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Anatomical studies transfer *Leucotaenius* from Achatinidae to Acavidae

(Pulmonata: Sigmurethra).

By

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With 11 figures.

Introduction.

The genus *Leucotaenius* has long been an engima. On the basis of the "einfachen Genitalien" in *Leucotaenius favannii*, THIELE (1929) removed the genus from the Enidae and placed it in the Achatinidae. His remarks were brief in the extreme and no illustrations were provided. For elusive reasons, and because of THIELE's terse description, there has been in the mind of the present author a deep and growing suspicion that *Leucotaenius* simply does not belong to the family Achatinidae (cf. BRUGGEN 1980a: 155, 1981: 123). The shells, which are found in most U.S. and European major natural history museums, offer no real clue to their relationships, except for the fact that the more conspicuous shell features are not shared with other achatinid genera. Preserved soft anatomies were needed. Fortunately, during the author's visit at the Forschungsinstitut Senckenberg in Frankfurt in 1980, the mollusc collection was found to have seven alcohol preserved specimens that had

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been removed from their shells. They were labeled "122046/7, Lebende Landschnecken, Dornwald, Kalkplateau-Ausläufer zw. Audvoka u. Bevoalavo; K. KOCH leg. Mai 1953 [Madagaskar]" The shells in the dry collection, bearing the same data, are extraordinarily large, fine specimens, the largest measuring h, w: 68×36 , Ap: 35.5×27 , last whorl: 46 mm. The third largest and clearly the finest specimen was illustrated by ZILCH (1959: fig. 1356). It measures h,w: 60.5×36.5 , Ap: 32×26 , last whorl: 43 mm. An additional alcohol preserved specimen, in shell, was found in the Muséum National d'Histoire Naturelle in Paris, but the soft anatomy was not examined. Specimens of *Acavus phoenix* and *A. superbis* dissected in the present study were collected in Ceylon by the author in Ratnapura and Kundasale, respectively, in 1954.

All dimensions of the soft anatomies were measured at least twice with ocular micrometers and microspanners.

History

The genus *Leucotaenius* was described by MARTENS in ALBERS (1860: 229) under "Genus XXII *Buliminus* EHRENBURG" [sic for EHRENBURG's *Bulimina*, 1831] with the type designated as "*B. favanni* LAM." It was treated as one of twelve "Gruppen" within and subordinate to *Buliminus*. His footnote on p. 316 explains why the specific name "*favanni* LAM." was placed under the generic name *Bulimus* in the index, rather than under *Buliminus*. In CLESSIN's opus postumum publication of PFEIFFER's Nomenclator Heliceorum Viventium (1881: 282), the generic name *Leucotaenius* is attributed to "ALBERS 1869" [sic] and is categorized as "Sect. 2" under "Genus LXI *Bulimina*" The type species is shown as "*B. favannii* F." KOBELT (1900: 647) more conventionally delineated the taxon as "*Buliminus (Leucotaenius) favannii* LAMARCK"

Earlier, ALBERS (1850: 172) proposed the genus-group name *Liparus* [non OLIVIER 1807], established it subordinate to *Buliminus*, and placed in it LAMARCK's "*favannii*", along with one other species. PFEIFFER (1856: 157) accepted essentially this arrangement. Although MARTENS (1860) retained *Liparus* as a "Gruppe" in genus *Buliminus*, he removed from it only "*favanni*" LAMARCK and "*crassilabris*" GRAY for his new genus *Leucotaenius*. ADAMS & ADAMS (1858, 2: 133) placed "Subgen. *Liparus*, ALBERS", including "*favanni*", under genus *Limicolaria* SCHUMACHER; but CLESSIN (1881: 282) retained *Liparius* and *Leucotaenius* as coordinate subsections under "*Bulimina*" In 1894b, PILSBRY pointed out the homonymic nature of ALBERS' *Liparus*, but regrettably treated neither the genus *Leucotaenius* nor its species in his Manual of Conchology.

FÉRUSAC (1822: 54, no. 408) proposed the species name *Helix favannii*, but since there was no description or figure, it became a nomen nudum at its inception. LAMARCK (1822, 7 [2]: 120), giving reference to FÉRUSAC's work, was the first to describe validly this species, designating it "*Bulimus favannii*"; hence, according to Article 32 of the "Code", this constitutes the "correct original spelling" of the specific name and thus should be retained. DESHAYES & MILNE-EDWARDS (1838, 8: 227) echoed the original description and correctly showed LAMARCK as the author of the species. GERMAIN (1913: 477) erroneously attributed "*Bulimus favannei*" to BRUGUIÈRE, followed KOBELT's transfer (1910, not 1901 or 1900 as GERMAIN indicated) of the species to the genus *Clavator*, established the new subgenus

Pseudoclavator, and designated its type as "*Bulimus favannei* BRUGUIÈRE" (cf. also GERMAIN 1921, 1935). The specific name has been variously spelled as "*favani*" (PETIT DE LA SAUSSAYE 1851: 76); "*favannei*" (CROSSE & FISCHER 1868: 185 [including their "var. β "]); FISCHER 1887: 472; MERMOD 1951: 726; GERMAIN (1913: 477, 1921: 17, 1935: 439); "*favanii*" (CROSSE & FISCHER 1868); and "*favanni*" (MARTENS in ALBERS 1860: 229; ADAMS & ADAMS 1858, 2:133; KOBELT 1910). TRYON (1884: 49), PAETEL (1889: 101), KOBELT (1900), HAAS (1929: 410) and others have followed LAMARCK's original spelling of the specific name.

