<i>Achatina (Lissachatina) panthera</i> (Férussac) . . . . .	226
<i>Achatina (Lissachatina) panthera lamarckiana</i> Pfeiffer . . . . .	228
<i>Achatina (Lissachatina) Layardi</i> Pfeiffer . . . . .	229
<i>Achatina (Lissachatina) glutinosa</i> Pfeiffer . . . . .	230
<i>Achatina (Lissachatina) albopicta</i> E. A. Smith . . . . .	231
<i>Achatina (Lissachatina) reticulata</i> Pfeiffer . . . . .	232
<i>Achatina (Lissachatina) iredalei</i> Preston . . . . .	233
<i>Achatina (Lissachatina) zanzibarica</i> Bourguignat . . . . .	234
<i>Achatina (Lissachatina) fulica fulica</i> Bowdich . . . . .	236
<i>Achatina (Lissachatina) fulica hamillei</i> Petit . . . . .	239
<i>Achatina (Lissachatina) fulica rodatzii</i> Dunker . . . . .	242
<i>Achatina (Euacchiopina) loveridgei</i> (Clench and Archer) . . . . .	242
<i>Archachatina (Archachatina) bicarinata</i> (Bruguère) . . . . .	244
<i>Archachatina (Culachatina) degneri</i> Bequaert and Clench . . . . .	245
<i>Archachatina (Calachatina) marginata ovum</i> (Pfeiffer) . . . . .	246
<i>Archachatina (Calachatina) marginata suturalis</i> (Philippi) . . . . .	247
<i>Archachatina (Tholachatina) simplex crawfordi</i> (Morelet) . . . . .	247
<i>Archachatina (Tholachatina) meadi</i> Bequaert . . . . .	248
<i>Archachatina (Tholachatina) osborni afromontana</i> (Bequaert and Clench) . . . . .	249
<i>Limicolaria kambeul</i> (Bruguère) . . . . .	250
<i>Limicolaria flammea</i> (Müller) . . . . .	252
<i>Limicolaria felina</i> Shuttleworth . . . . .	253
<i>Limicolaria saturata capitellum</i> Pilsbry . . . . .	255
<i>Limicolaria ussuwiensis</i> Kobelt . . . . .	256
<i>Limicolariopsis kiruensis</i> (Preston) . . . . .	257
<i>Pseudotrochus turbinatus mucidus</i> (Gould) . . . . .	258
<i>Pseudotrochus interstinctus insignis</i> (Pfeiffer) . . . . .	259

<sup>1</sup> Published with the aid of a grant from the Pacific Science Board of the National Research Council, Washington, D. C.

When this is once determined, it is usually not very difficult to make a correct identification even when the specimen is rather poorly preserved. Too often, though, a specimen such as this latter is used in setting forth the details of the genital anatomy. This is especially perilous where uniques are involved.

No matter what method is used in killing snails, there is always danger of producing at least a small amount of distortion in the genital system. Preserving in formalin after insufficient drowning will cause the animal to contract to such an extent that severe distortion of the soft parts will inevitably result. In addition, the acid in the formalin will not only attack the shell but will also dissolve the cementing substance that makes the periostracum adhere to the shell. Treatment with alcohol, under similar conditions is just as bad, as the dehydration will alter the general proportions, shrink the tissues and make the specimen hard enough so that it will be difficult to examine. Drowning to such an extent that there is little or no contraction when the specimen is immersed in a preservative still does not get away from distortion as the dead and dying tissues take on a great deal of water and thereby assume unnatural proportions.

Preserving the animal in formalin or alcohol while it is still in its shell, even under the best conditions, will create a real problem when attempts are made later to remove the soft parts without damaging or destroying completely the shell. A tearing of the visceral mass in its central portions is the usual result. Prolonged soaking in water or various solutions seldom is of any avail. Boiling will invariably cause it to shrink so badly that it is worthless as a scientific specimen.

The author has found that by far the best method is to plunge the partially drowned specimen into rapidly boiling water and examine it as soon as the columellar muscle has loosened sufficiently to permit extraction of the soft parts. This not only leaves the genitalia still very flexible but their immediate removal obviates the danger of making permanent any distortion due to the crowding effects of contraction. Added advantages are found in the ease with which the soft parts can be removed and in the undamaged shell specimen that remains. Too sudden cooling of the shell, however, may cause the periostracum to crack and flake off; the shell is therefore usually re-immersed in the hot water, after the soft parts are removed, and allowed to undergo gradual temperature changes as the water cools.

The soft parts, including the removed genitalia, are preserved in 6% formalin solution, as 70% alcohol dehydrates and shrinks the tissues and needs replenishing too often. Specimens that have become brittle with preservation in alcohol and even specimens that have been allowed to dry out completely have been restored to nearly

natural proportions and a most remarkable degree of flexibility through the use of an 0.8% solution of trisodium phosphate as recommended by Van Cleave and Ross (1947). Such specimens, whether genitalia or the entire snail, were soaked from a few hours to several days with never the slightest suggestion of maceration or distortion even in the longer period of time.

During the months of May and June, 1948, F. X. Williams, entomologist of the Hawaiian Sugar Planters' Association, sent, under special permission, live specimens of several species of the genus *Achatina* from Kenya Colony and Zanzibar. There is indeed little doubt that this is the largest shipment of live achatinas ever to be shipped to this country, and perhaps the western hemisphere. These formed the bulk of the live material examined in this study. The rest of the live material was collected in the Gold Coast and Nigeria by the author while on duty as Parasitologist of the Inter-Allied Malaria Control unit in British West Africa in 1944-45.

The examination of the live material sent by F. X. Williams was made possible by funds provided by the United States Navy and particularly the Office of Naval Research, enabling the author to go for the purpose to the Museum of Comparative Zoölogy of Harvard University. The author wishes to express his most sincere gratitude to Harold J. Coolidge, Executive Secretary of the Pacific Science Board of the National Research Council, for securing this grant; to William J. Clench for generously turning over to the author, for a period of a month, the complete facilities of the Mollusk Department of the Museum of Comparative Zoölogy; to his Assistant Ruth D. Turner for aid and assistance in many ways during his stay in Cambridge; to Joseph C. Bequaert for giving freely of his time and help during the course of this study and for identifying the species examined;<sup>1</sup> and finally to Henry A. Pilsbry of the Academy of Natural Sciences of Philadelphia, John Armstrong of the American Museum of Natural History, Yoshio Kondo of the Bernice P. Bishop Museum, W. Harry Lange of the University of California, and Dan Langford of the United States Navy, for the kind loan of preserved material.

<sup>1</sup>The taxonomic study of *Achatina* and *Archachatina* published in the same volume of this Bulletin (pp. 3-207) was written for the express purpose of clarifying the nomenclature, characters and classification of the species and subspecies examined anatomically by A. R. Mead and their close relatives. It was not possible to make at the present time a similar study of the other genera of Achatinidae dissected by Mead. I am however also responsible for the specific names he uses: in most cases shells of the lots or specimens he examined are now preserved at the M.C.Z., where they are available to future students and where their exact status may eventually be determined. The generic name *Pseudotrochus* is used by Mead in the customary sense of Pilsbry's Manual. It was shown recently that this name cannot be applied properly to this African group of snails. It seems hardly the proper place and would only cause confusion if the necessary change in nomenclature were proposed in a purely anatomical study.

## GENITAL ANATOMY

The basic achatinid genital anatomy is of the most simple, generalized type — the only specialization of any importance being the penial sheath. There is a complete lack of any accessory structures along either the male or female conduit.

There are described below the genitalia of twenty-eight achatinid species and subspecies which the author has examined. The reproductive system of the familial type, *Achatina achatina* L., Figs. 1, 2, will be examined first from base to apex and in detail to establish the terminology that will be used hereinafter. This being understood, the genital structures of the other achatinids can be correctly identified, interpreted and homologized.

The figures of this species, as of the others, have been shown devoid of most individual variations and insignificant details, such as wrinkles, folds, and the like, which, if included, would needlessly obscure the valid characters and make more difficult the drawing of homologies. Further, the genitalia have been shown in the ventral aspect as they can thus be seen to better advantage.

## ACHATINA (ACHATINA) ACHATINA (Linné)

Figs. 1, 2

In this species, the penis (P) is a very muscular, robust, hollow tube that projects approximately half its length above the basally placed, thick penial sheath (PS) or "ring muscle." At the junction of the penis and the slender basal vas deferens (BD) the penial retractor (PR) takes its origin. This passes posteriorly to insert on the right tentacular retractor (TR) which is a portion of the great columellar muscle system. The basal vas deferens is embraced by the penial sheath for a portion of its length and hence comes to rest between it and the penis. It leaves the sheath, however, about midway and descends to the crotch between the penis and vagina. H. B. Baker (1939, etc.) refers to this crotch in related mollusks as the "penioviductal angle", though peniovaginal angle would seem more correct even if it is less euphonic. The basal vagina (BV), which is approximately as large and as long as the penis, is a very muscular, whitish, hollow tube without modification. Apically it is joined, after a slight constriction, by a more glandular, tan-cream colored portion of the vagina (AV). These histological differences, which are scarcely apparent in the preserved specimen, indicate that the two parts of the vaginal tube undoubtedly have different functions during copulation and egg laying. Nearly the entire vagina, but especially its basal portion, is held in

place on the ventral body wall by an irregular, variable series of muscle slips which, together, act during copulation as a retainer of the vagina. As these are taxonomically valueless it has been thought advisable not to confuse the outlines of the vagina by their inclusion. Basally the vagina combines with the penial tube to form a shallow genital atrium (GA), opening to the exterior through a single genital orifice. It is unfortunate that certain American and German authors have used the unsuitable terms "cloaca" and "Geschlechtskloake" for this common chamber in related species.

The spermatheca arises as a diverticulum at the very apex of the vagina. In this species, the spermathecal duct (SD) is extremely short and the terminal, clavate spermatheca proper (S) is only slightly longer. In the literature, this structure is variously referred to as a seminal receptacle, bursa copulatrix, spermatheca and Samentasche, though spermatheca is by far the most generally used. Beyond the base of the spermathecal duct, the female conduit continues as the free oviduct (FO). This is only slightly larger and longer than the spermathecal duct.

The apical vas deferens passes in close juxtaposition to the vagina and is connected to it by thin slips of connective tissue. Apically, it joins the free oviduct to form the so-called spermoviduct (ovispermato-duct of Taylor, 1894, p. 146). Actually, this term is not wholly suitable as the entire oviduct, apical to the free oviduct, functions during egg formation as a uterus and only incidentally as an oviduct. As indicated below, the thin-walled, vitreous-yellow basal uterus (BU) probably forms the outer, yellow shell layer of the eggs, whereas the thick-walled, opaque-white apical uterus (AU) apparently forms the pale inner layers. The division between these two sections is pronounced.

At the point where the male and female conduits become confluent, the former develops a multifold, aciniform prostate gland (PA) which passes apically for the full length of the uterus and obscures from the outside the internally situated seminal duct, or spermatic duct. The interrelationships of these two conduits are discussed below under genital physiology. The female conduit is joined apically by a common duct from the reniform albumen gland (AG) and then fuses completely with the male conduit to form a very small, delicate tube. This common duct, which is sometimes referred to as the "carrefour" (H. B. Baker, 1939, etc.), soon gives off a short, irregular diverticulum termed the talon (T, Fig. 2). This indeed poorly understood structure consists of a basal sacculate portion and an apical digitiform diverticular process which in turn contains a varying number of smaller diverticula (*Cf.* Fig. 15). It has been variously, vaguely and erroneously

referred to in the literature of the achatinid genital system as "une poche ovarienne contenant les rudiments d'un œuf" (Deshayes, 1851), "vesicula seminalis" (Connolly, 1925), "spermatocyst" (Odhner, 1932), "Befruchtungstasche" (Simroth and Hoffmann 1908-28) and "caecum" (Reynell, 1906). Apical to the talon, the common duct becomes enlarged and extremely convoluted. The usual presence of a great mass of spermatozoa in this region of the duct vouches for the fact that it functions as a seminal vesicle (SV). In its apical portions, it may be found irregularly covered with a purple-black pigment. Somewhat beyond the middle, the ovotestis duct abruptly narrows to a very thin duct (OT) which passes to the ovotestis (O). This latter consists of five more or less distinct pinnate groups of acini embedded in the columellar surface of the antipenultimate whorl of the liver or hepatopancreas (L). In the freshly killed specimen, these are somewhat pinkish though they may be buried just deeply enough in the liver so that they are not apparent from the surface. And even in dissection, care must be taken in exposing them as they are very easily broken up and obscured in the all too soft liver substance.

Five specimens of *A. achatina* were examined. Three of these were collected by the author — one each from Accra, Gold Coast (June, 1944); Osenasi, Gold Coast (Oct., 1944), and Lagos, Nigeria (July, 1945). The female system in each of the latter two was markedly undeveloped though the male system was nearly as developed as that of the fully mature specimen from Accra. This undoubtedly is indicative of a protandrous condition in this species which also probably typically obtains in the other members of the family. The other two specimens were collected by Warren E. Buck in "Nigeria" some time in 1945 and were deposited in the California Academy of Sciences.

Measurements of Accra specimen in millimeters: P — 41, PS — 21x10, AV — 13, BV — 36, FO — 9, SD — 9, S — 10.

#### ACHATINA (LISSACHATINA) PANTHERA (Férussac)

##### Fig. 21

Semper, 1874, p. 143, taf. xii, fig. 17.

Brancsik, 1893, p. 116, tab. vi, fig. 2.

Martens and Wiegmann, 1898, pp. 85-92, tab. iv, figs. 5, 6.

Pilsbry, 1904-05, p. xii, pl. 63, figs. 30, 32.

Simroth and Hoffmann, 1908-28, p. 564, pl. xxxv, figs. 9, 10.

Semper first described the genitalia of this species but he unfortunately had it confused with *Achatina fulica*. His specimens were reportedly from Calcutta which probably persuaded him to believe



that he had *fulica* — the sole species of *Achatina* in India. Another specimen (also undoubtedly *panthera*), which he states came from Zanzibar, was compared with these at the time and it was found that they “stimmt . . . in allen Einzelheiten überein.” Since *panthera* has not been introduced into India, the validity of the locality of Semper’s specimens (from “Dr. Anderson”) is immediately open to question. Further, his illustration of the genital system clearly agrees with that of Brancsik<sup>1</sup> and those of Martens and Wiegmann and does not compare favorably with the existing illustrations of *fulica*. These three original illustrations all agree in the unique form of the penis. Pilsbry, and Simroth and Hoffmann copied the illustrations of Martens and Wiegmann.

A single large alcoholic specimen of the genitalia only of *A. panthera* was found in the collection at MCZ (58799). The information on the label leads one to believe that the specimen was collected on the island of Zanzibar by C. Cooke and given to F. C. Gray, and that he in turn gave it to MCZ on 26 March, 1862. Bequaert (1950), however, is convinced that *panthera* does not occur on Zanzibar and that “consul” Cooke probably obtained this specimen from some other East African place and shipped it from Zanzibar. Checking the shell under this accession number removed all doubt as to its being typical *panthera*. Furthermore, the form of the penis is indisputably like those of the illustrations mentioned above. It is extremely attenuate and, before connecting with the basal vas deferens, it folds back upon itself, well beyond the confines of the upper limits of its sheath, to form a conspicuous loop. Although the exposed basal vas deferens is, in diameter, only about half the size of the apical penis, this difference is superficially obscured by the broad origin of the penial retractor. This probably explains why these two adjacent parts have been shown in previous illustrations to be of the same caliber. The very slender sheath, which basally covers nearly three-quarters of the penis, is apically thin-walled and constricted by discernible circular muscle bands. In the absence of live material, the function of this constriction cannot be determined but it quite possibly is responsible for producing, during copulation, an unusual intromittent organ.

The sheath does not cover the most basal part of the penis, adjacent to the genital atrium, and there is thus formed what hereinafter will be referred to as a penial prepuce (PC). Its anatomical significance is treated below in the discussions of the penial types and copulatory anatomy. Basally, within the sheath, the penis becomes approximately twice the size of its most apical portion. A very short penial retractor

<sup>1</sup> Brancsik illustrates it under the new specific name, *mossambica*; this Pilsbry put in the synonymy of *panthera*.

inserts upon the tentacular retractor muscle. The vas deferens does not reach the penio vaginal angle. Just before its junction with the free oviduct, there is a fairly conspicuous, apparently lobulated and glandular mass whose possible function is explained below in the section on genital physiology.

The most striking element in the genitalia is the unusually attenuate vagina which basally is very muscular, thick-walled and thrown into a tight series of compound folds. The nature of the folds and the arrangement of the muscle bands seem to preclude any possibility of distortion, due to killing, being a factor in producing these folds. Previous illustrations of the genitalia of this species have shown what appeared to be very wrinkled vaginae; it is now quite apparent that these "wrinkles" were merely attempts to indicate the characteristic folds. Further, all specimens of the subspecies *lamarckiana* possessed similar but less pronounced folds. Upon dissection of the vagina, the lumen was found to be small and convoluted in conformity with the thick vaginal folds. Apically, the vagina is straight and thinner walled. The short free oviduct and the basal portion of the equally short spermathecal duct are of the same caliber as the apical vagina. The large, sacculate spermatheca is approximately twice the length of its slender duct. A distinct talon is present and, like the other apical structures, is typical of the group. The genital atrium is shallow.

Measurements in millimeters of the genitalia: P (apical to PS) — 30; PS — 42; PR — 13; AD — 57; BD — 3.5; V — 60; FO — 10.5; SD — 11; S — 23x7; AG — 21; No. compound curves, vagina — 8.

#### ACHATINA (LISSACHATINA) PANTHERA LAMARCKIANA Pfeiffer

Seven of sixteen alcoholic specimens of this subspecies (MCZ 4880) were examined. These were collected by Nicholas Pike in Mauritius on October 13, 1873. The seven were selected to give the greatest possible variation in body size.

No really tangible differences could be found between *lamarckiana* and typical *panthera* which could not reasonably be attributed to differences in size of the animal or artifacts of preservation. One significant fact was apparent, however; for though all specimens were sexually mature, none attained near the over all genital proportions of the single specimen of typical *panthera*. And to add significance to this, the two specimens of the closely related *A. layardi* were considerably larger animals than any in this series of *lamarckiana* and yet they both were quite immature. These findings, then, lend strong support to the assumption that *lamarckiana* is merely a small race of *panthera*.

Of particular importance, in the comparison of the seven specimens in this lot, is the great variability in the size of the penial "loop" that passes out of the sheath. It should be noted in the accompanying tabulation, however, that the length of the "loop" and the sheath are in inverse proportion, thus probably indicating a variable degree of contractility in these two organs. Of similar importance is the variable number of compound curves in the vaginae. Only one of the specimens possesses for certain, the circular muscle bands of the apical sheath found in the single specimen of typical *panthera*. Actually, a series of freshly killed specimens is needed to throw further light on these apparent differences. In all specimens, the penial retractor inserts upon the right tentacular retractor and the vas deferens does not reach the peniovaginal angle.

Measurements in millimeters of the genitalia:

P (apical to PS).....	32	32	34	39	1	32	4
PS.....	19	15	22	21	32	26	34
PR.....	6	3.5	8	5	10	10	6
AD.....	29	24	37	30	26	33	28
BD (apical to PS).....	3	5	2	4	—	8	1
V.....	22	23	27	24	25	31	24
FO.....	8	4	11	10	9	11	5
SD.....	10	6.5	13	8	11	11	6
S.....	10x4	10x3	13x6	11x4	18x8	15x5	13x5
AG.....	9	10	18	—	—	14	9
No. comp'd curves in vagina	2	6	4	5	3	7	3

#### ACHATINA (LISSACHATINA) LAYARDI Pfeiffer

Two alcoholic specimens (MCZ 82409), collected by J. H. Sandground at Lourenço Marques, Portuguese East Africa, were dissected. One was so immature as to be practically valueless. The other, though somewhat immature, gave a quite fair idea of the definitive genital anatomy of this species. Basically, the genitalia are strikingly like those of *A. panthera* in that both the penial sheath and the vagina are attenuate and that the penis forms a long apical loop. The only tangible differences are found in the vagina which is not as muscular nor does it show even the slightest suggestion of forming the compound curves so characteristic of *panthera*. To add significance to this, the smallest individuals of the series of *A. panthera lamarckiana* examined, were smaller than this specimen of *layardi* and yet they possessed very muscular, sinuous vaginae. This suggests then that these vaginal characters may prove, upon examination of full-grown specimens of *layardi*, to be the only fundamental differences that exist between these two obviously very closely related species.

Measurements in millimeters of the larger specimen: P (apical to PS) — 27, PS — 13, PR — 6.5, AD — 27, BD (apical to PS) — 3, V — 17, FO — 7, SD — 10, S — 10x2.5, AG — 6x2.

ACHATINA (LISSACHATINA) GLUTINOSA Pfeiffer

Fig. 20

There was but a single, fully mature specimen available for dissection. Its sole datum consisted of an American Museum of Natural History catalogue number "3221".

In many respects, the genitalia are intermediate between those of *A. reticulata* and *panthera*. As is shown in the conclusions, they thus form the last link in a series that nicely connects such anatomically diverse forms in this genus as *fulica* and *panthera*. The penis sheath is long and tubular. Apically, the penis is fairly large and projects for almost half its length beyond the sheath. Because in this specimen the adjacent basal vas deferens, which is less than half the caliber of the penis, is considerably shorter, it effects a sigmoid flexure in the penis thus producing a peculiar penial "loop." The very short penial prepuce is scarcely discernible. The vas deferens leaves the sheath in approximately its apical one-third and does not reach the penio-vaginal angle but passes directly to an apical swollen portion adjacent to the prostatic gland. An insertion on the right tentacular retractor is made by the fairly long penial retractor.

A very definite swelling is present in the basal vagina but it does not approach the rotundity or the cormoid proportions of those in *fulica* and closely related species discussed below. The apical vagina is slender in its mid-portions but nearly twice as large at the junction of the free oviduct and spermathecal duct. The latter is quite attenuate and terminates in a capitate spermatheca. The larger free oviduct narrows only slightly in its apical portions.

Of the species examined, *glutinosa* seems to be nearest to *reticulata* and differs only in that the basal vagina is more muscular, the apical vagina, the penis, and the sheath are longer and more slender. On the other hand, it can be distinguished from *panthera* in that the basal vas deferens forms a greater part of the "loop", the penial retractor is longer, the sheath is shorter, the shorter vagina is not sinuous, and both spermathecal duct and free oviduct are considerably longer. These differences notwithstanding, there is little doubt that *glutinosa* and *panthera* are definitely closely related.

Measurements of the genitalia in millimeters: P (apical to PS) — 15; PS — 20; PC — 3.5; PR — 28; BD (apical to PS) — 11; AD — 55x1.25; BV — 6x5; AV — 29x2-3.5; SD — 31x1.5; S — 9; FO — 28x2.25; AG — 28x11.

## ACHATINA (LISSACHATINA) ALBOPICTA E. A. Smith

Figs. 14, 15, 16, 18

The very robust, thick-walled, white penis sheath, which is approximately half as wide as it is long, stands out as the most striking feature of the genitalia of this species. In direct contrast, the penis was found, upon opening this sheath (Fig. 16) to be extremely slender, thin walled and scarcely as large around as the basal vas deferens. The process of extroversion of these structures to form the intromittent organ seemed enigmatic until copulation was observed in *Achatina fulica* (*vide infra*). No demarkation between the penis and basal vas deferens could be found; though, as in other species, the origin of the penial retractor indicates the region of this junction. The penial retractor in its basal one-seventh is embraced by the sheath; apically it inserts on the right tentacular retractor. At the basal limits of the sheath, the internally contained penis is enlarged and then suddenly constricted at its junction with the unensheathed, thin-walled penial prepuce. This latter, like the adjoining genital atrium is lined with a brownish, chrome yellow epithelium. The epithelium gives rise to thick, chrome yellow slime as do the rich-brown colored exposed portions of the body. The basal vas deferens leaves the sheath about midway and extends approximately two and one-half times the length of the sheath to its junction with the free oviduct to form the spermoviduct.

A dissection of the basal vagina (Fig. 18) revealed that a very thick muscular band is responsible for the cormoid proportions of this organ. The apical vagina is thin-walled and nearly three times the length of its basal portion. The slender free oviduct and spermathecal duct are only slightly longer than the apical vagina. These three structures are approximately the same caliber as the apical vas deferens. The spermatheca is variable in length but remains relatively slender and clavate.

The basal uterus is a pronounced military green-brown in the freshly killed specimen and has numerous longitudinal vermiculations indicating good accommodation for a sizeable batch of eggs. The apical uterus is pale yellowish basally and pale cream color apically with the usual abundant transverse folds. The talon (Fig. 15) has a variable number of diverticulations. The convoluted seminal vesicle is basally pale cream colored and apically dark purplish.

There were dissected four live specimens collected in May, 1948, by F. X. Williams at Diani Beach, south of Mombasa, Kenya. The single immature individual which was examined was quite apparently protandrous.

Measurements in millimeters of genitalia (the illustrated specimen is listed first):

P. ....	10	—	—	—
PS .....	14.5x7	16x7	15x9	16.5x8
PR (apical to PS) . . . . .	22	19	22.5	20.5
PC .....	2.5	5	5	6
VD .....	39	40	38	41
BV .....	5x8	4x5	6x10.5	4x9
AV .....	13	13.5	15	15
FO .....	15.5	16	19	22
SD .....	19	18	16	23
S .....	11	8	17	17
AG .....	16.5	11	29x9	30x9

ACHATINA (LISSACHATINA) RETICULATA Pfeiffer

Fig. 13

In spite of the great similarity in the form and sculpturing of the shells of this species and *albopicta*, the genitalia are quite contrasting. The penis, like those of *A. achatina* and some species of *Archachatina*, is very large and muscular and extends considerably beyond the upper limits of the fairly thin-walled sheath. There is a marked difference in the caliber of the apical penis and the basal vas deferens. From their junction, the penial retractor passes to the right tentacular retractor where it makes the insertion. The first specimen dissected, which is the one illustrated here, has a highly significant modification of this insertion. A description and a discussion of this will be found below under the topic of penial insertion. The sheath is approximately only twice as long as the apically exposed penis and four times as long as the penial prepuce. The basal vas deferens leaves the sheath in its apical one-third and passes nearly to the peniovaginal angle before joining the free oviduct.

In this species, in contrast to *albopicta*, there is a conspicuous lack of a muscular thickening of the basal vaginal wall. The vagina is evenly thin-walled throughout its entire length and is not differentiated into basal and apical portions. It is somewhat enlarged adjacent to the shallow genital atrium and more strongly enlarged in its apical portions before giving rise to the slender spermathecal duct and the larger free oviduct. The spermatheca is variable but in general clavopapitate. The basal uterus is canary-yellow and the apical uterus is pale cream in color; in other respects these structures are typical of the genus.

One juvenile and two adult live specimens, collected on the island of Zanzibar in June, 1948, by F. X. Williams, provided the material for the examination of the genitalia of this species. A fourth one was preserved but not dissected. The body is light tan in color with a washing of brown over the tentacles, head and neck. The largest one in the lot was seen twice to be rasping vigorously along the leading edge of its shell in an apparent robbing-Peter-to-pay-Paul attempt to add more calcium to its diet.

Measurements of genitalia in millimeters (in each case the first figure refers to the specimen illustrated): P (apical to PS) — 13, 8, 10; PS — 26, 12, 16; PR — 33, 13, 20; PC — 6, 2, 3.5; VD — 71, 32, 49; V — 39, 19, 20; FO — 29, 16, 23.5; SD — 32, 20, 26; S — 25x9, 9, 14.5; AG — 34x11, 9, 29x7.

#### ACHATINA (LISSACHATINA) IREDALEI Preston

Figs. 17, 19

Though this is a considerably smaller animal and its shell is of quite different form, the genitalia are infinitely more similar to those of *A. albopicta* than the latter are to those of the presumed more closely related *A. reticulata*. The penis sheath of this species, however, is much less incrassate than that of *albopicta*. The penis, which is typically completely contained within the sheath, is somewhat enlarged at its junction with the basal vas deferens. In only one case was this region seen to be projecting very slightly beyond the apical limits of the sheath. This apparent exception can be accounted for through the fact that, during the killing process, a greater contraction of the penial retractor tends to attenuate the ensheathed penis. The penial retractor takes its origin very broadly on the apical penis, the basal vas deferens and even the inner surface of the sheath. In every case, except one, the retractor inserts on the right tentacular retractor. The significance of this and other exceptions is discussed below. The sharp demarkation between the penis and the penial prepuce that was found in *albopicta* was also found in this species. The basal vas deferens leaves the sheath in its apical one-third and extends, as the apical vas deferens, approximately three and one-half times the length of the sheath.

