ON THE STATUS AND AFFINITIES OF
HYBOMYS PLANIFRONS (MILLER, 1900)
(RODENTIA: MURIDAE)

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Abstract. —The taxonomic status and phylogenetic affinity of *Hybomys planifrons* are reviewed and reassessed. This form, which Miller (1900) named from Mt. Coffee, Liberia, has been treated either as a subspecies of the Central African *H. univittatus,* as a subspecies of the West African *H. trivirgatus,* or as a species as originally described. Based upon principal component analyses of cranial variables, a cladistic evaluation of cranial and dental attributes, standard chromosomal preparations, and distributional information, we conclude that *planifrons* is a distinct biological species. *Hybomys planifrons* inhabits that portion of the West African high forest generally identified as the Liberian forest refuge. It bears closest relationship to *H. trivirgatus,* another West African species whose broader distribution covers high forest west of the Niger River; *H. planifrons* and *trivirgatus* are more distantly related to *H. univittatus,* found only east of the Cross River in Nigeria but extending over much of the great rainforest of Central Africa. New karyotypic information is presented for populations of *univittatus.* The karyotypic and morphological heterogeneity observed among our samples suggests that *univittatus* is a composite of two or more species.

In 1900, Gerrit S. Miller described the murid rodent *Arvicanthis planifrons* from "a damp, densely forested region" on the slopes of Mount Coffee, Liberia, elevation about 400 to 500 feet. He compared the new species, based upon two specimens, to the Central African *univittatus,* a form then placed either in *Mus* or *Arvicanthis.* In his description, Miller remarked upon the external resemblance of *planifrons* to *univittatus,* notably the presence of a black, mid-dorsal line without lateral stripes. However, he detailed numerous cranial differences, including the dorsal profile of the cranium, the depth of the rostrum, size and shape of the zygomatic plate, and robustness of the mandible, and concluded that (1900:642) "The external similarity of this animal to *Arvicanthis univittatus* forms a striking contrast to the distinctness of its cranial characters." Miller indicated that his comparisons to *univittatus* were based upon three specimens from Benito River, Cameroon, but nowhere mentioned *trivirgatus* (Temminck, 1853), another similar species described earlier from the Gold Coast of West Africa and one subsequently linked to the taxonomy of *planifrons.* In all likelihood, specimens of *trivirgatus* were not represented in the USNM collection at the time Miller named *planifrons.*

In the several decades following its description, Miller's *planifrons* seems to have drawn little notice in matters concerning the taxonomy of *univittatus* and *trivirgatus.* Instead attention focussed around the generic distinctiveness of *trivirgatus* and *univittatus* and the level of their interrelationship. Thomas (1910) erected the genus *Hybomys,* type-species *Mus univittatus* Peters, primarily because

the arched cranial vault of *univittatus* was quite different from either *Mus* or *Arvicanthis* as he understood them. His diagnosis of *Hybomys* failed to mention *trivirgatus* or *planifrons* or otherwise designate the contents of the new genus. The next year, Thomas (1911) diagnosed *Typomys*, type-species *Mus trivirgatus* Temminck, for the three-striped mice of West Africa then conventionally placed in *Arvicanthis* (Trouessart, 1898). Thomas' frequent contrasts to *Hybomys univittatus* reveal that he considered it and *Typomys trivirgatus* related to some degree, but in the same paper, he also emphasized what he saw as the strong dental similarity of *Typomys* to *Mylomys*. No reference was made to *planifrons*. Ingoldby (1929) questioned the generic separation of *univittatus* and *trivirgatus*, noting the intergradation of characters purportedly differentiating the two as observed in a population from Lagos, Nigeria; his description of these mice as *Hybomys trivirgatus pearsei* formalized that conviction. Hayman (1935) provided exceptions to Ingoldby's assertion about the absence of constant cranial characters distinguishing the three-striped and single-striped mice. Still he acknowledged Ingoldby's arguments for their generic association and listed two series from the Gold Coast as *Hybomys trivirgatus*.

Allen's (1939) checklist of African mammals stabilized the generic contents of *Hybomys* as its morphological limits are perceived today, but the affinity of *planifrons* has since fluctuated in interpretation. Allen (1939) placed *planifrons* as a subspecies of *univittatus*, together with the nominate subspecies and two others, *lunaris* Thomas, 1906, from Mt. Ruwenzori and *badius* Osgood, 1936, from Mt. Cameroon. *Hybomys trivirgatus* contained the nominate subspecies and Ingoldby's (1929) *pearsei*. Allen did not advance his reasons for listing *planifrons* under *univittatus*, but presumably the species' alignments reflected the pattern of striping of the dorsal pelage. Ellerman (1941), too, included *planifrons* as a race of *univittatus* but stated that skulls of *planifrons* were not examined, his arrangement primarily observing Allen's (1939) listing.

Rosevear's (1969) cogent analysis of the *Hybomys* situation in West Africa resulted in the transferral of *planifrons* to subspecific status under *trivirgatus*. Although recognizing the obvious difference in number of dorsal stripes, Rosevear emphasized the many cranial details shared by *planifrons* and *trivirgatus* and concluded (1969:372) that ". . . the skull [of *planifrons*], in size as well as form, is so extremely close to that of typical *trivirgatus* that there seems to be no reasonable probability of two different species being involved." Consequently, Rosevear maintained *planifrons* as a single-striped race of *trivirgatus*, considering it to be "not truly sympatric" with three-striped populations but rather "kept apart by ecological or other factors," and placed *pearsei* in synonomy under *t. trivirgatus*. In his key to African Rodentia, Misonne (1974) distinguished *trivirgatus* and *univittatus* on the configuration of their incisive foramina and remarked that lateral lines may be absent in some specimens of *trivirgatus*, diminishing the value of this pelage character for identification. Thus, Misonne, like Rosevear, aligned *planifrons* as a subspecies of *trivirgatus*, but curiously still listed *univittatus* as occurring in parts of West Africa. As a result of recent field work in West Africa, biologists have again questioned the synonomy of *planifrons* under *trivirgatus* because they have discovered the two forms living close together with little evidence of intergradation (Roche 1971; Coe 1975; Dosso 1975). In his

analysis of the Dahomey Gap as a faunal barrier, Robbins (1978) (following Misonne 1974) continued to recognize the single-striped mice of West Africa as *Hybomys univittatus*.

The last paper underscores the zoogeographic importance of reevaluating the affinity of taxa such as Miller's *planifrons* as a basis for understanding patterns of speciation of mammals inhabiting the high forest tracts of West Africa and the Congo Basin. Accordingly, we here review the status and relationship of *Hybomys planifrons* (Miller) and present new information on its morphology, karyotype, and distribution.

Materials and methods. — Study specimens consisted mainly of conventional study skins with associated skulls, and to a lesser extent, fluid-preserved whole carcasses, housed in the following museum collections, their acronyms listed in parentheses: American Museum of Natural History (AMNH); British Museum of Natural History (BMNH); Carnegie Museum of Natural History (CM); Field Museum of Natural History (FMNH); Harvard University, Museum of Comparative Zoology (MCZ); and the Smithsonian Institution, National Museum of Natural History (USNM).

In descriptions of the dentition, we have followed Miller's (1912) familiar t-system for the upper molars and Musser's (1981) terminology for the lower molars. Identification of the topographic features of the murid skull generally observes the terminology used in Musser (1981) and Carleton and Musser (1984).

To evaluate size and shape changes of the skull with increasing age and to improve comparability of the population samples, each specimen was assigned to one of five stages of dental wear. Comparative exemplars for the five wear stages were identified for a series of *H. trivirgatus* from Ghana, whose museum numbers are given below.

Stage I: M^3 unerupted or, if erupted, then scarcely worn, cusps of M^1 and M^2 prominent in relief, conical and acute; dentinal lakes of primary cusps isolated by inflexed enamel borders, which are in contact or nearly so (USNM 414482).

Stage II: M^3 wholly erupted and exhibiting moderate wear, that is, cusps still elevated with dentine of t8 confluent with t6 but not t4; dentine of chevrons of M^1 and M^2 confluent yet shape of cusps distinctly outlined by enamel constrictions; t8 of M^1 and M^2 not united with t6 or t4 (USNM 412823).

Stage III: M^3 heavily worn, that is, cusps nearly flat and enamel of t8 and t4 united but their dentinal basins still separated; cusps of M^1 and M^2 moderately worn and bluntly rounded, their dentine more broadly connected; t8 of M^1 and/or M^2 continuous with dentine of t6, either through annectant ridge or diminuitive t9, but not t4 (USNM 412813).

Stage IV: Central enamel island present on M^3, formed by union of dentine of t4-t5-t6-t8; cusps of M^1 and M^2 blunt and low but their definition still apparent; dentine of t8 continuous with t6 on both M^1 and M^2 and with t4 on M^1 and sometimes M^2 (USNM 412801).

Stage V: M^3 "dished out," central enamel lake obliterated; cusp definition of M^1 and M^2 poorly discernable, coronal surface almost flat (USNM 412822).

Having defined the wear classes based on examples of *H. trivirgatus*, it was discovered that recognition of wear classes (especially discriminating individuals in Stage II versus III) in samples of *univittatus* was sometimes ambiguous because of the stronger development and usual presence of t9. As a result, more attention

was placed on the wear sequence of M^3 and the prominence of cusps on M^1 and M^2 in assigning wear stages to individuals of *univittatus*.

Several measurements of the skin and skull were taken to characterize the morphology of the samples. Total length, tail length, and hindfoot length were extracted to the nearest whole mm from the skin tag. Twelve dimensions of the skull were measured to the nearest 0.1 mm by means of hand-held dial calipers accurate to 0.05 mm. These measurements, their abbreviations as used herein, and their definitions where necessary are as follows: (1) occipitonasal length, OcNL; (2) rostral length, LRos; (3) greatest zygomatic breadth, ZyB; (4) width of zygomatic plate, WZyP; (5) least interorbital width, IoC; (6) postpalatal length, PpL (from the posteromedial border of the basioccipital to the anterior margin of the mesopterygoid fossa); (7) length of hard palate, HPL (from the anterior border of the mesopterygoid fossa to the posterior edge of the incisive foramina); (8) length of incisive foramen, LIF; (9) diastemal length, LDia; (10) alveolar length of maxillary toothrow, LMax; (11) greatest breadth across upper molars, BMls (caliper jaws placed at labial margin of first molars); (12) depth of mandible, DMan (from ventralmost level of the angular process to the top of the condylar process).

In addition to the mensural variables, ten qualitative characters of the dentition and cranium were reviewed and tabulated for the specimen samples. The definition and abbreviation labels of these discrete variables are: (1) presence of a lateral bony strut at the base of the alisphenoid bone (AlSt); (2) presence of a t9 on the first upper molar (t9M^1); (3) presence of a t9 on the second upper molar (t9M^2); (4) presence of an anteromedian cusplet (AMCM_1), (5) an anterolabial cusplet (ALCM_1), and (6) posterlabial cusplet (PLCM_1) on the lower first molar; (7) occurrence of two medial rootlets on the lingual border (DLnRM^1) and (8) a single medial rootlet on the labial border (LbRM^1) of the first upper molar; (9) occurrence of accessory rootlets on the labial border (LbRM_1) and (10) lingual border (LnRM_1) of the first lower molar. Tabulation of dental structures was mainly restricted to specimens assigned to wear classes I–IV, while detection of molar roots was mostly confined to individuals in wear classes III–V.

Due to the high incidence of broken skulls and the small number of specimens generally available from a collecting site, localities were combined to achieve sample sizes suitable for statistical analyses. Twelve composite OTUs were so identified and are listed below, together with their sample size and identification code used in figures.