JAY (1839: 111, pl. 1 fig. 1) was the first to illustrate this species; but he identified it as his new "*Bulimus cinctus*", which early was shown to be in the synonymy of "*Bulimus favannii*" LAMARCK (PFEIFFER 1848, 2:185; REEVE 1848). The locality "Calcutta," cited by JAY, is erroneous. CHENU in DELESSERT (1841: pl. 27 fig. 8a, 8b), illustrated the type specimen of LAMARCK's *Bulimus favannii* (cf. also CHENU 1842-53: pl. 8 fig. 14); but as in REEVE's illustration (1848: pl. 29 fig. 179), a too intense sepia-pink wash was applied by the artist. Except for the remarkable detail of CHENU's illustrations, probably the best color illustration of this species is to be found in CROSSE & FISCHER (1889: pl. 21 fig. 6). This was reproduced by KOBELT (1900: pl. 98 fig. 2) with some loss of refinement. Black and white photographic illustrations are to be found in THIELE (1929: 561, fig. 645), MERMOD (1951: 727, fig. 77, type), and ZILCH (1959: 374, fig. 1356). The most recent selected synonymy of *Leucotaenius favannii* has been given by FISCHER-PIETTE (1963: 15). The holotype is in the Muséum d'Histoire Naturelle de Genève (MERMOD 1951).

Radula.

THIELE (1929) described the radula of *Leucotaenius favannii* in such brief terms that, in the absence of illustrations, little of substantive value was revealed except, "Mittelplatte der Radula ziemlich breit" This is uncharacteristic for the Achatinidae. The preparation and examination of the radula in the present studies were based on the fundamental works of RUNHAM (1969) and SOLEM (1972, 1973). In vertical aspect, the rachidian and early lateral radular teeth are broadly mesocone-unicuspid (fig. 1). Contributing to the anterior breadth of the mesocone are the vestigial ectocones, which were not discernible in transmitted light preparations. In the early laterals, the anterior edge of the basal plate is deflected medially to articulate supportively with the corresponding posterolateral deflection of the long basal plate of the tooth immediately anterior. The basal plates of the laterals thus are seen to be strongly asymmetrical. The slightly shorter rachidian cusps expose the long, symmetrical, posteriorly projecting basal plates that, at the crest of the rasping motion, squarely engage the teeth immediately posterior to them. Figure 2 shows these features in convincing detail and reveals in perspective the strong vertical structural support that is provided to the cusps. In contrast, this structural support, when seen under the compound microscope with transmitted light, produces apparent delineations at various levels of focus that confuse both outline and perspective. As the laterals progress towards the marginals, i.e. away from the greater stress of the rasping action, the basal plates become progressively shorter until they no longer articulate. Concurrently, the ectocones become larger and more pronounced and the mesocones become more slender and denticulate. In the marginals, the ectocones persist as obtuse spines, but the mesocones irregularly

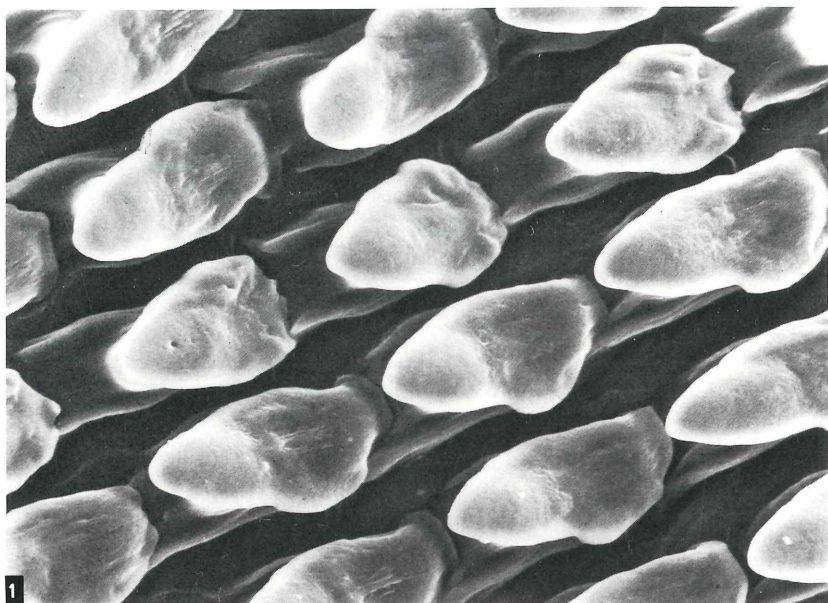


Fig. 1. Vertical view of the central-posterior radula of *Leucotaenius favannii* LAMARCK. The rachidian row is third from the top. x 464 (SMF 122046).

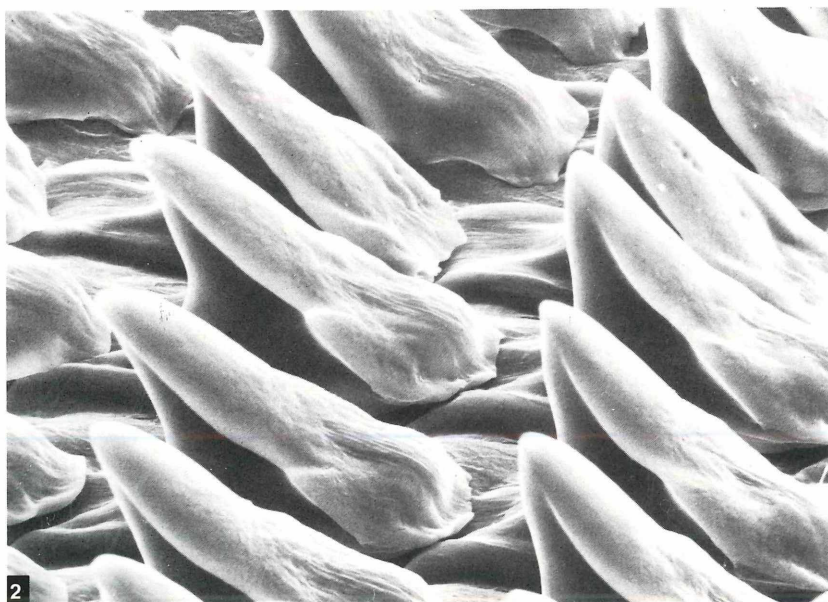


Fig. 2. High profile view of rachidian (second row from top) and early right lateral radular teeth showing vestigial ectocones and the interlocking of the extended basal plates. x 709.