The basal vagina is very muscular, enlarged and cormoid though not to the extent of that of *albopicta*. The most characteristic feature is the very abbreviated apical vagina which is approximately the length of the basal vagina. The free oviduct is slightly larger and the spermathecal duct is somewhat smaller than the apical vas deferens.

In general, these two structures closely resemble those of *albopicta*. The spermatheca is small and clavo-capitate. The basal uterus is bright butter-yellow in color. Other apical genital structures seem typical of the achatinas in general.

Five of the six live specimens, collected by F. X. Williams, were dissected. Two of these (Nos. 3, 20), including the one illustrated, were collected in May, 1948, at Diani Beach, south of Mombasa, Kenya; the other four (Nos. 12, 16, 21, 22) were collected in June, 1948, on the island of Zanzibar. One of these latter possessed a well-developed male system and a very immature female system indicating that protandry obtains in this species. No tangible differences whatsoever could be found in the anatomy of the specimens from these two localities. One specimen was found to contain five large albumen masses in the apical uterus; the significance of these is discussed below in the section on physiology.

Measurements of genitalia in millimeters (the illustrated specimen is listed first):

	#3	#12	#16	#20	#21
P.....	11	—	11	—	—
PS.....	11x4	10	11	10	13
PR.....	16	13	13	10	15
PC.....	2.5	2	2.5	3	2.5
VD.....	41	30	37	35	46
BV.....	5x5	2x4	3x5	2x4	3x4
AV.....	4	5	4	5	5
FO.....	13	11	17.5	13.5	18
SD.....	17	13	18	17	19
S.....	6.5	2.5	—	10	7
AG.....	38x7	4	24x7	27x7	23x9

#### ACHATINA (LISSACHATINA) ZANZIBARICA Bourguignat

Figs. 8, 10

There were dissected, in the study of the genitalia of this species, six of several specimens collected by A. Loveridge in Amani, Usambara Mountains, Tanganyika Territory, in November, 1926. Unfortunately, the killing medium, in which these specimens were placed, was so severe that in most cases extreme distortion was found to have taken place in the soft parts of the snail. One in this lot, however, seemed to be in better condition than the rest; the genitalia of this specimen have been illustrated.

The proportions of the genital structures are so nearly like those of *A. iredalei* and especially *A. loveridgei* that they can be distinguished



only with difficulty. The penis is so abbreviated that the fairly thick-walled sheath not only covers it completely, but also embraces the penial retractor for approximately half its length. The penis seems to be divided almost equally into three quite definite regions. The most apical portion is only slightly larger around than the basal vas deferens, and in its connection with this latter, it forms an oblique angle. Only the very shortest part of the basal vas deferens is embraced by the sheath. This is in contrast with the condition in *iredalei*. The mid-penial portion is a very narrow, thin-walled tube, only one-half the caliber of the apical portion. This becomes much broader, but not abruptly so, to form the shorter basal portion. The latter appears to join the penial prepuce broadly but upon closer examination, a very narrow constriction is found between the two structures. The penial retractor, apical to the sheath, is narrow and shorter than the sheath. In two specimens it inserts upon the right tentacular retractor, in three specimens it inserts in the approximate center of the diaphragm and in one specimen it splits terminally and attaches at both places. The significance of these variations in insertion is discussed under that general topic below.

The cormoid, muscular basal vagina is sessile upon the genital atrium. The slender, thin-walled apical vagina is twice the length, but only slightly longer than the width, of the basal vagina. The free oviduct and the spermathecal duct are of the same caliber. They are approximately half the length and almost as wide as the vas deferens. The clavate spermatheca is about half the length of its duct.

Two of the six specimens were gravid with fully formed embryos. One contained twenty-six. Some of these had apparently been quickly expelled during the killing process, for six were found discharged in the folds of the foot and mantle, one in the genital atrium, and two in the free oviduct. The rest were found in the greatly distended uterus going apically to a point adjacent to the albumen gland. This latter was very small indicating that its supply of albumen had been heavily drawn upon. The other gravid specimen had been dissected previously by other investigators (Clench and Archer, 1930). There was no way of determining the number of embryos that this one contained though a single one was found centrally located in the free oviduct. The embryos varied from  $3\frac{1}{2}$  to  $4\frac{1}{2}$  whorls and from 11x9 mm. to 14.5x11 mm. in height. This phenomenon of ovoviviparity is treated below in a discussion of genital physiology.

Due to excessive distortion in two of the specimens, the measurements, in millimeters, of only four are given here. The specimen illustrated is listed first.

P.....	7	—	—	—
PS.....	11x5	19.5	14	19
PR.....	7	8.5	10	6
PC.....	3.5	3	11	2.5
VD.....	40	40	56	46
BV.....	3x5	3x4.5	—	3x5
AV.....	5	6	5.5	6.5
FO.....	19	22	—	16
SD.....	20	12	26	22
S.....	11	22	9	11

ACHATINA (LISSACHATINA) FULICA FULICA Bowdich

Fig. 41

Quoy and Gaimard, 1832-34, **2**, pp. 152-155; **3**, pp. 879-880, pl. 49, fig. 21.

Keferstein, 1862-66, pl. 99.

Brancsik, 1893, p. 204, tab. vi, fig. 6.

With an illustration of the internal anatomy of *Achatina mauritiana* (= *fulica*), Quoy and Gaimard were probably the first to show the achatine genitalia. The lack of detail, however, makes it of little value, especially since much of their terminology is now known to be incorrect. Keferstein copied their illustration directly. Semper (1873) unfortunately used the name *fulica* in describing and illustrating *A. panthera* (*q.v.*) thus later persuading Pilsbry (1904-05, p. xii) to assume that the genitalia of these two species were similar. Brancsik illustrated, rather poorly, the genitalia of a *fulica* from Madagascar, therefore of the typical subspecies. The proportions of the basal female conduit are approximately correct; but the lack of detail in the male system makes the illustration practically valueless. Further, he erroneously interprets the penial retractor as the "flagellum."

In the present study of the genitalia of this species, there were dissected and examined: two specimens collected in Mauritius by Nicholas Pike in 1873; one specimen collected at Agaña Bay, Guam, by R. Tucker Abbott; two specimens raised in Hawaii in 1940-41 by Yoshio Kondo; three of several specimens collected on Saipan (one on November 11, 1947, and two on March 12, 1948) by W. Harry Lange; and two of several immature specimens and a number of empty shells collected on the Palau Islands in the fall of 1948 by Dan Langford. Before any of the material was examined, seven freshly killed specimens of *A. fulica homillei* from Kenya and Zanzibar and two freshly killed specimens of *A. fulica rodatzi* from Zanzibar were dissected and the relationships of the genitalia were determined and

illustrated (Figs. 5, 7, 11, 12). As there had not been found any appreciable difference in the genitalia of *hamillei* and *rodlatzi*, it was not expected that those of *fulica fulica* would prove different. The results of these examinations were confirmatory. The figures indicated above, then, will serve to illustrate as well the genitalia of the typical subspecies. The same degree of variability in the length of the penis, apical vagina, free oviduct and spermathecal duct was found in this series of typical *fulica*. In a smaller series, however, these differences might have been judged as significant. In every case, the penial retractor inserted on the right tentacular retractor. A generalized diagram (Fig. 41) based on the genitalia of all examined specimens of *fulica* subsp. has been prepared to demonstrate relationships and facilitate homology in the various penial types, which aspects are treated in detail below.

The specimens from Saipan and the Palau Islands show definite signs of being in an environment that is far from optimum for them. In the first place, nearly all of the shells showed the results of multiple, clean, sharp breaks with often as much as an inch or two of the last whorl of the shell being removed. In a couple of instances, new shell had been built up and this too had become broken. Breaks higher up on the shell had also been mended, leaving noticeable irregularities in the outline of the shell. To add to this effect, much of the tissue of the snail contained numerous whitish islets of calcification, giving a measly quality to the flesh. All this presented a superficial picture of a very unthrifty condition in the snails. And, as a matter of fact, these were sent to the author with the suggestion that possibly they were diseased snails.

In the absence of first-hand knowledge regarding the environmental conditions in the region where these specimens were collected, it is a bit difficult to state what caused these breaks. But a very likely guess can be produced. These giant snails have a rather bad habit of taking a short cut to the ground after foraging in the tree tops. In the West African rain forests, the author has observed *Archachatina degneri* dropping from the tree tops with impunity because of the dense undergrowth. However, in the region where the specimens of the former species were collected, the undergrowth quite likely was insufficient to break their fall. Beyond this, rough, coralline rock may have been in the way. This could have produced the sharp breaks evident in the shells. If a predatory vertebrate had produced the breaks, in the process of eating the snails, specimens would not be commonly found that had the snail still intact.

Another factor adds to this. There are definite periods of rain and drought in that region. Snails with badly broken shells would be hard

put to withstand the unfavorable conditions of increased dryness since they would be unable to withdraw completely into their shells and form the protective epiphragm. Such snails would eventually become sufficiently dehydrated to die, or become subject to the attacks of predators or disease agents.

The calcification of the tissues comes very naturally from a diet high in  $\text{CaCO}_3$ . The specimens raised by Yoshio Kondo in Hawaii were fed a diet high in  $\text{CaCO}_3$  (as evidenced by coralline flakes in the contents of the digestive tract) and the tissues of these were in the same condition. This has been observed in other mollusks on similar diets. Because of the unsightly nature of these pale beads of  $\text{CaCO}_3$  all through the tissues, however, one might be persuaded to believe that an actual pathogenic condition was present.

Absolutely no other factor could be found nor was there even the slightest evidence of any pathogenesis. On the contrary, the tissues looked very healthy and normal. It will, of course, take field work to determine for certain whether or not an actual "disease" has gotten started in *Achatina fulica* in these regions. One thing is certain though, the specimens at hand indicate nothing more than breaks in the shells produced by a mechanical force of considerable strength and calcification of the tissues due to the normal process of storing excess  $\text{CaCO}_3$  taken in a  $\text{CaCO}_3$ -rich diet.

The specimens in the lot collected on Saipan on November 11, 1947, were remarkable in that they were all very small, yet several of them were gravid. Somewhat over seventy eggs were found in the one specimen that was dissected. Though the genitalia were histologically mature, they were diminutive in size. This "dwarfism" is undoubtedly attributable to limited feeding imposed by the marked dry periods on that island. There are also strong indications, in the material from the Palau Islands and Saipan, that these periods of dryness effect at least a partial seasonal atrophy of the genital system inasmuch as in some cases the genital structures are markedly reduced in caliber though not immature. In some of these and in some of the functionally mature specimens, the apical portion of the penis forms a very definite loop, of one to three millimeters, apical to the apparently shortened or contracted sheath. It is quite obvious that field work in these regions is needed to determine for certain the significance of these variations.

Actually, it was the study of the genitalia alone that provided the first tangible evidence of the true conspecific nature of these three subspecies. Further, this study has at last permitted us to connect indisputably the "*fulica*" that has spread from Mauritius to India to the Dutch East Indies to China to Japan to the South Pacific

Islands to Hawaii and even to unsuccessful invasions of our own country, with the prototype stock (*fulica hamillei*) of continental East Africa. Such information is obviously of great importance in determining more effective control of this rapidly spreading agricultural pest as it indicates where a study can be made of this snail in its native environment.

With the genitalia of these three subspecies being essentially identical, Bequaert (1950) has distinguished them on the basis of minor differences in the shells.

Measurements of genitalia in millimeters:

	Mauritius		Guam	Hawaii		Saipan		
P.....	13	—	—	12	15	9	16	8 <sup>1</sup>
PS.....	14	15	12.5	14	14	6	15	7
PC.....	5	5	3	6	3	3	2	4
PR.....	15	9	40	20	32	37	33	—
VD.....	51	40	49	48	57	43	46	27
BV.....	4x5	3.5x4.5	4x5	3.5x5	4x5	2x2	3x4	3.5x3
AV.....	10	10	13	10	12	7	8.5	5
SD.....	20	14	31	21	34	32	30	11
S.....	10	10	12	14	13	7	9	5
FO.....	22	12	31	21	37	33	29	8
AG.....	—	—	—	62x14	—	5	15x4	13x7

<sup>1</sup> Gravid.

#### ACHATINA (LISSACHATINA) FULICA HAMILLEI Petit

Figs. 5, 7, 11, 12

Pilsbry, 1904-05, pp. xiii, 45, 216, pl. 65, figs. 65, 66.

Bacci, 1939, p. 335, fig. 1.

As shown below, Pilsbry first described the genitalia of this subspecies (as *A. leucostyla*), from Wasin Id. near Mombasa. Bacci dissected specimens from Italian Somaliland, which he called "*Achatina fulica* (Fér.)." His illustration was mediocre. His description of a peculiar "piccolo diverticolo cieco . . . con due piccole protuberanze sferoidali" probably refers to the talon though his illustration suggests that adjacent larger genital structures may have confused him.

Seven live specimens collected by F. X. Williams were examined. Four of these (Nos. 1, 6, 13, 18) were collected at Diani Beach, near Mombasa, Kenya in May, 1948. The other three (Nos. 7, 11, 19) were taken on Zanzibar in June, 1948.

The penis sheath is slender, but quite muscular, and often subarcuate. Thin muscle bands originating in the basal portion of the

sheath pass onto the thin-walled penial prepuce and may obscure the junction between these two structures. In every case the penial retractor inserted on the right tentacular retractor. The penis, like those of the closely related *Achatina albopicta*, *iredalei*, *zanzibarica* and *loveridgei*, is very slender and completely enclosed by the sheath. A great deal of variation was seen in the length of the penis. In some (Fig. 5) it is so short that it joins the basal vas deferens almost at right angles. In others (Fig. 11) there is formed a definite hairpin loop which very nearly projects beyond the confines of the sheath. There is no evidence that differences in the degree of contraction could make up more than a fraction of this difference. Besides, the shorter penes do not appear to be contracted any more than the longer ones. The basal portion of the penis is swollen and is about as thick-walled as the penial prepuce, between which two structures there is a noticeable constriction. Centrally, the penis is very slender and thin-walled; whereas in its apical portions it is large and clavate. In this latter region, the muscular wall is far thicker than any place along the vas deferens and hence an ejaculatory function can probably be assigned to it (Cf. Fig. 41). As will be seen below, a study of the copulatory anatomy tends to substantiate this assumption. Numerous fine muscle strands pass from the point of origin of the penial retractor, on the penis and adjacent vas deferens, to many points on the inner wall of the sheath. The vas deferens reaches the peniovaginal angle.

The basal vagina is thickly muscular and cormoid as it is in the four achatine species mentioned above. Apically the vagina is slender, thin-walled and proportionately longer than any of those except *albopicta*. There is a definite variability in the length of the spermatheca duct and the equally slender free oviduct which is approximately the caliber of the vas deferens. Similarly, the spermatheca may be clavo-capitate or so slender that it forms only the slightest terminal enlargement. There are shown in Figs. 7 and 12, from Kenya and Zanzibar respectively, these extreme variations, which also have been found occurring at random and without significance in populations of the typical subspecies. The apical genital structures are typical of the genus in form and color. Specimen No. 11 was observed in copulation with a specimen of *A. fulica rodatzki* and details of the observations are discussed below under that topic. Upon dissection, specimen No. 19 was found gravid with 292 lemon-yellow colored eggs which had heavy calcareous shells measuring 4x5 mm. The relationships of the eggs to the genital system are treated below in the discussion of that general topic.

Pilsbry described members of this subspecies as the new subspecies *leucostyla* of *Achatina panthera*; but in the same manuscript, he later

(p. 216) elevated the name to full specific standing, with this statement, "This form proves to be so different in genitalia from *A. panthera* that it will stand as a species." There was thus established for the first and only time in this group, until the present study was undertaken, a new species on the basis of genitalia.

The paratypic series of four specimens of Pilsbry's *leucostyla*, from Wasin Island, Kenya Colony, was loaned to the author by the Academy of Natural Sciences of Philadelphia to permit a comparison with the live material from Zanzibar and Diani Beach, Kenya. As suspected when the first specimen from this latter place was dissected, *leucostyla* and *hamillei* are conspecific. Their genitalia compare favorably in every detail. Since this confirmation was made upon the examination of the first paratypic specimen of *leucostyla*, the other three paratypes were left undissected for possible future anatomical examinations. The single specimen examined had been previously only partly dissected, presumably by H. A. Pilsbry, and the genitalia were still left intact save for the basal parts which had been freed at the genital orifice and lifted out a ways. When the penial retractor was fully exposed, it was found to be bifurcated at the tip with part inserting normally on the right tentacular retractor and the other part passing around the sagittal myoseptum in straddle fashion and inserting on the columellar muscle. As will be seen below in the general discussion of the insertion of the penial retractor, it was such specimens as this that finally solved the mystery of the occasional and overrated diaphragmatic insertion of this muscle.

Measurements of genitalia in millimeters (those marked with an asterisk have been illustrated in this paper):

	#1*	#6*	#7*	#11*	#13	#18	#19	<i>leucostyla</i>
P.....	14	11	12	—	10	12.5	11	14
PS.....	14	13	12	—	12	15	11	17
PC.....	5	5	6.5	—	4.5	5	3.5	3.5
PR.....	24	19	19	18	24	20	14.5	50
VD.....	67	56	48	56	51	57	55	58
BV.....	3.5	3.5x5.5	4x5	4x6	3x4.5	3x5	3x7.5	4x5
AV.....	9.5	8	11	11	8.5	7	14	16
SD.....	40	28	18	28	28	33	—	40
S.....	12	9	12x5	15x4	8	11	—	10
FO.....	35x1.5	26	18	28	27	27	20	35
AG.....	25	18	29	33x10	21x7	35x12	24x10	48x17

ACHATINA (LISSACHATINA) FULICA RODATZI Dunker

Pilsbry, 1904-05, p. xiii, pl. 64, fig. 68.

The genitalia of this subspecies were illustrated by Pilsbry under the new name *Achatina chrysoleuca*. The completely enclosed penis was not shown, though he states that it is "similar to that of *leucostyla* but longer." It should be recalled that *leucostyla* has been shown above to be synonymous with *A. fulica hamillei* and that there is a natural marked variation in the length of the penis in both that subspecies and typical *fulica*. This would then suggest that there was little or no real difference between *hamillei* and *rodatzii*. Examination of other subspecies complexes has taught us so far that tangible subspecific differences in the soft anatomy do not exist. It was therefore assumed that the genitalia of *rodatzii* (= *chrysoleuca*) would be like those of the other two subspecies. An examination of the two live mature specimens of *rodatzii*, collected by F. X. Williams on Zanzibar in June, 1948, clearly indicated that this assumption was a correct one. Further, the "type" specimen of *chrysoleuca* (Acad. Nat. Sci. Phila. 68113, collected by Dr. A. Donaldson Smith in Tulu Didirko, E. Africa on March 27, 1895) was examined by the author and was found to be mature and essentially identical to the Zanzibar specimens. Once again, subspecific characters seem to rest exclusively in the shell characters. In this pale subspecies, the body is a yellow-tan color and the head is slightly brownish.

The second of these two specimens copulated with a specimen of *A. fulica hamillei* and the details of this process and their anatomical significance are discussed below under a separate heading.

Measurements of genitalia in millimeters (in each case, the number in parentheses refers to the type specimen of *chrysoleuca*): P — —, 11, (7); PS — 14, 14, (14); PC — 4, 4, (—); PR — 14, 15, (26); VD — 59, 57, (35); BV — 4x6, 3x5, (3x4); AV — 11.5, 9.5, (8); SD — 27, 20, (18); S — 9, 15, (12x5); FO — 27, 21, (16); AG — 38x15, 39x15, (26x10).

ACHATINA (EUAETHIOPINA) LOVERIDGEI (Clench and Archer)

Figs. 6, 9

Two paratypic specimens collected in Bagilo, Uluguru Mts., Tanganyika Territory, were examined. These had been previously dissected by Clench and Archer (1930).

In only a few respects do the genitalia differ from those of *A. iredalei* and even less so from *A. zanzibarica*. The penis and the basal half of



the penial retractor are completely embraced by the sheath which is proportionately somewhat shorter than in *zanzibarica*. With respect to its sheath, however, it is proportionately larger in its apical third and smaller in its basal two-thirds. Apically, the penis joins the basal vas deferens at right angles. The very wide penial retractor originates broadly on the apical portion of the penis, the entire ensheathed portion of the basal vas deferens and adjacent portions of the inner sheath wall. No evidence of the manner of insertion remained in either specimen though Clench and Archer maintained that the retractor "inserted on the diaphragm." The vas deferens is somewhat shorter than in *zanzibarica* and leaves the sheath in its apical one-third.

The cormoid basal vagina is as long as, or almost as long as, the abbreviated, thin-walled, apical vagina. In this respect, it compares more favorably with *iredalei*. Basally, the free oviduct and the spermathecal duct are nearly the same caliber, though the latter is as slender as the vas deferens throughout most of its length. The former is approximately one-third the length and twice the diameter of the vas deferens. The spermatheca is capitate. No significant difference was found in the apical genital structures.

Clench and Archer (1930, p. 297) give the following characters to distinguish from *Limicolaria* the new genus *Euaethiops* (= subgenus *Euaethiopina* of *Achatina*) in which they had placed *loveridgei*: ". . . a larger, thicker albuminiparous gland; a shorter hermaphroditic duct, smoother above but heavily granulose at its entrance into the spermo-viduct instead of consisting of a long series of granulations as in *Limicolaria*; a large uterus; a wider, fatter and shorter spermatheca; a longer, more twisted vas deferens; a larger penis; and a much shorter, thicker penial retractor." None of these characters is of generic grade. As a matter of fact, the first two can never be safely used even in distinguishing species. An examination of their dissections revealed the fact that only the outer layers of the thick penis sheath had been removed and the slender, tubular penis was therefore not seen by them at all. Hence the penis was reported and illustrated as being much larger than it actually is. As will be seen in a discussion of *Limicolariopsis kivuensis* (*vide infra*), this misinterpretation caused them to miscalculate in constructing the affinities of *Euaethiops*. Further, they incorrectly describe the ovotestis as "short, granulose and bound tightly to the albuminiparous gland." This gland is very disperse and located in the antipenultimate whorl of the liver as in other achatinas. It is the apical uterine folds that they apparently described. They made other observations which are at variance with the author's findings; but as they are less significant, space will not be taken here to comment upon them. Actually, there is little doubt that the general

form of the genitalia places *loveridgei* in the genus *Achatina* and close to the *zanzibarica-iredalei-fulica-albopicta* complex.

Measurements of genitalia in millimeters (the first figures, in each case, refers to the specimen illustrated): P — 11, (—); PS — 10x3, (12); PR — 4, (5.5); VD — 31, (34); BV — 2.5x4, (3x4); AV — 4x2, (3); FO — 11, (12); SD — 15, (11); S — 8, (10); AG — 23x9, (22x5).

ARCHACHATINA (ARCHACHATINA) BICARINATA (Bruguière)

Fig. 25

Deshayes, 1851, 2, pp. 154–155, pls. 127A (colored), 127B (colored), 127A127B (one uncolored plate).

Pilsbry, 1904–05, p. xiv, pl. 63, fig. 29.

This remarkable, large, sinistral snail was first anatomically examined by Deshayes (1851). He referred to it, however, as *Achatina sinistrorsa* Chemnitz. Though he did not discuss the genitalia, his exquisite illustrations of the animal, in successive stages of dissection, and the extensive labeling (explained in the Atlas, 1, p. 18) leave little to the imagination. It is understood, of course, that at that early date, some of the genital structures were not correctly interpreted. For example, he refers to the prostate gland as a “portion du testicule”, the ovotestis duct as “l’ovaire”, the talon as “une poche ovarienne contenant les rudiments d’un œuf” and the vagina as “le col de la matrice.” Pilsbry reproduced the illustration showing the genitalia of this species and pointed out that the manner of insertion of the penial retractor is “unknown.”

Very fortunately, three alcoholic specimens of this genotype were obtained on loan from the American Museum of Natural History to permit a rechecking of the genital anatomy. These carried the following data: “J. G. Comia, San Thomé Is. A.6280.” It was only with the greatest difficulty that two were removed from their shells, and then only after prolonged soaking in 0.8% solution of trisodium phosphate. As two specimens were adequate for the present study, it was thought advisable to leave the third one for possible future investigations.

It must not be forgotten that not only the shell is sinistral, but the entire animal is just the reverse of one that is dextral. The genitalia are therefore shown in Fig. 25 quite differently arranged, though with the same orientation as the other illustrated genitalia.

The species has, without question, the most muscular and proportionately the largest of the achatinid genitalia examined. The relatively huge penis is a hollow, muscular structure that projects apically

beyond the sheath one and one-half times the length of the latter. In both specimens, the apex of the penis is bent back on itself. A possible explanation for this is found in the fact that the penis apex tightly abuts against a vertical sheet of tissue (the sagittal myoseptum) a small portion of which is shown at the insertion of the very short penial retractor on the *left* tentacular retractor. The significance of this sheet of tissue is discussed below under the heading, "Insertion of the Penial Retractor." When the sheath was longitudinally cut, it was found to increase in thickness basally. Conversely, the penis was found to be reduced to approximately one-quarter of its apical width; thus the entire structure appeared markedly clavate. At the very base in both specimens, the sheath becomes somewhat sacculate, but this may be only an artifact of preservation. The vas deferens is of small caliber. It leaves the sheath approximately midway and passes to the peniovaginal angle. Internally, the penis is lined with a most remarkable papillo-rugate reticulation that is reminiscent of the lining of a rumen. It must, indeed, make a formidable organ when everted as the papillate rugae are so arranged that they would still remain distinct on the extroverted and distended organ. These papillate rugae are less abundant basally though they do continue right into the almost non-existent genital atrium.

The vagina is shorter than the penis sheath and is without any noticeable differentiation. Apically, it is continuous with the free oviduct, of approximately the same caliber. At the junction of these two structures is the very narrow spermathecal duct which terminates in a capitate spermatheca.

With a penis of this caliber, a short vagina, and a very slender spermathecal duct, it is difficult indeed to understand how the genitalia function during copulation.

Measurements of genitalia in millimeters (the first figure, in each case, refers to the specimen illustrated): P (apical to PS) — 60x8-10, (47x9-12); PS — 41, (31); PR — 18x8, (21x8); BD — 58, (78); V — 31, (32); SD — 31, (27); S — 19x9, (32x2); FO — 21x8, (28x10); AG — 38x14, (—).

#### ARCHACHATINA (CALACHATINA) DEGNERI Bequaert and Clench

Fig. 4

Unlike that of the preceding species, the penis sheath extends only about a third of the way up the penis and the slender vas deferens leaves it somewhat below the half-way mark. From there it passes to the peniovaginal angle. There is a strong tendency for the basal

vas deferens to be shorter than the penis and as a consequence, the penis is drawn partly or often almost completely back upon itself. The penial retractor is long and inserts, in all cases observed, on the right tentacular retractor.

The vagina is shorter than in the anatomically similar *A. achatina* and enlarges gradually in its apical portions. Internally, there is a strong circumferential thickening of the muscle layers in the female conduit at the junction of the free oviduct and the vagina which is apparent externally as a shallow crease. It is conceivable that this acts during copulation as a sphincter to insure the entry of the penis into the spermatheca rather than the free oviduct. In contrast to that of *A. achatina*, the spermathecal duct is very long and slender and only a quarter to a third the size of the very robust free oviduct. The capitate spermatheca is sharply set off from its duct. Further apically, the structures are typical of the genus and bear no specific difference.

As will be shown in the conclusions, the similarity between *A. achatina* and the dolichophallate species of *Archachatina*, because of convergent evolution, is more apparent than real.

Twelve specimens, all collected by the author in Accra, Gold Coast, or its immediate vicinity, were examined between June and November, 1944. Immature specimens indicated the presence of protandry. One of the half-grown specimens was kept in a container without food or water and in a few days responded by forming a very thick, calcareous epiphragm that was complete except for a thin slit over the pneumostome. It remained quiescent for nearly six months and actually did not break the epiphragm and crawl about until water was sprinkled over the specimen.

Average adult measurements in millimeters: P — 51, PS — 18, V — 25, FO — 14, SD — 16, S — 10.

#### ARCHACHATINA (CALACHATINA) MARGINATA OVUM (Pfeiffer)

##### Fig. 3

Semper, 1873, p. 144.

Semper examined but did not illustrate the genitalia of "*Achatina marginata*" and found them typical and similar to those of *Archachatina granulata*.

In this species, the penial sheath is twice as long as in *Arch. degneri* and therefore the penis-sheath linear ratio nearly exactly attained the proportions (2 : 1) of the same structures in *A. achatina* (Fig. 1). As in *Arch. degneri*, though, the real differences are found in the female conduit. The vagina is large, tubular and unmodified save for a

whitish, more muscular basal portion that often is set off from the more glandular apical portion by a slight constriction. The spermathecal duct is very slender and in strong contrast to the capitulate spermatheca. The free oviduct is equally long and approximately three times as large around as the spermathecal duct.