Hybomys planifrons, p: Ivory Coast, Liberia, and Sierra Leone, N = 14.
Hybomys trivirgatus, t1: Ghana, N = 16; t2: Ivory Coast, N = 22; t3: Liberia, N = 7; t4: Nigeria, N = 10; t5: Sierra Leone, N = 3.
Hybomys univittatus, u1: Cameroon, Batanga, N = 17; u2: Cameroon, Eseka and vicinity, N = 15; u3: Cameroon, Lolodorf, N = 23; u4: Gabon, Cap Esterias, N = 9; u5: Zaire, Upper Congo area, N = 17; u6: Zaire, Kivu Prov., N = 21.

Standard descriptive statistics (mean, range, standard deviation, variance, standard error) were derived for the twelve OTUs. One-and two-way analyses of variance were performed to assess the effects of sex and age on nongeographic population variation. In evaluating the age factor, we excluded the youngest and

oldest cohorts, the analyses being restricted to specimens in wear classes II–IV. Similarly, we restricted our multivariate analyses to individuals in the same three wear-classes, although this range of classes still introduced significant age variation that might complicate a comparison of samples with dissimilar age profiles. However, we did not feel constrained to correct statistically for possible age differences among our OTUs, since the magnitude of inferred species differences exceeded the intraspecific geographic and nongeographic variation apparent. Principal components were extracted from a variance-covariance matrix and computed using only the 12 cranial variables transformed to natural logarithms. A principal component program was preferred over canonical variate and discriminant function analyses because no a priori designation of groups is required nor assumptions about multivariate normality. In view of some of our small samples sizes, occurrence of multivariate normality is highly suspect. All analytic procedures were carried out using Systat, a series of statistical routines on diskette programmed for microcomputers.

Preparation of chromosomal material, and descriptive terminology for chromosomal morphology follow Patton (1967), except that we include the sex chromosomes in our calculation of fundamental number (FN), given their ambiguous identification in *Hybomys*. Karyotypes of specimens from the following localities were examined.

Hybomys planifrons.—Sierra Leone: Meema (USNM 463386 ♀); 10.1 km E Fintonia (USNM 546938 ♀).

Hybomys trivirgatus.—Sierra Leone: Belebu, (USNM 463170 ♀).

Hybomys univittatus.—Cameroon: 11 km S, 1 km E Bamenda (CM 58832 ♂, 58833 ♀); 6 km S, 5 km E Eseka (CM 58834 ♀). Gabon: Estuaire Prov., 1 km SE Cap Esterias (CM 90809 ♂, 90812 ♂, 90813 ♂). Zaire: Yalosemba (USNM 537813 ♂, CM 86727 ♀).

Qualitative Character Variation

External.—As suggested by the specific epithets *trivirgatus* and *univittatus*, the striping pattern of the dorsal pelage has historically received important attention in the diagnosis and recognition of mice now placed in the genus *Hybomys*. Thomas (1911) emphasized the tri-striped pattern in examples of *trivirgatus* in erecting his genus *Typomys*. And the single, black dorsal line evident in *planifrons* persuaded earlier workers to align it as a West African subspecies of the Congo Basin form *univittatus*, which also possesses but a single mid-dorsal stripe (Allen and Coolidge 1930; Allen 1939; Ellerman 1941). This taxonomic placement was later reversed when investigators attributed greater significance to the cranial similarities of *trivirgatus* and *planifrons* (see below), and consequently viewed *planifrons* as a single-striped race of *trivirgatus* (Rosevear 1969; Misonne 1974). From this perspective, the pattern of dorsal striping was interpreted as variable at the population level and hence unsuitable as a character for species diagnosis and identification. For instance, Misonne (1974:19), who included *planifrons* under *trivirgatus*, stated that "These lines [i.e., lateral lines of *trivirgatus*] may disappear so that they are of little use for identification."

Although some variation obtains, the pelage patterns observed in our West African samples assignable to *planifrons* or *trivirgatus* suggest a greater constancy

than previously supposed. Compared to the medial stripe, the lateral ones are paler, sometimes very faint, in specimens of *trivirgatus*; the weakest definition of lateral lines occurs among our Nigerian samples. Nevertheless, a trilinear arrangement of stripes is discernable even in the faintest examples, unlike the complete lack of lateral stripes as observed in true *planifrons*. In addition to the consistency of stripe definition, the medial stripe in *trivirgatus* extends onto the animal's forehead, reaching between the eyes and less commonly onto the rostrum; whereas the mid-dorsal stripe possessed by specimens of *planifrons* usually terminates at the level of their pinnae (Fig. 1), a distinction noted by Rosevear (1969). Aside from the pronouncement of dorsal stripes the ground color of the fur appreciably differs too. In *trivirgatus,* the general appearance of the dorsum is paler, more speckled, and harsher, qualities imparted by the greater predominance of yellow-tipped hairs. In contrast, specimens of *planifrons* contain more reddish-tipped hairs in the dorsal coat, giving them a richer and more uniform dark brown tone. The venters of both forms are more variable, but examples of *planifrons* typically exhibit a stronger suffusion of reddish overlaying dark gray bases, while those of *trivirgatus* have a more yellowish wash with bases of a paler gray. These tonal contrasts are subtler than the stripe differences, yet they reinforce the impression that *planifrons* is something more biologically distinct than a variant of *trivirgatus* that lacks lateral stripes.

In certain respects, populations assigned to *univittatus* display more striking chromatic variations of the fur. The black dorsal stripe (which, in contrast to *planifrons,* usually ends on the nape) may be very faint and virtually undetectable in some individuals. The indistinctness of the stripe seemingly arises in two ways. In one, hairs constituting the stripe itself are paler such that the stripe fades into the dorsum ground color. The two USNM specimens from Uganda, for example, exhibit this condition, but we observed it in individuals from other parts of the range of *univittatus* as well. In the other, the overall darker saturation of the pelage almost matches the black tone of the dorsal line and obscures it. This appearance characterizes the holotype of *H. univittatus badius* Osgood, which possesses a rich dark brown dorsum with a reddish tinge and a similarly colored venter. The underparts of most *univittatus* are some shade of grayish.

Thomas (1910, 1911) reported the number of mammae as 0-2 = 4 or 1-2 = 6 for *univittatus* and 0-2 = 4 for *trivirgatus,* but Rosevear (1969) noted that all female *univittatus* in BMNH have the 1-2 = 6 mammary distribution, and that 0-2 = 4 is characteristic only of *trivirgatus.* Females of *planifrons* also apparently lack anterior pairs; no axillary or pectoral teats were detected on dried skins, and one live-trapped, lactating female from Sierra Leone possessed only two inguinal pairs.

The fifth digit of the hindfoot of *Hybomys* barely exceeds the first in length and extends only to the bases of digits two to four. *Hybomys* possess only five metatarsal pads on the bare plantar surface, a number substantiated in fluid-preserved examples of *planifrons, trivirgatus,* and *univittatus.* The pad missing from the usual muroid complement of six is the lateral one (=hypothenar pad) of the posteriorly placed metatarsal pair. Both Tullberg (1893) and Sanderson (1940) illustrate the hindfoot conformation of *Hybomys univittatus* and accurately depict the number and position of the metatarsal pads.

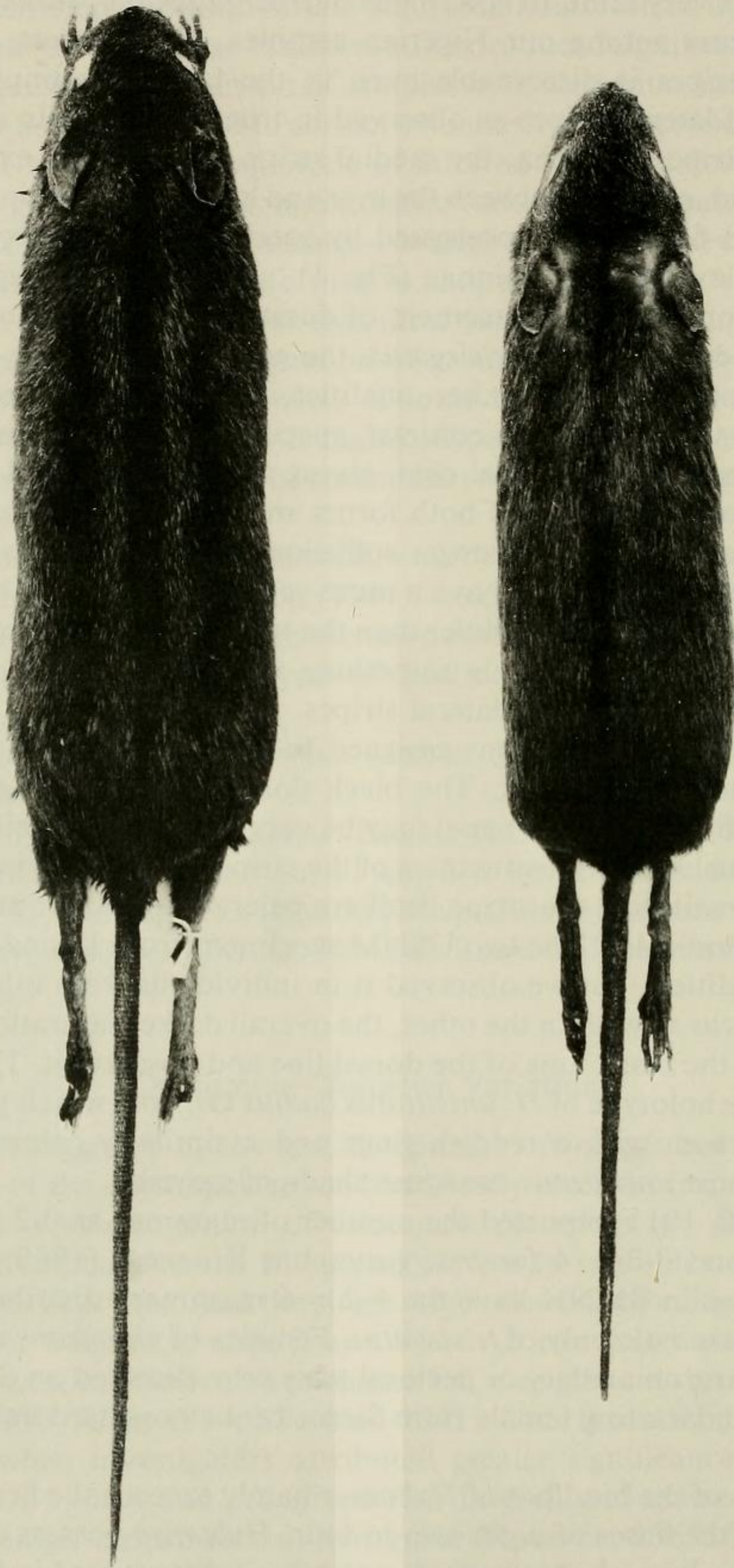*Cranial.* —As remarked by Rosevear (1969), the subgeneric archetypes *H. (Hy-*

Fig. 1. Dorsal view of skins of: Left, *Hybomys trivirgatus,* adult female (USNM 545624) from Lalehun, Sierra Leone; Right, *Hybomys planifrons,* young adult female (USNM 466767) from Niebe, Ivory Coast.

bomys) *univittatus* and *H.* (*Typomys*) *trivirgatus* exhibit such striking conformational differences of their skulls that characterization of the cranium for the genus proves difficult. With this obstacle in mind, the following description of cranial morphology treats first those characters general for the genus, next those that separate *univittatus* from both *planifrons* and *trivirgatus,* and last, traits that provide discrimination of *planifrons* from *trivirgatus.*