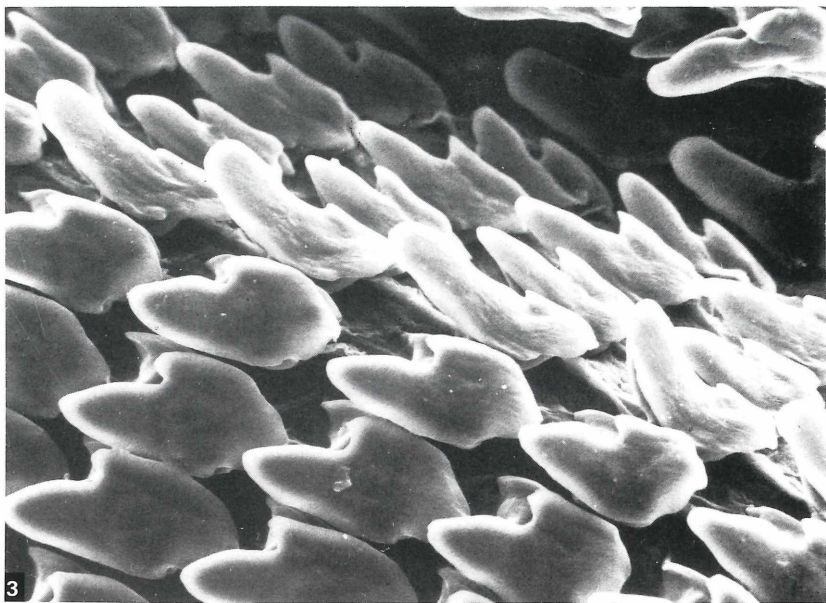


Fig. 3. Transition zone between the dentate far left laterals and the lingulate early marginals, both of which have prominent ectocones. x 464.

become attenuatedly lingulate and oriented slightly medially, with the abbreviated basal plates far separated from each other in adjacent rows (fig. 3). At the lateral extremes, these mesocones become shorter and shorter, multilobed or fused, and eventually reduced to irregular basal plate blocks, similar to those that RANGLES (1900) reported for *Acavus* and *Oligospira*. In the examination of three *L. favannii* radulae, there was found a surprising amount of irregularity and abnormality, particularly in the longitudinal rows (figs. 4, 5). As a consequence, the demarcation between laterals and marginals in transverse rows was variously fairly sharp or, more often, obscure. H. WATSON in CONNOLLY (1915: 137) found somewhat similar abnormalities in the dorcasiids. On average, the radulae of *L. favannii* were ca. 7×2 mm, contained ca. 150 nearly transverse rows, and had a formula of 53-1-53, for a total of ca. 16,000 teeth.

In apparent order of descending relationship, the radula of *L. favannii* is similar to those of the acavid genera *Acavus* (BINNEY 1884, PILSBRY 1894a, RANGLES 1900), *Oligospira* (RANGLES 1900), *Helicophanta* (PILSBRY 1894a, FISCHER-PIETTE 1950, FISCHER-PIETTE & LOUBRESSE 1965), *Ampelita* (PILSBRY 1894a, FISCHER-PIETTE 1952, FISCHER-PIETTE & LOUBRESSE 1965), and *Strylodon* (BINNEY 1884, PILSBRY 1894a) in the following features: conspicuously long basal plates of rachidian and early laterals, absence of endocones, suppression or absence of ectocones, broad mesocones of early laterals, slightly shorter broad mesocones of rachidian teeth, and lingulate marginals. It is unfortunate that in the anatomical studies of *Clavator* by

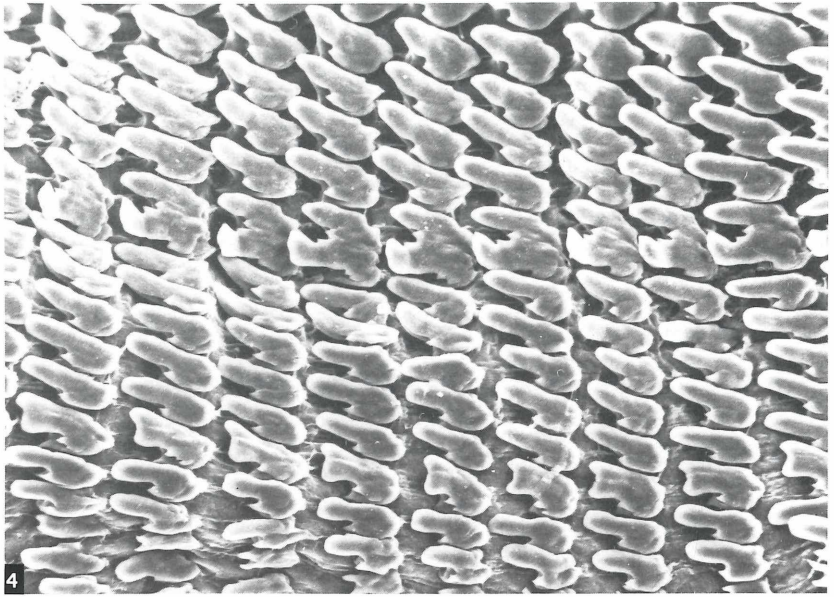


Fig. 4. Vertical view of mid-right radula showing abnormalities in the transition zone between laterals and marginals. Note: The normally reduced basal plates, fused sixth and seventh rows from the top, bilobed mesocones of thirteenth row, and diminutive mesocones in the sixteenth row. x238.

FISCHER-PIETTE et al. (1975), the nature of the radulae was not reported; but it is a quite safe prediction that in these same basic features, the radula will be found to be similar.

The shorter basal plates of the early laterals in the radulae of the caryodid genera *Pedinogyra*, *Hedleyella*, *Anoglypta* and *Caryodes* (PILSBRY 1894a) appear to set these genera apart from the acavid genera, despite the basically similar, large, broad mesocones. WATSON (in Connolly 1915) illustrates the sharply contrasting radulae of the dorcasiid genera *Trigonephrus* and *Dorcasia*, emphasizing the more primitive nature of the former; however, the radula of the latter is considerably more like that of the acavid genera, particularly with respect to the broadly conical mesocones. The presence of reduced ectocones in the transitional laterals and marginals, so far reported only in *Stylodon* (Acavidae) and *Leucotaenius*, has its counterparts in the DorcasIIDae (Connolly 1915) and in the Strophocheilidae (HEYNEMANN 1868, SEMPER 1874, BINNEY 1884, PILSBRY 1895-1896, 1901-1902). This fact, in addition to the acavid character of greatly extended basal plates atypically in the strophocheilid *Gonyostomus multicolor* (BINNEY 1884) is probably not so much a phylogenetic enigma as it is a reflection on feeding adaptations. In contrast, however, RANGLES (1900) does not show in the Acavidae substantively convincing differences between the radulae of the arboreal *Acavus* and the ground-dwelling *Oligospira*.