In every case, the long penial retractor inserted on the right tentacular retractor. As in the two previous species, and in *A. achatina*, the sheath is situated so far basally that a penial prepuce is not apparent.

Eight specimens collected for the author in the market place at Lagos, Nigeria, (5 in March and 3 in June, 1945) were examined. All possessed the diagnostic rich apricot-yellow columella.

Average measurements in millimeters: P — 63, PS — 32, AV — 20, BV — 5, FO — 13, SD — 17, S — 9.

#### ARCHACHATINA (CALACHATINA) MARGINATA SUTURALIS (Philippi)

The genitalia of this subspecies are so nearly identical to those in *Arch. marginata ovum* that they could not be distinguished. The three functionally hermaphroditic specimens that were examined, were collected in Lagos, Nigeria, in June, 1945, along with the specimens of *ovum*. It is not probable that a larger series will disclose consistent differences in the genitalia. The columellae of all three specimens were vinaceous-red in color.

#### ARCHACHATINA (THOLACHATINA) SIMPLEX CRAWFORDI (Morelet)

Figs. 27, 28, 29

Pilsbry, 1904-05, p. xiii, pl. 64, figs. 69-71.

Two fully mature specimens, bearing the data: "Port Elizabeth, So. Africa, John Ponsonby 1889. Acad. Nat. Sci. Phila. 60967", were examined. One of these had been dissected and illustrated by Pilsbry as "*Cochlitoma crawfordi*." In this specimen, Pilsbry found the penial retractor attached to the floor of the diaphragm; this was confirmed by re-examination. The second specimen was still in its (broken) shell. This was removed and dissected. The short penial retractor was found to attach, as in most other achatinines, to the right tentacular retractor! Had Pilsbry dissected this along with the other specimen, he would have found that he could not safely give taxonomic significance to diaphragmatic insertions of the penial retractor. Actually, the penial retractor inserts at the junction of the right tentacular retractor and a vertical sheet of tissue, the sagittal myoseptum (discussed below). A portion of this latter is shown attached (SM) in Fig. 27.

When the thin-walled penial sheath was cut, a truly unique clavo-capitate penis was exposed. It was found to be broadly convex on one side and deeply concave on the opposite side, thus appearing thickly "U"-shaped in cross section (Fig. 29). The basal vas deferens attaches to the dorsal fold of this "U". It is this concave or infolded portion that Pilsbry considered a continuation of the vas deferens into an internal "fleshy pilaster." An examination of this latter, however, shows it to be of the same thickness and histological construction as the convex portion. It would undoubtedly form an asymmetrical swelling on the distended intromittent organ but it would not act as a pilaster *per se* as such would presumably be a stimulatory, solid ridge. The basal portion of the penis is thicker walled. The vas deferens reaches the peniovaginal angle and is embraced in that region by the penial sheath. In this specimen, the vagina is short and appears to be excessively wide because of pressure from adjacent structures. Both the free oviduct and the capitate spermatheca and its duct are longer than the penis.

The specimen that Pilsbry examined is almost identical in every respect with the exception of the vagina which is longer and more slender and in these respects is probably more typical. In Pilsbry's illustration, the spermathecal duct seems disproportionately long.

Measurements of genitalia in millimeters (the first figure, in each case, refers to the specimen illustrated): P — 6.5x2.75, (5); PS — 7x3, (—); PR — 2.25, (2); VD — 19, (20); V — 4.5x4, (5.5x2); SD — 11, (12); S — 5x2.5, (4x1.5); FO — 9, (12); AG — 8, (9).

#### ARCHACHATINA (THOLACHATINA) MEADI Bequaert

##### Fig. 22

A single completely dehydrated specimen (MCZ 81351), collected in Ngosi Volcano, Rungwe, Tanganyika Territory by A. Loveridge on April 17, 1930, was soaked forty-eight hours in an 0.8% solution of trisodium phosphate. At the end of this time, the tissues were very pliable and, with the exception of the large, thin-walled spermatheca and its duct, the genitalia were removed without damage.

This specimen had been labeled "*Euacthiops loveridgei*." An examination of the genitalia, however, immediately indicated that a quite different animal was at hand. A comparison of the shell under this accession number with the types of *loveridgei* proved confirmatory. The penis is large, muscular and in every respect typical of the genus *Archachatina*. No internal papilla or verge is formed, though the apical third of the penis projects well out of the fairly thin, basally

located sheath. A very abbreviated penial prepuce is scarcely discernible. The basal vas deferens joins the apical penis to form a conspicuous loop apical to the sheath. The vas deferens is approximately one-half the diameter of the penis, leaves the sheath in its apical third, does not appear to reach the peniovaginal angle and describes a quite direct route to the spermoviduct. The very narrow, long retractor takes a broad origin on the penial loop and passes by a devious route, described in greater detail below in the discussion of this general topic, to an insertion centrally on the diaphragm.

The vagina is thin-walled, quite evenly tubular throughout its length and without any basal muscular swelling. Only the frayed basal part of the spermathecal duct was recovered; its proportions are therefore unknown. The cylindrical free oviduct is slightly smaller and shorter than the vagina. Nothing of significance was found in the apical genital structures.

Measurements of genitalia in millimeters: P (apical to PS) — 2.5, PS — 5x3, PR — 23, VD — 15, V — 9x2, FO — 8, SD — ?, S — ?, AG — 8x5.

ARCHACHATINA (THOLACHATINA) OSBORNI AFROMONTANA  
(Bequaert and Clench)

Figs. 23, 24

There were examined in the anatomical study of this species, five preserved specimens collected for the Institute of the Belgian Congo National Parks, bearing the data "Kamatembe (North of L. Kivu, Belgian Congo) 1059, G. F. de Witte."

In direct contrast to *bicarinata*, the genitalia of this species are proportionately so small that they probably represent the ultimate or near-ultimate in reduction in this genus, and perhaps even in the Achatininae. The penis, though diminutive, is not the delicate structure that is found in the *fulica* complex. It is fairly thick-walled, quite wide, without verge formation and entirely enclosed within the sheath. A definitely shaggy appearance is given to this latter because its surface is covered with many thin, narrow muscle bands which originate more or less centrally, become more abundant basally, and insert on or adjacent to the atrial wall. In two of the five specimens, the short penial retractor inserts medially on the diaphragm near its junction with the anterior lip of the mantle and the body wall. In the other three, it inserts on the body wall, in the neck region, anterior to this junction. The combination of a short penis and a short retractor has quite probably predisposed the retractor to this unusual insertion.

From the broad origin of the retractor on the penis and adjacent basal vas deferens, numerous muscle bands, similar to those on the outer surface of the sheath, interlace and pass to the inner wall of the sheath. These are made more apparent by similarly inserting muscle bands that have their origin in the outer muscle layer of the penis. This multiplicity of muscle bands produces a general untidy effect. Apical to the sheath, the basal vas deferens doubles in size with increased musculature. Further apically, it is somewhat reduced in size but becomes typically enlarged at its junction with the spermoviduct. This latter enlargement was cut open. Its walls did not seem excessively glandular and internally there were numerous, longitudinal trabeculate ridges.

The completely unmodified vagina is even shorter than the penis and almost as wide. The very large, sacculate spermatheca is disposed so far basally that early in the dissecting it might easily be mistaken for the penis. The free oviduct is proportionately long.

Only one specimen was immature. In this, the penis projected for half of its length beyond the short sheath thus creating a condition that superficially seemed in strong contrast to that in mature specimens. The rest of the structures, though reduced in size, were fairly typical — including the enlarged spermatheca.

Measurements of genitalia in millimeters (the first listed is illustrated in Fig. 23, the third is illustrated in Fig. 24):

P.....	7.5	—	—	—
PS.....	9.5	7	7x4.5	8
PR.....	15	—	8	12
VD.....	41	32	32	34
V.....	6.5	4	5x3	6.5
SD.....	4	4	4	4
S.....	22x8	21x8	15x6	12x7
FO.....	21	25	21x2.5	24
AG.....	19x4	22x4	11x4	20x5

#### LIMICOLARIA KAMBEUL (Bruguière)

Figs. 26, 30

Lehmann, 1864, p. 48, pl. 1, fig. 3.

In this species the penis sheath is apically so situated that it actually embraces the basal portion of the relatively short penial retractor, which latter inserts upon the right tentacular retractor. Since the sheath muscular elements pass imperceptibly onto the basal vas



deferens, there is no detectable division between the two structures. Basally, the sheath is delimited approximately half-way down the penis, though very thin muscle strands are seen to pass further down and blend with the otherwise naked muscle wall of the basal penis. Though the vas deferens, which does not reach the peniovaginal angle, is apically a fairly large duct, it is found basally to be about half that diameter. The vagina is only slightly larger at its apex than at its base and appears to be more or less evenly muscular throughout. The free oviduct, which attains a greater length than the penis, has only half the diameter of the very short spermathecal duct. The spermatheca is a broadly spatulate structure which attenuates apically and then enlarges somewhat to form a terminal bulbous portion. The genital atrium is pronounced. The basal and apical portions of the uterus are distinct. The prostatic acini are proportionately large and fewer than in any of the preceding species.

The thin-walled sheath was cut to expose the internally contained penis. The musculature of the penial retractor, the penis proper and the penial sheath is so extensive that it appears to be but a single tissue entity. A dissection of the penis itself, however, revealed relationships quite unlike anything found heretofore (Fig. 26). In approximately the middle of the penial organ is a pronounced circumferential thickening of the inner wall so that the lumen in this region is reduced to a very narrow passage. As this conical thickening projects into the basal half of the penial tube, it assumes the form, and undoubtedly the function, of a verge (penis papilla). Apical to the verge, the penial wall is quite thick and muscular, but at its apex it makes a turn and quickly reduces to the caliber of the histologically similar basal vas deferens. The epithelium facing the lumen of the penis in this region is strongly vermiculate. The outer spongy muscle layer of the penis seems continuous with the fibers of the penial retractor. Basal to the verge, the penial wall is thinner and internally thrown up into bifurcating and anastomosing longitudinal rugae. Basal to the level where the sheath leaves the penis, the penial wall is still thinner and externally ragged appearing because of the many irregular muscle bands passing to the genital atrium wall. Some anatomists might be tempted to refer to the apical portion of the penis as the epiphallus; but the use of that term here is not necessary. And further, as is often the case with this basically vague term, it would give no indication of function and would actually obscure homologies. The subject of penial homology is discussed in detail below.

Lehmann described and illustrated the genitalia of *Bulimus (Limnicolaria) adansoni* Pfr. which since has been placed as a synonym of *L. kambeul*. His illustration, unfortunately, is not sufficiently detailed to

enable the author to make a positive statement in support of this reduction to synonymy, though there is nothing to indicate that it could not be *kambeul* that Lehmann had. He describes a unique "darmförmiges Organ" near the penis; this without much doubt is not part of the genital system but a slip of adjacent tissue — perhaps the body-wall. The ovotestis is shown, probably incorrectly, as a single mass of acini rather than the typical 4-5 smaller masses.

Four specimens from the Gold Coast were examined; one collected at Achimota in June, two at Labadi in July, and one at Nsawam in August, 1944. All specimens were collected by the author.

Measurements in millimeters of genitalia of three typical specimens: P — 12; 17, 16; PS — 7, 10, 9; PR — 7, 3, 10.5; VD — 23, 24, 21; V — 6, 9, 8; SD — 2, 3, 5; S — 17, 20, 19; FO — 16, 17, 18.

### LIMICOLARIA FLAMMEA (Müller)

Figs. 31, 32

The penis in this species peculiarly attains a gamma-shape and, like that of *L. kambeul*, its sheath is apically placed and tightly fitted, extending only slightly beyond the tip to embrace the very base of the short penial retractor which similarly inserts upon the right tentacular retractor. Sheath muscle elements pass onto the basal vas deferens forming a distinct enlargement which might be mistaken for a small epiphallus. Internally, the vas deferens in this region is much thicker walled than it is apically and it therefore might be presumed that this portion has an ejaculatory function. Basally the sheath enlarges slightly to pass over the swollen angle of the penis and then immediately terminates after making a second constriction. This gives an external appearance of the penis ending at the angle and the sheath extending in prepuce fashion considerably beyond it and at right angles to it. Wide, thin muscle bands originating in the sheath muscle, extend from a point near the very base of the sheath to the basal portion of the penis. Apically, the vas deferens is noticeably enlarged. The long slender free oviduct attains a diameter scarcely larger than the middle portion of the vas deferens. The spermatheca is a very large sacculate structure having both a terminal and a basal bulbous portion. In some specimens, the central constriction was more pronounced so that two globose portions were formed. The spermatheca duct is about the same diameter and half the length of the completely unmodified vagina. There is a deep genital atrium which appears to be directly continuous with the penis. As far as could be determined, there were no specific differences in the apical genital structures.

When the thin-walled penis sheath and the penis were cut open to determine the nature of the internal structures, a basically similar condition to that of *L. kambeul* was found. The verge, however, was more pronounced and situated at the angle of the penis, hence being responsible for the previously observed swelling in that region. Because of this more apical location of the verge, the rugate penial wall below the verge makes up the greater portion of the penial tube. Conversely, the portion of the penis above the verge, though vermiculate internally and otherwise similar to that of *kambeul*, is considerably reduced. There is little question that *flammea* and *kambeul* are quite closely related.

Four from a lot of ten specimens were examined; all were collected by the author in Weija, Gold Coast, in December, 1944. The uterus of one specimen contained forty canary-yellow, obovate (3x4 mm.) eggs. Their extremely thick, porcelain nature seems to preclude the possibility of ovoviviparity, which Robson (1912) suspected in an unnamed species of *Limicolaria* and *L. smithi*.

Measurements of genitalia in millimeters: P — 13, 12, 12, 12; Verge — 2, -, -, 1.5; PS — 7, 7, 7, 7; PR — 6, -, 7, -; VD — 15, 15, 17, -; V — 9, 9, 6, 10, SD — 4, 3, 3, 3; S — 15, 14, 20, 12; FO — 10, 10, 12, 11.

#### LIMICOLARIA FÉLINA Shuttleworth

Figs 33, 34

Semper, 1873, pp. 142-143, taf. xii, fig. 1.

The penis sheath in this species is more basally placed so that the apex of the penis, the origin of the longer penial retractor and the base of the vas deferens are not obscured. Basally, the sheath is longer on one side than the other and its margin seems ragged with irregular muscle bands trailing down to thin points of attachment on the wall of the prominent genital atrium. The basal vas deferens is embraced by the uppermost portion of the sheath. The apical vas deferens is typical in that it is enlarged. In every case, the penial retractor inserts upon the right tentacular retractor. The unmodified vagina, which is conspicuously longer than the penis, narrows slightly towards its base. The free oviduct is long and of noticeably greater diameter than the vas deferens. Like the preceding species in this genus, the spermatheca consists of terminal and basal sacculate portions joined by a more narrow median portion. The basal portion, however, joins the vagina so broadly that a spermatheca duct, as such, is not apparent. No character of the apical genital structures appears to be peculiar to this species.

The thin-walled penis sheath and penis were dissected with the expectation that a condition similar to that of *L. kambeul* and *flammea* would be found. In the basal portions and in the formation of a verge, this actually proved to be the case; but apically, quite a different situation was found. Apparently the muscle layer of the apical portion of the penis has become so hypertrophied that the penial lumen has been seriously encroached upon — so much so, in fact, that it is not appreciably larger than that of the vas deferens. The apical penis thus consists largely of a thick, spongy mass of muscle strands which blend imperceptibly with those of the penial retractor. And this matting of muscle tissue, containing both longitudinal and circular muscle fibers, has altered somewhat the nature of the nearly centrally located verge. Instead of its being a more or less solid structure consisting of an outgrowth of the inner epithelium and the adjacent compact muscle layers, it is made up of this same epithelium and packed with a very loose, spongy muscle layer. In two of the three specimens examined, this verge is asymmetrical in that it is noticeably smaller and shorter on one side. This may be an artifact of preservation though it should be remembered that the sheath was similarly asymmetrical. Basally the penial tube is like that of the previously dissected limicolarias with the exception of the facts that internally it is thrown into numerous longitudinal, vermiculate ridges and externally it is nearly completely embraced by the sheath.

Without having first seen the penes of *kambeul* and *flammea*, these relationships would probably not have been correctly interpreted; for it appears as if the wall of the basal vas deferens, along with an apparently enlarged penial retractor, had greatly hypertrophied. The vas deferens thus seems to pass directly down into the verge and this latter seems to mark the apical termination of the penis proper. With the exception of the presence of an outer sheath, then, the penial components would seem to assume the relationships found in the land slugs *Hesperarion niger* and *Ariolimax columbianus* of western North America (Mead, 1943).

Semper illustrated and described very briefly the genitalia of *Achatina* (*Limicolaria*) *turbinata* "Reeve."<sup>1</sup> An examination of Semper's illustration does not make it possible to determine whether there exist tangible anatomical differences between the genitalia he describes and those described here for *felina*. Semper seems to have been "loop" conscious, probably through the fact that he was overly impressed by the conspicuously looped condition of the apical penis and basal vas

<sup>1</sup> Reeve's *Bulimus turbinatus* is a *Limicolaria* but Lea's *Achatina turbinata* is a *Pseudotrochus*. Pilsbry (1904-05) referred Reeve's figure to his *L. felina* var. *zebra*. There seems to be no way of determining whether Semper dissected typical *felina* or the variety *zebra*.

deferens of *A. panthera* (which he mistakenly refers to as *A. fulica*). He thus shows "*turbinata*" as well as other species with a more pronounced loop than probably actually exists. The rest of the genital system, except the unilobulate ovotestis, seems thoroughly within the bounds of *felina*. Though he does not mention it, his illustration indicates that the penial retractor makes its insertion on the tentacular retractor.

Three Gold Coast specimens were examined; two were collected by the author at Kumasi in November 1944 and one at Aburi (20 miles east of Accra) in October, 1944.

Measurements of genitalia in millimeters: P—6.5, 6, 6; Verge—1.5, 1.3, 1.7; PS—5, 5, 4; PR—8, 9, 9; VD—15, 12, 10.5; V—7, 8.5, 7; SD+S—11, 11, 9; FO—6, 6, 7.

### LIMICOLARIA SATURATA CAPITELLUM Pilsbry

Figs. 35, 36

A paratyptic series (46479) of five specimens (two very immature) from the Academy of Natural Sciences of Philadelphia was examined. These were collected in November, 1919, at Medje, Belgian Congo.

The sheath extends further down than in any of the previously examined species of this genus. Actually, its basal limits are nearly completely obscured by many thin muscle bands originating in the sheath and passing to points of insertion on the penial prepuce and the wall of the genital atrium. In two of the specimens, the long penial retractor inserted upon the right tentacular retractor; in the third specimen, it inserted on a vertical sheet of tissue, the sagittal myoseptum (discussed below). The immature specimens were not examined. The vas deferens leaves the sheath close to its apex and, without approaching the peniovaginal angle, it passes to an apical swollen portion that joins the free oviduct.

The tubular, unmodified vagina is approximately twice as long as the penis sheath and seems to bifurcate to form the free oviduct and the shorter spermathecal duct. This latter gives rise to the spermatheca which consists of a basal bulbo-sacculate portion narrowly joined to an apical clavo-sacculate portion.

The fairly thick-walled sheath was cut to expose a penis whose proportions are very similar to those of *L. felina*. However, the spongy mass of muscle strands, that makes up the penis apical to the centrally located verge, and the tubular portion basal to the verge are proportionately longer than in *felina*. But aside from this, the very different sheaths make it easy to distinguish these two closely related species.

An abbreviated penial retractor and a much larger verge in the very closely related *L. ussuwiensis* set that species off as still different.

Inasmuch as the second specimen dissected was abnormally attenuated, apparently during preservation, the measurements in millimeters, of only two specimens are given here. The first figure in each case refers to the specimen illustrated. P — 6, 5; PS — 6x3, 5.5x2; PC — 2x1, 2; Verge — 1.5, 1; PR — 16, 10; VD — 18, 21; V — 12, 11; SD — 3, 3; S — 15x1-4, 14; FO — 6.5, 8; AG — 14, —.

#### LIMICOLARIA USSUWIENSIS Kobelt

Figs. 37, 40

There were examined six specimens collected for the Institute of the Belgian Congo National Parcs, labeled "Burunga (Mokoto), Belgian Congo. Mission de Witte No. 288." In all six specimens, the very short penial retractor inserted upon the diaphragm; and in all but two of these, the insertion was quite near the anterior rim of the mantle. Though the penial sheath is, in general, more slender, it still is very similar to that of *L. saturata capitellum* in that it covers all but the very basal portion of the penial tube. The vas deferens is swollen apically and is typical of the genus as it does not reach the peniovaginal angle. Basally, the vagina tends to be enlarged to such an extent that the genital atrium is obscured and the penial prepuce is encroached upon. In this respect, it is in contrast with *L. flammea* (Fig. 32). The free oviduct is approximately the size of the vas deferens. There occurs between the two sacculate portions of the spermatheca, not a simple constriction but a very definite isthmus which is approximately the length of the spermathecal duct. The form of the spermatheca as depicted in Fig. 40 is consistent throughout the series and is probably typical for the species.

Cutting the sheath, which is slightly thicker in its apical portions, revealed a penis of the type found in *Limicolaria felina*, *saturata capitellum* and *Limicolariopsis kivuensis*. The reduced muscular network of the apical penis, however, emphasizes the fact that the verge in this species is larger than in any of the others. Longitudinal vermiculations mark the lining of the penis basal to the verge.

Diagnostic characters of this species, then, rest in the penial retractor, verge, vagina and spermatheca.

Measurements of genitalia in millimeters (the illustrated specimen is the first one listed):

P.....	5	—	—	—	5	—
PS.....	8	6	8	7	6.5	7
PR.....	3	2	4	2	2.5	2.5
PC.....	2	—	—	—	—	2
Verge.....	3	—	—	—	3	—
VD.....	16	19	19	14	13	13
V.....	11	12	9	15	10	11
SD+S.....	14	10	15	12	16	15
FO.....	8.5	8	8	8	6	7
AG.....	20	7	9	15	10	16

## LIMICOLARIOPSIS KIVUENSIS (Preston)

Figs. 38, 39

A single specimen of this species, (MCZ 77059) collected on the "trail from Burunga, Belgian Congo", had been dissected and reported upon by Clench and Archer (1930). The carefully removed genitalia, however, were not figured by them but are shown here.

The penial tube is entirely enclosed within the thin-walled sheath with the exception of a very short basal piece, the prepuce, close to the shallow genital atrium. The sheath was rather acutely bent in its basal one-third, as shown in the figure. This bending has been observed in preserved specimens of other species and though it is not felt here that this is a naturally occurring feature, it is not forgotten that *Limicolaria flammea* (Fig. 32) has a consistently angulate, diagnostic apical penis and sheath. Freshly killed material is actually needed to determine for certain the nature of this character. Immediately after the penial retractor leaves the confines of the sheath, it becomes very narrow and long. It clearly inserts upon the diaphragm. Muscle elements from the sheath pass out on the basal vas deferens obscuring its point of departure from the sheath. The vas deferens does not even approach the peniovaginal angle but enlarges slightly before joining the free oviduct. Like those of *Limicolaria*, the prostatic acini are noticeably larger than those of *Achatina* and *Archachatina*. The vagina also is similar to those of the examined species of *Limicolaria* in that it is very long (one and one-half times the length of the penis sheath) and tubular. Its apparent angulate nature is probably an artifact of preservation. The similarity to *Limicolaria* is carried still further, for the spermathecal duct has two distinct sacculations. The free oviduct is not as long as the sheath and is only slightly larger in diameter than the vas deferens.

Upon cutting the thin-walled sheath, which was very thin in its basal portions, it was seen that the relationships of the penial com-

ponents were like those of *Limicolaria felina*, *saturata capitellum* and *ussuwiensis*. The nearly centrally located verge is not as large as in this last species but it is definitely larger than in either of the other two. The basal penial retractor and the loose matting of muscle fibers of the apical penis are so intimately intermingled that the retractor seems to be basally very massive and to have a very broad origin on and in the verge. The lining of the basal portion of the penial tube seems to be thrown up into dense, depressed papules.

Clench and Archer (1930) point out the great similarity of this species to *Achatina* (= *Euaethiops*) *loveridgei* on the basis of the penes; but as indicated in the discussion of this latter species, the penis of *loveridgei* was not properly interpreted. In view of this re-examination, their relationship is without question quite distant, a great similarity in the flared lip of their shells notwithstanding. On the other hand, their conclusion that *Limicolaria* and *Limicolaria* are closely related is a thoroughly sound one. And as a matter of fact, this anatomical study of *Limicolaria kivuensis* shows that this species apparently is more closely related to the three species of *Limicolaria* mentioned above than any one of these latter is to either *Limicolaria kameul* or *flammea*.

Measurements of the genitalia in millimeters: P — 10x3; PS — 14.5; Verge — 4; PR — 28; PC — 2; VD — 25; V — 20; FO — 9.5; SD + S — 22; AG — 12.

#### PSEUDOTROCHUS TURBINATUS MUCIDUS (Gould)

Figs. 42, 43, 44, 46

Three rather badly dehydrated specimens preserved in alcohol were soaked twenty-four hours in an 0.8% solution of trisodium phosphate before they were examined. These were collected by Joseph C. Bequaert near Doblí Island, Liberia, on April 12, 1944.

A very noticeable reduction in the vascularization of the roof of the pulmonary chamber was found. As Clench and Archer (1930) report, a similar condition is found in *Achatina loveridgei*, though not to this great extent.

Of the three specimens, two had been removed from their shells and one was left intact. The larger of the first two was dissected (Fig. 43) and it was found to be gravid with embryos. The penis (Fig. 42) is clavate, hollow, and with the exception of the very abbreviated prepuce, the penial tube is completely embraced by the thin-walled sheath. The short penial retractor is broad at the point of origin and attaches to the right tentacular retractor. A subterminal junction



occurs between the penis and the very slender basal vas deferens. The latter apically folds back upon itself, leaves the sheath in its basal two-fifths, and passes to the peniovaginal angle. At its junction with the spermoviduct, there is an asterisk-like, lobulated gland whose possible function is discussed below.

In the middle of the tubular, essentially unmodified vagina, is a transverse constriction that may well be an artifact produced when the animal was killed. The spermatheca duct is only slightly over half the length of the vagina and the free oviduct is scarcely one-fifth its length. Eight fully formed embryos, 4x5 mm., extend from the free oviduct to the albumen gland, *i.e.* throughout the entire length of the apical and basal parts of the uterus. Each has a well calcified shell of two and one-half whorls covered by a thin, transparent membrane (Fig. 44). A talon is present and is typical of the other achatinids examined.

The smaller specimen was very immature and no significance could be obtained from its examination except for the fact that the sheath was short and the penis projected apically well beyond it as it did in the immature specimen of *Arch. osborni afromontana*.

The third specimen was removed from its shell and though it was mature, as evidenced by the presence in its oviduct and uterus of several homogeneous albumen masses as large as the embryos in the first specimen, the sheath-penis relationships (Fig. 46) were like those in the immature specimen. The sheath did appear contracted, though it is not possible in the absence of fresher material to determine the significance of this variation nor to establish accurately the basic genital plan from which relationships can be drawn. Some light seems to be thrown on this by the study of the single immature specimen of *P. interstinctus insignis* (*vide infra*). Only slight differences were found in the other structures.

Measurements of genitalia in millimeters (the two specimens are listed in order of examination): P — 7, 9.25; PS — 9, 5; PR — 5, 8; VD — 12.5, 12; BV — 4, 4.5; AV — 4, 4.5; FO — 1.5, 3.5; SD — 4.5, 2.5; S — 3.5, 2.75; AG — 10.5x3, 6.

#### PSEUDOTROCHUS INTERSTINCTUS INSIGNIS (Pfeiffer)

A single specimen collected on April 12, 1944, near Dobi Island, Liberia, by Joseph C. Bequaert was examined. The genitalia were so immature and attenuate that they were practically valueless in this study. The penis sheath, however, was short and only one-third the length of the attenuate penis. This would seem to lend support to a

presumption that the specimens of *Pseudotrochus turbinatus mucidus* with the shorter penial sheath (Fig. 46) are more normal than the one with the longer penial sheath (Fig. 43). Dissections of other achatinines have shown that the immature specimens often tend to have a short penis sheath even when it is normally long in the adults. But these observations still leave unexplained the reason for the apparent dimorphic condition of the sheath in *P. turbinatus mucidus*.