The skull in *Hybomys* is medium-sized (occipitonasal length = 31–36 mm) with a rounded, smoothly contoured braincase (Fig. 2). Temporal and lambdoidal ridges are scarcely evident even in old animals. The interparietal is relatively long but narrow, its lateral apices terminating far short of the squamosal-parietal suture. A narrow but distinct bead extends from the frontal-parietal junction just past the narrowest portion of the interorbital constriction and delineates the arcuate supraorbital edges. The zygomatic arches are not bowed laterally but appear parallel over their midsection. The squamosal part of the arches seems to be slung unusually low on the side of the skull, dipping to the plane of the maxillary alveoli (Fig. 3). A weak short ridge extends caudad from the squamosal root of the zygoma. The area covered by the squamosal bone posterior to the root of the zygomatic arch is diminuitive, a condition which suggests a small surface of origin for the temporalis muscle. The rostrum appears relatively long and broad, the anterior nasal tips normally tapering, not broadly expanded. The bullae are medium-sized and otherwise unremarkable; a groove indicating passage of the internal carotid artery scores their anteromedial surface. A large stapedial foramen penetrates the posteromedial wall of the bullae at the petrotympanic junction, but no squamosal-alisphenoid groove exists, nor does a sphenofrontal foramen. This combination of features suggests a carotid circulatory pattern like that typical of other murines, in which the supraorbital branch is lacking and supply of the orbit instead arises from the infraorbital vessel (Bugge 1970; Musser 1982). The triangular-shaped pterygoid fossae are little recessed and border the moderately long mesopterygoid fossa, the palatal end of which is bluntly u-shaped or sometimes bears a medial promontory. Well-defined sphenopalatine vacuities perforate the dorsal walls of the mesopterygoid fossa at the level of the basisphenoid-presphenoid suture. The hard palate is relatively flat and unmarked by ridges and corrugations. The posterior-palatine foramina are usually located in the palatine-maxillary suture and emerge at a point even with the middle of the second molar. The incisive foramina are notably wider at their midsection and strongly convergent anteriorly. The spacious postglenoid foramen is crescentic and sometimes confluent with the middle lacerate foramen or separated from it by a flange of the periotic bone. No squamosomastoid (=subsquamosal) foramen occurs in *Hybomys.* A conspicuously large optic foramen penetrates the orbitosphenoid bone in *Hybomys,* perhaps reflecting their diurnal habits; the opening of the optic foramen is two-thirds to subequal the size of the sphenoidal fissure. The dentary bone lacks a capsular projection on its lateral face, the incisive alveolus terminating about the level of the front edge of the coronoid process.

Rosevear (1969) thoroughly enumerated the trenchant points of contrast distinguishing the "*Hybomys*-type" of skull from that of the "*Typomys*-type," the latter designation applying both to *trivirgatus* and *planifrons.* The dorsal cranial profile is notably arched in *univittatus,* its outline curved symmetrically both
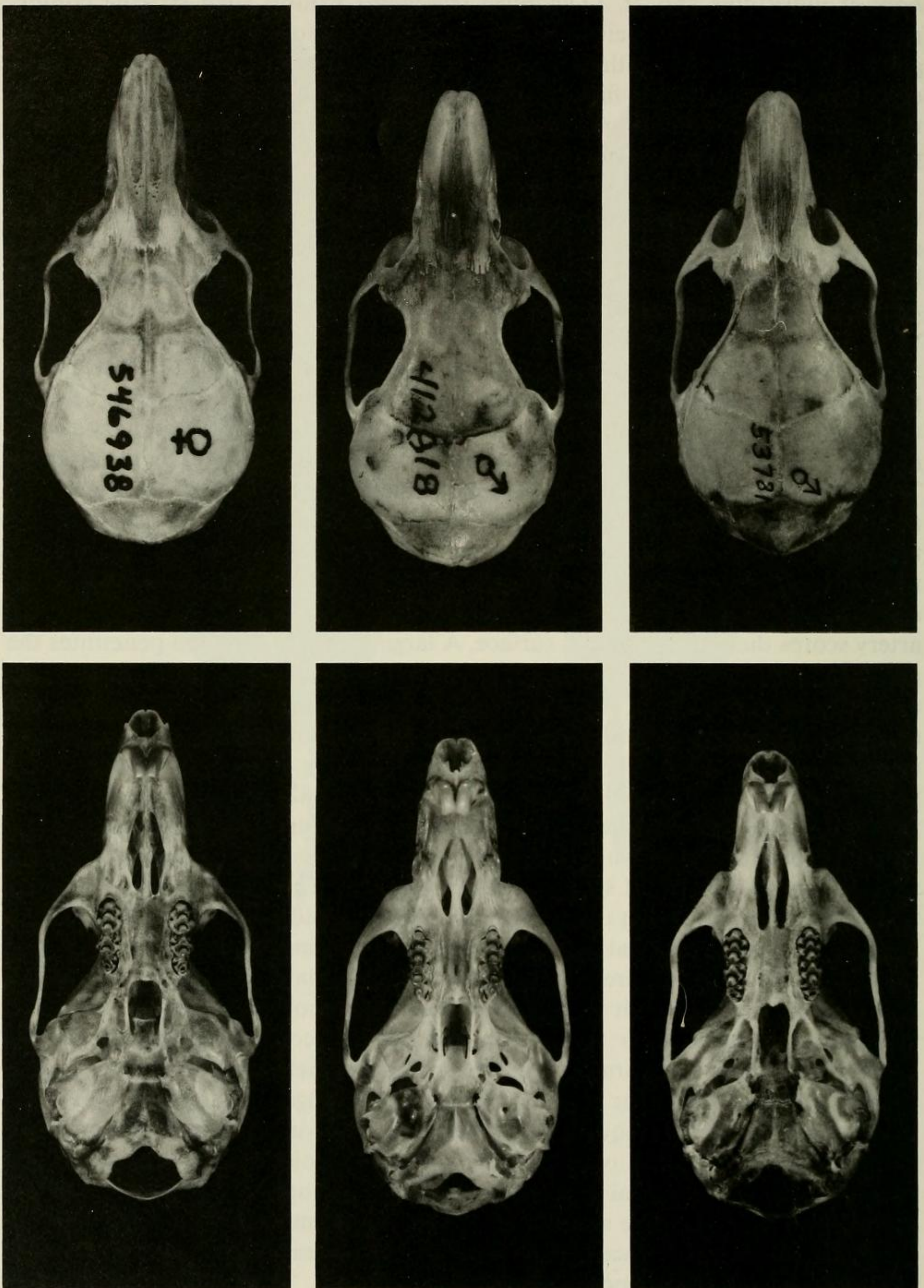
Fig. 2. Dorsal (upper) and ventral (lower) view of skulls of: Left, *Hybomys planifrons,* adult female (USNM 546938) from 10.1 km E Fintonia, Sierra Leone; Middle, *Hybomys trivirgatus,* adult female (USNM 412818) from 1 mi N Berekuso, Ghana; Right, *Hybomys univittatus,* adult male (USNM 537814) from Tandala, Zaire. Approximately 2×.

anteriorly and posteriorly from the apex of the cranial vault located approximately at the midpoint of the orbit (Fig. 3). In *planifrons* and *trivirgatus,* the highest point of the cranial vault is displaced more posteriad, near the rear of the orbit, which imparts a flatter, longer slope to the facial region in contrast to the arcuate curve of the braincase. The rostrum in examples of *trivirgatus-planifrons* is relatively longer but not as deep as that seen in *univittatus.* Moreover, the nasal tips are more attenuate in *trivirgatus-planifrons* compared to rounded in *univittatus.* The anterior ends of the supraorbital ridges recurve laterad in *trivirgatus-planifrons* but terminate parallel to one another in *univittatus,* giving a more hourglass-shape to the interorbital region of the former and cuneate appearance to the latter (Fig. 2). The maxillary portion of the zygomatic arch features several points of dissimilarity. In *univittatus,* the zygomatic plate is broader with a vertical leading edge and deeper zygomatic notch; whereas in *trivirgatus-planifrons,* the zygomatic plate is narrower, its leading edge inclined and the zygomatic notch shallow. In addition, the zygomatic plate seems shifted forward on the skull of *univittatus,* the posterior edge of the plate aligned with the anterior root of the first molar. A line projected along the rear edge of the plate in *trivirgatus-planifrons* intercepts the first lamina of the first molar. The length of the incisive foramen in *univittatus* surpasses that in *trivirgatus-planifrons,* but the difference is more striking in comparisons of *univittatus* and *trivirgatus* skulls (Fig. 2; Appendix 2). The incisive foramina of *trivirgatus-planifrons* appear broader and their ends noticeably converge both anteriorly and posteriorly. *Hybomys univittatus* possess a significantly deeper, more robust mandible, the greater depth especially evident between the condyloid and angular processes (Fig. 3). The more deeply excavated notch above the angular process accentuates the gracile appearance of the mandible in *trivirgatus-planifrons.*

Other authors had previously emphasized the diagnostic value of many of the cranial traits discussed above, particularly the dorsal contour of the skull (Miller 1900; St. Leger 1931), the morphology of the zygomatic plate (Miller 1900; Thomas 1911; Ingoldby 1929), and the size and shape of the incisive foramina (Miller 1900; Thomas 1911; St. Leger 1931; Hayman 1935). In a morphometric study comparing large samples of *univittatus* and *trivirgatus,* Van der Straeten and Verheyen (1982) quantitatively verified the discriminatory power of several of the same variables identified through visual inspection of skulls by earlier systematists.