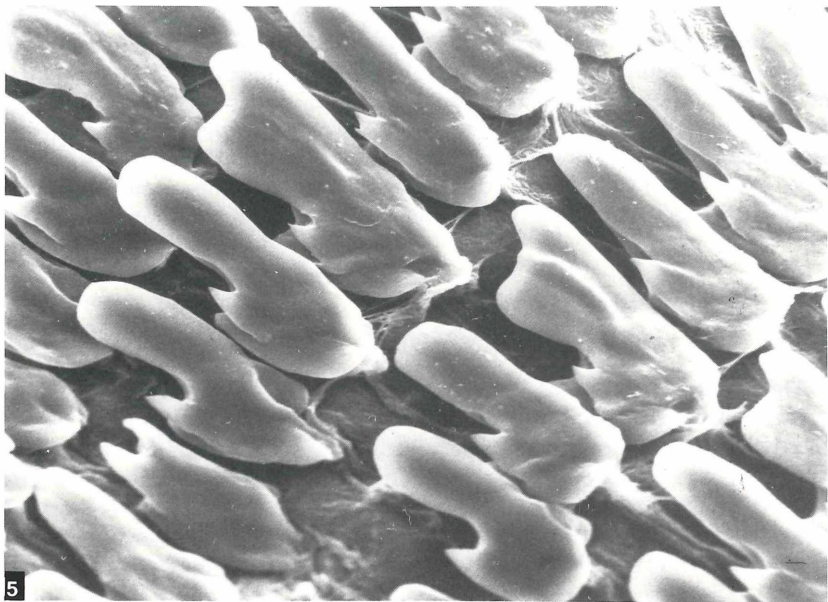


Fig. 5. Higher magnification and slightly posterolateral view of abnormal thirteenth and sixteenth longitudinal rows of fig. 4. x 689

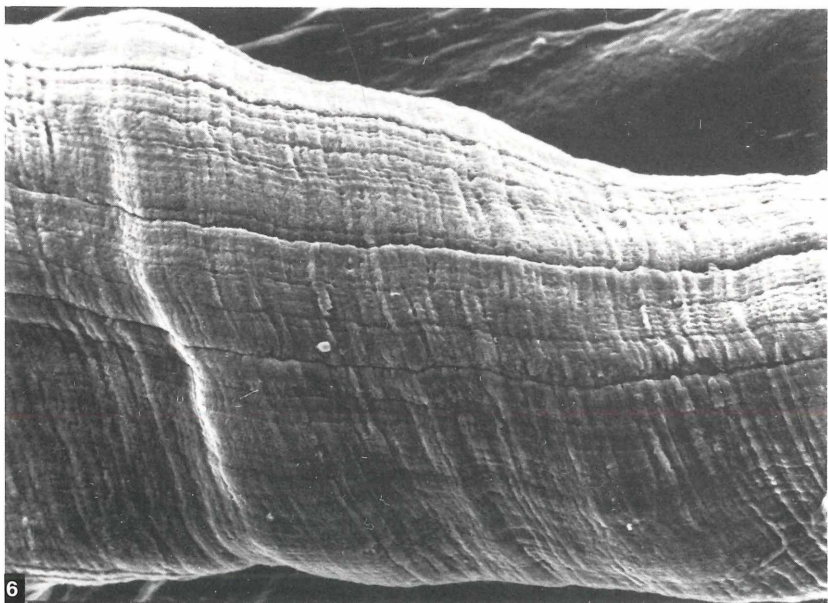


Fig. 6. Midsection of the jaw. x 238

The characteristically diminutive rachidian tooth of the Achatinidae (SEMPER 1874, PILSBRY 1904-1905, CONNOLLY 1939) is virtually or completely non-functional and is in contrast to the somewhat reduced but functional rachidian tooth of the Acavidae. This character in the achatinid radula, in addition to the shorter basal plates and the prominence of the ectocones, convincingly differentiates between the two families. The uncharacteristically larger, functional rachidian tooth of *Callistoplepa* (Ailly 1896) is only one of several anatomical features, currently being explored by the author, that reveal the deviant nature of this achatinid genus.

Jaw

The jaw of *L. favannii* is broad, slightly arcuate and without ribs, vertical plicae or discernible median projection. Under the scanning electron microscope, the fine growth lines are seen to dominate transversely on an otherwise fairly homogeneous surface (fig. 6). In shape and texture, it conforms to what emerges in the cited literature as the typical acavid jaw, quite in contrast to the plicate, ribulate or striatulate jaw of Achatinidae (PILSBRY 1904-05) and the striatulate jaws of Dorcasiidae (CONNOLLY 1915) and Strophocheilidae (HEYNEMANN 1868).

Genital System.

The most striking feature of the basal genital system of *Leucotaenius favannii* is its tripartite nature (fig. 7). The vaginal portion of the female conduit has become foreshortened to the point where the spermathecal duct and the free oviduct branch off independently and directly from the genital atrium, as does the penis. The clearly dominant element is the muscular basal two-thirds of the spermathecal duct (BSD), which, because of its axial alignment and extraordinarily thick wall (1.0 mm), surely functions as a surrogate vagina, although it is the homolog of the slender, thin-walled basal portion of the spermathecal duct of most stylommatophorans. The apical one-third (ASD) is characteristically thin-walled, as is the discoid-clavate spermatheca (S). In contrast to the typically thin-walled straight, tubular free oviduct (FO) of the Achatinidae, this structure is inordinately muscular and asymmetrical. It appears to branch off laterally from the basal spermathecal duct. As revealed in a histologically cleared specimen, there is internally a slender, strongly sigmoid canal that connects the lumen of the spermoviduct (SO) with the genital atrium (GA). It is likely that this muscular portion of the female conduit assists in expelling the eggs during ovulation.