## SURVEY OF THE LITERATURE

An exhausting but probably not completely exhaustive search of the literature has been made in order to determine the extent to which the genitalia of the Achatinidae have been examined and illustrated. The search yielded illustrations of nineteen species and subspecies of which six have been re-examined, re-illustrated and re-described above in the light of a more clear understanding of the genital components and interrelationships. The nonexistence or unavailability of preserved material has prevented a similar rechecking of the remaining thirteen species and subspecies. Therefore in order to make the record as complete as possible, it has been necessary to make outline copies of the original illustrations for reproduction in this present paper. These original illustrations were so variously executed that it was thought advisable to reproduce them in such a manner that all would be similarly arranged and brought to approximately the same size (Figs. 54-63). A study, then, of such a series of illustrations, in conjunction with the original illustrations which the author has contributed, will not only permit of more accurate drawing of homologies, but the relative taxonomic value of the genital system can be more nearly ascertained. In this process of re-drawing, every precaution was taken to preserve the same dimensional ratios as appeared in the original illustration. Here and there, however, liberties were taken in incorporating characters where they were clearly described in the text but not or poorly shown in the originals. These are accurate, then, only in so far as the original investigators were accurate in their observations and illustrations.

There is presented below, with brief annotations, a list of these thirteen species and subspecies whose genitalia have been illustrated or discussed in the literature.

## ACHATINA (ACHATINA) DAMMARENSIS Pfeiffer

## Fig. 54

Degner, 1922, pp. 37-38, figs. 12c, 13.

We have in this species apparently a genuinely unique form in the male genitalia inasmuch as the penis and vas deferens are reported to be peculiarly bulbous in the region where they join each other and where the penial retractor has its origin. On the other hand, it is thoroughly possible that severe contraction of the penial sheath at the time the specimen was killed has produced these swellings as artifacts. Degner describes in detail the external and internal anatomy of the basal structures. He describes a wide fold on the inner wall of the penis which is presumed to be a stimulatory organ (Reizorgan). The vagina is divided into basal and apical portions. The penial retractor was found to make its insertion on the floor of the lung, on the strength of which he incorrectly links this species with *Limicolaria vanattai* and *Archachatina simplex crawfordi*. The significance of variations in the insertion of the penial retractor is discussed below.

## ACHATINA (ACHATINA) SCHWEINFURTHI v. Martens

## Fig. 55

Pilsbry, 1919, pp. 72-73, figs. 31, 32.

Pilsbry's photographic plate of the genitalia of this species gives quite a fair idea of all the basal structures except the length and form of the spermatheca. It was hoped that the original specimen could be re-checked to determine this but efforts to locate it were not met with success. Examination of other species in this genus has shown, however, that in general the spermatheca is coextensive with the free oviduct and contiguous with the basal spermoviduct. With this thought in mind, there is indicated by a dotted line an attempt to approximate its probable dimensions.

The term "epiphallus", which Pilsbry used in referring to the basal vas deferens, is misleading.

## ACHATINA (ACHATINA) ZEBRA ZEBRA (Bruguière)

Semper, 1874, p. 144.

Pilsbry, 1904-05, p. xiii.

Semper did not illustrate this species but described its genitalia in the most brief and general terms, presenting as the only significant

character the fact that the spermathecal duct was short. Pilsbry also referred to this character.

ACHATINA (ACHATINA) ZEBRA OBESA Pfeiffer

Fig. 56

Robson, 1921, p. 256, fig. p. 257.

Robson described in considerable detail the genitalia of "*Cochlitoma zebra* var. *obesa* (Pfeiffer)" which, like the parent species, reportedly possessed a short spermathecal duct. He was in error, however, when he referred to the free oviduct as the "vagina" and to the vagina as the "common duct of vagina and spermatheca." The penis sheath was found to be "complete" and the penial retractor "a branch of the right ocular band." It seems apparent from his findings that one of the two specimens he had ("z<sub>2</sub>") was an attenuated immature specimen. His reference to an "anomalous condition" of the vas deferens (p. 262) in that specimen, therefore, is probably not a valid one.

ACHATINA (ACHATINA) ZEBRA FULGURATA Pfeiffer

Fig. 57

Robson, 1921, p. 262, fig.

Pfeiffer (1851) originally described this as a new species of the genus *Achatina*. Pilsbry (1904-05) relegated the species to the genus *Cochlitoma*. Robson retained it in the genus *Cochlitoma* but like his fellow British predecessors, considered it a subspecies of *zebra*. He was able to show, on the basis of his anatomical study of two individuals, differences between this and "var. *obesa*" in the length of the free oviduct (which he mistakenly calls the "vagina") and the spermathecal duct. His findings led him to "conclude that the present concept of the genus *Cochlitoma* is unsound." Connolly (1939) avoids the issue completely and cautiously takes the classification of Melvill and Ponsonby.

If the anatomical differences between *obesa* and *fulgurata* prove constant, and if these two are still to be considered mere subspecies of *zebra*, then there exist greater differences between them than between any other subspecies so far examined.

## ACHATINA (LISSACHATINA) LACTEA Reeve

Fig. 59

Bacci, 1939, p. 337, fig. 2.

In this species, Bacci has made an even less correct interpretation of the structures than he did in *fulica hamillei* (q.v.). To the fact that he was unable to find a talon, which unquestionably is present, he assigned the absurd reason, "In questa specie il condotto ermafrodita non dà luogo alla formazione di un diverticolo." The greater length of the vas deferens is given undue significance. The nature of the penis is completely confused not only because he fails to distinguish between it and its sheath (though he implies it is completely covered by the sheath), but he creates out of the swollen basal portion of the penial retractor "un epifallo piriforme." The characters of the basal female conduit seem to be significantly different from those of *fulica*.

## ARCHACHATINA (THOLACHATINA) GRANULATA (Krauss)

Fig. 58

Semper, 1874, p. 143, taf. xii, fig. 2.

It is apparent from Semper's illustration that what he refers to as the loop of the vas deferens is actually the apical penis and the adjacent basal vas deferens. These project considerably beyond the confines of the penis sheath and, along with the greater length of the vagina, are in contrast with the other illustrated species put in the genus *Cochlitoma* by Pilsbry. It was this contrast that stimulated Robson (1921) to point out that *granulata* "does not fall into line in the character of its penis sheath" and was used by him to support his contention that the genus *Cochlitoma* was of questionable status. Semper considered the genitalia similar to those of *Archachatina marginata*.

## BURTOA NILOTICA NILOTICA (Pfeiffer)

Reynell, 1906, p. 197, pl. 17, fig. 2 a, b, c.

The typical form of this species has been examined and illustrated by Reynell. He shows the conspicuously slender penis somewhat enlarged at its apex and projecting with the slightly smaller basal vas deferens in loop fashion a short ways beyond the apical rim of the apparently quite thick sheath. He is inconsistent, however, in indicating the length of the vagina, for in one of his figures it is longer than

the penis and in another it is considerably shorter. Just the reverse is shown in the length of the spermathecal duct. The spermatheca is shown as a large, irregularly sacculate structure; but he reports that it varied in the "pregnant and non-pregnant animals." He reports that the penial retractor inserts "distally on the diaphragm." In two of his specimens, he found 154 eggs each "contained in a calcareous shell." No free embryos were found.

BURTOA NILOTICA OBLIQUA (v. Martens)

Fig. 60

Pilsbry, 1919, p. 81, fig. 34.

In spite of Pilsbry's feeling that Reynell and Pollonera had different subspecies than the one he examined (*obliqua*), the figures of the three authors compare very favorably. Pilsbry's illustration of the basal genital structures of this subspecies is reproduced here as there are inconsistencies in the illustrations of Reynell and misinterpretations in those of Pollonera. In a second diagram, Pilsbry shows the penial retractor originating all along the portion of the vas deferens embraced by the sheath; this, of course, is not unique (*Cf. e.g.* Figs. 11, 17). The spermatheca is shown as small and globose and the penial retractor is reported to insert on the diaphragm.

BURTOA NILOTICA MINOR Pollonera

Pollonera, 1909, p. 197, pl. 19, figs. 6, 7.

Though Pollonera does not discuss the genital structures of this subspecies, he has illustrated them. In his two figures, he shows at the apex of the penial sheath (which he calls the "pene") some peculiar structures. To one who is acquainted with achatine genital anatomy, it is easily seen that what he terms the "flagellum" is actually the basal stub of the penial retractor. That which he terms the "retrattori" is the thin penial artery, with its adjacent muscle fibers coming from the ganglionic region and passing into the inner walls of the sheath via its apex. The remaining, and unlabeled, structure in his illustration is obviously the loop formed by the apical penis and basal vas deferens. The spermatheca, labeled the "borsa copulatrice", is globose and like that of *obliqua*.

## LIMICOLARIA VANATTAI Pilsbry

Fig. 61

Pilsbry, 1904-05, p. xi, pl. 65, fig. 42.

In his discussion, Pilsbry points out that the penis sheath envelops the entire penis, the basal portions of the vas deferens and the retractor muscle. He describes the penis as "thick and short" though he does not attempt to show it in his illustration. The spermathecal duct is conspicuously longer than the free oviduct and the sheath embraces the vas deferens only in its most basal portion in the region of the apical penis. The penial retractor attaches to the "lung floor or diaphragm."

## PSEUDOTROCHUS ALABASTER (Rang)

Fig. 62

Semper, 1874, p. 145, taf. xii, fig. 3 [not fig. 1 as he reports in the text].  
Pilsbry, 1904-05, p. xi, pl. 1, fig. 1.

This species is conspicuous in that the vagina is long, the spermathecal duct is very short and the robust penis projects considerably beyond the short, basal penial sheath. In these respects, the genitalia are similar to those of *A. achatina*, *P. turbinatus mucidus* and *P. interstinctus insignis* and further substantiates the thesis that the sheath is normally short in this genus. The penial retractor is reported to connect with the columellar muscle.

## ATOPOCOCHLIS EXARATA (Müller)

Fig. 63

Furtado, 1888, pls. 2, 3.  
Pilsbry, 1904-05, p. x, pl. 1, figs. 8, 9.

Furtado has shown the genitalia of this species in fair detail; Pilsbry has reproduced his illustrations exactly. The penial retractor is reported to make its insertion on the columellar muscle. The basic plan of the genital system is not tangibly different from that of the examined species of *Pseudotrochus*. This lends significance to the fact that some authors consider *Atopocochlis* congeneric with *Pseudotrochus*.

## THE BASIC PLAN IN PENIAL ANATOMY

A comparative study of the genitalia of the several species in the subfamily Achatininae has revealed that the most complex and taxonomically most significant achatinine genital structure is the penis with its sheath and retractor. It was found that in spite of striking differences, all penes could be reduced to a common, basic plan, the establishment of an understanding of which permitted for the first time a correct interpretation of the intricate, variable and heretofore apparently indecipherable relationships of the penis and its attendant structures.

In the material examined, the genitalia of *Achatina fulica* are very nearly the least specialized and therefore will serve as a good example to illustrate this basic plan. Further research may possibly show that these are not prototypic in this group. At present, however, all others that are known can be derived from a plan similar to the one demonstrated in this species. With the help of the schematic and idealized illustration in Figure 41, then, let us examine the basal portion of the male conduit in *A. fulica* to get an understanding of the basic interrelationships of its component parts. With this established, it will not be difficult to homologize them in the other species. As will be seen in the conclusions, where each species is discussed in the light of all of its significant characters, homologizing from this basic plan will help to establish a concept of phylogeny in this group which seems entirely impossible from the study of the shells alone.

First of all, it helps to keep in mind that the male conduit, basal to the spermoviduct, is essentially a long, hollow tube which is apically reduced to form the vas deferens and basally enlarged to form the penial tube. The latter is able to pass out in part or in its entirety as the intromittent organ during copulation. At the junction of the apical and basal parts, a slip of muscle arises from the outer muscular wall of the conduit and passes normally in this group to the right tentacular retractor, though as explained below, it occasionally inserts at other places. The principal modification in this conduit is the formation of a penis sheath. It will be seen that the sheath (PS) is not a separate entity but merely a continuation, a doubling back and a thickening of the outer muscular wall of the penis (OP) and the vas deferens (OV). As it passes apically then, it embraces the basal vas deferens a second time and completely surrounds the penis including the basal portion of its retractor (PR). In this process, the penial artery (PT, Cf. also Figs. 7, 50) is not embraced but pushed apically so far that it must make a hairpin loop in order to reach the inner wall of the sheath where it breaks up into smaller vessels. This artery



arises near the circumesophageal nerve ring as a branch of the right cephalic artery which, in turn, is a branch of the anterior aorta. Because this artery is surrounded by a thick band of connective tissue, it is quite prominent and in some cases has confused investigators. Poltonera's reference to it as a "retrattori" in *Burtoa nilotica* is a case in point. Other investigators, who stopped too soon in their dissections, were misled by the prominence of the penial sheath and have erroneously referred to it as the penis proper. This has led to some gross misunderstandings as to the relationships of certain species.

Internal to the outer muscular layer of the vas deferens (OV) is an inner more or less spongy, muscle layer (IV) and an epithelial layer (EV) which are continuous with those of the penis (IP, EP). The same two layers are seen to make up entirely the walls of the genital atrium (GA) and the unensheathed basal portion of the penial tube (PC). This latter has been frequently referred to in related groups as the "penial prepuce." The nature of its walls indicates that it is a direct extension of the genital atrium and it might therefore be considered a "penial atrium." This term, however, is no better than the other one as far as indicating what its true function is in copulation. The term "basal penis" has the right connotation but it would obviously lead to ambiguities. It is with some reluctance, then, that the term "penial prepuce", or simply "prepuce" has been used in this paper. A very pronounced constriction occurs in the penial tube at the base of the sheath; hence there is a definite demarkation between penis and prepuce. The much more delicate epithelial layer of the penis further emphasizes the difference in these two structures. Externally, however, the sheath often appears to pass all the way to the atrium. The reason for this is found in the fact that a variable number of muscle bands (MB), that have their origin in the sheath, pass basally and insert in many places on the prepuce and the genital atrium. Connective tissue (CT) also adds to the illusion. Often these must be cut away to determine the basal limits of the penial sheath.

In the achatinines that are known anatomically, the deviations from this basic penial plan seem to fall into six definite groups. The first, characterized by *A. fulica*, which has a very slender penis completely enclosed by a thick walled sheath, also includes the closely related *A. iredalei*, *zanzibarica*, *loveridgei* and *albopicta*. The penes in the second group are also short and confined to the sheath but they are quite robust. This group includes *Arch. osborni* *afromontana* and *Arch. simplex crawfordi* and apparently *A. zebra* and *A. schweinfurthi*. In the third group, to which belong *Pseudotrochus turbinatus mucidus*, *P. interstinctus insignis*, *A. dammarensis*, *Burtoa nilotica*, *Arch. meadi* and *Arch. granulata*, there is a definite tendency toward elongation

of the penis beyond the confines of the sheath. Pronounced elongation of the penis is demonstrated in the fourth group by *A. reticulata*, *A. glutinosa*, *A. layardi* and finally *A. panthera*. This tendency is carried to the extreme in the fifth group with the formation of a very robust, muscular penis which extends considerably beyond the sheath. This group includes *P. alabaster*, *Atopocochlis exarata*, *Arch. degneri*, *Arch. marginata*, *A. achatina* and *Arch. bicarinata*. In the sixth group, however, quite a different trend has taken place. In *Limicolaria kambeul* and *L. flammea*, the penis proper is completely surrounded by the sheath; but the prepuce has become so greatly elongated that the sheath appears to be apically situated. Further, there arises at the junction of the penis and the prepuce (which is an area of constriction in *fulica*) a basally directed, circumferential outgrowth of the inner muscle layer and the epithelial layer thus forming a distinct verge or penis papilla. In *L. felina*, *saturata*, *ussuwienensis* and the obviously closely related *Limicolariopsis kivuensis*, the penis proper has become obscured through the hypertrophy of the middle muscle layer. This has not only reduced the lumen of the penis to a narrow passage, hardly larger than that of the vas deferens, but has formed a packing between the walls of the verge to make it a more pronounced structure. Actually, before the penis sheath is cut, the genitalia of members of this group look superficially quite similar to those of the first two groups above — hence the need for careful dissection of the penis itself.

#### INSERTION OF THE PENIAL RETRACTOR

Pilsbry (1904-05) found that the penial retractor of his *Limicolaria vanattai* attached to the "lung floor or diaphragm" and from this assumed that this character was typical for the genus. He also found a similar attachment in *Cochlitoma* (= *Archachatina*) *crawfordi*. Reynell (1906) found the same character in *Burtoa nilotica* and Pilsbry (1919) supported his observation by finding it in *B. nilotica obliqua*. On the strength of the fact that this character was found in *Achatina dammarensis*, Degner (1922) attempted to link this species with the others above. It is significant that each of these four species is in a different genus and, as far as the genital anatomy is concerned, is quite distinct from the others. This suggests immediately that caution should be exercised in assigning any taxonomic value to this character and that an extensive investigation is indicated so that its true value can be ascertained.

Though it was not possible to undertake such an investigation in the present study, a great deal of light has been shed on this general problem. In order to make as understandable as possible the complex

factors apparently responsible for the great variation in the attachment of the penial retractor, there has been prepared in Fig. 49 an idealized stereogram, basically typical of all genera studied, which is exaggerated in some dimensions to emphasize relationships.

First of all, it should be understood that the *origin* of the penial retractor (PR), as Hoffmann (1922, p. 521) has shown in his embryological study of *Limax maximus*, is on the apex, or near apex, of the penis (P). The *insertion*, then, will be found at the opposite end. And typical of insertions, it demonstrates greater variability in its attachment. This point frequently has been confused in the literature.

When the mantle (M) is cut away, in dissecting a specimen, the lung or pulmonary cavity is exposed. The muscular lung floor or diaphragm is traversed, from posterior to anterior, by the large, prominent anterior aorta (AA). Well before the anterior thickened rim of the mantle (AM) is reached, this aorta passes ventrally through the diaphragm to the ganglion masses where it gives rise to a number of arteries including a fairly large one to the penis. This penial artery, as explained in the discussion of penial anatomy, has been confused with the penial retractor. In examining the diaphragm lying to the left of and anterior to the anterior aorta (LD, LD) it is found to be muscular but very thin-walled. In contrast, the diaphragm lying to the right of and posterior to the aorta (RD) is much more muscular and approximately twice as thick. It was not understood why the anterior aorta seemed to rest in a very marked depression between these two sections of the diaphragm until the haemocoel (RH + LH), or main body-cavity, was exposed. A very definite vertical sheet of muscle and connective tissue (SM), oriented in a postero-anterior direction, was found to connect the diaphragm, immediately below the anterior aorta, with the giant, ventral columellar muscle (CM) hence dividing the haemocoel into right (RH) and left (LH) portions in this region of the body. This sagittal myoseptum, as it will be called, is of highly variable nature, for it may terminate abruptly with a considerably thickened edge at the level where the anterior aorta passes ventrally, or it may continue anteriorly to the penio vaginal angle and thereby put the penis and vas deferens (VD) in the left haemocoel with the crop and odontophore, and the entire female conduit by itself in the right haemocoel. If it does extend this far anterior, the right tentacular retractor (TR) is diagonally traversed by the sagittal myoseptum. Modifications of this have been found wherein this myoseptum passed more and more strongly toward the right until it passed not between penis and vagina but transversely over the lower portion of the spermoviduct until all of the basal genital structures rested in the left haemocoel with the crop.

Posteriorly the sagittal myoseptum gradually breaks into separate muscle bands that become smaller, shorter and more sparse. Shortly posterior to the last band, the right tentacular retractor joins with the left tentacular retractor (TL) which latter has already joined with the combined left (OL) and right (OR) retractors of the odontophore. These four muscle bands then, join the columellar muscle in its most posterior portions to form a single contractile unit. It should be borne in mind that the tentacular retractors not only attach to the two tentacles on their respective sides but to several other places on the head and neck regions.

Springing from the sagittal myoseptum is another nearly vertical sheet of muscle and connective tissue, the transverse myoseptum (TM). This connects dorsally, in an arc, along the left diaphragm and finally makes a terminal attachment in the region where the diaphragm attaches to the columellar muscle. A separation of the left haemocoel into an anterior portion, containing the crop, and a posterior portion, containing the stomach, is thereby effected. As both myosepta are quite muscular and are vertically oriented, it is very possible that they supplement the work of the diaphragm.

By far the majority of the achatinid specimens examined had the insertion of the penial retractor on the right tentacular retractor either at a point (A) anterior and to the left of the sagittal myoseptum; or, when the myoseptum was shorter or turned more sharply to the right, at a point (B) further up the right tentacular retractor and therefore sometimes to the right of the myoseptum. This, without much doubt, is the *normal* type of insertion for this group.

In one of the specimens of *A. simplex crawfordi* the insertion of the penial retractor was found to be perfectly normal. In the other, it was such that some of the fibers fused with the right tentacular retractor and the rest fused with the adjacent portion of the sagittal myoseptum (at C). A small piece of this myoseptum remained at the apex of the penial retractor when the genitalia were removed (Fig. 27, SM; Cf. also Fig. 25). A large specimen of *A. reticulata* (Fig. 13), went one better by having apical fibers passing not only to these two points but to the columella (at D) as well. For a still different combination, one of the paratype specimens of *A. leucostyla* (= *fulica hamillei*) had an apically bifurcated retractor that inserted on the right tentacular retractor and on the columella. And on the other hand, single specimens of *A. iredalei* and *L. saturata capitellum*, from series of otherwise normal specimens, had insertions entirely upon the sagittal myoseptum (at E).

Working still further dorsally, one of six specimens of *A. zanzibarica* had a retractor that inserted on the right tentacular retractor, the

sagittal myoseptum and on the ceiling (at F) of the diaphragm or lung floor; or to be more accurate, on the ceiling of the left haemocoel. Several species had one or more individuals with retractors that passed vertically along the left side of the sagittal myoseptum, over the crop and inserted centrally on the diaphragm; these are *A. zanzibarica*, *loveridgei*, *Arch. simplex crawfordi*, *meadi*, *osborni afromontana*, *Limicolaria ussuwiensis* and *Limicolariopsis kivuensis*. In all six specimens of *L. ussuwiensis* the insertion was on the diaphragm but in four cases the insertions were anteriorly placed very close to the junction of the left diaphragm and the mantle (at G). Still greater anterior progress was made in *Arch. osborni afromontana*. Two of the six specimens examined had insertions centrally on the diaphragm and four of them had insertions on the body-wall (BW) anterior to the diaphragm and the anterior lip of the mantle (at H).

From these observations, the following conclusions can be made relative to the insertion of the penial retractor: (1) The sagittal myoseptum interferes with the normal insertion of the penial retractor by acting as a physical barrier. This interference may cause the retractor to insert upon the myoseptum itself or be deflected over the crop to the diaphragm, or it may cause a splitting of the terminal retractor with slips passing to two or three different points of insertion. (2) Orientation of the penis anlage undoubtedly predisposes a certain type of insertion. The short, often anteriorly directed penis in *Arch. osborni afromontana* may be a case in point. (3) Deviations from the normal insertion have occurred sporadically a good many times in the Achatininae for the reasons indicated above; and actually, they are by no means limited to the subfamily Achatininae, for Connolly (1925), in his discussion of the subulinine genus *Pseudoglossula*, points out that he found the penial retractor attached to the "retractor of the right tentacles" *i.e.* "the columellar muscle, as in so many of the Achatinidae and not from the diaphragm, as Pilsbry [1919] states that it does in *Ps. stuhlmanni* (Mts)." These deviations cannot therefore be considered of taxonomic significance, though there remains the possibility that when very large series of *Arch. osborni afromontana*, *L. ussuwiensis* and perhaps others are examined, they may be found to be secondarily consistent in their deviations because of an inherent consistency in the predisposing factors. (4) Pilsbry (1904-05, p. xi) has assumed that the diaphragmatic insertion in this group is indicative of a "true" penial retractor and a "normal insertion" whereas the insertion on the "right ocular retractor" is a "secondary" one. The present investigation does not support this assumption. On the contrary, it indicates that just the reverse is more likely the case.

## COPULATION AND COPULATORY ANATOMY

Most of the achatinids studied possess a simple tubular penis which may be short as in *Archachatina osborni afromontana* or long as in *Achatina achatina*. In either case, it is not difficult to imagine how the intromittent organ is formed during copulation or what is extroverted in the process. And even in *A. panthera* with its very long, sinuate vagina, the mechanics of copulation would seem fairly simple. It is quite different in *Achatina fulica*, *iredalei*, *zanzibarica*, *loveridgei* and especially *albopicta*, however, as the extremely small, thin penis and the very thick, muscular sheath give no idea as to what takes place in extroversion. It was soon apparent that the answer would be found only in witnessing the actual extroversion process itself.

The opportunity very fortuitously presented itself at 10:30 p.m. on June 27, 1948, when the author made his final evening check of the terrarium containing two specimens of *A. fulica hamillei*, three of *A. iredalei*, three of *A. reticulata* and one of *A. fulica rodatzki*. All specimens were actively crawling about or feeding on lettuce and carrot. The single specimen of *rodatzki* from Zanzibar, that hereinafter will be referred to as "A", was seen to be approaching one of the *iredalei*, which hereinafter will be referred to as "B", from the rear and to be moving at least twice as fast as the rest. As it contacted the posterior portion of the foot of "B", the rhinophores, which were fully extended and forming about a 90° angle, were brought very close to the shell of "B". In this fashion, they skimmed over the surface rising and lowering with each elevation and depression as "A" progressed anteriorly over the shell of "B". The appearance was very much like that of a bull that has its head and horns lowered for a charge. The head of "A" was seen to swell very noticeably. As "A" continued to move forward, now more slowly, the genital atrium completely everted as did the penial prepuce. The orifice leading into the vagina was apparent and the whole structure looked not unlike the folded hand with the index finger extended. "B", however, did not respond to this approach and "A" moved from side to side several times almost as if in confusion, and then slowly crawled away. The genital atrium and penial prepuce were gradually invaginated again.

But "A" seemed charged with persistence. It next moved over to the shell of a giant *A. reticulata* — again approaching it from the rear. As it neared the anterior end of the shell, once again the atrium and penial prepuce became more and more extended and the rhinophores were held close to the shell and at the same angle. Again, there was no response and the withdrawing action of "A" was the same as before.

A smaller specimen of *A. fulica hamillei* from Kenya, which herein-

after will be referred to as "C", was then approached head on. The movements of "A" did not seem purposeful but it moved to one side of "C" and after an irregular course approached "C" from the rear as it had the others. The same response was noted in its basal genital structures as before. At the same instant, "C" showed an identical response and began to rise upright as "A" approached the neck region, just as it had done with the others. As "A" buried its head deeply between the neck and the anterior rim of the shell of "C", the latter rose still higher and more vertically off the terrarium floor. "A" seemed to be half rasping, half caressing the neck region of "C" and at the same time, "C" was beginning to lean further and further back onto the dorsally situated "A". Each individual had the genital atrium and the penial prepuce fully extended. "C" showed a great deal of activity by way of contracting and extending the four tentacles and the anterior region of the head in general.

Finally "C" began to turn to its right so that "A" brushed against its expanded atrium and prepuce more and more as it moved up higher and higher on the neck region of "C". Reciprocally, "A" turned slightly to its left so that its corresponding genital structures were also being brushed continually against the neck region of "C" as they both passed each other in wider and wider sweeping motions of the head and neck. It was now quite apparent that the everted genital atrium and penial prepuce were functioning as a stimulatory organ<sup>1</sup>.

As the activity became more and more pronounced, the genital regions came closer and closer together. Finally, a large, very clear but yellowish drop of very viscous fluid was produced simultaneously at the tip of each stimulatory organ (thus coming from the male system) and the next time the individuals brushed against each other, these drops were each deposited close to the mouth of the other. With this, the two individuals tightly appressed their stimulatory organs together and simultaneously contracted the head and neck regions so that a fair amount of altitude was lost. There was a very definite high rate of internal activity for the first minute, at which time the extroversion of the genital structures was doubtlessly taking place. At first, all genital structures were completely obscured from view; but within a minute's time, both animals began to relax in opposite directions and ultimately to a distance of a good half inch. It could be seen then that there was reciprocal concurrent copulation taking place; for in each case the extended intromittent organ of one was clearly entering the pronounced vaginal opening on the evaginated genital atrium of the other. Mohr (1935) shows a somewhat dark illustration of a copulating pair of *A. fulica* in just this stage.

<sup>1</sup> Also known as egersidium, Reizkörper and Reizorgan.

A great deal of clear slime had been secreted by "A" over the right side of its body, posterior to the genital region, though "C" did not show this. After fifteen minutes, the two individuals had withdrawn considerably and the intromittent organs were obviously being pulled upon. Nothing but the gripping action of the thick basal vaginal muscle could account for the fact that these intromittent organs were being held in place. "A" began to be active at this time and by another five minutes (twenty minutes after complete union) it was very active — extending its tentacles and moving slightly to one side and then the other. During this time, "C" was completely inactive and lay back on the dorsal surface of its shell. In a few minutes, "A" had quieted down once again. Forty minutes after complete union, "C" finally became slightly active by slowly extending and contracting the tentacles. But by this time, "A" had become completely inactive and had withdrawn all its tentacles. "C" soon took up, in a deliberate fashion the task of cleaning up the slime that had accumulated on the anterior portion of its foot, including the clear drop that the other had deposited there. This it did without disturbing the other or without any noticeable tugging on the genital structures. There were frequent rests from this activity and after a full hour of complete union, the two subsided into complete quiescence with the intromittent organs extended until the more attenuate portions could be seen.