Still other cranial attributes differentiate *univittatus* from *trivirgatus* and *planifrons.* The cross-sectional area of the optic foramen appears approximately equal to that of the sphenoidal fissure in examples of *trivirgatus-planifrons;* whereas in *univittatus,* the optic foramen is smaller, about two-thirds the size of the sphenoidal fissure. Comparison of the basal portion of the alisphenoid bone discloses another reliable means of separation. Specimens of *univittatus* possess a strut of bone that partitions the combined masticatory-buccinator foramen from the foramen ovale accessorius (Fig. 4). Examples of *trivirgatus-planifrons* usually lack this strut of the alisphenoid. Instead, the spacious opening found represents a coalescence of the masticatory-buccinator foramen and the foramen ovale accessorius. In this condition, the anterior end of the alisphenoid canal and the foramen ovale are visible laterally, their position no longer obscured by the alisphenoid
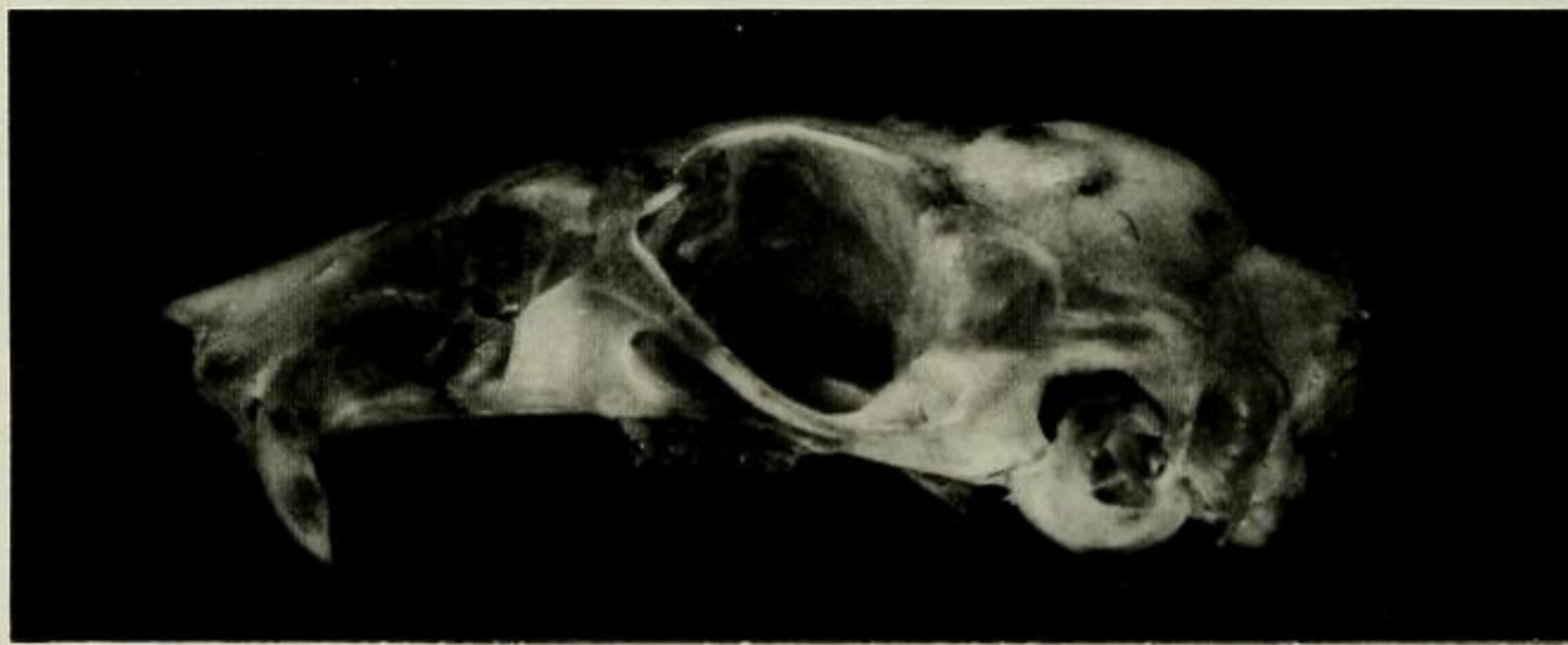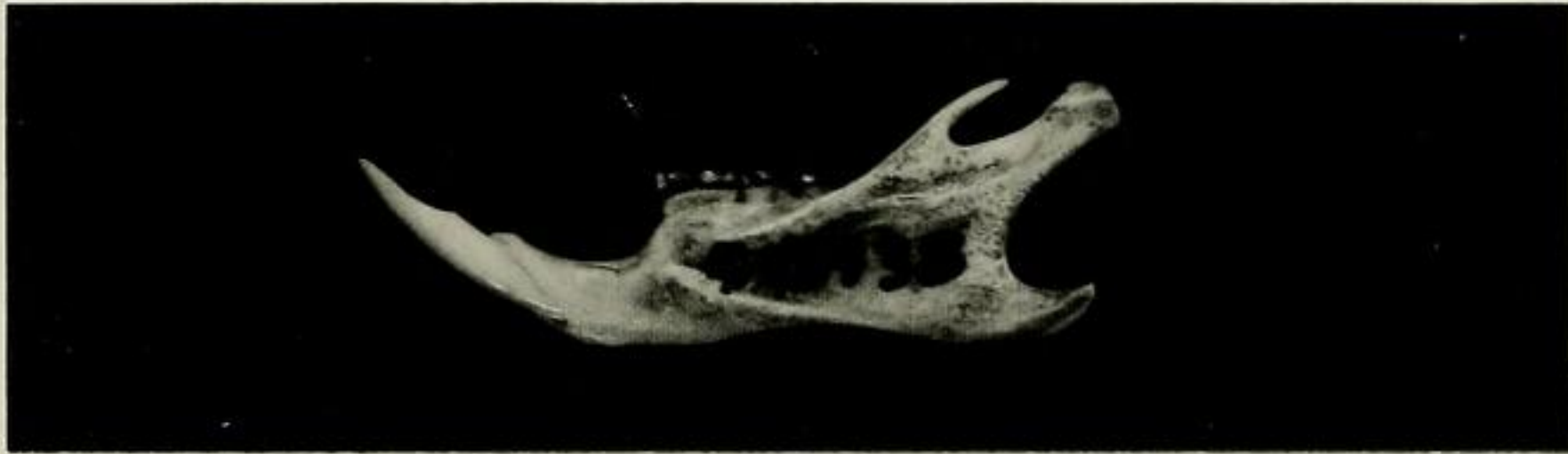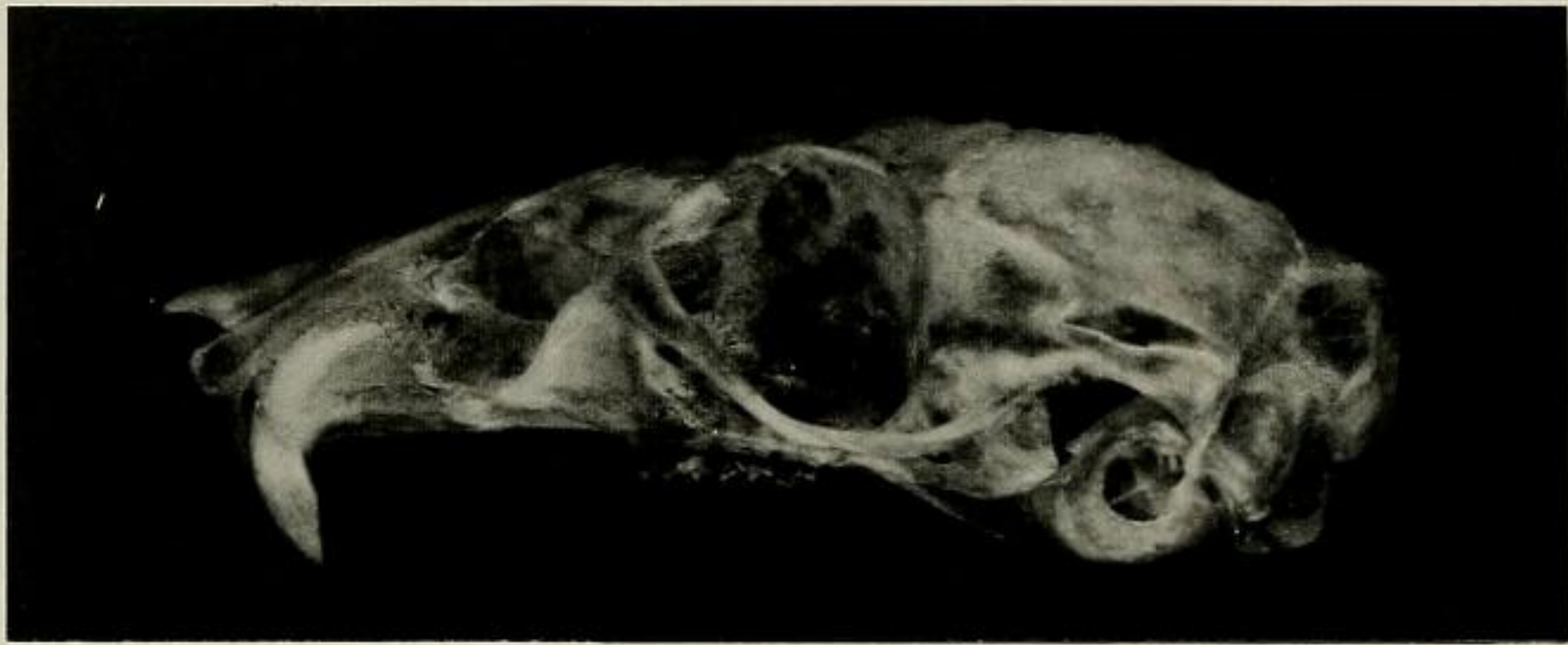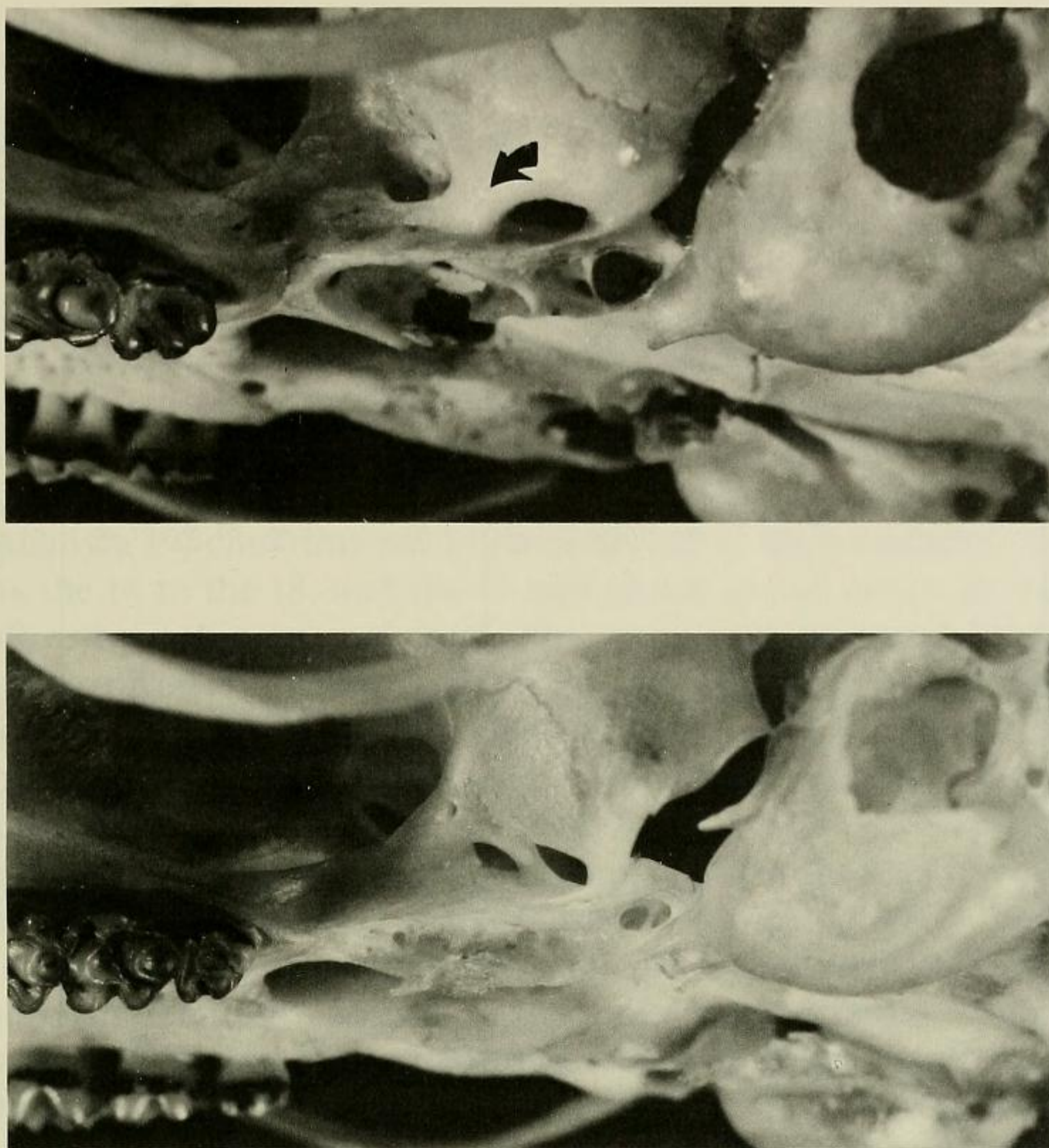
Fig. 4. Ventrolateral view of alsiphenoid region of: Top, *Hybomys univittatus* (USNM 101982) from Gabon; Bottom, *Hybomys trivirgatus* (USNM 420628) from 6 mi N Kade, Ghana. Arrow denotes the alisphenoid strut characteristic of *univittatus*. Approximately 5×.

strut. The alisphenoid strut was observed in 94% of the specimens of *univittatus* examined, but in only 6.4% of *trivirgatus* and none of *planifrons* (Table 1).