The penis (P) is short, broad and without a sheath. Because of contraction in the process of preservation, the penial retractor (PR) varies in length, but tends to be short and broad. It inserts narrowly near mid-diaphragm in all three specimens examined. The vas deferens (VD) is not differentiated into apical and basal portions, although it becomes convoluted 3 mm before joining the free oviduct. Instead, it seems disproportionately short, passes ventrally and diagonally across from its junction with the free oviduct, goes between the penis and the basal spermathecal

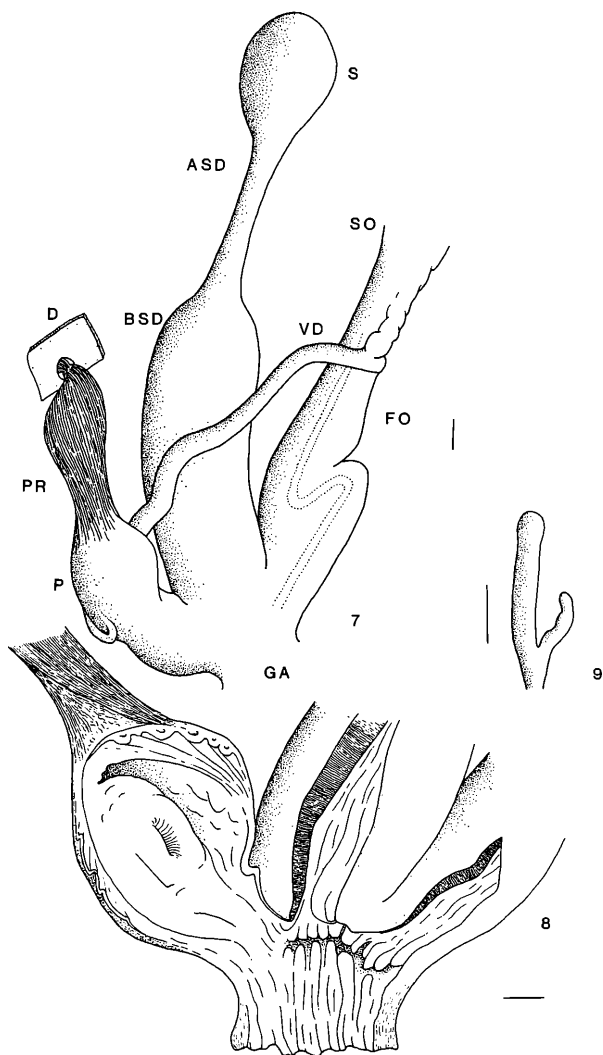


Fig. 7-9. — 7) Genitalia of *Leucotaenius favannii* LAM., ventral view. Penis rotated ca. 35° counterlockwise to show point of insertion of vas deferens on dorsal surface. Bar scale, 1 mm. ASD, apical spermathecal duct; BSD, basal muscular spermathecal duct; D, portion of diaphragm showing insertion of penial retractor muscle; FO, free oviduct; P, penis; PR, penial retractor; S, spermatheca; SO spermoviduct; VD vas deferens. — 8) Ventral view of basal genital system incised and extended to show tripartite nature and relationships with the genital atrium. The ventral half of the penis has been cut and elevated dorsally to reveal the large penis papilla within. Bar scale, 1 mm. — 9) Talon with diverticulum. Bar scale, 1 mm.

duct, circumvents the penis basally, narrows abruptly to less than half its caliber, goes a short way apically as it blends with the tissues of the penis, and finally inserts diffusively about midway on the dorsal surface of the penis. Internally, nearly half of the dorsal surface of the penis is occupied by a gross, elevated, rugose penis papilla (fig. 8). On the summit of this papilla, a smooth, muscular elevation surrounds a 1.2 mm long orifice. Deep in this orifice is the conduit of the vas deferens, which has narrowed to 0.2 mm. The inner ventral surface of the penis is ridged with coarse, rounded rugae that are oriented diagonally toward the genital atrium in a fan-shaped pattern. The caliber and pattern of these suggest a pilaster function. The irregular rugae of the muscular spermathecal duct and the free oviduct terminate abruptly at the junction with the more regular, slender, axial rugae of the genital atrium. The truly tripartite nature of the basal genital systems is most evident in this aspect.

The spermoviduct (SO) appears disproportionately long and nearly evenly sinuate in $10 \pm$ folds. Ova were not found in any of the seven specimens. The albumen gland (AG) and the highly convoluted hermaphroditic duct (HD) are typically stylommatophoran. A slender, digitiform talon (T), with a thumb-like appendix is present (fig. 9). How this actually compares with the simple, elongate talon in *Acavus* (RANGLES 1900) and the multidiverticulate talon in Achatinidae (MEAD 1950) is elusive at this state of our knowledge. The acini of the ovotestis are not bound together into a discrete organ as in *Acavus*, but are loosely aggregated in 5-6 acini and embedded immediately below the columellar surface of the right (posterior) lobe of the digestive gland. The retractor muscle of the right ommatophore passes deeply in the angle between the penis and the muscular spermathecal duct.

Following are the measurements of the illustrated specimen. Measurements of two other dissected specimens varied insignificantly. AG 16×4.5 , ASD 5.5×1.5 - 0.7 , BSD 10×3.5 , FO 11×1.5 - 3.4 , GA 3.5 , HD 17×0.5 - 0.6 , P 4×2.5 - 3.0 , PR 5×2.2 - 1.8 , S 4×3 , SO 37×3 , VD 21×0.3 - 0.8 , T 3×0.4 .