Fearing that there would be a very protracted period of quiescence and fearing that there would be a gradual withdrawal of the intromittent organs without any indication of the function of the various male parts in this extroversion process, the intromittent organ of "C" was quickly cut with the scissors as far basally as possible. This brought about a very rapid, simultaneous withdrawal of the intromittent organ of "A" and the complete drawing in of the head of "C" until only the foot projected from the shell. With the forceps, the amputated intromittent organ was removed from the genital orifice of "A". This is shown in lateral and dorsal views in Figs. 52 and 53, respectively.

Very soon, "A" began busying itself with removing the thick mass of slime that it had secreted on its right side. This it rasped at until it was nearly gone and then proceeded to wander about the terrarium. The actions of "C" were quite different. It started several times to crawl but each time it retracted violently, reflecting the reaction to the amputation. In fact the retraction was so sudden that air passed through the pulmonary orifice, or pneumostome, rapidly enough to produce a pronounced squeaking sound. This phenomenon has been observed by Gammon (1943, p. 178) in the so-called "singing snail", *Helix aperta*. In about ten minutes, however, it moved off perfectly



naturally and rasped at a piece of carrot. Later it crawled on "A" and finished up a small stringy mass of slime that "A" had missed. As observed in many other snail groups, there seemed to be a very definite taste for this slime secreted prior to and during copulation. Both snails continued to crawl about more or less together and occasionally rasped at bits of slime on the shell or foot of the other. Even an hour later, "C" showed very intense reaction to the slightest jarring and would pull back into its shell as quickly as if it had been touched with an open flame. The rest, including "A", did not respond to this type of stimulus.

The following morning, "C" was killed and its reproductive tract examined to determine what parts had been amputated as the intromittent organ. As seen in Fig. 50, all but the most apical portion of the penis had been removed as had the basal third of the penial sheath, the entire penial prepuce and a small portion of the apical genital atrium. Next, the intromittent organ was dissected to determine the relationships of these amputated parts (Fig. 51). A re-examination of Figs. 11 and 41 and a comparison of them with Fig. 51 will assist in understanding the confusing reversal of relationships in the extroversion process. This process is initiated by the evagination of the genital atrium (GA) and the penial prepuce (PC) to form the stimulatory organ. This brings the basal portion of the penis proper (BP) to the very tip of the evaginated prepuce. The constriction between these two structures probably prevents further initial eversion. When complete union is effected, there doubtlessly is a contraction of the muscle bands (MB) connecting the sheath (PS) and the prepuce, which pulls the muscular sheath out into the evaginated prepuce. At the same time, there is a complete evagination of the swollen basal portion of the penis (BP) as well as a good share of the very slender middle portion (MP) of the penis. This latter, then is responsible for the very attenuate tip of the intromittent organ. The eversion of these structures pulls the apical portion of the penis (AP) into the intromittent organ. This, of course, becomes very attenuate especially with the squeezing effect produced by the extended basal portion of the sheath. This is further attested to by the fact that it is greatly contracted in the amputated intromittent organ. Since it is a highly muscular structure and was found to be filled with spermatozoa, it is presumed that it has an ejaculatory function. Normally, when the penial retractor (PR) contracts, all these structures are pulled back into the body in their original positions as they are all attached in series. In this case, however, its violent contraction succeeded only in pulling what was left of the apical penis apically right out of the sheath (Fig. 50).

During copulation, no such pronounced "glans" structure could be seen; instead, the intromittent organ seemed very attenuate. This is probably explained by the fact that there was not only a general contraction of the muscular tissue in the intromittent organ at amputation, but the sheath muscle bands (MB) contracted to such an extent that the prepuce wall (PC) became bunched up adjacent to the genital atrial wall (GA, Fig. 51). And even this latter contracted and was pulled distally by the contracting prepuce considerably beyond the level at which it was cut. As Fig. 51 is examined, then, it should be borne in mind that the cut surfaces of the apical penis, genital atrium and penis sheath were originally at the same level and the entire assemblage was much more attenuate.

In general, and as indicated specifically in the anatomy of *Arch. degeneri*, probably the contraction of a circular muscle band in the basal portion of the free oviduct insures the insertion of the intromittent organ into the spermathecal duct. The entire length of the vas deferens was inspected and several white sperm masses were found. There was no evidence of spermatophore formation. Only a small amount of seminal fluid was found in the spermatheca.

One interesting factor in this copulation is that two different subspecies from two completely separated localities were sexually compatible. Several instances of the pre-copulatory behavior were noticed in the specimens of *A. iredalei* and they were characteristically the same as observed in this case. These observations, then, probably are typical for the group.

The absence of a thick sheath and the presence of a verge set up still a different problem in *Limicolaria* and *Limicolariopsis*. It is most probable that in these genera the penis proper does not evaginate. Instead, the prepuce must evaginate so as to bring the verge or penis papilla into terminal position. The penis and its thin-walled sheath would then give support to the prepuce to form a substantial intromittent organ.

Webb (1942, etc.) has done a great deal of work on the anatomy of the extroverted copulatory organs in several North American genera and has made some exceedingly interesting and significant observations. He regularly plunges the copulating pair into boiling water to secure the genitalia in the extended condition. With such large animals as the achatinas, however, a more drastic measure had to be taken. If one is seized with a profound conviction that mayhem has been committed, it might help to know that the North American giant land slugs of the genus *Ariolimax* practice auto-amputation of the intromittent organ, or apophallation, as a regular, but not too fitting, culmination to copulation (Mead, 1943).

## GENITAL PHYSIOLOGY

During the course of the present study, there have been examined a great number of specimens, varying considerably in form, size and maturity. Many of the observations made, reflect on the very complex interrelationships of the male and female conduits and the function of their component parts. Though a number of these will need rechecking by way of carefully controlled physiological experimentation or histological examination, it seems advisable here to indicate what has been found and what the apparent function, relationships and implications are so that the way might be pointed toward further research along these lines.

As has been pointed out above, it seems perfectly clear that the basal portion of the ovotestis duct, or hermaphroditic duct, acts as a seminal vesicle. It has been found crammed with spermatozoa in every case where the genital system was mature and functioning. There was no exception even in those specimens found in the midst of producing eggs. The question of autofertilization or the existence of some incompatibility factor is immediately suggested. It might be mentioned here that the author has research in progress which should give the answers to this problem.

The talon in general has long been considered a sort of fertilization chamber or "Befruchtungstasche." There is absolutely no evidence in this group of its being anything more than a diverticulum, or caecum, of the ovotestis duct. It frequently contains a mass of spermatozoa which is confluent with that in the ovotestis duct.

Apically, the male and female conduits are intimately associated as will be seen in the examination of the diagram of the spermoviduct in cross section (Fig. 47). The male conduit ( $\sigma$ ) is poorly set off from the female conduit ( $\varphi$ ) by two unequal, whitish, overlapping walls. These, in turn, are overlapped by an adjacent small portion of the uterine wall which seems to consist of the same type of whitish, firm tissue. The rest of the uterine wall is of softer consistency and cream-colored in the apical uterus and butter-yellow or ochre-colored in the basal uterus. The lumen of the uterine portion of the oviduct is lunate in the individual that is not gravid. This seems attributable to the fact that the voluminous, cream-yellow, compound prostatic acini (PA) are tucked deeply into the infolded portion of the uterine wall and are held in place by connective tissue. The compound acini open basally between the two walls of the male conduit through conspicuous, slightly raised pores (Fig. 45). This whole assemblage, plus a branch of the genital artery (G), is suspended from the diaphragm by a very thin sheet of mesentery (M).

In one of the specimens of *A. iredalei*, which had been killed by plunging in boiling water, there were found high up in the apical uterus five firm, coagulated albuminous masses which were approximately 6 mm. in diameter. These were perfectly homogeneous and contained no sign of an outer calcareous layer. Both these and the very large albumen gland were approximately of the same consistency and color. It is apparent, then, that the ova at this stage were being surrounded by albumen from the albumen gland and were being temporarily stored in the apical uterus. The basal uterus looked perfectly normal.

A gravid specimen of *A. fulica hamillei*, treated in the same way, was found to be in a later stage of egg formation. Both apical and basal portions of the uterus were crammed with 292 thick-shelled, butter-yellow eggs approximately 4x5 mm. When these were removed and the uterine wall was examined, it was found that a portion of the wall adjacent to the male conduit was thrown up into two very irregular longitudinal folds (Fig. 48, F, F) which contained numerous secondary folds. The arrangement of these was such that nearly every egg was somewhere in contact with the uterine wall or its proliferations. The eggs in the apical uterus were just as completely formed as were those in the basal portion. It seems quite apparent that this modification in the uterine wall greatly increases the surface of the shell depositing tissue. The presence of a smooth, even, calcareous covering of the eggs doubtlessly rests in the fact that the eggs are moved about in the uterus during the process of shell deposition — quite after the manner of sugar-coating pills. It is possible that the cream-colored apical uterus lays down the inner pale layers of the shell whereas the butter-yellow basal uterus lays down the outer, butter-yellow shelly layer. One of the eggs was broken open and the embryo within was found to be completely formed and apparently ready to hatch. This near-ovoviviparity is probably attributable to the fact that the snail was held in prolonged conditions unfavorable for oviposition thus forcing a retention of the eggs. As a matter of fact, in response to these unfavorable conditions, the snail had formed a rather thick epiphragm at the time it was killed.

The author has examined specimens of *A. achatina*, *fulica hamillei*, *fulica fulica* and *Limicolaria flammea* that contained well-formed eggs. These and probably most other achatinines are oviparous. Ovoviviparity was suspected in one or two species of *Limicolaria* (Robson, 1912). Its sporadic appearance suggests that it has arisen independently several times. The two obvious elements of greater survival value rest in the economy of lime and in the greater protection afforded by prolonged retention in the uterus. The very thin, transparent membrane that covered the embryos of *A. zanzibarica* did not

pass over the aperture of the shell and there was fair evidence that intra-uterine feeding on a mucoid secretion had been taking place. This obviously is a point that needs further investigation.

One thing that was abundantly apparent in this study is that the size of the so-called prostate gland is all out of keeping with its presumed prostatic function, as only a small amount of mucoid fluid accompanies the spermatozoa during copulation. The only other function that could be ascribed to it would be the production of some substance during egg formation, egg laying, or retention of the embryos. When the uterus is full of eggs, the two walls that delimit the male conduit are pulled so far apart that the male and female conduits are completely confluent (Fig. 48). At that time, the pores between these two walls (Fig. 45) face into the lumen of the uterus. Thus it is physically possible for the prostate gland to have a role, for example, of pouring out the large amount of mucus that accompanies egg laying; or to have some similar function in addition to a prostatic function. Apropos of this, there still remains unknown the source of the clear, yellowish drop of fluid that appeared at the tip of the stimulatory organs immediately prior to physical union in copulation (*vide supra*).

At the very apex of the vas deferens, that is, just before it joins the free oviduct, there is a pronounced swelling and, in the freshly killed specimen, a change in color from a pale cream to a light gray-tan or purplish. This swelling was found especially pronounced in the examined specimens of *Limicolaria*. At first, it was thought this was a glandular structure as it seemed to be made up of barely distinguishable acini (*Cf.* Figs. 21, 43). On cutting open several, however, it was found that they were not excessively glandular. Instead, in each case the lumen was found to be quite large and the thin walls densely covered with deep, branching and anastomosing rugae. Sperm was often found present and packed deeply between the rugae, hence giving this structure an external appearance of being an aciniform gland. In the specimen of *A. fulica hamillei*, discussed above, which had been killed shortly after copulation, this structure was found jammed with sperm. From these observations, it would appear that this enlarged region of the vas deferens possibly functions as a sort of subsidiary seminal vesicle. A relay ejaculatory function should be considered.

Frequently there is encountered in the spermatheca a pinkish viscous substance that gives every appearance of being a polysaccharide. Investigations are in progress in related gastropods to determine the exact nature and function of this. It is very possible that it is a nutritive substance desquamated from the spermathecal lining and that it sustains the life and viability of the otherwise short-lived spermatozoa.

Direct and indirect evidence of protandry and seasonally imposed periods of genital atrophy have been found in a number of specimens.

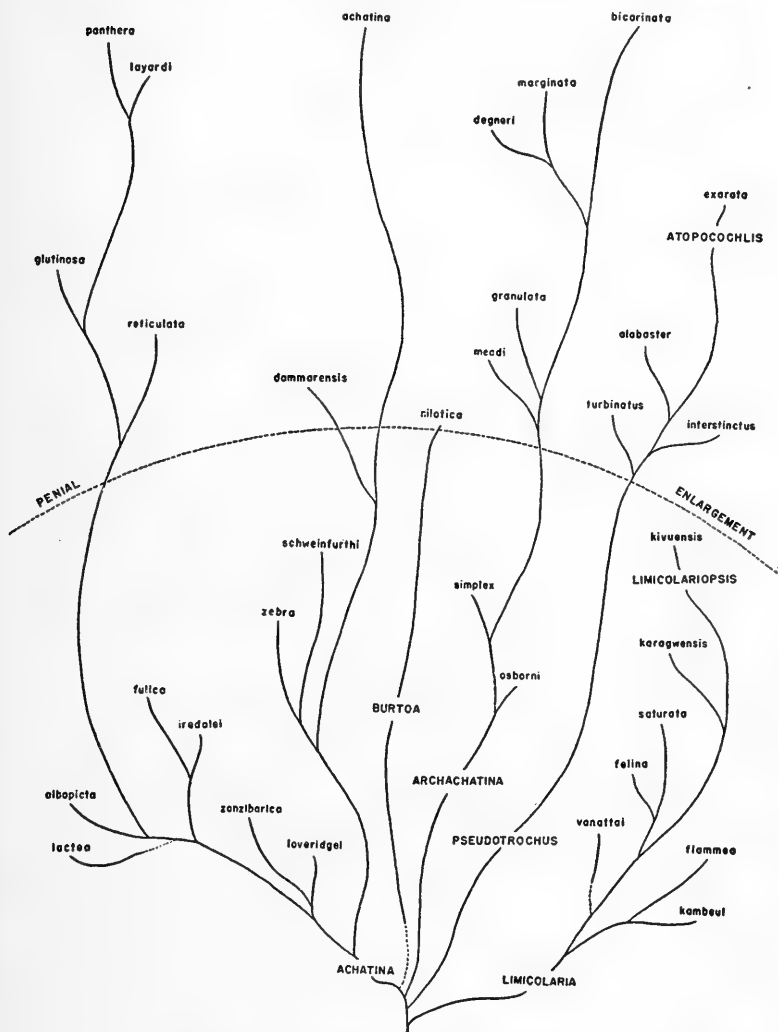
### CONCLUSIONS

In spite of the fact that a great number of specimens and a good many achatinid species and subspecies have been examined during the course of this study, they represent only a small portion of what should be examined before any real conclusions or broad generalizations can be safely made. Nonetheless, at this time it is possible to indicate certain obvious trends, affinities, correlations and other factors of phylogenetic significance which should elucidate considerably this whole subject and point the way toward further investigation. Even though subsequent findings may prove to be at variance with the interpretations and provisional conclusions reached in this paper, the effect probably will be largely one of reorientation rather than an actual changing of the fundamental ideas involved. Besides, any means, such as phylogeny, that tends to pull together and put sense into an otherwise meaningless jumble of variously related species is a step in the right direction in clarifying the issue so that eventually the real truth might be reached.

Let us re-examine, then, the several illustrated species with the thought of homology, and therefore phylogeny, foremost in mind. To depict graphically the relationships indicated, there has been prepared a phylogenetic tree of the anatomically known achatinines (Text Fig. 1).

*Achatina zanzibarica* and *loveridgei* possess proportionately the most diminutive penes of all those examined and despite the fact that Bequaert (1950) has put them in separate subgenera on the basis of shell characters, their genitalia are remarkably similar. The genitalia of *A. iredalei* and *fulica* are of this same general type though the penes are less tripartite and tend to become more elongate. The specimens of *fulica* were especially variable in this latter character. In *A. albopicta*, the genitalia have not departed from this same type though the basal structures have become exceedingly muscular. In each species of this group of five, the basal vagina is short, muscular and cormoid in form. The apical vagina, on the other hand, is short, tubular, and unmodified but indicates a tendency toward greater elongation.

Because of the similarity in shells, it might be presumed that *A. reticulata* is an overgrown version of *albopicta*. The genitalia, however, indicate marked differences. The penis of *reticulata* has become quite robust and so elongate that it projects considerably beyond the apical limits of the sheath. Though there is a very slight enlargement in the



Text Fig. 1 Outline of the phylogenetic relationships of the anatomically known Achatininae. For *karagwensis* read *ussuwiensis*.

basal region of the vagina, it is not cormoid nor is the wall thicker than the rest. The genitalia of *glutinosa* seem to have carried this general attenuation still further with a concomitant reduction in

thickness of the sheath. This trend is culminated in *A. layardi* and *panthera*, as the penis is extremely slender and forms, with a small portion of the basal vas deferens, a pronounced loop apical to the sheath. The immature paratypic specimens of *layardi* showed in the basal vagina no tendency toward the formation of the striking sinuations so evident in *panthera*. Along with this development of the vagina in *panthera*, there has been a reduction in the length of the spermathecal duct and free oviduct.

Quite another line of evolution within the genus *Achatina* seems to have taken place in *zebra*, *schweinfurthi*, *dammarensis* and *achatina*, which Bequaert (1950) has put in the subgenus *Achatina*. Only the latter species has been examined by the author. It represents an advanced stage in the development of greatly enlarged basal genitalia. The illustrations in the literature of the other three species, which have been reproduced in this work, suggest that this trend may have started with the enlargement of the penis while it was still confined to the thin-walled sheath. This is in contrast to the first group wherein the penis was reduced and the sheath was considerably thickened. However, the greatly elongated vagina, along with the shortened spermathecal duct and free oviduct, in *dammarensis* and *achatina*, indicates either convergent evolution or affinities in the direction of *panthera*. To determine this for certain, it will take a re-examination of *schweinfurthi*, *zebra* and others in this group, which unfortunately has not been possible.

Robson (1921) indicates sufficient anatomical difference between the subspecies *obesa* and *fulgurata* of *A. zebra* so that their presumed subspecific status is immediately open to question. This is especially the case when it is recalled that no tangible anatomical character of subspecific value has been found in any other examined group of subspecies.

Specimens of *Burtoa nilotica* could not be secured for examination, but the illustrations of the genitalia in the literature suggest that it has arisen from brachyphallate stock close to the stem of the typical *Achatina* as did probably the more primitive members of the genus *Archachatina*. Again, in this latter genus, progressive enlargement of the penis seems to have taken place, for the penis in *osborni* *afromontana* and *simplex* *crawfordi* are enlarged, though confined to the short sheath; in *meadi* and *granulata* it projects with the basal vas deferens a short ways beyond the sheath; in *degneri* and *marginata* it is more robust and projects still further; and finally in *bicarinata* it projects as far but has become extremely massive. Of all the achatinids studied anatomically so far, *Arch. simplex crawfordi* is unique in that it possesses a peculiar subterminal partial evagination of the penis.



The genus *Pseudotrochus* also seems to have arisen from stock that had the penis completely ensheathed as indicated in the gravid specimen of *P. turbinatus mucidus* (Fig. 43). It will be recalled, however, that one other fully mature specimen of this same species (Fig. 46) had a basally placed sheath as did the single immature specimen of *P. interstinctus insignis* and the illustrated specimen of *P. alabaster* (Fig. 62). A trend toward an enlargement of the penis beyond the upper limits of the sheath seems therefore to be in progress. The illustration of the genitalia of *Atopocochlis exarata* indicates that this species and the examined species of *Pseudotrochus* are apparently quite closely related thus supporting the contention in some quarters that all these are congeneric. The very elongate vagina and the abbreviated free oviduct and spermathecal duct in this group are reminiscent of the condition in *A. achatina* and *panthera*.

The evolution of the genus *Limicolaria* has been quite distinct as indicated by the fact that the species illustrated in this paper are in agreement with each other, and distinguished from all other achatinids examined, in the following characters: the formation of a definite verge through no addition of new structures but merely through changed relationships of those already present, a great development of the muscle tissue in the penis proper, larger and fewer prostate gland acini, and a large spermatheca with both apical and basal swellings. Further, they all have in common a vas deferens that does not reach the penio vaginal angle and a vagina that is long and unmodified.

The retention of a fairly large lumen in the penis proper, the development of a long penial prepuce which makes the penial sheath appear apically placed, and a vagina that is shorter than the penis plus its prepuce, set off *L. kambeul* and *flammea* from the others. A development of a loose spongy mass of tissue by the walls of the penis proper with a concomitant reduction of the penial lumen to a narrow canal equivalent to that of the vas deferens, the retention of a fairly short penial prepuce, the enlargement of the verge, and the presence of a vagina longer than the penis plus its prepuce, characterize *L. saturata*, *felina* and *ussuwiensis*. *L. vanattai* unfortunately has not been shown in sufficient detail by Pilsbry to make it possible to determine what its real affinities are in the genus. The apparently clavate spermatheca is in contrast with the other examined species. Pilsbry's assumption that a diaphragmatic insertion of the penial retractor is typical in this genus is no longer tenable. *Limicolariopsis kivuensis* is so strikingly like the latter group of *Limicolaria* species that one might well question the reason for its being placed in a different genus. Actually, these are more similar than the two groups of *Limicolaria* are to each

other. The examination of the genitalia of other species of *Limicolariopsis* should prove enlightening as would a much needed detailed anatomical study of the large and confused genus *Limicolaria* which will never be in taxonomically sound status until this is done.

To sum up then, the present study has revealed convincing indication that there are in *Achatina*, *Archachatina* and *Pseudotrochus* strong tendencies toward the maintenance of a simple tubular penis, the enlargement of it, and finally the extension of it beyond the sheath with a concomitant almost complete reduction of the prepuce. In *Limicolaria*, on the other hand, the tendencies seem to be directed toward the formation of a verge, elongation of the prepuce and reduction of the penis proper to a thick mass of muscle fibers through the hypertrophy of the middle muscle layer.

The whole worth of a study of this sort depends not only upon anatomical variability, but variability of a tangible and significant nature. The real problem, therefore, rests first in discerning the presence of variability and then determining its nature. It is only after a good many dissections that a concept of this latter begins to emerge. The factors responsible for and influencing the expression of variability in this group should be examined at this time.

First of all, individual differences are ever present and confuse the picture, especially when too small a sample is taken. The talon, for example, is always present but varies greatly from specimen to specimen. The type of insertion of the penial retractor, as shown above, is also a highly variable and undependable factor and is therefore taxonomically valueless; though there is some indication that it may prove constant enough to be a helpful character in the identification of some species. Another factor is the degree of maturity. This greatly influences the expression and relationships of the anatomical characters in the genitalia. For this reason, the nature of the albumen gland can never be used for more than determining the degree of maturity and in some cases determining whether eggs are soon to be formed or have just been formed. In very immature specimens, the genitalia are of small caliber and tend to be strongly attenuated and quite translucent. Immature specimens of several species that normally have the penes completely ensheathed in the adult animal (*e.g. Arch. osborni afromontana*), were found with the penis projecting atypically well beyond the sheath. In somewhat more mature specimens, proandry, which seems to be universal in this group, adds its bit of confusion. The possibility of genital atrophy, imposed by seasonal changes, must also always be considered. In such cases, the genitalia lack the attenuate nature of those in the immature specimen, are proportionately reduced in caliber, and retain the coloration and opaque-

ness of the mature system. Specimens of *A. fulica* from Saipan and the Palau Islands rather clearly demonstrated this phenomenon. One thing is certain though, large immature specimens can be distinguished anatomically from small mature specimens. This is not always possible in the study of the shell alone, as witnessed by the fact that in the past immature and adult individuals of the same species have been described as specifically distinct.

As explained in the introduction, killing by any method will produce at least some distortion through contraction. For this reason, the length of the penial retractor is usually a very variable factor and therefore not a dependable one; however, in some species it is found quite consistently very short or very long. A similar variable degree of contractility in the vas deferens will determine how closely this structure will approach the peniovaginal angle. Severe contraction in the penis may cause it to rest in a reverse direction or become acutely angulate as, for example, shown in Pilsbry's illustration (1904-05, pl. 65, Fig. 42) of *L. vanattai*. Such cases must be distinguished from cases of natural angulation such as found in *L. flammea*.

The most tangible and constant specific, and to some extent generic, anatomical variations are found in the basal genital structures, and especially in the penis and its sheath. Before we seek an explanation for this, let us examine some of these variations or modifications.

As in any other evolving group, various combinations of characters are tried and often carried to extremes. Gigantism has always been a popular variation and it has been independently attempted in the genitalia of this group, by way of penial enlargement, several times. This, then, introduces an element of convergent evolution which invariably complicates interpretation. All the evidence indicates that penial enlargement is an experimentation in this group and is not a prototypic feature. Attenuation of the penis is another trend that has been tried, often concurrently with penial enlargement. Myopachynsis or muscle hypertrophy has been tried in the basal vagina of *A. fulica*, and closely related species, and in the penial sheath of *A. albopicta* as a still different type of variation. And as a final main type of variation found in the examined species, verge formation with attendant penial alterations has been undertaken by *Limicolaria* and *Limicolariopsis*. Some of these variations have initially taken place within the confines of the penial sheath and for this reason, brachyphallate species of wholly different stocks tend to look superficially very much alike until the penes are exposed.

A profound question is immediately apparent. Why is it that variations and modifications in the internal anatomy have been limited almost entirely to the basal genital structures and especially to the

penis and its sheath? An attempt to answer this cannot be made without indulging in dangerous speculation. Nonetheless, what seems to the author to be a plausible explanation is given here. The intromittent organ, which is formed often in a complex manner by the penis, the prepuce and the sheath, is the only internal structure that comes in direct contact with the external environment. Any variation in the form of the intromittent organ, such as would be caused if the proportions of its components were altered, might introduce an element of physical incompatibility with the receiving components of the female genital tract. There would thus be a premium of survival value put on the effecting of reciprocal changes in the complementary form of the female tract. A series of such variations and reciprocal changes in a given stock could lead to a definite trend that might eventually be culminated in a very exaggerated condition in certain structures. It is not a mere coincidence that the vaginae of the dolichophallate *A. panthera* and *achatina* are very long or that the basal vagina of *A. reticulata* has lost the cormoid proportions possessed by the closely related brachyphallate *A. albopicta* or that both penis and vagina are short in *Arch. osborni afromontana* and *Arch. simplex crawfordi*.

To hypothecate a strange, greater natural stability in all internal structures except the basal genitalia is but to beg the question. The basal genitalia have, because of copulation between different individuals, structural interrelationships of a variable nature not found between any of the other internal structures. The radula is the only other internal structure that can begin to approach this nature and it is notoriously a variable structure in most groups.

Of all the species examined, *A. fulica* proved to be genitally the most variable. This fact might be interpreted as an index of a general, basic genetic instability which could explain the great adaptability this species has demonstrated in the many different types of environments into which it has been introduced in the past hundred years.

Finally, the author wishes to make perfectly clear that it is not his intention to propose or even suggest that the achatinid genital characters should take precedence over those contained in the shell but, rather, that the two be used together to construct a sound classification in this confused group. In the past, the use of the shell characters alone, in most cases by sheer necessity, has been far from satisfactory as altogether too frequently such characters have proven to be intangible, over-lapping variations in degree of color, size, shape or sculpture. It has been shown in this study that many rather minor shell characters can be given real significance when they are backed by tangible differences in the genitalia. With the correlation once established, these minor shell characters are then used with confidence

in the absence of, or when it is not practicable or desirable to examine, the soft parts. As an example, a comparison at first of the very similar reticulately sculptured shells of *A. albopicta* and *reticulata* indicated no more than a subspecific difference between the two. An examination of the genitalia, however, revealed striking differences which most certainly were of specific caliber. On the strength of these differences alone, the two were set up as distinct species.

Cummings and Robson (1914) suggested in their short article that internal structures would probably be found to be of generic and ordinal value, whereas the external structures would be more valuable in determining specific and varietal differences. This belief was later retracted by Robson (1921) with the statement, "There would now be grounds for considering that the internal anatomy is neither more nor less variable than the external structures." In the light of the present study, neither the original suggestion nor its retraction leave what is believed to be the correct implications. Actually, a great deal of evidence has been brought forth in support of the contention that the genital characters are not only helpful but often indispensable in determining species and higher categories. Further, they have been shown to hold forth the only hope of determining the exact status of some of the apparently bastard genera in this family whose present status is based solely upon shell characters. On the other hand, this study has shown that the lower categories, in probably every case, must be determined entirely upon the basis of shell characters as witnessed, for example, by the condition in the three examined, anatomically indistinguishable subspecies of *A. fulica*.