Compared to the suite of cranial features that separate *univittatus* and *trivirgatus-planifrons*, those that discriminate *trivirgatus* from *planifrons* are few and subtler. The interorbital region in *planifrons* appears more constricted and does average smaller than *trivirgatus*, but their ranges overlap substantially (Appendix 2; Fig. 1). The incisive foramina of *planifrons* are broad like those of *trivirgatus*, but unlike *trivirgatus*, the posterior ends of the incisive foramina usually reach the level of the front edge of the first molars and hence are longer (Appendix 2; Fig. 1). This characteristic of *planifrons* illuminates the ambiguities Rosevear (1969) encountered in identifying specimens from certain localities in West Africa (for example, Mt. Bintamane, Sierra Leone), where mice exhibited a *trivirgatus-*

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Fig. 3. Lateral view of skull and mandible of: Top, *Hybomys planifrons*, adult female (USNM 546938) from 10.1 km E Fintonia, Sierra Leone; Middle, *Hybomys trivirgatus*, adult female (USNM 412818) from 1 mi N Berekuso, Ghana; Bottom, *Hybomys univittatus*, adult male (USNM 537814) from Tandala, Zaire. Approximately 2×.

Table 1.—Percent occurrence of certain cranial and dental traits in samples of *Hybomys* (sample sizes in parentheses).*

Species and country	AISt	T9M[1]	T9M[2]	AMCM1	ALCM1	PLCM1	LbRM[1]	DLnRM[1]	LbRM1	LnRM1
H. planifrons										
All localities	0.0 (34)	5.5 (36)	0.0 (36)	0.0 (36)	0.0 (36)	25.0 (36)	0.0 (33)	15.1 (33)	0.0 (33)	9.0 (33)
H. trivirgatus										
Ghana	2.8 (35)	96.7 (31)	32.2 (31)	0.0 (34)	0.0 (34)	35.2 (34)	0.0 (27)	0.0 (27)	0.0 (28)	3.6 (28)
Ivory Coast	2.7 (36)	85.2 (34)	23.5 (34)	0.0 (34)	0.0 (34)	23.5 (34)	6.2 (32)	3.1 (32)	0.0 (32)	0.0 (32)
Liberia	0.0 (12)	84.6 (13)	15.3 (13)	0.0 (13)	0.0 (13)	30.7 (13)	0.0 (11)	0.0 (11)	0.0 (11)	0.0 (11)
Nigeria	0.0 (17)	75.0 (16)	0.0 (16)	0.0 (16)	0.0 (16)	18.7 (16)	0.0 (11)	9.0 (11)	0.0 (11)	0.0 (11)
All localities	6.4 (108)	86.4 (103)	22.5 (102)	0.0 (105)	0.0 (105)	26.6 (105)	2.2 (90)	2.2 (90)	0.0 (91)	1.0 (91)
H. univittatus										
Gabon	86.6 (30)	100.0 (41)	90.0 (40)	92.3 (39)	27.5 (40)	100.0 (40)	100.0 (33)	24.2 (33)	100.0 (31)	100.0 (31)
Cameroon	94.1 (120)	100.0 (114)	97.3 (114)	90.9 (110)	50.0 (110)	99.0 (110)	96.8 (95)	28.7 (94)	100.0 (92)	93.5 (93)
Zaire	96.3 (82)	100.0 (92)	98.9 (92)	96.6 (89)	55.0 (89)	98.8 (89)	98.8 (84)	23.8 (84)	100.0 (85)	100.0 (86)
All localities	94.1 (239)	100.0 (253)	96.8 (250)	93.4 (244)	48.1 (245)	99.1 (245)	98.1 (218)	25.3 (217)	100.0 (213)	97.2 (215)

* Grand totals for "All localities" include all specimens examined of a species.

like skull but possessed long incisive foramina as seen in *univittatus*. The greater length of the incisive foramina in *planifrons* is reflected in its concomitantly shorter hard palate compared to the longer one recorded for specimens of *trivirgatus*.

Dental.—The molars of *Hybomys* are strongly cuspidate, the triserial arrangement of the major cones well-marked even in worn teeth (Fig. 5). The central row of cusps (t2, t5, and t8) in the upper molars of young animals are inclined posteriorly, but this orientation is obscured in older specimens. The cusps of each chevron are united transversely but retain their distinctiveness until extremely worn. The anterior chevron (consisting of t1, t2, and t3) of the first upper molar is isolated from the second (t4, t5, and t6); however, cusps of the second and third (t8 and usually a t9) chevrons are interconnected at their margins. A low lingual ridge joins the t4 to the t8, and the t6 and t8 are united either by a small intermediate t9 or by a thin enamel crest. The cusps composing the first and second chevrons are arrayed almost symmetrically, the t1 and t4 set only slightly posterior to and being slightly larger than their buccal counterparts, the t3 and t6. The second upper molar contains a t1 and diminuitive t3 representing the first chevron, the full complement of t4-t5-t6 of the second, and a large t8 comprising the third (a small t9 is consistently found in some forms). The connections of the t8 to the second chevron are the same as described for the first molar. The third upper molar is approximately one-half the size of the second and exhibits lower cusp height and cusp definition relative to the anterior cheekteeth. A conspicuous t1 is present but unites with the anterolingual border of the t5 after little wear. A definitive t3 is absent but may be represented by an enamel spur extending from the anterobuccal margin of the t5. The second chevron is apparently complete but the individual cusps are broadly connected. The t8 consists of a round to oval heel, which eventually unites with the second chevron to enclose a central enamel island. Posterior cingula are usually absent, but where found, they resemble a minute posterolabial spur off of the t8 and become indiscernible after little wear. A t7 does not occur in the upper molars of the genus *Hybomys*.

The lower molars present a biserial arrangement of cusps that are more confidently homologized to those of a cricetid molar. In the first and second molars, the protoconid-metaconid and hypoconid-entoconid form opposite pairs; the primary cusps comprising each pair unite at their anteromedial borders (Fig. 5). The anteroconid of the first molar is deeply bifurcate, the anterolingual and anterolabial cusps so well defined that they almost match the major cones in prominence. The anterolabial-anterolingual cusps and protoconid-metaconid join medially in an x-shaped configuration, but a deep trough separates the hypoconid-entoconid and protoconid-metaconid. Both first and second molars possess a posterior cingulum, situated at their posteromedial margin. This structure is lower in relief compared to the major cusps; it is conically shaped in younger animals and assumes an oval appearance with wear. As in its upper homolog, the lower third molar displays lower cusp relief and definition. The broad talonid heel of the third molar presumably consists of a fused hypoconid-entoconid; no posterior cingulum is present.

The above description generally characterizes the molar dentition of *Hybomys*, but differences do occur between the named forms with respect to the presence and development of certain minor coronal features. These variations include the
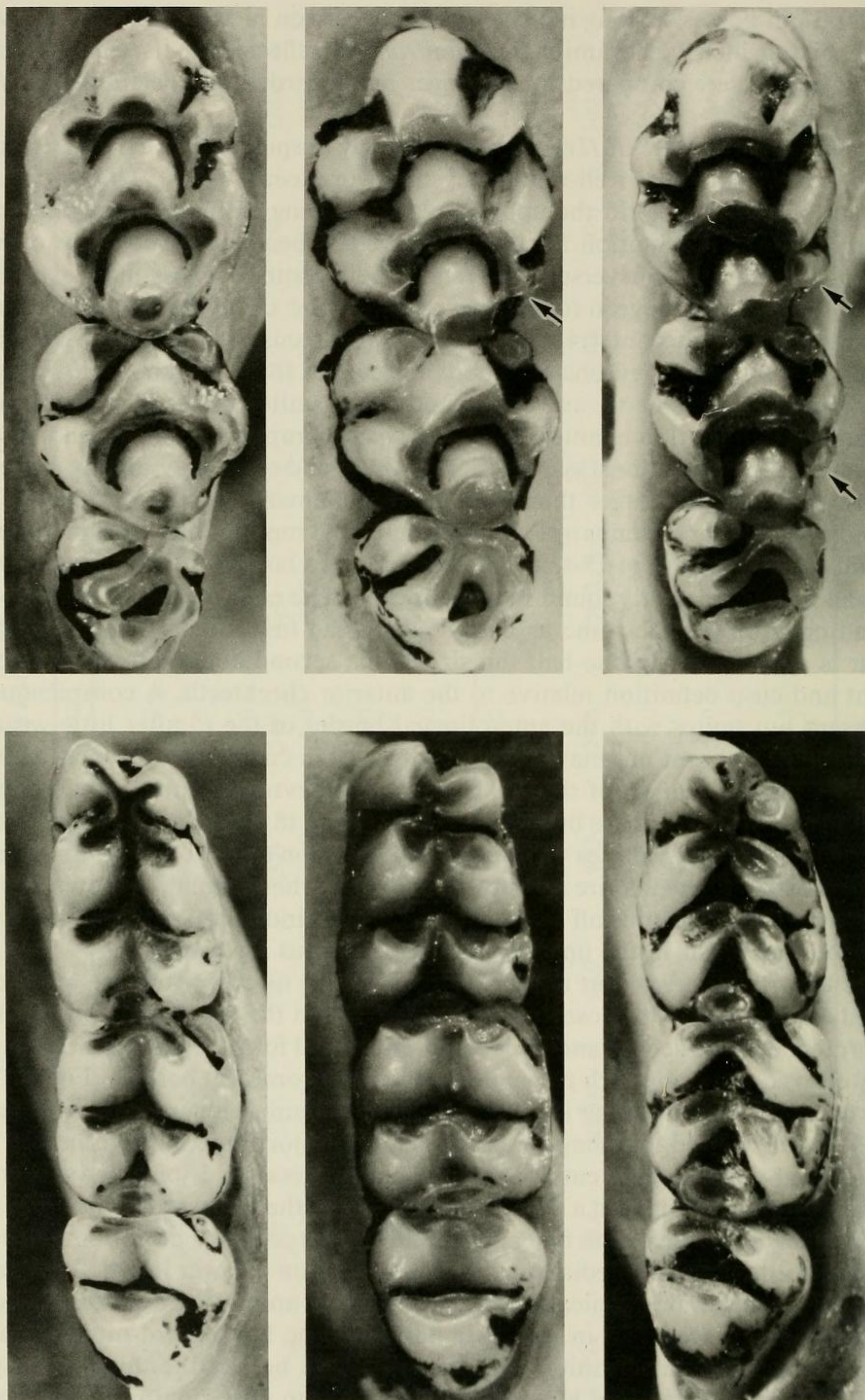
Fig. 5.   Upper left (top) and lower right (bottom) molar toothrows of: Left, *Hybomys planifrons* (USNM 546936) from 10.3 km SE Fintonia, Sierra Leone; Middle, *Hybomys trivirgatus* (USNM 481859) from 25 km N Zwedru, Liberia; Right, *Hybomys univittatus* (USNM 535545) from Irangi, Zaire. Arrows indicate the presence of a t9 in the M^1 of *trivirgatus* and M^1 and M^2 of *univittatus*. Approximately 15×.

occurrence and size of the t9 on the first and second upper molars, and the presence of an anteromedial cusplet (AMC), anterolabial cusplet (ALC), and posterolabial cusplet (PLC) on the lower first molar.