On the basis of comparative anatomical studies of the genital system *Leucotaenius favannii* is found to be most closely allied to the Acavacea, and more specifically, the genus *Acavus*. As emphasized in earlier studies (MEAD 1950, 1979), a routine examination of the internal structure of the penis should be made because it often reveals phylogenetically important characters that too often in the past have been overlooked. A simple outline of the genital system is not enough. The present study adds further support to this belief. RANGLES (1900) demonstrated distinctive differences in the penial pilasters and associated structures in the six species of *Acavus*. Two of the species, *Acavus phoenix* and *A. superbus*, were examined anatomically in the present study. The simplest structural pattern internally in the penis of this genus is an elongate furrow bordered by an acutely elliptical elevated ridge in the dorsal wall. Adjacent to this ridge is one or more coarsely rugose-papillate pilasters. Unfortunately, RANGLES confused dorsal and ventral, and further, did not realize that the vas deferens, on the dorsal surface of the penis, emptied directly but obscurely into this furrow. He therefore presumed the necessary presence of a "not very conspicuous" penis papilla in the extreme apex of the penis. This simple basic pattern is found in *A. phoenix*. The other species have modified this pattern through the process of fusion and elaboration. For example, the elaboration of tissue in the elevated ridge around the penial furrow in *A.*

superbus has produced a high, steep-sided mound around the thin slit exit of the vas deferens. By definition, it became a penis papilla. Somewhat differently, in *A. haemastomus*, the adjacent pilasters fused and encroached upon the penial furrow. A combination of the modifications in these two species of *Acavus* produces the homologous pattern found in *Leucotaenius favannii*. In the latter, however, the elevation has become so profound that it essentially is a pilaster as well as a penis papilla. Regrettably, however, the internal penial anatomy of other Acavacea is not known.

Leucotaenius and *Acavus* also share another remarkable feature in the genitalia that imparts a tripartite nature to the basal genital structures. Both have a spermathecal duct, the basal portion of which is a robust thick-walled surrogate vagina, that completely dominates the basal genital structures. It is oriented on a straight axis with the genital atrium and is so close to it that in *Leucotaenius* no vagina remains, and in *Acavus* it is unclear, even on examination of the rugae within, whether the vagina is vestigial or whether the genital atrium is slightly attenuated. It is understandable why RANGLES (1900) labeled this structure the vagina.

Although the tripartite basal genital system is strange in appearance, it obviously has independently evolved many times as evidenced by its sporadic appearance in such diverse families as Endodontidae, Arionidae, Limacidae, Helicarionidae, Zonitidae and Camaenidae. Not only does the basal part of the spermathecal duct apparently function as a vagina, but in the closely related *Clavator clavator*, the free oviduct appears to serve this function (cf. FISCHER-PIETTE et al. 1975).

In the genital system, other differences and similarities between *Leucotaenius* and *Acavus* were found, but until more is known about the comparable structures in presumed related forms, these cannot be evaluated.

After *Acavus*, *Ampelita* is probably next most closely related to *Leucotaenius*. Nine of the thirteen species of this genus, for which the genital system has been illustrated (FISCHER-PIETTE 1952, FISCHER-PIETTE & LOUBRESSE 1965, FISCHER-PIETTE et al. 1975), have a large basal spermathecal duct that produces a tripartite or near tripartite arrangement of the basal genital structures. In the process of interpreting illustrations, particularly in the more subtle aspects, there is always the question of whether it is variation or orientation; witness the differences in the illustrations of different specimens of *Ampelita sepulchralis* (FISCHER-PIETTE 1952: 44, FISCHER-PIETTE & LOUBRESSE 1965: 149) and of *A. xyxtera* (PILSBRY 1894a: pl. 51A, FISCHER-PIETTE 1952: 33). The similarly stout, short penis in most of the illustrated species of *Ampelita* and the reported "corrugated" penial wall of *A. xyxtera* (PILSBRY 1894a) suggest provocatively that internally they are similar to *Acavus* and *Leucotaenius*. At the least, they emphasize the need for additional anatomical studies.

Of the six species of *Helicophanta* in which the nature of the reproductive tract is known, only *H. amphibulima* appears close to *Ampelita* and thus *Leucotaenius* (PILSBRY 1894a, FISCHER-PIETTE 1950, FISCHER-PIETTE & LOUBRESSE 1965, FISCHER-PIETTE et al. 1975). The two illustrated species of *Clavator* (FISCHER-PIETTE et al. 1975) and the single illustrated species of *Stylodon* (PILSBRY 1894a) show in their reproductive tracts no close relationship to *Leucotaenius*. The same holds for the differences revealed in the illustrated genital systems of the genera of the Dorcasiidae, Caryodidae and Strophocheilidae (PILSBRY 1894a, CONNOLLY 1915, LEME 1973 et seq.).

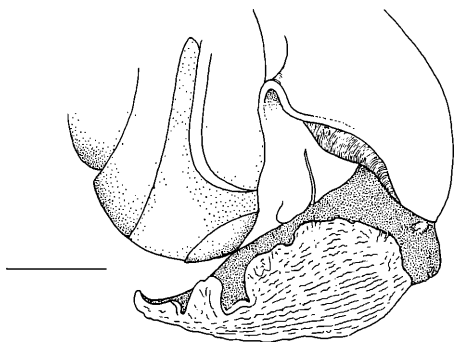
Pallial Complex.

The strongly attenuated triangular kidney (K) dominates the pallial complex in *Leucotaenius favannii* (fig. 11). It is four times as long as it is wide at its broadest point, three times the length of the pericardium (PC) and three-quarters the length of the lung cavity. Its minute (0.4 mm) aperture (AK) is surrounded by two diminutive, elevated lips located at the extreme tapering anterior tip of the kidney. The large primary ureter (U) is 10 percent longer than the kidney; anteriorly it is thin-walled and saccular; it broadly embraces nearly half of the kidney surface facing the lung cavity; it extends anteriorly ca. 1.5 mm beyond the kidney; and it abruptly terminates posteriorly in a ca. 1 mm transverse apertural slit (AU), just before which the ureteral wall becomes glandular. The ureteral channel, at that extreme posterior tip of the lung cavity, continues in a sharp arc, immediately dorsal to the rectum (R), as an open secondary ureter or ureteral trough (UT), the floor of which is folded into tightly and evenly spaced darker colored plicae.