Once again then, both conchological and anatomical data are required and their differences must be reconciled in order to put the Achatinidae in sound taxonomic status. But this cannot be realized until a great deal more anatomical data have been gathered. That is the immediate need in this problem.

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**PLATES**



**PLATE 1**

PLATE 1

Fig. 1. *Achatina achatina* (L.), genital structures. X  $\frac{3}{4}$ .

Fig. 2. *Achatina achatina* (L.), apical genital structures.

Fig. 3. *Archachatina marginata ovum* (Pfeiffer), basal genital structures. X  $\frac{3}{4}$ .

Fig. 4. *Archachatina degneri* Bequaert and Clench, genital structures. X  $\frac{3}{4}$ .  
AD — apical vas deferens; AG — albumen gland; AU — apical uterus; AV — apical vagina; BD — basal vas deferens; BU — basal uterus; BV — basal vagina; FO — free oviduct; GA — genital atrium; L — liver; O — ovotestis; OT — ovotestis duct; P — penis; PA — prostate; PR — penial retractor; PS — penis sheath; S — spermatheca; SD — spermathecal duct; SV — seminal vesicle; T — talon; TR — right tentacular retractor.

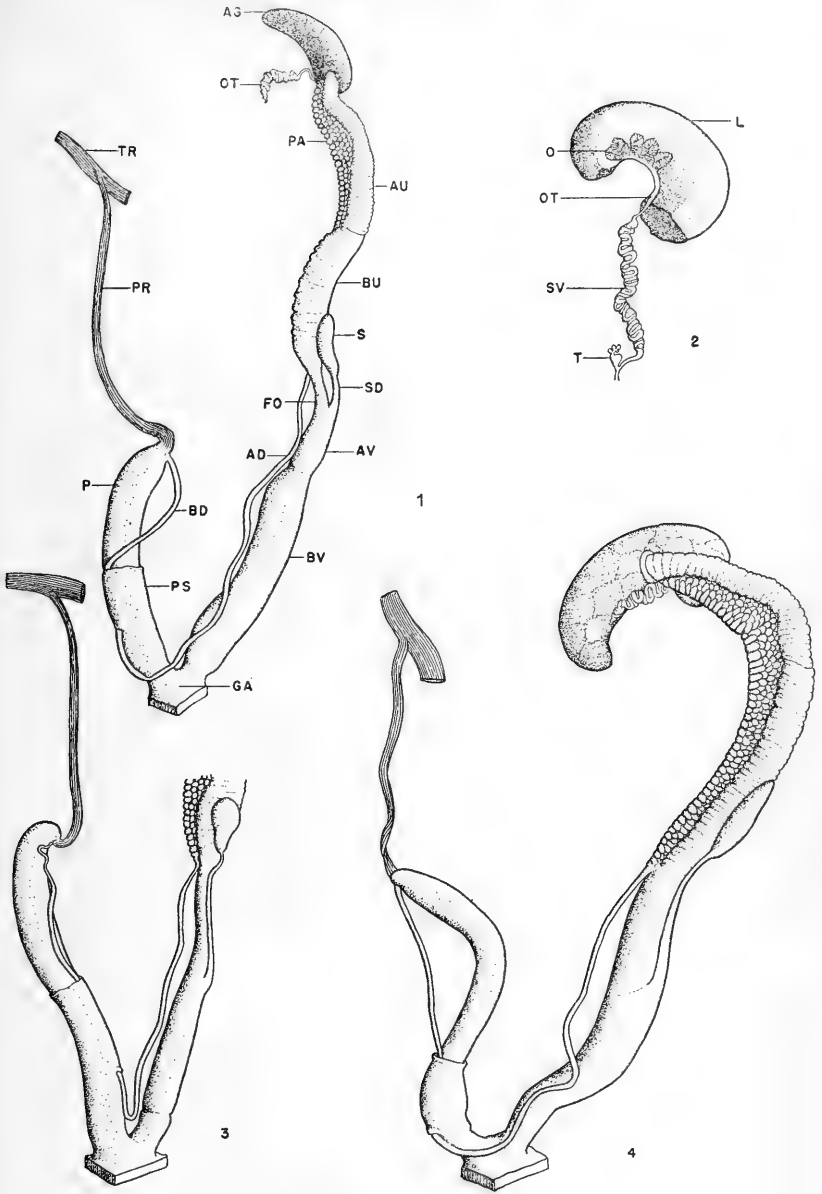






PLATE 2

PLATE 2

Fig. 5. *Achatina fulica hamillei* Petit, sheath cut to expose the short type of penis. X  $2\frac{1}{2}$ .

Fig. 6. *Achatina loveridgei* (Clench and Archer), basal genital structures. X  $1\frac{1}{2}$ .

Fig. 7. *Achatina fulica hamillei* Petit, genital structures. Natural size.

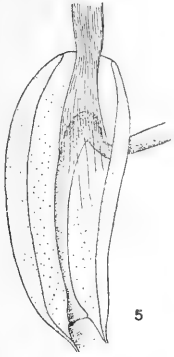
Fig. 8. *Achatina zanzibarica* Bourguignat, sheath cut to expose penis. X  $4\frac{1}{2}$ .

Fig. 9. *Achatina loveridgei* (Clench and Archer), sheath cut to expose penis. X  $2\frac{1}{2}$ .

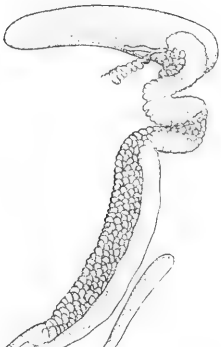
Fig. 10. *Achatina zanzibarica* Bourguignat, basal genital structures. Natural size.

Fig. 11. *Achatina fulica hamillei* Petit, sheath cut to expose the long type of penis. X  $2\frac{1}{2}$ .

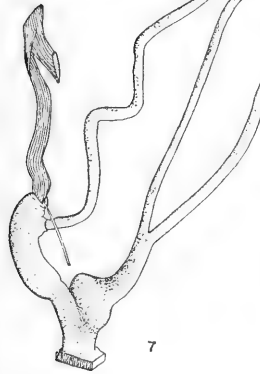
Fig. 12. *Achatina fulica hamillei* Petit, basal genital structures. Natural size.



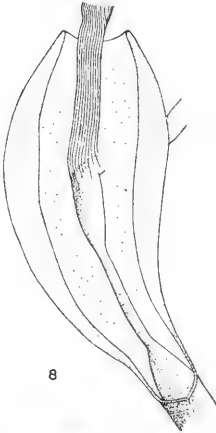
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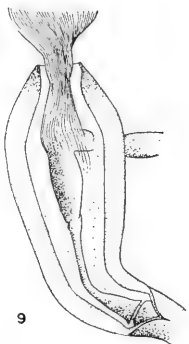
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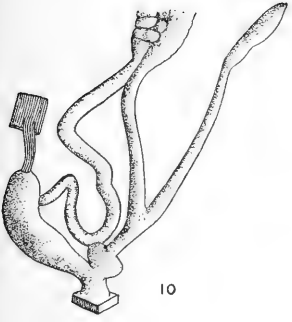
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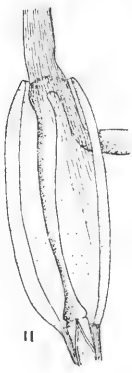
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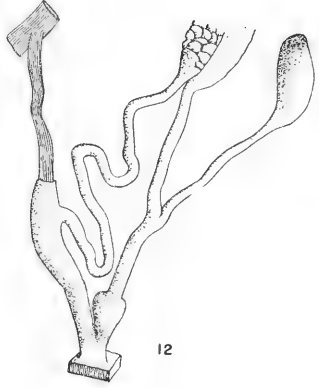
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**PLATE 3**

PLATE 3

- Fig. 13. *Achatina reticulata* Pfeiffer, basal genital structures. Natural size.  
Fig. 14. *Achatina albopicta* E. A. Smith, basal genital structures. Natural size.  
Fig. 15. *Achatina albopicta* E. A. Smith, talon.  
Fig. 16. *Achatina albopicta* E. A. Smith, sheath cut to expose penis. X  $2\frac{1}{4}$ .  
Fig. 17. *Achatina iredalei* Preston, sheath cut to expose penis. X  $2\frac{1}{2}$ .  
Fig. 18. *Achatina albopicta* E. A. Smith, basal vagina cut to expose lumen. X 2.  
Fig. 19. *Achatina iredalei* Preston, basal genital structures. Natural size.

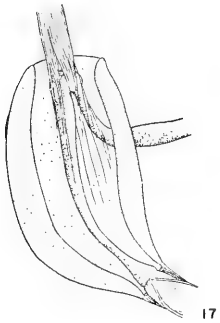
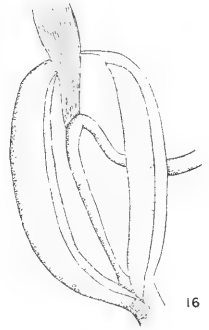
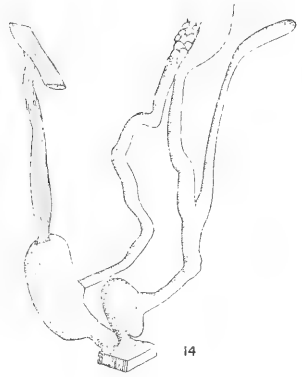
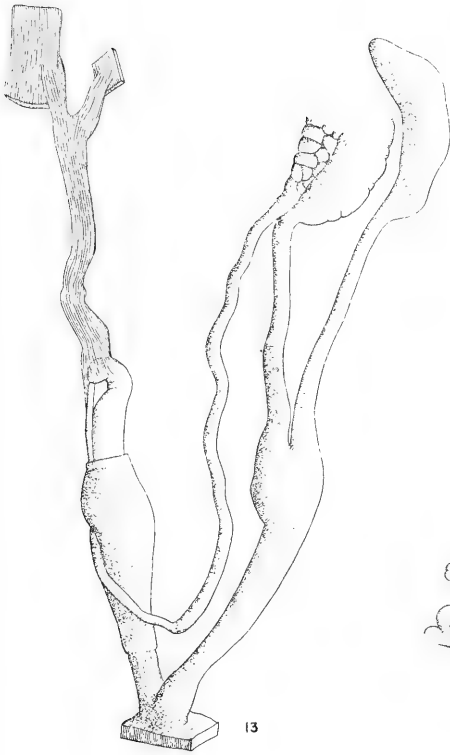


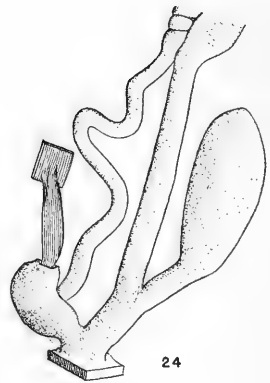
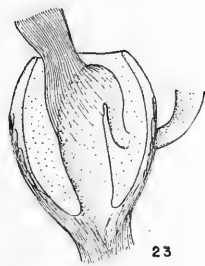
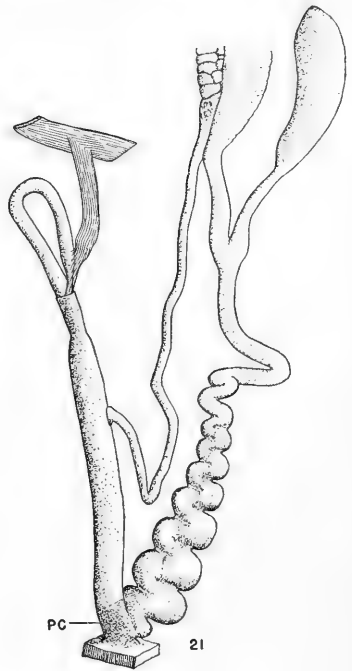
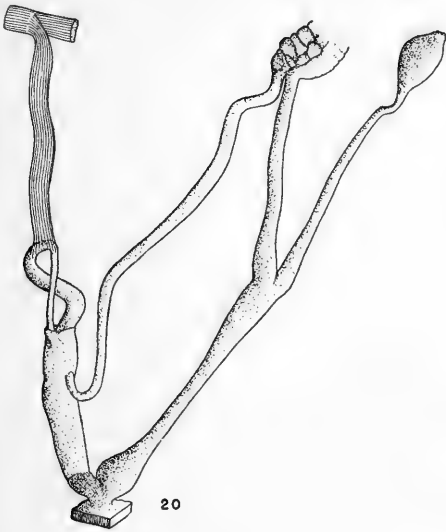




PLATE 4

PLATE 4

- Fig. 20. *Achatina glutinosa* Pfeiffer, basal genital structures. Natural size.
- Fig. 21. *Achatina panthera* (Férussac), basal genital structures. Natural size. PC—penial prepuce.
- Fig. 22. *Archachatina meadi* Bequaert, basal genital structures. X 2.
- Fig. 23. *Archachatina osborni afromontana* (Bequaert and Clench), sheath cut to expose penis. X  $2\frac{1}{2}$ .
- Fig. 24. *Archachatina osborni afromontana* (Bequaert and Clench), basal genital structures. X  $1\frac{1}{2}$ .





**PLATE 5**

PLATE 5

Fig. 25. *Archachatina bicarinata* (Bruguière), basal genital structures. X 11/20.

Fig. 26. *Limicolaria kambeul* (Bruguière), longitudinal section through basal male conduit. X 2½.

Fig. 27. *Archachatina simplex crawfordi* (Morelet), basal genital structures. X 2.

Fig. 28. *Archachatina simplex crawfordi* (Morelet), sheath cut to expose penis. X 3.

Fig. 29. *Archachatina simplex crawfordi* (Morelet), transverse section through apical penis and basal vas deferens.

Fig. 30. *Limicolaria kambeul* (Bruguière), genital structures. X 1½.

Fig. 31. *Limicolaria flammea* (Müller), longitudinal section through basal male conduit. X 2½.

Fig. 32. *Limicolaria flammea* (Müller), basal genital structures. X 2.  
SM — portion of sagittal myoseptum.

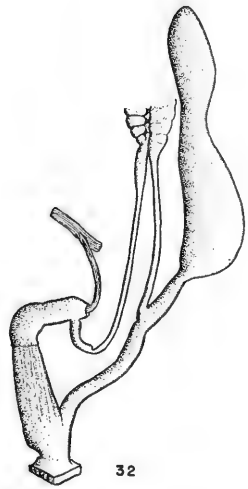
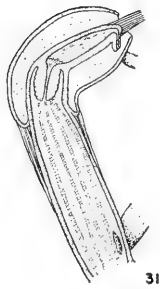
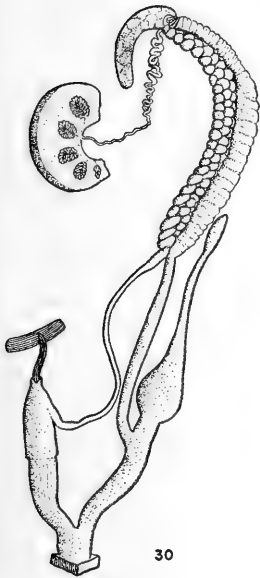
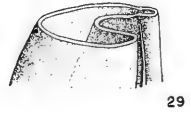
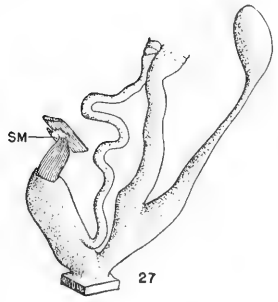
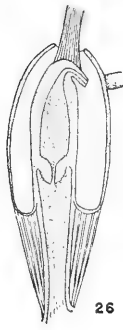
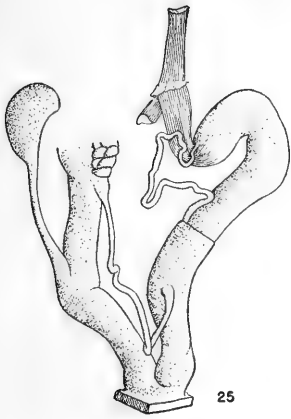


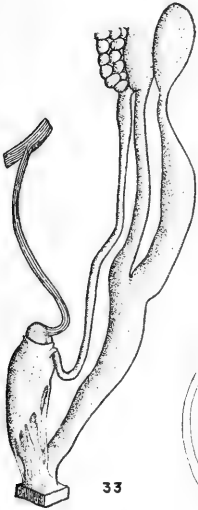




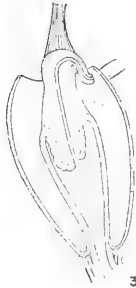
PLATE 6

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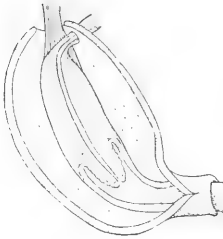
- Fig. 33. *Limicolaria felina* Shuttleworth, basal genital structures. X  $3\frac{1}{2}$ .  
Fig. 34. *Limicolaria felina* Shuttleworth, longitudinal section through basal male conduit. X 4.  
Fig. 35. *Limicolaria saturata capitellum* Pilsbry, longitudinal section through basal male conduit. X 4.  
Fig. 36. *Limicolaria saturata capitellum* Pilsbry, basal genital structures. X  $2\frac{1}{2}$ .  
Fig. 37. *Limicolaria ussuwiensis* Kobelt, longitudinal section through basal male conduit. X 4.  
Fig. 38. *Limicolariopsis kivuensis* (Preston), basal genital structures. X  $1\frac{1}{2}$ .  
Fig. 39. *Limicolariopsis kivuensis* (Preston), longitudinal section through basal male conduit. X  $2\frac{1}{2}$ .  
Fig. 40. *Limicolaria ussuwiensis* Kobelt, basal genital structures. X  $2\frac{1}{2}$ .



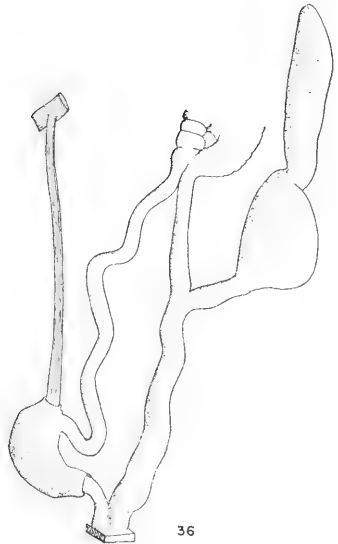
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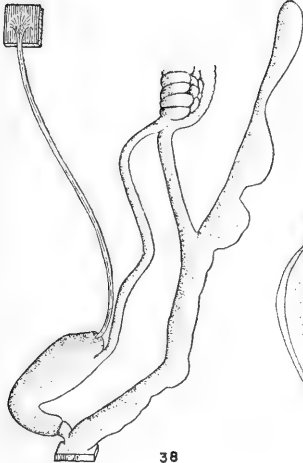
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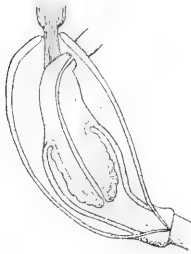
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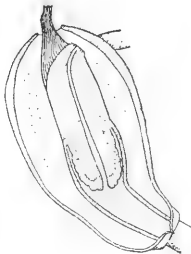
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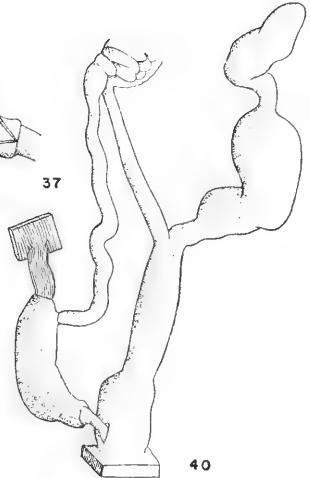
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PLATE 7

## PLATE 7

Fig. 41. Diagram of longitudinal section through the basal male conduit of the *Achatina fulica* type, showing basic relationships of the component parts.

Fig. 42. *Pseudotrochus turbinatus mucidus* (Gould), sheath cut to expose penis. X  $3\frac{1}{2}$ .

Fig. 43. *Pseudotrochus turbinatus mucidus* (Gould), genital structures. X  $1\frac{1}{2}$ .

Fig. 44. *Pseudotrochus turbinatus mucidus* (Gould), embryo within thin membrane. X  $2\frac{1}{2}$ .

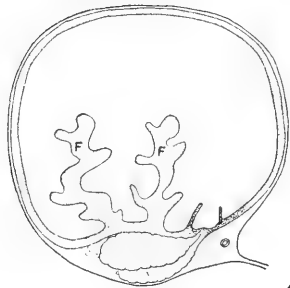
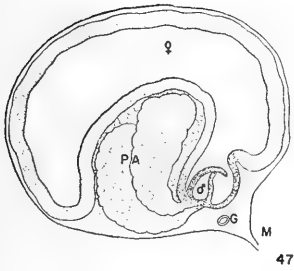
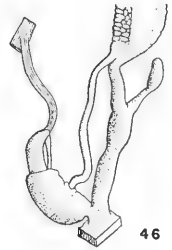
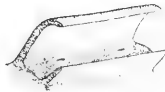
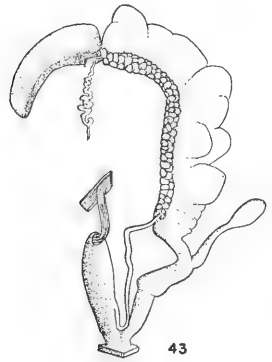
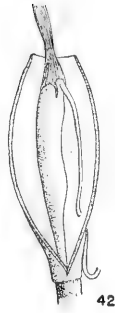
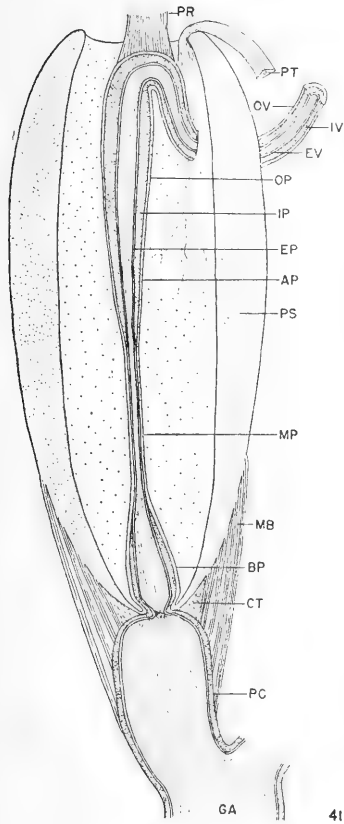
Fig. 45. A portion of the spermatid duct with the walls spread to show prostatic pores.

Fig. 46. *Pseudotrochus turbinatus mucidus* (Gould), basal genital structures of form with abbreviated sheath. X  $1\frac{1}{2}$ .

Fig. 47. Transverse section of achatine spermoviduct showing relationships of male and female conduits.

Fig. 48. Transverse section of gravid achatine spermoviduct.

AP — apical penis; BP — basal penis; CT — connective tissue; EP — epithelial layer of penis; EV — epithelial layer of vas deferens; F — longitudinal folds of uterine wall; G — genital artery; GA — genital atrium; IP — inner muscle layer of penis; IV — inner muscle layer of vas deferens; M — mesentery; MB — muscle bands; MP — medial penis; OP — outer muscle layer of penis; OV — outer muscle layer of vas deferens; PA — prostatic acini; PC — penial prepuce; PR — penial retractor; PS — penial sheath; PT — penial artery.



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PLATE 8

PLATE 8

Fig. 49. Stereographic antero-dorsal view of achatine anterior haemocoel, showing structures concerned in penial retractor insertion.

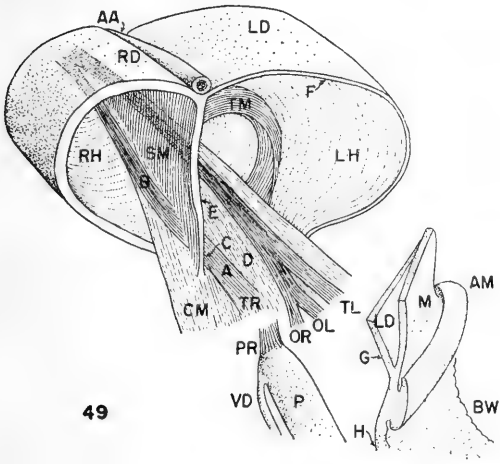
Fig. 50. *Achatina fulica hamillei* Petit, basal portion of male genital structures remaining after amputation of intromittent organ.

Fig. 51. *Achatina fulica hamillei* Petit, amputated intromittent organ cut open to expose internal components.

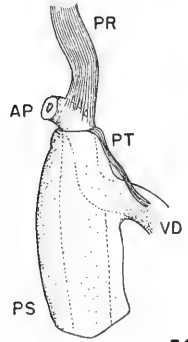
Fig. 52. *Achatina fulica hamillei* Petit, amputated intromittent organ, lateral view. X 2½.

Fig. 53. *Achatina fulica hamillei* Petit, amputated intromittent organ, dorsal view. X 2½.

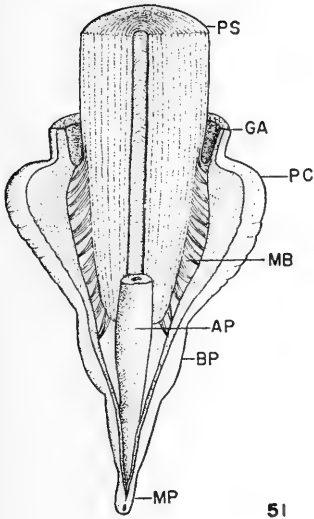
A — point of insertion of penial retractor; AA — anterior aorta; AM — anterior rim of mantle; AP — apical penis; B — point of insertion of penial retractor; BP — basal penis; BW — body wall; C — point of insertion of penial retractor; CM — columellar muscle; D — point of insertion of penial retractor; E — point of insertion of penial retractor; F — point of insertion of penial retractor; G — point of insertion of penial retractor; GA — genital atrium; H — point of insertion of penial retractor; LD — left diaphragm; LH — left haemocoel; M — mantle; MB — muscle bands; MP — medial penis; OL — left retractor of odontophore; OR — right retractor of odontophore; P — penis; PC — penial prepuce; PR — penial retractor; PS — penial sheath; PT — penial artery; RD — right diaphragm; RH — right haemocoel; SM — sagittal myoseptum; TL — left tentacular retractor; TM — transverse myoseptum; TR — right tentacular retractor; VD — vas deferens.



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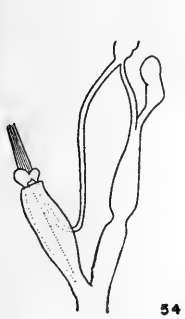
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PLATE 9

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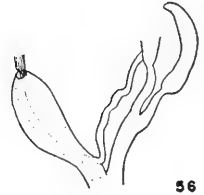
- Fig. 54. *Achatina dammarensis* Pfeiffer (after Degner, 1922).  
Fig. 55. *Achatina schweinfurthi* v. Martens (after Pilsbry, 1919).  
Fig. 56. *Achatina zebra obesa* Pfeiffer (after Robson, 1921).  
Fig. 57. *Achatina zebra fulgurata* Pfeiffer (after Robson, 1921).  
Fig. 58. *Archachatina granulata* (Krauss) (after Semper, 1874).  
Fig. 59. *Achatina lactea* Reeve (after Bacci, 1939).  
Fig. 60. *Burtoa nilotica obliqua* (v. Martens) (after Pilsbry, 1919).  
Fig. 61. *Limicolaria vanattai* Pilsbry (after Pilsbry, 1904-05).  
Fig. 62. *Pseudotrochus alabaster* (Rang) (after Semper, 1874).  
Fig. 63. *Atopocochlis exarata* (Müller) (after Furtado, 1888).



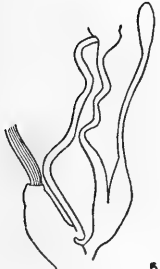
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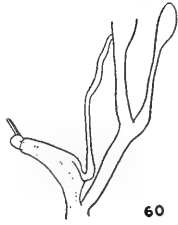
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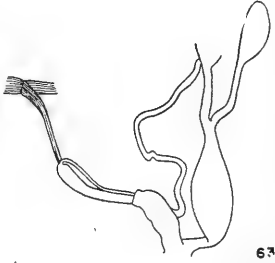
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AT HARVARD COLLEGE

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LIFE-HISTORY STUDIES OF EAST AFRICAN  
ACHATINA SNAILS

BY FRANCIS X. WILLIAMS

WITH FIVE PLATES

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# No. 3—*Life-History Studies of East African Achatina Snails*<sup>1</sup>

By FRANCIS X. WILLIAMS<sup>2</sup>

## CONTENTS

	PAGE
Introduction.....	295
Ecology of <i>Achatina</i> .....	297
1. <i>Achatina zanzibarica</i> Bourguignat.....	297
2. <i>Achatina fulica hamillei</i> Petit.....	298
3. <i>Achatina reticulata</i> Pfeiffer.....	300
4. <i>Achatina albopicta</i> E. A. Smith.....	300
Enemies of <i>Achatina</i> .....	304
1. Vertebrates.....	305
2. Crustacea.....	305
3. Mollusca.....	306
4. Insecta.....	308
Conclusions.....	317

## INTRODUCTION

The giant African land snail (*Achatina fulica* Bowdich) has been introduced mainly by the Japanese — as food and medicine — into many tropical and subtropical islands of the Pacific as far eastward as the Hawaiian Islands. In some of these islands it has increased enormously and is inflicting considerable damage to certain truck crops and to garden plants.