A conspicuous, well-defined t9 exists on the first and second molars of all sampled populations of *univittatus* (Figs. 5, 6; Table 1). This cusp is more closely apposed to the t6 than to the t8 and unites with the posterobuccal border of the t6 in early wear stages. Rosevear (1969:371) recognized this condition in *univittatus* and contrasted it with the morphology of West African forms ("*Typomys*-type") as follows: "In M^1 and M^2 t9 is often (but not always) reduced to little more than a ridge, especially in M^2 where the reduction is sometimes so great that the cusp appears to be lacking." This description is adequate, but collation of the occurrence of the t9 among West African populations reveals sharp discontinuity along taxonomic lines. A t9 was observed on the first molar of most individuals (average = 86.4%) of *trivirgatus* examined (Figs. 5 and 6; Table 1). The t9 evident in *trivirgatus* usually does not equal in size and discreteness that found in specimens of *univittatus*; still a noticeable enamel indentation of the labial border of the first molar marks its usual presence. In contrast, a t9 was documented in few individuals of *planifrons* (average = 5.5%), and its development, if present, resembles little more than a bulge of the crest connecting t6 and t8. In such instances, identification of a t9 as present or absent was subjective for examples of both *planifrons* and *trivirgatus*. Whereas a t9 occurs on the second molar of most *univittatus* (96.8% of all samples), its presence is infrequent in *trivirgatus* (22.5%) and unknown in *planifrons*. Among the population samples of *trivirgatus*, the lowest frequency occurrence of the t9 was recorded for the Nigerian series (Table 1).

No distinction between *planifrons* and *trivirgatus* was discovered for the occurrence of the supplemental conulids of the lower first molar, but both differed substantially from *univittatus* (Figs. 5, 6; Table 1). An anteromedian cusplet (AMC) projects from the junction of the anterolabial and anterolingual cusps in over 90 percent of the specimens of *univittatus*; whereas, this trait was not detected in any *planifrons* and *trivirgatus*. The presence of an anterolingual cusplet (ALC) and posterolingual cusplet (PLC) on the buccal cingulum of the lower first molar was frequently tabulated for *univittatus* but never (ALC) or infrequently (PLC) recorded for *planifrons* and *trivirgatus*.

The number of molar roots also provides a reliable criterion for distinguishing *univittatus* from *planifrons* and *trivirgatus*. The typical root formulae observed on the upper and lower molars are as follows (less frequent character state in parentheses): *univittatus*—4(5)/4, 3(4)/4, 3/3; *planifrons* and *trivirgatus*—3(4)/2, 3/3, 3/3.

The disparities in root number arise in a different manner according to the molar and/or species in question, and these variations were scored for the upper and lower first molars only (Fig. 7; Table 1). A small labial rootlet, situated midway to the large anterior and posterior roots, is visible in virtually every suitable specimen of *univittatus* but seldom detectable in *planifrons* and *trivirgatus*. St. Leger (1931) earlier drew attention to this dissimilarity and noted that when a labial rootlet is present in *trivirgatus*, it is located more medially compared to *univittatus*. The five-rooted condition of the upper first molar of *univittatus* and four-rooted variant of *planifrons/trivirgatus* occur when the large medial root is subdivided, a trait observed infrequently in all forms. In addition to the large
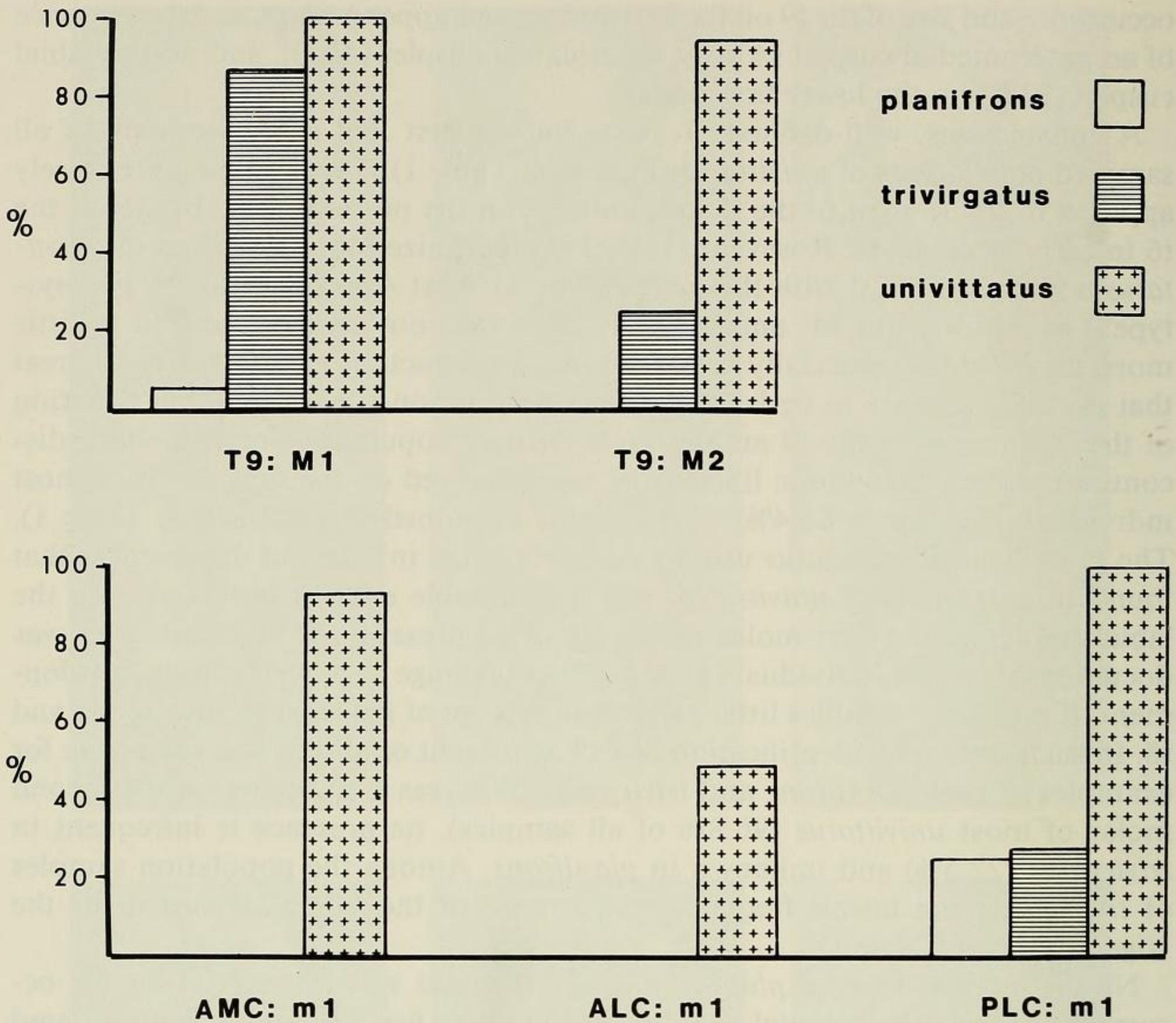
Fig. 6. Histograms illustrating percent occurrence of certain dental traits within three species of *Hybomys* for all specimens examined (see Table 1 for sample sizes and Materials and Methods for identification of character abbreviations).

anterior and posterior roots, satellite rootlets typically anchor the labial and lingual margins of the lower first molars of *univittatus* (hence M_1 four-rooted), but not *planifrons* and *trivirgatus* (M_1 two-rooted).

Numerical Analyses

Mice of the genus *Hybomys* display little sexual dimorphism in size, a conclusion supporting the previous finding of Van der Straeten and Verheyen (1982), who critically analysed large homogeneous population samples of *trivirgatus* and *univittatus*. Males did average 0.5 to 1.0 percent larger than females in the majority of cranial dimensions, but the slight disparity did not contribute significantly to deviations from the population mean (Table 2). Only the results for six cranial variables, several of which (for example, OcNL, LRos, ZyB) might be expected to exhibit sexual dimorphism, are given here, but the pattern is typical. We interpret the sole exception of statistical significance, $BMls$ in *planifrons*, as a Type I sampling error, in view of the absence of appreciable sex effects documented for all other dimensions recorded for *planifrons, trivirgatus,* or *univittatus* and in
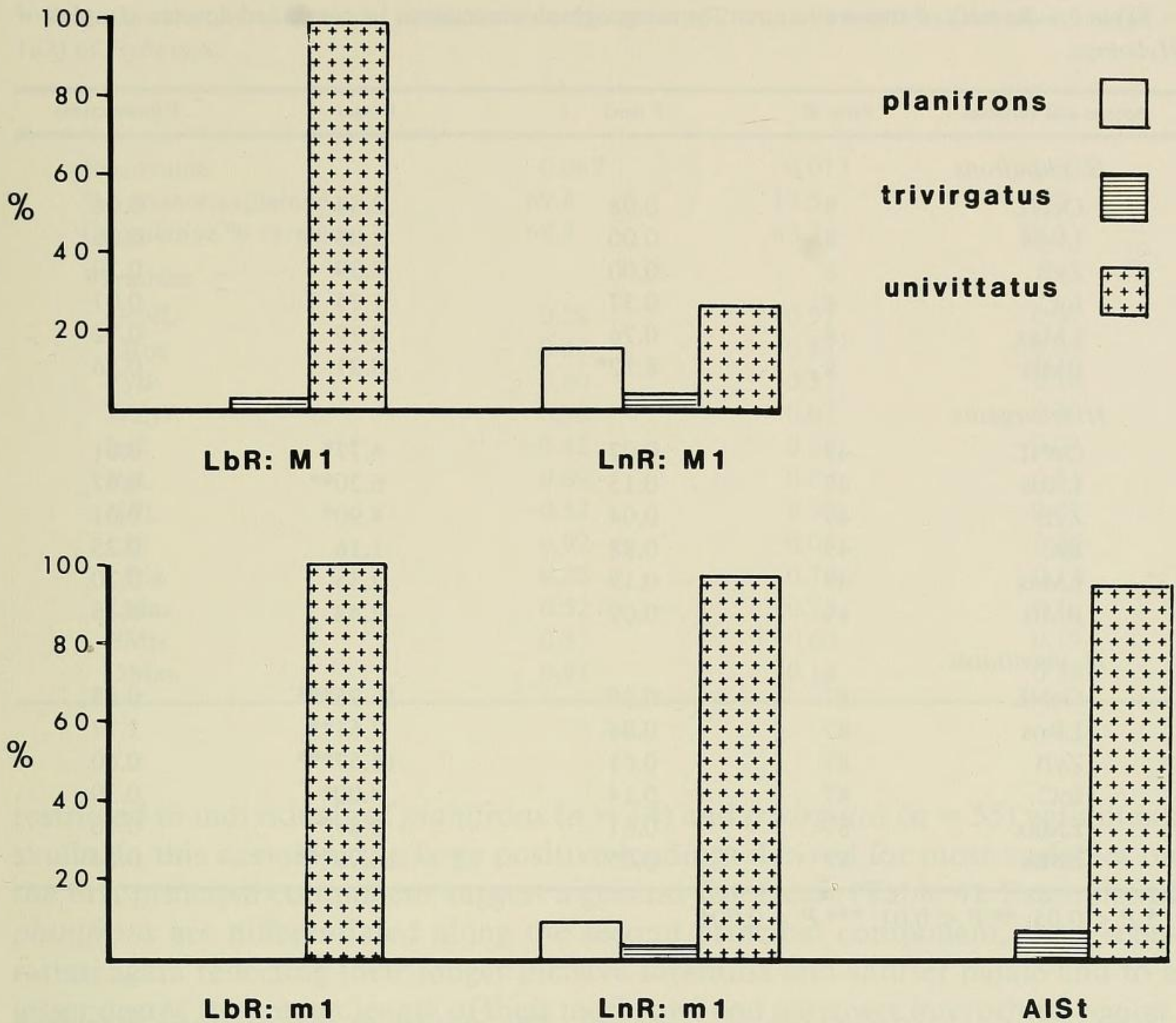
Fig. 7. Histograms illustrating percent occurrence of certain molar roots and one cranial trait within three species of *Hybomys* for all specimens examined (see Table 1 for sample sizes and Materials and Methods for identification of character abbreviations).

view of the small number of *planifrons* available. Sexes were pooled in the subsequent multivariate programs.