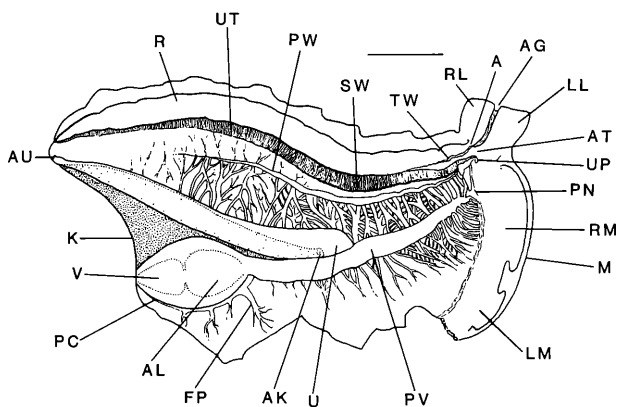
A series of three ureteral walls, parallel to the rectum, channel the excretory fluid more and more precisely to the aperture of the ureteral trough (AT). The primary wall of the ureteral trough (PW) is remarkably like a major pulmonary vein in appearance. It starts imperceptibly in the dorsal wall of the lung, at the mid-pericardial level, and elevates about midway to a 1 mm high, solid wall. Some of the broader small blood vessels impinge directly upon its dorsal surface. Anteriorly this wall once again becomes diminutive and appears to form the triangular ureteral-pneumostomal valve (UP) that dorsally separates the apical anal groove from the pneumostome (PN). The secondary wall of the ureteral trough (SW) starts imperceptibly somewhat anterior to the origin of the primary wall. Unlike the latter, however, this wall is acutely crenulate-convoluted and retains throughout its length a rather uniform, low profile (0.2 mm). The tertiary wall of the ureteral trough (TW) is less than half the length of the secondary wall. This also has a low, crenulate-convoluted profile. From its obscure origin immediately dorsal to the rectum, it gradually passes to the ventral surface of the rectum, and becomes fairly coarse just before it terminates at the junction of the anus (A), the anal groove (AG) and the aperture of the ureteral trough (AT). These three walls in apposition conduct the fluid dorsally into the apex of the anal groove. At this point, there is adjacent but discrete channeling of fecal and excretory substances, ventrally and dorsally respectively, into the anal groove. This latter is formed by the right and left perianal lappets (RL, LL), which are adjacent to the mantle collar (M) and the right mantle lobe (RM). These structures can be seen in situ in fig. 10. In contrast to the situation in the observed achatinids, the pneumostome (PN) is a wholly separate aperture ca. 2 mm away. It is independent of the anal groove and well under the right mantle lobe, in the far dorsal left lateral corner of the left perianal lappet.

The large primary pulmonary vein (PV) originates near the right anterior corner of the lung and passes diagonally to the auricle (AL), dividing the lung unequally into a densely vascular right side and, with the exception of the far anterior end, a sparsely vascular left side. Commensurate with this latter, the first branch of the pericardial vein (FP) is greatly reduced. Its status thus appears intermediate between the condition in *Acavus* (RANDLES 1900: pl. 9 fig. 1) and the dorcasiids (CONNOLLY 1915: pl. 4), wherein this vein is conspicuous in an evenly vascularized lung, and the condition in *Achatina*, wherein this vein is diminutive in a sparsely vascularized left side of the lung.

Efforts to discover, on the basis of the pallial complex, the phylogenetic affinities of *Leucotaenius* have been frustrated at the outset by the paucity of published anatomical information concerning suspected related forms. In this respect, it is regrettable that FISCHER-PIETTE et al. (1963-75) in their studies of Madagascan terrestrial snails did not include information on the pallial complex.



10



11

Fig. 10-11. — 10) Ventrolateral view showing right mantle lobe partially overhanging the two perianal lappets and obscuring the pneumostome (dotted). Note kidney and first loop of the intestine. Bar scale, 10 mm. — 11) Pallial complex. Bar scale, 10 mm. A, anus; AG, anal groove; AK, aperture of kidney; AL, auricle; AT aperture of ureteral trough; AU aperture of primary ureter; FP, first branch of pericardial vein; K, kidney; LL, left perianal lappet; LM, left mantle lobe; M, mantle collar; PC, pericardium; PN, pneumostome; PV, principal pulmonary vein; PW, primary wall of ureteral trough; R, rectum; RL, right perianal lappet; RM, right mantle lobe; SW, secondary wall of ureteral trough; TW, tertiary wall of ureteral trough; U, primary ureter; UP, ureteral-pneumostomal valve; UT, ureteral trough; V, ventricle; A. R. MEAD del.

The presence of an open ascending or secondary ureter immediately sets *Leucotaenius* apart from the Achatinidae, all known members of which have a completely closed secondary ureter. In *Leucotaenius*, the aperture of the primary ureter faces posteriorly at the far posterior end of the lung. Fluids pass into the lumen of the lung per se before being diverted by three ureteral walls to the anal groove. In *Acavus*, the closed portion of the ureter extends considerably beyond the kidney and well into the ascending branch; the aperture thus faces anteriorly. At that point, the ureteral wall is longitudinally slit, giving rise to a very small ventral and a much larger dorsal wall. These are homologous to the secondary and primary ureteral walls, respectively, of *Leucotaenius*. As in *Leucotaenius*, the larger wall forms a triangular ureteral-pneumostomal valve that separates the upper anal groove from the pneumostome. CONNOLLY (1915: 135, pl.4 fig.4) reports that HUGH WATSON found in the mantle cavity of *Dorcasia* and *Trigonephrus* "a slight ledge or fold... overhanging... a band of modified epithelium [that] occupies the position usually held by the ureter in the more highly organized Sigmurethra" Increasing complexity, seriatim, thus appears to be, dorcasids, *Leucotaenius*, *Acavus* and achatinids.

Anteriorly, the primary ureter is swollen and conspicuous in both *Leucotaenius* and *Acavus*, and as it passes posteriorly, it covers approximately fifty and fifteen percent, respectively, of the ventral surface of the kidney. Contrastingly in the achatinids, the primary ureter is substantially or nearly completely obscured ventrally by the encroaching and embracing kidney (cf. GHOSE 1964). Although there are considerable differences in the shape and length of the kidney in these and related forms, no phylogenetic pattern has emerged.