Prior to these introductions by the Japanese, *Achatina fulica* had found its way into other tropical countries: Ceylon, Malaya, Java, etc. And at a later date, it has threatened the Pacific coast of the United States by its temporary appearance there.

Since the United States Navy has taken over the government of the Pacific Islands formerly mandated to Japan, and governs other Pacific Islands as well, it is naturally concerned with the welfare of the inhabitants of these lands. In order to safeguard the agriculture of some of these Micronesian islands, it was necessary to combat plant pests chiefly through biological control, that is, by the introduction of suitable natural enemies of these pests. Hence, entomologists were assigned to this work. I was assigned the field study of the giant

<sup>1</sup> Published with the aid of a Grant from the Pacific Science Board of the National Research Council, Washington, D. C.

<sup>2</sup> Entomologist on a Navy Request Mission sponsored by the Pacific Science Board of the National Research Council, Washington, D. C.

African snail (*Achatina fulica*) and its enemies, with a view to the possibility of introducing some of its enemies into the Pacific islands.

After a brief stay in Washington, D. C. in November, 1947, in conference with Mr. Harold J. Coolidge, Executive Secretary of the Pacific Science Board of the National Research Council, from whom I received my directions, I went to Cambridge, Massachusetts, for a ten-day tutelage under Dr. Joseph C. Bequaert, Consultant for the giant African snail project, and Entomologist at the Museum of Comparative Zoölogy at Harvard University. Dr. Bequaert is a malacologist, of first standing, particularly as regards species inhabiting Africa, in which continent he has collected extensively.

On November 27, 1947, Mrs. Williams and I emplaned at New York for Africa. We stayed in British East Africa until June 19, 1948, returning to New York on June 21.

With the exception of a week's stay at Amani in Tanganyika Territory, situated in the Usambara Mountains at an elevation of 3,000 feet and about fifty miles by road from the coast, my work on *Achatina* was confined to the coast or within a very few miles of it. Here the rock, as exposed, was of coral formation with pockets or larger areas of soil interspersed. The forest, where still existing, was low and scrubby increasing to fairly lofty and often characterized by many thorny plants such as occur in xerophytic regions where the rainfall is sharply seasonal.

The British East African coast was examined at several points for about 200 miles, beginning at Malindi, some 70 miles north of Mombasa, and extending south through Mombasa and on into Tanganyika to Tanga, about 70 miles south of Mombasa, then to Zanzibar Island still farther south and some 22 miles off the Tanganyika coast, lying in latitude 6°10' S. The longest stay was in the Diani District, about 20 miles south from Mombasa, where most of my observations were made, from March to June. Here the rainy season, though rather abortive in 1948, made conditions favorable for my work. The *Achatina* involved was *A. albopicta* Smith, a species extremely abundant in and about the low coral-base forests around the Diani Beach Hotel, especially. Other species of *Achatina* on which data were secured were *A. fulica hamillei* Petit from Mombasa, Tanga and Zanzibar and *A. fulica rodatzki* Dunker from Zanzibar.

The writer desires to acknowledge his indebtedness here to the Insect Control Committee for Micronesia of the Pacific Science Board of the National Research Council, who selected him for this assignment and rendered every possible assistance. The United States Navy and particularly the Office of Naval Research approved and granted the funds to finance this research project and demonstrated their efficiency

in the matter of transportation and dealing with what is known as "red tape." I am also under obligation to Mr. Harold J. Coolidge, Executive Secretary of the Pacific Science Board of the National Research Council, for his kind personal concern and able management; and to Dr. Joseph C. Bequaert for his encouragement, helpful advice, and generous imparting of useful knowledge of African malacology that I would not have acquired otherwise. All the Mollusks referred to in this paper have been determined by Dr. Bequaert. Also, I wish to make grateful acknowledgement to numerous government officials and scientists who furthered my work in Africa most generously. Some of the photographs of live snails were taken in Cambridge by Miss Ruth Turner; those of material in East Africa are by Mrs. F. X. Williams, to whom I am further indebted for assistance in many ways in the field.

Cambridge, Massachusetts  
November 7, 1948

## ECOLOGY OF ACHATINA

### 1. ACHATINA ZANZIBARICA Bourguignat

This rather small to medium-sized species was taken in late January and early February, 1948, a short distance within the forest surrounding the East African Agricultural Research Institute, at Amani, in Tanganyika Territory. It did not appear common. A single well-grown individual was found in the forest in the shelter of a root of a large tree, and three other large ones were secured by agricultural workers. By scraping off the litter in the forest, several dozen living young with shells from 8 to 18 mm. long were found. The great majority of these were in one or more scattered colonies at or near the base of a huge buttressed tree. They were in a resting state, their shells being very generally closed by an epiphragm. Other small *Achatina* shells were cleanly empty and sometimes with the rim broken back, indicating the presence of enemies. Some of the young shells placed in alcohol yielded one or two rather large dipterous larvae, the status of which was not determined.

A large specimen of *A. zanzibarica* was kept for several days in a jar with leaf portions of cabbage, celery and lettuce. The leaf portions remained untouched. But the dark brownish excrement of the snail indicated that it may have fed upon a portion of a fleshy seed pod, which had also been enclosed in the jar. It is quite likely that when the snails are activated by the wet season, green leaves would be eaten.

More than thirty of the young *A. zanzibarica* were kept for over six weeks in a large jar in which leaf trash and paper had been added. Upon the addition of a little water the snails became active and ate holes in the paper, and probably devoured some of the dead leaves, as considerable excrement accumulated in the jar.

## 2. *ACHATINA FULICA HAMILLEI* Petit

This is a large snail with a very dark foot and a moderate to short spire. It was observed from Malindi to Mombasa, at Tanga and on the island of Zanzibar. Of the several colonies of this mollusk observed at Mombasa, the one occupying an old and abandoned Mohammedan cemetery, amply shaded, and with the monuments and enclosures, of calcareous stone, often in sad disrepair among the weeds, proved the most populous and interesting. This two-acre snail center, so easy of access, would seem an ideal spot for extended biological observations, were it not for the fact that, however neglected, it still was a cemetery, and for one to rummage among graves would be to invite suspicion among the crowded populace as well as instilling a certain feeling of guilt in oneself. However, keeping on good terms with the head grasscutter of this rather unsanitary area, helped a good deal.

When I visited this cemetery in early December, 1947, the weather was hot and dry, and the few *Achatina* that I examined were aestivating, being often slightly buried in the litter, and with a calcareous epiphragm bearing a slit-like groove upon its surface, closing the mouth of the shell. Most of the shells containing mollusks were of considerable size and a number were mature. Some shells had suffered much injury and showed obvious repairs thereto. Several *Achatina* were found at a height of 4 to 6 feet wedged in a deep groove in the trunk of one of the baobab trees there, aestivating. The presence of very young shells, all empty, showed that there had been some oviposition not very long previously. And elsewhere in Mombasa, on December 6, I found a cluster of eggs in a depression, corresponding to about half a tennis ball, in the shelter of a coral stone that bordered a path. The eggs were pale sulphur yellow, short-oval and about 5 mm. long. Some of the eggs occupying the deeper, slightly moist strata had hatched.

On December 13, there was a morning rain sufficient to wet the streets of Mombasa and to cause some of the *Achatina* to cast off their epiphragms. On December 15, a heavy morning shower brought out a number of the big fellows. Night activity probably also took place. A few days later, under the influence of dry weather, snails were again observed slightly buried in the soil. There had been some feeding by

the snails, however, as indicated by green droppings. When, on May 7, 1948, I again visited Mombasa to make observations on *Achatina*, monsoon rains had already fallen and fields and gardens were green. In the cemetery many large *Achatina* were crawling over the ground and one small group was revelling in a meal of damp old paper and cardboard. A large brood of recently hatched young were observed at the base of a sheltered wall and on and in the soil adjoining. Some weeks later a group of young, about double in size of shell than when just hatched, were seen on a wall. Enemies such as beetle larvae of the families Lampyridae and Drilidae and small streptaxid snails had already attacked these baby *Achatina*.

*Achatina fulica hamillei* was common on the island of Zanzibar. In January, 1948, I secured through the kindness of one of the government officials at the Kizimbani Agricultural Experiment Station, a large quantity of these snails collected when they were on the move at night. Most of these snails were immature. Among them were a few specimens of *Achatina fulica rodatzki*, an albino phase of the species, and some *A. iredalei*, a species of smaller size. *A. f. hamillei* was a familiar sight on the trunks of coconut palms, where they were stationed at heights from near the ground to at least ten feet and rarely ascending to as much as fifteen, as shown by the snail excrement adhering at that height.<sup>1</sup> Some of the snails were in movement on the trunks. I recall seeing on the trunk of a palm two specimens of the yellowish white *A. f. rodatzki* side by side among typical forms.

When I revisited Zanzibar in early June, young *Achatina fulica hamillei* of considerable size were in evidence. The snails, however, were still laying eggs, as shown in cleaning out the shells. On June 10, fair numbers, ranging in size from about 28 to 75 mm., were observed high up on tall cassava (*Manihot*) plants. I was told however, that they did no damage. Farmers in general seemed to pay little heed to these mollusks, although I was informed that years ago *Achatina* had become numerous enough to damage cassava and some other plants.

My few inquiries in East Africa as to whether these snails were ever eaten by man, brought negative replies. In this connection however, it is interesting to quote M. Connolly (A Monographic Survey of South African Non-marine Mollusca, Annals of the South African Museum, **33**, p. 326, 1939). In referring to the wide distribution of *Achatina fulica*, he concludes: ". . . , a remarkable fact when we remember that in their natural home on the east coast these creatures

<sup>1</sup> In July, 1948, on Koror, Palau Islands, in the tropical Pacific, the writer observed *Achatina fulica* quite commonly on trees and steep rocky banks. It ascended trees to an altitude of perhaps twelve feet, and sometimes small clusters of the snails could be found on the stems. The shells, particularly the last whorl were sometimes much broken due perhaps to falling off their perch.

do no harm whatever, save it to be to give possible indigestion to the indigenes who regard them as a culinary delicacy.”

For an account of *Achatina fulica* in Hawaii the reader is referred to an excellent paper by C. E. Pemberton (Hawaiian Planters' Record, **42**, pp. 135-140, 1938). A bibliography referring chiefly to its introduction elsewhere is included. See also Jarrett, V. H. C., The Occurrence of the Snail *Achatina fulica* in Malaya (Singapore Naturalist, No. 2, pp. 73-76, 1923). Further information on this snail in the Pacific (Marianas: Saipan) is given by Dr. W. H. Lange, Field Associate in Entomology, Pacific Science Board, in a mimeographed First Report of the Pacific Science Board of the National Research Council—Insect Control Committee for Micronesia—1947, on pp. 6-8. The most recent account that I have seen is by R. Tucker Abbott: The spread and destructiveness of the Giant African Snail, *Achatina fulica* (The Nautilus, **62**, pp. 31-34, 1948). See also an informative report by E. E. Green on the history of *Achatina fulica* in Ceylon (Report on the Outbreak of *Achatina* in Ceylon; Circulars and Agricultural Journal of the Royal Botanic Garden, Ceylon, **5**, No. 7, Aug. 1910, pp. 55-64).

For damage to crops by *Achatina* in East Africa, see Entomological Leaflet No. 17, Dept. Agric. Tanganyika Territory, Dar es Salaam, 1938; Entomologist's Report (*Achatina craveni* Sm. damaging sesame and coffee).

### 3. ACHATINA RETICULATA Pfeiffer

Two brief visits to Chwaka Bay, on the east coast of Zanzibar, sum up my acquaintance with this large snail. It was rather common at a few hundred feet in from the seashore in the dense brush growing on a difficult terrain of rough coral formation. All that I recognized as *reticulata* were of large size. In June, one of these in a sheltered place in the rather moist environment still retained its epiphragm. None was observed on bushes or the coral banks. A single fire-killed specimen contained some eggs, well roasted.

### 4. ACHATINA ALBOPICTA E. A. Smith

On March 12, 1948, we arrived at Mombasa from a scouting trip in Uganda. The monsoon rains had not yet fallen and the country remained dry and very warm. Time was pressing, and we immediately set about looking for a permanent station where I could make extended field studies on *Achatina* and its enemies. One of the important officials of a larger Mombasa hotel kindly gave us a list of likely little country



hotels along the coast adjacent to Mombasa, and of which there were a surprising number tucked away among the trees along the magnificent beaches bordering the Indian Ocean. The first place, a very short distance from Mombasa, proved unsuitable, although dead shells of *Achatina* were found there. Pursuing our way further to the south along a road of very indifferent quality, for a distance of twelve or fourteen miles, we entered a side road, bordered by lantana and other bushes and small trees, that passed through a terrain composed largely of coral. As the rather decrepit vehicle bounced along, I peered over the side and with some difficulty fixed my gaze along the side of the road to perceive *Achatina* shells present in very gratifying numbers. The road soon terminated at the Diani Beach Hotel, in the Diani District. Arrangements were immediately made to occupy one of the bandas, a little two-room cottage plus bath: cement floor, coral-block walls, whitewashed exteriorly, and a roof of coconut palm thatch. The veranda extending along three sides of the building was covered with clean coral sand. We moved in on March 16. The spare room and veranda adjoining constituted the laboratory. Situated among trees, some 200 to 300 feet from the seashore, it was backed by a scrubby forest, much of it being of a thorny character, with many perennial vines and interspersed with large trees, such as the baobab, and an occasional branching palm (*Hyphaene coriacea* Gaertner). Nearby was an area of taller forest. The country, at least for a considerable distance inland, showed a coral formation,<sup>1</sup> with shallow soil and soil pockets. The soil composing these pockets and even that beneath the rather heavy forest litter was somewhat moist, and while the dry season still prevailed, many plants were in flower and tufts of green grass sprang up plentifully. This condition may be attributed in part to the heavy morning dew that was said to be then prevalent.

March 16. The whole forest abounded in *Achatina albopicta*. Most of the shells in full view were empty; some recently so and hence still well marked, while others had weathered over a long period and showed little or no pattern. It was chiefly among the latter that the largest shells, very rarely attaining a length of 175 mm., were found. But living snails were numerous under debris as well as slightly in the soil at the bases of trees and bushes, so that hundreds could be easily collected in a single day. Mollusks with shells over 100 mm. long were found only in moderate numbers, those between 50 and 80 mm. were abundant, while still younger living *Achatina* with shells 22 mm. or less were not commonly found. But there were many very young shells frequently broken and with the mollusk cleanly removed; these probably indicated the presence of enemies, and would also

<sup>1</sup> The coral deposit is so massive that it is quarried into large building blocks.

appear to indicate that, from one to several months previously, there had been considerable oviposition among the *Achatina*. Most of these snails and some other kinds as well, were in the resting condition, with an epiphragm sealing the mouth of the shell. There was however, some little activity among them, probably during the hours of darkness, for droppings and trails of slime were present here and there.

This *Achatina*, though essentially terrestrial, does climb trees and walls. It also climbs down from these heights — the spire then pointing downward —, and I believe, often falls to the ground, from the stress of sheer weight, particularly when it is awakening from its resting stage and would then attempt to seize hold of the substratum. A word here about the epiphragm elaborated by the snail to seal its shell when it is about to aestivate, will be appropriate. When passing the dry season more or less buried in loose soil or debris, it consists only of a calcareous sheet — with a narrow, slit-like groove — that extends conformably across the aperture at a slight distance from its margin. But when *Achatina* aestivates on a tree trunk it must adhere there. Perhaps it glues the margin of the shell to the bark, but this is hardly sufficient, at least in the case of a big heavy shell and mollusk. Hence one finds that the middle of the epiphragm has been widely and ovably extended as a shelly tube — perhaps to one half of an inch in length — to the bark to which it is glued, with a sort of pedestal effect. When the snails awaken and move away, these delicate calcareous objects, often more or less broken, may be quite numerous adhering to the huge trunk of some baobab tree, from a few inches to rarely twelve or thirteen feet up (Pl. 4, Fig. 1). Some of these modified epiphragms may date back to more than one season. I do not recollect seeing very small epiphragms upon the trunks of trees. *Achatina* often rests in the grooves or folds on the trunks of trees (Pl. 3, Fig. 3).

Early April rains at Diani brought out many *Achatina albopicta*. The majority remained on the forest floor, but some were ascending trees and shrubs. Later in the month heavier precipitation activated quantities of snails, so that in sheltered places, such as in the shade of a baobab, many were moving about or feeding until well in the middle of the afternoon. At dusk, numerous *Achatina*, usually not mature, ventured on roads, so that some were crushed by vehicle or pedestrian. On the evening of April 3rd, Mrs. Williams and I counted approximately 150 *Achatina* in a roadside area of about thirty square feet. This was a density greater than usual, in our experience.

These snails were seen climbing trees late in the afternoon or early in the evening. The greatest height at which I have seen one of these *Achatina* was an estimated nineteen feet, up the vertical trunk of a

baobab. Another was observed descending the trunk of such a tree from a height of about twelve feet. On June 3, three large *Achatina* were noted on the straight, relatively smooth trunk of tall forest trees at a height of about eight, ten and fifteen feet respectively. In places in the low forest they became common on the small trees, occasionally ascending to thirteen or fourteen vertical feet. More often than not they were well within the reach of the hand. It was evident that many remained on shrubs or trees for some time and often their excrement was deposited on the tree trunk or branch just above and to one side of the shell. Sometimes snails were found upon the leaves of a bush, the mollusk travelling along so slender a twig that its foot clasping this twig met broadly on the far side. Deposits of excrement, some of it greenish, occurred on bushes, tree trunks and on the ground.

Considerable rain seemed to be required to bring out quite small *Achatina*. They would then emerge from among soil and debris at the base of shrubs and trees and climb up the stems. Decaying heaps of trash thoroughly wetted by drenching rains in late April, produced multitudes of *Achatina*, both large and small.

Feeding. *Achatina albopicta* may eat a great variety of food, its tastes evidently being about the same as those of *Achatina fulica*. When freshly out of aestivation I have observed them many times munching at decaying leaves on the forest floor, their jaw often producing a fine scratching sound as they feed. The rind of an orange and the pulp in the pod of the baobab is to their liking. Yellowing leaves and green ones are also eaten. Among the plants that serve as food are *Commelina* sp., *Haemanthus* (Liliaceae), *Lantana camara* (Verbenaceae) *Carica papaya* (Caricaceae), *Boerhaavia diffusa* L (Nyctaginaceae), a small Euphorbiaceous weed, *Plumeria* (Apocynaceae), a leguminous shrub, a slender weed with a milky juice (Compositae), and lettuce. The leaves of many undetermined plants also served as food. A certain, finely branched shrub with soft leaves that was growing near the beach, was much patronized, particularly by the younger *Achatina*. But the eating of its leaves was not severe. They were often found high up on lantana bushes, while leafy bits of lantana branches that had fallen along the road were sure to be visited by them in the evening. These snails nibbled at fallen wild fruit, including the tough husks of the nuts of *Hyphaene coriacea*. Small groups of *Achatina* were seen feeding upon their fellows crushed on the roadside. They nibbled at the tough droppings of the pigmy deer, and I have seen as many as thirty individuals gathered about human excrement. *Achatina* is known to ingest coral, upon which I have often observed them apparently engaged in eating. Holes that appear to have been rasped, in empty shells suggest the work of *Achatina*. Furthermore, these snails climb the whitewashed coral walls of build-

ings, presumably in their search for lime. To complete this inadequate list of what *Achatina* swallows, the drinking of rain water accumulated in old shells was observed.

In all its feeding *Achatina*, though easily disturbed, impressed me as being leisurely, even desultory, in contrast to the brisk activity of a caterpillar engaged upon the same task. However, they can occasionally do considerable damage to succulent plants.

Breeding. The first observed mating was on April 27, the two snails joined by their sexual organs, lying side by side. Examination at this time of the ovaries of an *Achatina*, showed eggs not yet separating and but slightly developed. The next matings observed in the forest were on the mornings of May 1, 2, 3 and 4. Although some of the snails involved were of considerable size, none was mature. The following are the measurements of the pairs in mm.: 70 and 83, 73 and 117, 75 and 85, 78 and 115, 80 and 100, 82 and 120, 90 and 90, and 93 and 100.

On May 4th I discovered an *Achatina albopicta* with a shell 98 mm. long, in an area recently cleared of weeds. The mollusk, which had probably been sun-killed, contained a number of eggs visible within its last whorl. Further within the shell were numerous fly maggots. On May 31, just off a roadside, I found an overturned *A. albopicta*, its shell being 130 mm. long. It had probably been sickened by the sun for it was still alive. A large quantity of its pale yellow eggs lay alongside on the ground. They numbered approximately 330.

On May 25, and June 3, I examined some cut stems of the papaya "tree." These stems are largely hollow, juicy and brittle, though quite heavy. They had been placed several together on the ground near a pile of weeds alongside a thicket. The tissues of this plant are very attractive to *Achatina*. The rind had been scored rather deeply by their feeding, and where accessible the hollow interior of the stems was crowded with the snails. Even withered and dry papaya leaves were being munched. Under a felled papaya trunk there were numerous tiny *Achatina*, of two broods or sizes, and some young just hatched (May 25), besides a few eggs. Some of the tiny snails were feeding at the rind where it had been scored by the large *Achatina*.

#### ENEMIES OF ACHATINA

In places disturbed by man *Achatina* may be killed off in large numbers. Fires destroy a great many; quantities are crushed on roads; others that did not retire to a dependable shade by sunrise, may in the open spaces be killed by the heat of the sun.

The enemies of *Achatina* are fairly numerous. Among them are carnivorous snails (Streptaxidae), carabid beetles, and drilid and lampyrid beetle larvae. Certain vertebrates also feed on these snails.

### 1. Vertebrates

*Bdeogale tenuis* Thomas and Wroughton, of the Viverridae or civet cat family, is a mongoose-like animal known to feed extensively on *Achatina*. The animal holds the mollusk between its paws and strikes it rapidly against some hard object until the shell is broken. While in Zanzibar, where *Achatina fulica hamillei* is prevalent, some natives showed me five places near their village where the *Bdeogale* broke these shells, the noise of its operations being sometimes heard at night. In two instances the animal used coral outcrops as breaking blocks, in two others the base of a smooth-stemmed tree, while in the fifth instance a stone that had become firmly lodged near the level of the ground between the branches of a small tree served this purpose. Such places may be used over a considerable period, as shown by the quantity of broken shells and by the degree of weathering among them. As many as fifty shells, mostly broken ones, were found strewn about an eight-inch tree trunk, over a diameter of several feet. Generally, the shells were immature and about three inches long with the margin thin, though strong, and quite a task even for a man to break by striking it against some hard object.

At Diani Beach, on the mainland, I found evidence of the work of *Bdeogale* among *Achatina albopicta*. The species involved here was probably *B. crassicauda* Peters; or, it could have been a species of another genus of the Viverridae.

The *Bdeogale*, like some other members of the family Viverridae of shell-breaking habits, no doubt has tastes that would render it undesirable as an introduction elsewhere.

Scattered over the forest floor are many empty *Achatina* — and other shells — particularly quite immature ones, cleanly empty ones and frequently with their thin margins broken back. Among the several factors that may be responsible for the premature death of those mollusks, rodents must play a part here, as they are known to do elsewhere.

### 2. Crustacea

Land crabs. A sturdy, pinkish or light brown crab living in holes in the sand-mixed soil at some distance behind the beach in the Diani district, is an enemy of *Achatina*. The large mollusk literally swarms

in parts of the scrubby forest that may extend to the seashore, so that it not infrequently falls a victim to the redoubtable crustacean. On three occasions the crab was observed feeding on *Achatina* at the mouth of its burrow, to which it had probably dragged the mollusk. With its strong chelae, it cuts out portions of the shell to enable it to reach the meat within (Pl. 3, Fig. 2; Pl. 5, Fig. 5). One rather small crab, with a carapace one and three-fourth inches across, was found to have overcome an *Achatina* with a shell nearly two and one-half inches long.

Other observed prey of this land crab were a large cylindrical millipede, in this case four inches long, the body of which had been deeply cut into by the crab's sharp nippers, and a stout four-inch long black and brick red caterpillar with strong spines, of a ceratocampid (?) moth. Numerous such caterpillars were observed one morning descending the trunk of a tree to enter the ground or hide beneath debris for pupation.

### 3. Mollusca

Streptaxidae (Carnivorous or rapacious snails). Probably the most effective enemies of *Achatina* as observed in East Africa, are the carnivorous snails. With this statement Dr. J. C. Bequaert, who has long studied the *Achatinae* in Africa, concurs. Although naturally less abundant than their prey, the Streptaxidae are numerous in species. As far as I have observed, they are of generally secretive habits and very seldom found off the ground. They are frequently active under the cover of dead leaves and sometimes seek their prey barely beneath the loose soil. Some of the small species may occur under logs and large stones. *Edentulina affinis* C. R. Boettger, a large species, was found in a single instance about two feet off the ground on the underhanging side of the partly dead trunk of a sloping tree. It seemed to have followed an *Achatina* there, for the empty shell of the latter was resting on a small projection at a little distance below the streptaxid. Rarely, dead shells of *Edentulina* were found on the spreading roots overlying the ground, of a large tree.

Nearly all my data referring to *Edentulina* and *Gonaxis*, comprising the larger predacious snails, were obtained in the Diani District in the months of March, April and May. Under dry conditions, during the first part of my stay there, many of these snails were in a resting condition, having sealed the aperture of their shell a short distance within with a thin epiphragm. While they kill large numbers of *Achatina*, they are not selective and likewise attack other species of snails — and slugs — in laboratory experiments. They will eat their

own kind in the laboratory and at least sometimes in the field. One species of terrestrial snail that to some extent appeared successful in resisting the attacks of the carnivorous species was *Maizania magilensis* (Craven), which is provided with a strong corneous operculum.

*Edentulina affinis* has a whitish convexly-conic shell that reaches a length of about 50 mm. The mollusk itself is orange. Empty shells were far more commonly found than living specimens. The former were scattered over the forest floor, so that thirty or more specimens might be collected in half a day. Living *Edentulina* were found under dead leaves, in soil pockets among the coral substratum, and more or less secreted under large root bases overlying the ground. They occurred singly or, as once noted, as a small colony of half-grown, well-spaced individuals. They were not often found in exposed places. On April 2, a young one was noted upon a leaf on the ground; on May 10, an adult was found resting about two feet up the under slope of a tree trunk; and on the same date another grown *Edentulina*, 43 mm. long, was observed on the forest floor devouring an *Achatina* with a shell 55 mm. long, the slender fore part of the carnivore being deeply inserted into the aperture of the shell of its victim (Pl. 3, Fig. 5). On May 2, towards evening, another adult *Edentulina* was taken in the middle of a wooded road where it had been feeding upon the crushed remains of an *Achatina*.

Most of these findings were during the wet season.

Wholly consuming as they may their so often relatively large victims, both *Edentulina* and *Gonaxis* are frequently too gorged to immediately attack another snail. Not only is the mollusk itself devoured but the shell may, in the need for lime, be scraped to a point of local collapse.

It is probable that the biotic potential of *Edentulina* is less than that of *Achatina*. It probably lays fewer eggs, and, being specialized to a diet of flesh, would turn to (greater ?) cannibalism in times of scarcity. These large carnivores have their enemies also. Drilid beetles reduce their numbers, and it was not unusual to find both young and mature shells of *Edentulina* as well as *Gonaxis* containing the bristly, caudally pronged moult skin of a drilid larva.

Along the coast some eight or nine miles north of Mombasa, the empty shells of the smaller *Edentulina obesa* (Taylor) were found.

*Gonaxis kibweziensis* E. A. Smith. This smaller, apparently more hardy and adaptable species outnumbered *Edentulina affinis* roughly five or six to one. The shell is wide and dorso-ventrally distorted, as if stepped upon obliquely, so that the aperture is far off center. The whorls are delicately ribbed. It is translucent whitish so that the orange mollusk is visible through the shell. The greatest length is about 22 mm.