Age, in contrast, contributed substantially to nongeographic variation, despite our elimination of individuals from the youngest and oldest wear-classes in the two-way ANOVA (Table 2). The influence of sample sizes on the significance levels realized is apparent in the comparison of results for *planifrons* and *univittatus*. With large samples, even variables known to be relatively age-invariant, such as LMax and IoC, attained significant F-ratios. Our measurement of the maxillary toothrow was an alveolar length, and individuals in older wear-classes seemed to undergo some erosion of bone away from the dental roots so that alveolar length increased with age. In their discriminant function analysis of *trivirgatus* and *univittatus*, Van der Straeten and Verheyen (1982) too remarked upon the positive association of overall cranial size and age (they recognized two age groups), but the within-group, age-class differences did not approach the dispersion observed between the centroids of the two species.

We initially applied principle component analysis to all specimens of *Hybomys* with complete cranial measurements (variables = 12; n = 162), although only the

Table 2.—Results of two-way anova for nongeographic variation in combined species samples of *Hybomys*.

Species and variables	Error df	F (sex)	F (age)	F (interaction)
H. planifrons				
OcNL	8	0.08	2.54	0.06
LRos	8	0.00	2.03	0.05
ZyB	8	0.00	2.39	0.20
IoC	8	0.37	1.75	0.07
LMax	8	0.76	0.79	0.72
BMls	8	8.12*	0.91	0.16
H. trivirgatus				
OcNL	49	0.07	4.77*	0.01
LRos	49	0.15	6.20**	0.07
ZyB	49	0.04	4.90*	0.01
IoC	49	0.88	1.16	0.25
LMax	49	0.19	2.35	0.70
BMls	49	0.09	2.42	0.16
H. univittatus				
OcNL	87	0.69	16.95***	0.88
LRos	87	0.84	7.61**	1.17
ZyB	87	0.61	15.57***	0.60
IoC	87	0.14	4.00*	0.39
LMax	87	0.61	3.87*	0.10
BMls	87	0.25	14.99***	0.64

$* P < 0.05; ** P < 0.01; *** P < 0.001.$

centroids of our 12 OTUs are portrayed. The results of this analysis disclosed three aggregations of OTUs that correspond to the named taxa represented. Samples of *univittatus* were separated from those of *planifrons* and *trivirgatus* on the first principal component (Fig. 8); no discrimination between *planifrons* and *trivirgatus* was apparent on this component. Only three variables—WZyP, LIF, and DMan—conspicuously contributed to the sharply defined hiatus between *univittatus* and *planifrons-trivirgatus* (Table 3), a separation which underscores the pronounced contrasts in shape of the "*Hybomys*-type" versus "*Typomys*-type" cranium. Two of these variables (WZyP and LIF) are among the several identified by Van der Straeten and Verheyen (1982) as providing the best discrimination of *trivirgatus* and *univittatus*. Interestingly, the magnitude of these shape contrasts overshadows size as the principal source of variation on principal component one. Instead, the grading of OTUs, particularly those of *univittatus*, along principal component two conforms to one's expectation of a general size factor. The several length variables (OcNL, LRos, PPL, HPL, LDia) that load most heavily on this component support this interpretation (Table 3). Principal component three emphasizes the distinctiveness of specimens representing *planifrons*, a segregation principally due to their possession of relatively long incisive foramina and a short hard palate. The discontinuity of *planifrons* surpasses that evident among the geographic representatives of *trivirgatus*.

Because of the predominant influence of those variables that accounted for the segregation of *univittatus* on principal component one, the analysis was next

Table 3.—Results of principal component analysis using 12 cranial variables of all specimens (n = 162) of *Hybomys*.

	I	II	III
Eigenvalue	0.067	0.013	0.005
% variance explained	69.8	13.5	5.2
Cumulative % variance	69.8	83.3	88.5
Variables			
OcNL	0.28	0.91	0.07
LRos	−0.27	0.84	0.05
ZyB	0.60	0.57	0.14
WZyP	0.98	0.02	−0.20
IoC	−0.42	0.59	−0.07
PpL	0.09	0.82	0.11
HPL	−0.33	0.70	−0.41
LIF	0.92	−0.05	0.28
LDia	0.35	0.72	0.12
LMax	0.52	0.28	0.16
BMls	0.37	0.60	0.19
DMan	0.91	0.13	0.25

restricted to individuals of *planifrons* (n = 14) and *trivirgatus* (n = 55) with intact skulls. In this iteration, the large positive loadings derived for most variables on the first principal component suggest a general size factor (Table 4). Examples of *planifrons* are differentiated along the second principal component, their separation again reflecting their longer incisive foramina and shorter palate and to a lesser degree the greater length of their toothrows and narrower interorbital region. Although some overlap of individual scores occurs on this component, the mor-

Table 4.—Results of principal component analysis using 12 cranial variables of specimens of *H. trivirgatus* (n = 55) and *H. planifrons* (n = 14).

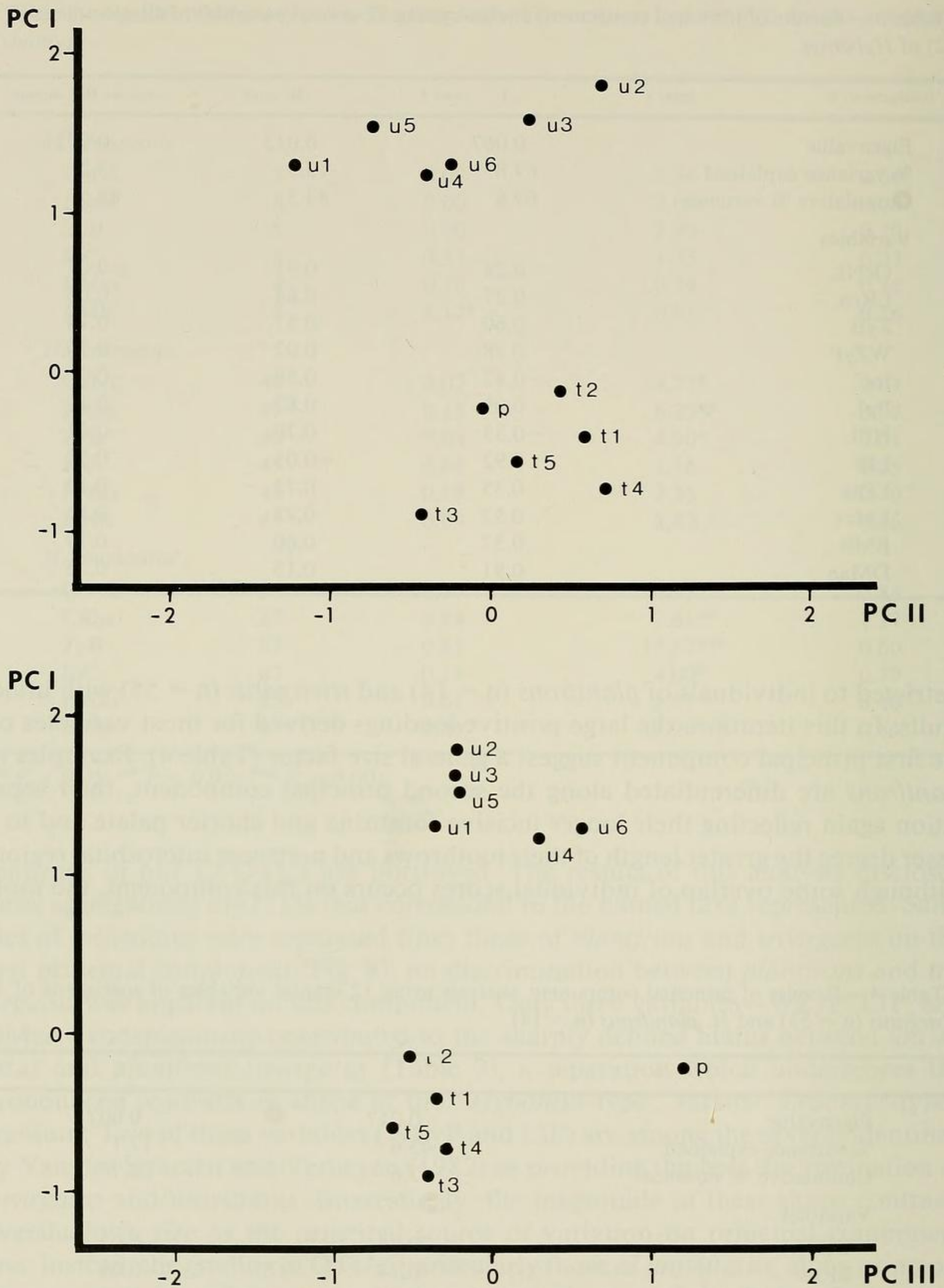|	I	II
Eigenvalue	0.017	0.007
% variance explained	43.6	17.1
Cumulative % variance	43.6	60.7
Variables		
OcNL	0.77	−0.02
LRos	0.74	0.04
ZyB	0.68	0.09
WZyP	0.84	−0.36
IoC	0.40	−0.44
PpL	0.67	0.02
HPL	−0.01	−0.66
LIF	0.59	0.63
LDia	0.75	0.15
LMax	0.26	0.44
BMls	0.56	0.22
DMan	0.61	0.38