The primary pulmonary vein is dominant in the lung of *Leucotaenius* (fig. 11), *Acavus* (RANGLES 1900), the achatinids (PILSBRY 1904-1905), the dorcasids (CONNOLLY 1915, LEME 1980), and the strophocheilids (LEME 1973, 1974, 1975, LEME et al. 1979). Tangible variability, however, is found in the first branch of the pericardial vein. The explanation for this may be found in the fact that this vein is in an area subject to reduction in width and vascularization. In *Acavus*, the dorcasids and the strophocheilids this vein is conspicuously the second largest in the lung. It is present in *Leucotaenius*, but it has been reduced to a short, coarse spur. Its presence as a broad-based vein, along with the nature of the ureters, further aligns *Leucotaenius* with the acavids.

The presence of perianal lappets and the dorsal substantial separation of the pneumostome from the anal groove in *Leucotaenius* is, so far, uniquely in contrast to the condition in the achatinids and *Acavus*. In these latter, there are no perianal lappets and, obversely, the anal groove dorsally embraces the pneumostome in what appears to be a single, elongate external aperture arcuately parallel to the mantle rim. These features need to be explored in other Acavacea.

Other Structures.

Both a sagittal myoseptum and a transverse myoseptum were found in this species (cf. MEAD 1950: 269-270, fig. 49). The former is a thin, diaphanous membrane apparently composed mostly of connective tissue with some muscle and vascular elements. It extends anteriorly from the albumen gland, diagonally across the juxtaposed slender apical spermathecal duct and apical free oviduct, binding them

tightly together, and stops near its junction with a transverse myoseptum. The anterior aorta passes anteriorly along the haemocoel surface of the diaphragm rather than on the lung floor, as it does in the achatinids that have been anatomically examined. As it turns ventrally, it forms the abrupt anterior edge of the sagittal myoseptum and passes between the crop and the basal spermathecal duct, partitioning the latter and the free oviduct to the right of the sagittal myoseptum. The more muscular, discrete transverse myoseptum, which is broadly attached dorsally to the diaphragm and may function as its depressor, crosses from the left side, over the crop at the level of the posterior extensions of the salivary glands, and joins the sagittal myoseptum, contributing further at that point to the binding together of the slender spermathecal duct and the apical free oviduct. Thus, the two myosepta create anterior and posterior chambers, or blood sinuses, in the unequal right and left halves of the haemocoel, with the penis and crop remaining in the left anterior chamber. This more conspicuous myoseptum was referred to in the Dorcasiidae by WATSON as seeming "to form a partial septum across the body cavity" (CONNOLLY 1915: 139). CARRIKER (1946) found a possibly homologous structure, the "cervical septum" in the Lymnaeidae.

In the achatinids, the anterior aorta is visible on the floor of the posterior lung (MEAD 1950: fig. 49). It is not visible in this region in either *Leucotaenius* or *Acavus*. The stomach was the only other anatomical feature showing tangible differences. In both *Acavus* and the achatinids this organ is grossly saccular and in strong contrast in caliber to the crop and intestine. But in *Leucotaenius* the stomach is surprisingly slender — scarcely more than a slightly enlarged (6×4 mm) acute turn between the adjacent slender crop and intestine, being 3 mm and 2 mm in diameter respectively. No consistent differences were found in the mantle lobes nor in the columellar muscle system. The striking similarity in the circumapertural areas of the shells of *Leucotaenius* spp. and some species of *Trigonephrus* (but not *Dorcasia*) is provocative, but the inference is elusive.

Conclusions.

Primary anatomical features in the radula, jaw, reproductive system and pallial complex of *Leucotaenius favannii* have characters in common with, or very similar to, those found in *Acavus*, and to a lesser known extent in the other acavid genera. Of special importance are the following: the large rachidian tooth, the ribless jaw, the large thick-walled muscular basal spermathecal duct serving as a surrogate vagina, the absence or near absence of a vagina, the vas deferens opening into an elevated dorsal pilaster, the absence of a penial sheath, the open secondary ureter, and the basally large first branch of the pericardial vein. With the single exception of the broad rachidian tooth in *Callistoplepa*, these characters are unknown in the Achatinidae. Regarding the penial sheath, it is relevant to point out that it is present in the closely allied Subulinidae and Achatinidae as well as in the Ferussaciidae.

In the process of establishing relationships, some inferences have had to be drawn from excessively limited information and they are of necessity tentative. In other instances, no interpretation could be made. For example, the muscular, sigmoid free oviduct in *Leucotaenius favannii* appears to be unique, although this section of the female conduit is suspiciously large in various other acavids. As the anatomies of others become better known, the affinities of this species, and

therefore the genus, can be brought more sharply into focus. One thing is certain at this point, the anatomy of this species departs so far from the known spectrum of variability in the Achatinidae that it no longer can justifiably be retained in that family. Nor does any other gondwanan family provide at present a more promising slot for this genus. *Leucotaeniinus* therefore is herewith transferred from the Achatinidae to the Acavidae.

This transfer thus eliminates the Achatinidae, as the family is presently conceived, from the endemic fauna of Madagascar and restricts it to continental Africa, the western equatorial islands of Fernando Poó, Príncipe, São Tomé, and some of the small, coastal islands, e.g. Zanzibar and Mafia. In its dispersal from its origin in tropical central Africa, west, east and then south, it did not reach Madagascar before its separation from continental Africa, which is believed to have occurred in the Jurassic $130-140 \times 10^6$ years ago (SMITH et al. 1981, OWEN 1983). The explanation for the presence on Madagascar of *Achatina fulica* and *A. immaculata*, with its "subspecies" *A. i. antourtourensis*, as apparent indigenous taxa was well researched and explained by BEQUAERT (1950: 70, 113), who believed the subspecies to be merely "a depauperate albino race". He reported that GERMAIN was strongly of the opinion that these two species "are recent arrivals in Madagascar and most probably accidental introduction by man". This is the opinion of the present author, reinforced by conversations with Dr. BEQUAERT. BRUGGEN (1981: 120, 124) considers *A. immaculata* indigenous on Madagascar, but "somewhat suspect".

Major contributions to the relevant topic of the distribution of gondwanan pulmonates are found in PILSBRY (1911), CONNOLLY (1915), GERMAIN (1925), C. R. BOETTGER (1935), LEME (1975) and BRUGGEN (1980b), among others.

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