*Gonaxis* was for a time rather easy to find under leaf cover and in the loose, often sandy soil at the base of grass clumps; similarly under small low spreading trees, at the base of a coral escarpment and in soil pockets. Usually this snail was more readily found during the dry season when there was less vegetation to interfere with its search. I once found a number of young *Achatina*, from about 15 to 35 mm. long, among dead leaves and slightly moist soil at the foot of a small tree. In this colony were three adult *Gonaxis* each of which was feeding upon an *Achatina* somewhat smaller than itself. Later on, I uncovered two adult *Gonaxis*, the one being devoured by the other, the victor with its fore part deeply inserted into the nearly empty shell of the vanquished. On the other hand, a *Gonaxis* in the laboratory was observed feeding side by side with an *Edentulina* upon an *Achatina* 60 mm. long, which the larger carnivore had overcome. A single *Gonaxis kibweziensis* evidently killed by the heat of the sun was collected on a road, beside an *Achatina* that had been crushed by pedestrian or vehicle.

*Gonaxis* also feeds extensively on *Pseudoglessula boivini* (Morelet), a rather small snail with an oblong-conic, finely striated shell that dwells among dead leaf cover and soil.

Young *Gonaxis* were not uncommon, but no eggs of this snail were certainly identified as such.

Among the few other species of carnivorous snails observed were some belonging to the genus *Gulella*. These small, often strongly sculptured snails are probably effective enemies of quite young *Achatina*, among which they may sometimes be found.

#### 4. Insecta

Carabidae (ground beetles). A number of Carabidae of large size were found in East Africa. Species representing several genera, including *Anthia*, *Calosoma*, *Galerita*, *Psecadius* and *Tefflus*, were given laboratory tests to determine if they would feed on living *Achatina* snails.

*Anthia* sp. This black beetle marked with whitish, of rather savage disposition, emits a strong defensive secretion. It would not touch small *Achatina*. Neither would a smaller, roughly sculptured, all-black species of *Anthia*.

*Calosoma* sp. A swift black beetle over an inch long. It savagely ripped open and devoured the hairy caterpillars I offered it. Under stress of hunger it devoured young *Achatina*. Two of its victims had shells 30 and 38 mm. long, respectively.

*Galerita* sp. This slender beetle refused small *Achatina*.



*Psecadius*. Nearly three-fourths of an inch long. Shaped somewhat like a *Cychnus*. Elytra spotted. They refused several freshly hatched *Achatina* offered them.

*Tefflus* spp. A purely African genus. The fore part is relatively narrow with the thorax heart-shaped and the strongly-grooved wing covers fused together, gently tapering at either end; apex subtruncate in the female. Running with moderate speed. They appear to be rather uncommon.

Three or four species of these rather mild-mannered beetles were found. Smaller species, a little more than an inch long, taken at 3,000 feet in the Usambara Mts., and in the Diani District near Mombasa, would not eat *Achatina*, even quite young ones. It is possible, however, that my tests were not sufficiently extensive and that they, eventually feeling more at home, would have attacked *Achatina*.

But a species of *Tefflus*, somewhat less than two inches long, is definitely a feeder on snails (Pl. 3, Fig. 4). My first acquaintance with it was at Mombasa on the mid morning of December 18, 1947. Here on one of my rounds of inspection of a little colony of *Achatina fulica hamillei* in a small wooded area, I came upon one of these beetles on a coral outcrop, with its head and thorax in part inserted into a 30 mm. *Achatina* shell. The beetle, which lacked one of its middle legs, was very much engrossed in its meal. I pulled it free of the shell and brought it to my room where it again returned to its feeding, turning over the shell with its feet so as to conveniently reach the aperture. After settling down in the Diani District, I kept a constant lookout for this *Tefflus* during my forest ramblings. On a very few occasions portions of its elytra were found showing that it had some enemies. Finally, on April 30, 1948, following some rains, a fine specimen was captured among debris lodged a short distance up a hollow tree trunk in a scrub forest. For some days it refused *Achatina* in its large jar prison, but finally it consumed them regularly, so that by May 31 it had devoured completely or in great measure, eighteen *Achatina* ranging in length of shell from 20 to 50 mm. These were mostly attacked toward and during the evening when *Tefflus* came out of hiding from among the dry leaves in its jar. It would turn over the shell with its legs and quickly bite the withdrawing mollusk. Whether the carabid injected a liquifying fluid into its victim, was not determined; at any rate there was often much liquid at the aperture and the mollusk would eventually become loose from the innermost whorls. If the shell aperture crowded the large beetle, the outer whorl would be broken down sufficiently by means of the stout jaws. It seems that *Tefflus* may not finish its meal at one sitting, revisiting the shell so that we sometimes found it eating in the morning.

As the time for my return to the United States was drawing near and I had hunted in vain for additional large *Tefflus*<sup>1</sup>, recourse was had to Native help in the Diani District, for additional live specimens. An offer of a shilling apiece for these beetles soon set a number of eager Africans searching under heaps of weeds, among dead leaves beneath mango trees, etc. Thus, in eight or nine days, about fifteen of the beetles were secured. Male specimens predominated at first.

In addition, a number of smaller species of carabid beetles were brought to me with some confidence. But when I informed the bringers that these were not the kind of beetle desired, my pronouncement was regarded with suspicion, since it was claimed that these smaller specimens were but young of the larger one!

Kept in pairs in large glass jars, *Tefflus* mated readily enough and several individuals lived amicably in one receptacle. Small *Achatina* snails were consumed in some numbers. Apparently no eggs were laid.

A few live *Tefflus* were brought to Honolulu for experimentation under quarantine conditions. Several survived four months in captivity.

I believe that in the coastal regions of East Africa *Tefflus* feeds primarily on *Achatina*.

A taste for snails is of course found in species of large Carabidae in other parts of the world.

Drilidae. Drilid beetles are important enemies of snails. Their peculiar life-history — involving a protracted larval stage interrupted by pseudo-pupal phases — has made them the object of study chiefly in Europe and North Africa.

My first view of a drilid was of a large larva with sickle-like jaws, collected by Dr. J. C. Bequaert from the shell of an *Achatina* in Sodu, Liberia, in 1944. Mention is made of finding Drilidae in *Achatina* in British East Africa in E. Olivier's: *Insectes, Coléoptères, VII, Lampyridae et Drilidae. Voyage Alluaud et Jeannel Afr. Orient. Angl. (1911-12), 1914. With Appendix by P. de Peyerimhoff, Sur deux femelles larviformes de Malacodermes.*

As studied in material from East Africa, the male drilid is of normal malacoderm appearance and is capable of flight; the female is a great heavy wingless creature with short antennae (Pl. 4, Fig. 3). After laying her eggs she contracts a good deal and then suggests, somewhat, a fat wingless cockroach. She is little more than an egg-laying machine. Neither sex appears to eat snails, and I do not know if the adults eat at all. The larva has strong curved jaws and is quite bristly beyond the thorax, the posterior end terminating in a pair of lobes or

<sup>1</sup> On June 7, I found my third specimen. It was under a piece of coral at Mombasa.

more conical processes bearing several stout spines, among the shorter bristles (Pl. 5, Figs. 1, 3, 4). In this stage it spends most of its time in snail shells, devouring first, as befits its size, very small snails, then attacking others of larger and larger size — perhaps not invariably larger — undergoing moults in the shells, and transforming to the adult in the shell of its last victim. The finding of drilid larvae wandering about at large indicates that the desired snail victim is not always soon found.

The last victim of drilids that feed upon *Achatina* may be quite large — up to 115 mm. in length of shell, as observed in the case of *Achatina f. hamillei* at Mombasa. The male drilid being much smaller than the female does not require so large a shell.

The larval stage in drilids is by far the longest part of their existence. I have followed but little of their development and reared none to maturity. Only a few larvae were found, although a considerable number of moult skins, often in poor condition, were obtained. These were chiefly from *Achatina f. hamillei*, rarely from *A. iredalei*. They were common in *Edentulina* and *Gonaxis* and very rare in *Pseudoglossula* and in another very small species of land snail. But to attempt to work out the stages of these Drilidae, constituting perhaps more than one species, on this incomplete data would be to fail in exactness. However, L. C. Crawshay in England has worked out the life-history of *Drilus flavescens* Rossi (Trans. Ent. Soc. London, 1903, pp. 36-51, Pls. 1 and 2), while A. Cros has done the same for *D. mauritanicus* Lucas, in Algeria (Bull. Soc. Hist. Nat. Afrique du Nord, 1926, **17**, pp. 181-206, Pls. VIII, IX (IX) and X). Here the larval stages, involving resting forms, may extend into the third or fourth year. Prior to pupation there is a sort of false pupal stage involving a moult. These two drilids are a good deal smaller than the one in *Achatina* considered here. Other references on North African Drilidae are: Lucas, H., 1842, C. R. Acad. Sci. (Paris), **15**, pp. 1187-1189; Lucas, H., 1870, An. Soc. Ent. France, (4), **10**, Bul. Séances, pp. lvii-lviii; and Lucas, H., 1871, An. Soc. Ent. France, (5), **1**, pp. 19-28, Pl. 1.

With the coming of the rains, the *Achatina* lay their hard-shelled pale sulphur-yellow eggs. These soon hatch and the tiny young, gregarious for a time, are attacked by enemies of several kinds. Thus, during May, I located, chiefly at Mombasa, several perhaps first stage drilid larvae, each within the shell of a young *Achatina*. At Diani Beach, I collected one of these drilid larvae, pale yellowish, 3.5 mm. long, at large in the leaf debris of a tamarind tree. Placing this larva in a vial with a young epiphragmed *Gonaxis* 7.5 mm. in diameter, it showed some interest in the mollusk, attempting to bite through its epiphragm, but soon gave up the attempt and wandered off. The next

day, I offered it a new born *Achatina fulica hamillei*. It took immediate interest in this snail, clinging to the shell and moving about on it. The larva seemed to be chewing at the shell. It remained thus exposed upon the shell for some hours. By the following morning the little drilid, now healthily distended, was located in the last whorl of its host. Small grains of sand, glued to the edge of the shell, suggested that an effort had been made to seal the shell. Another tiny *Achatina* shell that contained a young drilid lay mouth down in its jar of sand, its aperture lightly plugged by a slightly moist ball of sand.

On May 7 I discovered a dead female drilid beetle in the *Achatina* colony in the old Mohammedan cemetery at Mombasa. She appeared rather recently dead, being soft and well preserved, and contracted because she had already laid her eggs. The color was chestnut brown, with the shining tergal plates largely blackish. The length was 32 mm. and the widest part of the abdomen was 18 mm. The dark apical portions of the mandibles were only slightly curved and these organs were hardly as well developed as in the larva. The antennae were seven-jointed with a small conical bristle-bearing tubercle on the last joint. The sides of the abdomen were drawn out rather triangularly and the abdomen terminated in a small subquadrate segment bearing a pair of papilla-like processes. The vestiture consisted of short brown hair. Altogether, this insect somewhat resembled a cockroach of the burrowing type. It was quite likely that she was the mother of some of the tiny drilids infesting the newly hatched *Achatina* nearby.

At least at the beginning of its life, the drilid larva moults at relatively short intervals. A specimen collected on May 27 in an *Achatina f. hamillei* shell 7.5 mm. long, moulted in this shell on May 30, to enter a shell of the same species 14.5 mm. long. This larva was of an orange color, with a dark segmental spot each side of the dorsal line. A larger drilid larva, perhaps 11 mm. long, was found wandering over the ground at Diani Beach on May 4. I placed it in a jar with a small *Achatina* and a mature *Edentulina*. It took no interest in these snails, but finally after some days of crawling and resting it went under the light soil and evidently moulted there. Soon afterward it attacked and entered the shell of a small *Achatina* offered it.

The female drilid larva grows to a considerable size, probably to at least 50 mm. judging from exuviae of the last active larval stage. It is provided dorsally with orange segmental plates with two black spots. These plates are armed with bristly hairs, while laterally on each abdominal segment are slightly curved, chitinized, somewhat finger-like processes that are quite bristly, as is the stout terminal lobate process, each lobe terminating in a stout spine and two smaller subterminal ones. The antennae are short, two-jointed and with a

terminal process; the jaws are stout and evenly curved. This larva eventually moults into what is apparently a non-feeding form, less bristly anteriorly and with the lateral abdominal processes more stubby, and with the bristly hair shorter giving it a coarse velvety appearance, the terminal thorn-tipped lobes being shorter and more or less buried in the stiff hair. The head is less developed and the jaws much weaker than in the previous stage. I found one such larva in an *Achatina* shell at Mombasa on December 19. Its fore part, relatively unarmed, was twisted and crammed quite out of sight in the spire, while the rather depressed abdominal portion was about 22 mm. long. The formidable bristly posterior suggested an adaptation for defence. On about January 5, 1948, it had shed its bristly skin, thereby exposing a delicate pale yellow "pseudopupa." This was capable of some stretching and wriggling and thus varying in length from 38 to 45 mm. It now looked very naked there being only some short hairy vestiture. There appeared to be no eye spots, the antennae were very short and papilla-like, the jaws small and encased, the legs weak. There were eight finger-like lateral abdominal lobes and a single short spine each side of the broad apex of the last segment. By about January 18 or 19, this "pseudopupa" had cast in part its thin exuviae, and showed a pale yellow true pupa with the head better developed, eye spots plainly visible, antennae still short though larger and with many segments, abdominal processes greatly reduced, and cauda hidden by crumpled and adhering skin. This pupa soon died. However, apical portions of pupal skins taken out of other *Achatina f. hamillei* shells show the two-fingered membranous case that envelops the subquadrate segment bearing two papilla-like processes, of the adult female beetle.

Portions of all four of these pre-adult skins were found in one *Achatina* shell. These are: 1, the last stage black-spotted bristly larva; 2, the first resting? stage with shorter but dense bristles having a coarse velvety appearance, jaws probably not functional; 3, the pseudopupa, almost naked and with a single short spine each side of the broad apex of the last segment, jaws still weaker; and 4, the true pupa, with the apical part much as the adult female, jaws stronger.

These beetles are rather effective enemies of *Achatina f. hamillei* and probably other species. At Mombasa, out of 48 empty shells ranging from 53 to 115 mm. long, seven contained drilid exuviae. These exuviae are not usually visible at the aperture of the larger shells, which must be broken down to reveal them, or the skins dislodged by jarring or by means of water. Quite young, thin shells when held up to the light may show the pronged outline of the posterior portion of small drilid exuviae.

Despite the examination of hundreds of *Achatina albopicta* shells in the Diani District, in but one, a doubtful instance, did I find evidence of a drilid, although exuviae of Drilidae were of frequent occurrence in the shells of both *Edentulina* and *Gonaxis* there.

According to excellent authority at the Coryndon Museum at Nairobi, the commonest drilid on the east coast of Africa is *Selasia pulchra* Pascoe. The male of this species is largely yellow with the antennae flabellate. It is to be taken at light.

Lampyridae (Fireflies and glow-worms). The larvae of these beetles are among the best known natural enemies of land snails, and studies on their habits date back to at least the middle of the last century.

Only a few observations were made on these insects in East Africa. Nearly all the lampyrid larvae found there readily attacked quite small *Achatina*, and it seems probable that they are generally non-selective as regards the kind of snail eaten. One larva consumes several snails in its lifetime. In Mombasa, small lampyrid larvae were found among newly hatched *Achatina f. hamillei*, which they were devouring.

In Ceylon, the larva of *Lamprophorus tenebrosus* Walker, a large lampyrid found also in Malaya and India, is predacious on the introduced *Achatina fulica*. Two important papers dealing with its habits are: one by C. A. Paiva, on this glow-worm as occurring in India (Rec. Indian Mus. **16**, pp. 21-28, Pl. 8, 1919), another by J. C. Hutson and G. D. Austin, as occurring in Ceylon (Dept. Agric. Ceylon, Bull. **69**, 16 pp., 1 Pl., 1924).

Histeridae. A small beetle of this family was once found among fly maggots in a dead *Achatina* at Diani Beach. It probably fed on these maggots, as many of the Histeridae are partial to larvae of other insects.

Scarabaeidae, subfamily Coprinae. Beetles of this subfamily were frequent visitors at dead *Achatinae*. A small, brilliant green species was common among crushed snails along the roadside at Diani Beach. One such beetle was observed cutting off a portion of the ovary of an *Achatina*, forming it into a ball which it rolled to the middle of the road, and there dug a hole in which to bury it. This provender would serve as food for its young.

This coprid beetle and a larger one of duller greenish hues, both kinds usually working in pairs, dig a steep hole more or less beneath a dead *Achatina*, the shell aperture of which faces downward. The soil which the beetles bring to the surface often fills a large portion of this shell, in which the coprids may sometimes be found. Presumably, portions of the dead mollusk are detached and buried in the hole.

Diptera (Flies). Although several muscoid flies are definitely known to be parasites of certain land snails, I was unable to prove that the

two or more species of muscoid flies (*Sarcophaga*, *Panaga* and *Aethiopomyia*), that I bred from *Achatina* ever attacked healthy snails.

Here are some findings at Diani Beach:

1. A very sick specimen of *Achatina albopicta* with a few tiny fly maggots on its foot, was found afield. It was taken to the laboratory and placed in a jar somewhat loosely closed with a lid. In about 21 days it yielded *Sarcophaga* flies.

2. An *Achatina* in the laboratory was killed and partly eaten by one of the carnivorous snails (Streptaxidae). I marked it and placed it at the foot of a baobab tree in forest where it remained for two days, after which it was placed in a screw-top jar in the laboratory. In about 15 days after the exposure some *Panaga* flies emerged, and 9 or 10 days later, 2 *Sarcophaga* issued.

3. Two mature *Achatina albopicta* were submerged in water until nearly drowned. Then they were placed at the foot of a baobab tree. They were very weak, but lived well on into the second day. I took them to the laboratory and placed them in a jar, where they soon were seething with maggots. From one or both of these snails *Sarcophaga*, and one *Panaga* fly issued. There was a possibility of contamination in the laboratory by some of these flies.

It seems to me doubtful if the several sick, fly-infested *Achatina* that I found afield had in the first place sickened because of the attacks of these flies. *Achatina* are often killed in exposed situations by the heat of the sun.

A fly of ordinary *Sarcophaga* appearance is often seen on dead *Achatina*, even in the hot sunshine. It appears to deposit its tiny maggots only on sick and dead snails. On reaching maturity these maggots transform into rather slender fusiform puparia. The life-cycle, from larviposition to the hatching of the adult fly, was estimated at about twenty-one to slightly more, days.

There are several species of the *Panaga* complex found at Diani. The commonest of these stout brown flies is about 7 to 8.5 mm. long. A second species is much larger, measuring about 13 mm. long. These flies are shade lovers and are often active towards sunset. They may be of common occurrence on the lower portion of the huge trunks of baobab trees (*Adansonia digitata* L.), about shaded coral cliffs, and in the shade along roadsides where they are often attracted to the crushed *Achatina*. The smaller species was often abundant on the forest floor, often perching among fallen fruit there. Certain individuals fly in zigzags or curves low over the ground, with a shrill buzz. None was ever seen attacking a living *Achatina*, although occasionally alighting on shell or mollusk as a convenience. One of these smaller *Panaga* was observed ovipositing on a drowned *Achatina*. The egg is about

2.25 mm. long, white and tough, fusiform, with a sort of wide flange extending from either side of the length that is to be glued down. The larvae are active in the foul-smelling liquid that accumulates in the shell, and are found on the flesh itself. The puparia are arranged more or less in rows, being glued to the aperture, in view to far out of sight within. They are stout, broadly rounded at the ends and somewhat arcuate from the substratum. In the few cases studied, the time from the laying of the egg to the hatching of the adult fly occupied from fifteen to twenty days. Over eighty flies hatched from a large specimen of *Achatina f. hamillei*, and it is probable that this number may be greatly exceeded.

The smaller of these *Panaga* flies finally became very numerous about the laboratory at Diani Beach where I cleaned out *Achatina* shells. They deposited their strongly adhering eggs, often in large numbers, on the foot, and particularly the shell, of drowned snails, or at the water's edge of a bucket, or where the lid fits the jar that contained these dead mollusks. One of these *Panaga* even entered the aperture of *Cypræacassis rufa* (L.), a large marine shell, the mollusk of which had been dead for at least a week and of which only a small portion remained in the shell. These flies could become a nuisance. The larger, more feral *Aethiopomyia*, was not often seen in the laboratory. It too, breeds in *Achatina* as well as in one or both of the large carnivorous snails, if the large puparia found in these shells belong to this species.

At least some of these snail flies are attacked by wasp parasites. Small chalcids were reared from one *Achatina* shell that contained fly puparia. A large black chalcid with legs in part red, attracted by the odor (?) of dead or sick snails, follows closely upon the ovipositions and larvipositions of these muscoid flies. One of these wasps was observed jabbing at a small fly maggot on the surface of a dead or nearly dead *Achatina albopicta* snail that I had exposed to the attack of these flies. Similarly this wasp is attracted to snails drowned in a bucket of water. And occasionally one finds a *Panaga* puparium with the emergence hole of what may well be this chalcid.

Keillin (Parasitology, 1919, **11**, pp. 430-455, Pls. 22-25) in writing of *Mydaea*, under (2) Carnivorous Forms, remarks: "*Mydaea* sp. allied to *Mydaea bivittata* Macq. In a recent paper by Rodhain and Bequaert (1916, p. 248) we find the following observation on the feeding habit of the larvae of this Anthomyid: "The genus *Mydaea* exists in Central Africa and its larvae are carnivorous; one of us bred at Kivou a great number of a species allied to *M. bivittata* Macq. (identified by Dr. Villeneuve) from the larvae devouring a big terrestrial mollusk (*Burtoa nilotica* Pfeiff.). . . ."



For a comprehensive paper on the arthropod enemies of mollusks, see J. C. Bequaert (Medical Rept. Hamilton Rice 7th Exped. to Amazon, 1926, pp. 292-303. Harvard University Press, Cambridge).

During the rains many dead and empty *Achatina* shells that rest mouth upwards in the forest, may receive a good deal of water that is retained over a considerable period. Thus, a large number of such containers serve as breeding places for certain mosquitoes (*Aedes* and *Eretmapodites*). In places along the East Coast of Africa, such breeding places for mosquitoes are destroyed by order of the Department of Public Health.

Less commonly, *Achatina* shells at Diani Beach containing rain water provided a breeding place for a species of toad, *Bufo micranotis* Loveridge, subsp. (as determined by Mr. A. Loveridge). Two such shells containing a few tadpoles were found in a well-shaded spot in the forest. Several of these amphibians were reared to the juvenile adult condition.

### CONCLUSIONS

The following are the most important conclusions reached from my study of the predacious enemies of *Achatina* in East Africa. No true parasites were found.

The Streptaxidae, or rapacious snails, are ruthless enemies of snails in general. Probably they are the most effective natural control of *Achatina* in Africa. No such snails are native in the Pacific Islands.

The larvae of drilid and lampyrid beetles also destroy a great many *Achatina*. Some of the Lampyridae (fire flies) are able to climb trees.

The adults of the large ground beetle, *Tefflus*, seem to feed principally on *Achatina*, but probably are a less effective control than the Streptaxidae, Drilidae and Lampyridae.

If these predators were successfully established on some of the Pacific Islands where the giant African snail (*Achatina fulica*) is present, undoubtedly they would reduce the *Achatina* population considerably. However, the native terrestrial, but probably not the whole arboreal, land snail fauna undoubtedly also would be reduced, though perhaps not exterminated.

As these predators multiply rather slowly, results would not be apparent for a year or more.

I doubt very much if there are any enemies strictly specific to *Achatina*.



PLATE 1

PLATE 1

Fig. 1. *Achatina reticulata* Pfeiffer.

Fig. 2. *Achatina fulica hamillei* Petit.

Fig. 3. *Achatina iredalei* Preston.

Living snails at Cambridge. Photographs by Miss Ruth Turner. Greatly reduced.

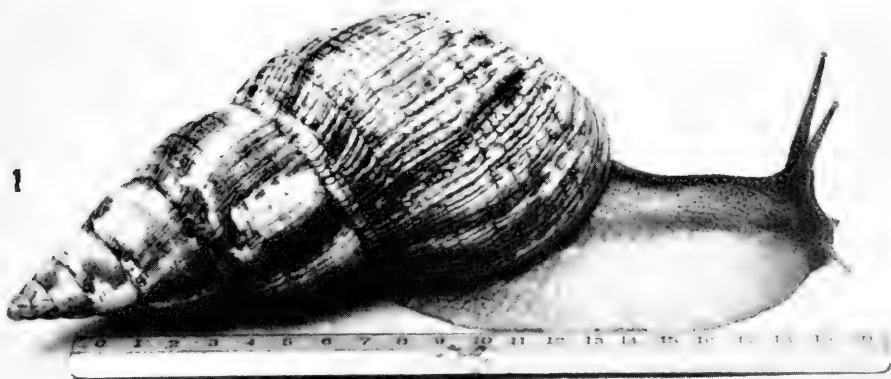




PLATE 2

PLATE 2

Fig. 1. *Achatina reticulata* Pfeiffer.

Fig. 2. *Achatina albopicta* E. A. Smith.

Fig. 3. *Achatina fulica rodatzii* Dunker.

Living snails at Cambridge. Photographs by Miss Ruth Turner. Greatly reduced.



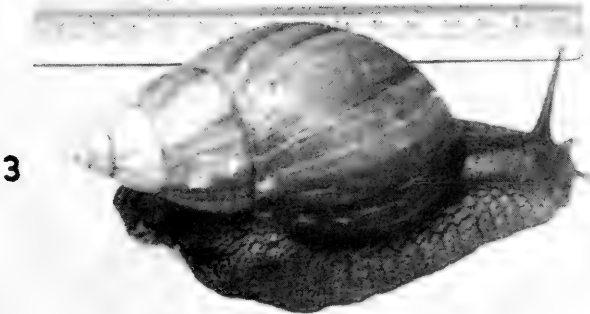




PLATE 3

PLATE 3

- Fig. 1. *Achatina albopicta* E. A. Smith. In bush at Diani Beach.  
Fig. 2. Land crab attacking *Achatina albopicta* at Diani Beach.  
Fig. 3. *Achatina albopicta* wedged in furrow of a tree at Diani Beach.  
Fig. 4. *Tefflus* beetle devouring young *Achatina fulica hamillei* at Mombasa.  
Fig. 5. *Edentulina affinis* C. R. Boettger devouring *Achatina albopicta* at Diani Beach.

All photographs by Mrs. F. X. Williams.





PLATE 4

PLATE 4

Fig. 1. Two epiphragms built by *Achatina albopicta* and left behind on a tree trunk after the snails moved away. Lower one shows tubular extension to the bark. Diani Beach. Photograph by Mrs. F. X. Williams.

Fig. 2. Group of *Achatina fulica hamillei* Petit and *A. f. rodatzii* Dunker on trunk of coconut palm about 9 ft. from the ground. Zanzibar Id. Photograph by Mrs. F. X. Williams.

Fig. 3. Adult female, after oviposition, of Drilid which in the larval stages attacks *Achatina*. Diani Beach. X 2.

Fig. 4. *Achatina albopicta* showing large numbers of eggs deposited by female *Panaga* flies. Mombasa.

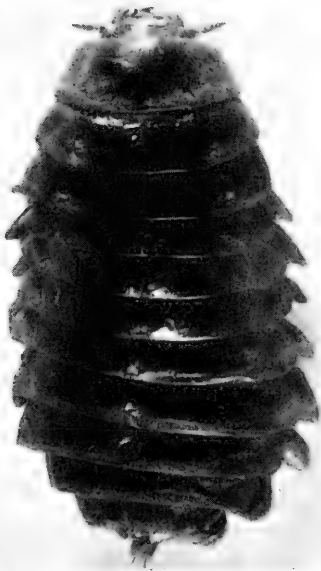




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**PLATE 5**

PLATE 5

Fig. 1. Exuviae of last active larval instar of Drilid feeding on *Achatina fulica hamillei* at Mombasa. Dorsal view. X 2.

Fig. 2. Top of broken *A. f. hamillei* showing hatched puparia of *Panaga* flies.

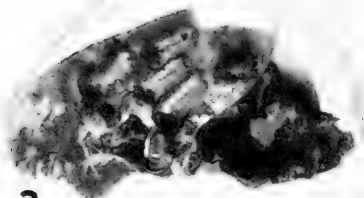
Fig. 3. Caudal portion of a resting stage larva of the Drilid attacking *Achatina*. Dorsal view. X 2.

Fig. 4. Apical portion of abdomen of active larval instar of the Drilid attacking *Achatina*; probably preceding the stage shown in Fig. 1. Dorsal view. X 2.

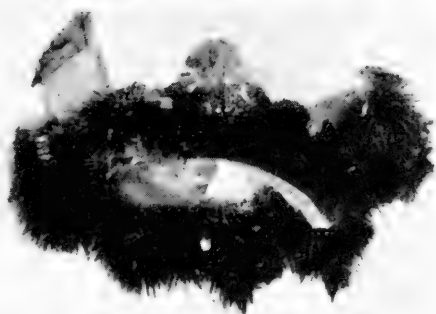
Fig. 5. *Achatina albopicta* cut into at the edge of the mouth by a land crab. Diani Beach. Natural size.



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