Fig. 8. Scatter plots of principal components using all intact specimens representing 12 samples of *Hybomys: Top,* PC I versus PC II; and *Bottom,* PC I versus PC III (see Table 3; identification of sample codes given in Materials and Methods).
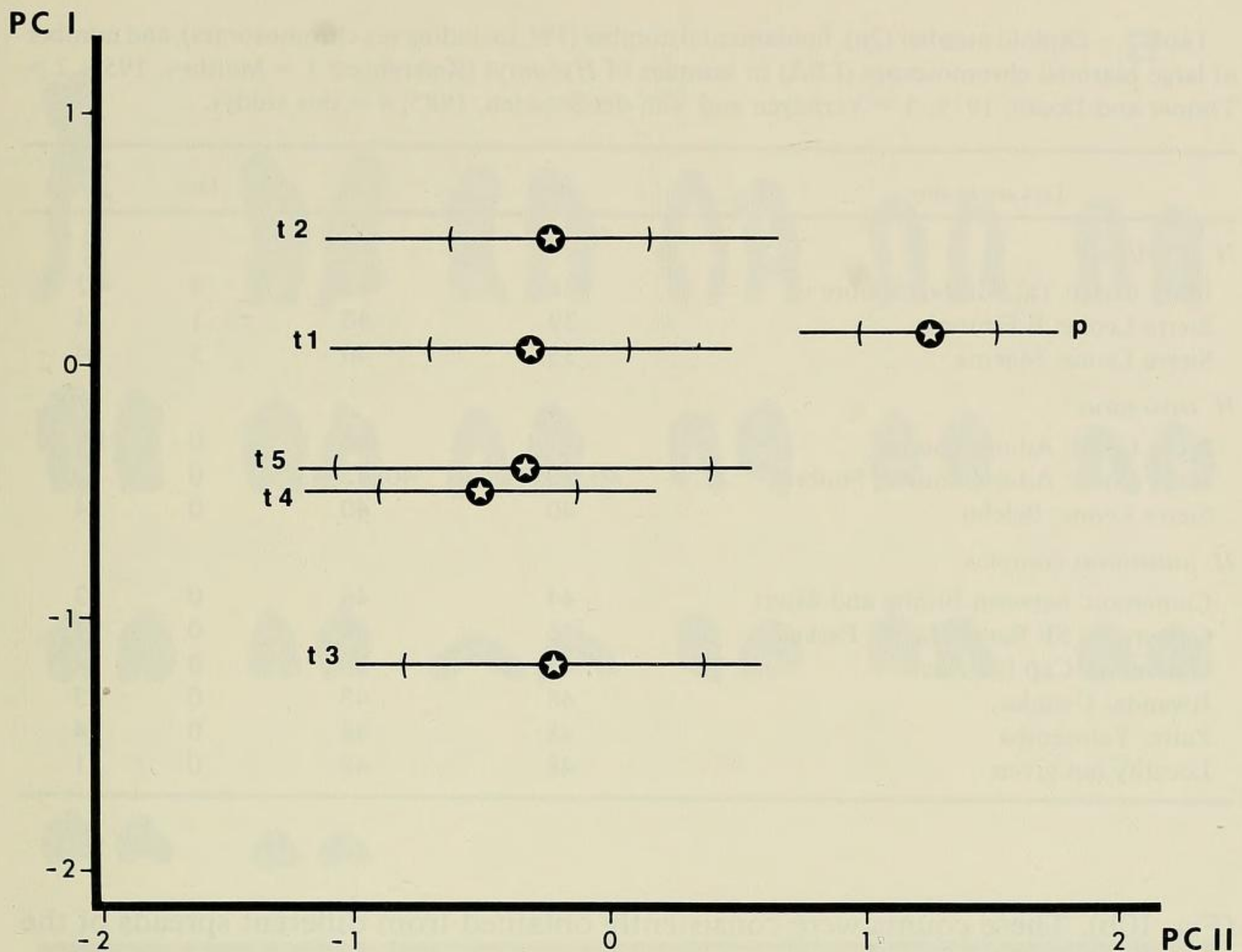
Fig. 9.   Scatter Plot of principal component I versus II using all intact specimens representing *Hybomys planifrons* and five samples of *Hybomys trivirgatus* (see Table 4; identification of sample codes given in Materials and Methods). Horizontal lines delimit ±1 SD of individual scores around a group's centroid on Pc II, and parentheses indicate ±2 SE of the mean. To avoid visual congestion, dispersion statistics are not depicted for PC I.

phological singularity of *planifrons* readily contrasts with the five samples of *trivirgatus* (Fig. 9).

Karyology

Our knowledge of chromosomal variation for the genus *Hybomys* includes information on the forms *planifrons, trivirgatus, univittatus,* and *lunaris,* as contributed by the studies of Matthey (1959), Tranier and Dosso (1979), and Verheyen and Van der Straeten (1985) (see Table 5). We shall report and compare our findings in light of those previous works.

Our two Sierra Leonean specimens of *planifrons,* both females, possess odd-numbered diploid counts that differ from one another yet exhibit the same total number of chromosomal arms. The one from 10.1 km E Fintonia has a 2N of 39, which consists of one large submetacentric and 19 pairs of acrocentric chromosomes graded evenly in size from small to large (Fig. 10a). The other female, from Meema, has 35 chromosomes, including the unpaired large submetacentric, two pairs of large submetacentrics, and 15 small to large pairs of acrocentrics

Table 5.—Diploid number (2n), fundamental number (FN, including sex chromosomes), and number of large biarmed chromosomes (LBA) in samples of *Hybomys* (References: 1 = Matthey, 1959; 2 = Trainer and Dosso, 1979; 3 = Verheyen and Van der Straeten, 1985; 4 = this study).

Taxa and locality	2n	FN	LBA	References
H. planifrons				
Ivory Coast: Tai, Grabo, Soubre	38	42	4	2
Sierra Leone: E Fintonia	39	40	1	4
Sierra Leone: Meema	35	40	5	4
H. trivirgatus				
Ivory Coast: Adiopodoume	40	40	0	3
Ivory Coast: Adiopodoume, Soubre	40, 42, 43	40, 42, 43	0	2
Sierra Leone: Belebu	40	40	0	4
H. univittatus complex				
Cameroon: between Bimba and Mieri	44	46	0	3
Cameroon: SE Bamenda, SE Eseka	46	46	0	4
Gabon: SE Cap Esterias	48	48	0	4
Rwanda: Uwinka	48	48	0	3
Zaire: Yalosemba	48	48	0	4
Locality not given	48	48	0	1

(Fig. 10b). These counts were consistently obtained from different spreads of the same individual.

Trainer and Dosso (1979) first reported a karyotype for *planifrons* for specimens collected from southwestern Ivory Coast. (Since the karyotype was not figured, Tranier kindly lent us the original negatives; however, due to their age, we could not critically compare the chromosomal morphologies of the Sierra Leone and Ivory Coast specimens. Therefore, our comments are based upon their published description.) These exhibited a 2N of 38 with 2 pairs of metacentric-submetacentric chromosomes and 17 pairs of acrocentric elements. This condition falls between that observed in our two specimens, both in diploid number and in number of biarmed elements. Tranier and Dosso (1979) identified the X as a large metacentric and the Y as a medium-sized submetacentric; however, this configuration seems highly unlikely given the chromosomal assortment observed in our 2N = 39 female. Based on the studies to date, a karyotype having at least one large biarmed chromosome is unique within the genus but the disparity in diploid numbers recorded from just three localities suggests remarkable polymorphism within *planifrons* that deserves further investigation.

Our one example of *trivirgatus*, a female from Belebu, Sierra Leone, has a 2N of 40, all pairs consisting of small to large acrocentrics (Fig. 11). This diploid complement agrees with the typical condition Verheyen and Van der Straeten (1985) reported for a series of *trivirgatus* from Adiopodoume, Ivory Coast, although one of their specimens had 2N = 42 as the modal count. Tranier and Dosso (1979) also recorded a diploid number of 40 for a specimen of *trivirgatus* from Soubre, Ivory Coast, but in two others, a male and female, they found 2N = 43 and 2N = 42, respectively. All of the diploid variants thus far documented for *trivirgatus* retain an entirely acrocentric chromosomal complement. The mech-
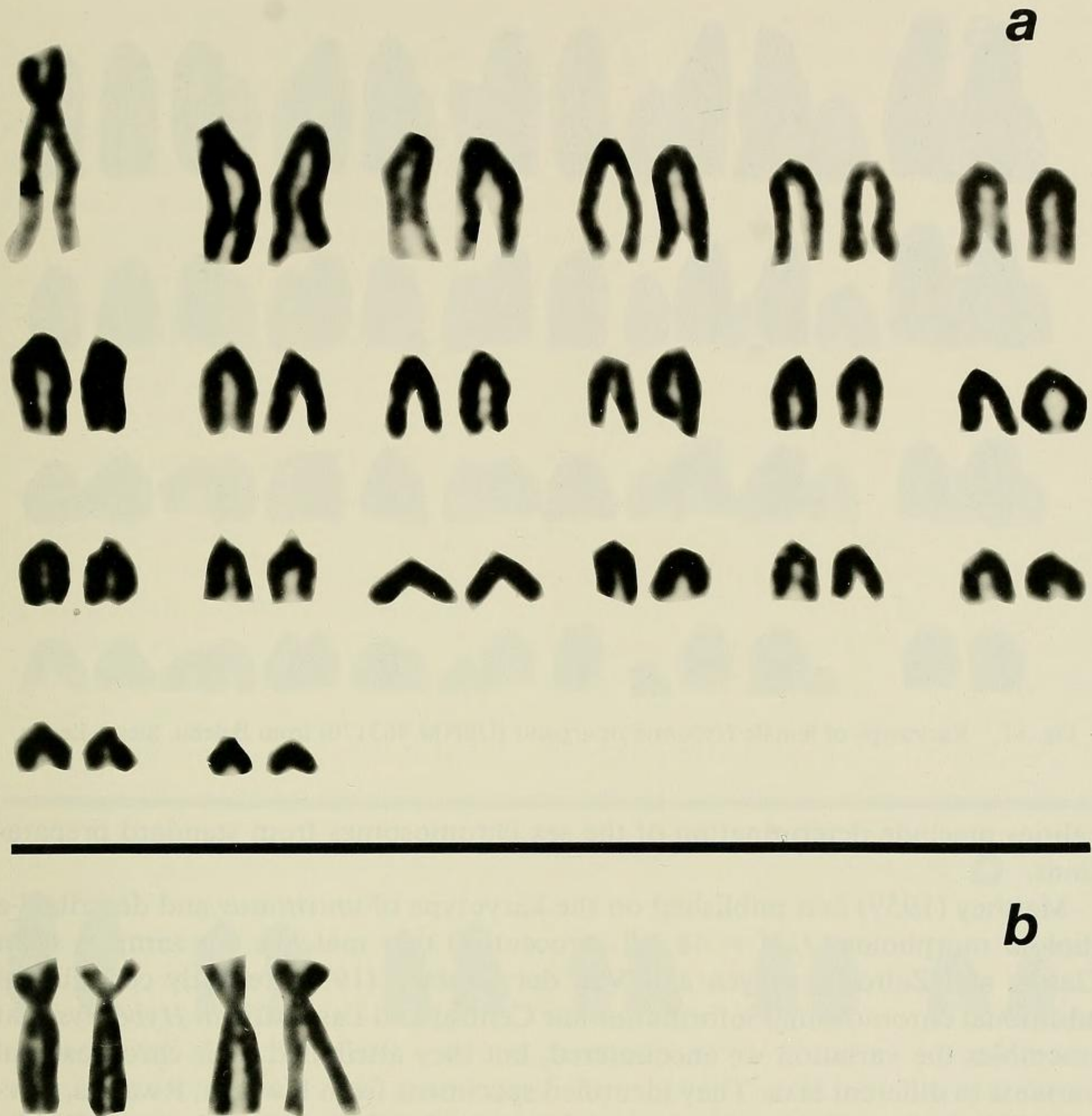
Fig. 10.　Karyotypes of *Hybomys planifrons*: a, female (USNM 546938) from 10.1 km E Fintonia, Sierra Leone, with 2N = 39; b, four additional large biarmed chromosomes found in female (USNM 463386) from Meema, Sierra Leone, with 2N = 35.

anism of sex determination warrants clarification for *trivirgatus*. Tranier and Dosso (1979) suggested an XY1Y2 system to account for the 2N = 43 male, but Verheyen and Van der Straeten (1985) postulated an XX′Y system and assumed that the largest pair of acrocentrics represent the sex chromosomes. These are heteromorphic in arm length in their female specimens, a condition observed in our single example (Fig. 11).

Two chromosomal morphologies were observed among our samples of *univittatus*. The Cameroon specimens (from the vicinity of Bamenda and Eseka) have a total of 46 chromosomes, all acrocentric ranging in size from small to large (Fig. 12a). In contrast, the Gabon (Cap Esterias) and Zaire (Yalosemba) mice possess a diploid count of 48, again all acrocentric elements sorted from small to large in size (Fig. 12b). The almost identical male and female karyotypes from both lo-
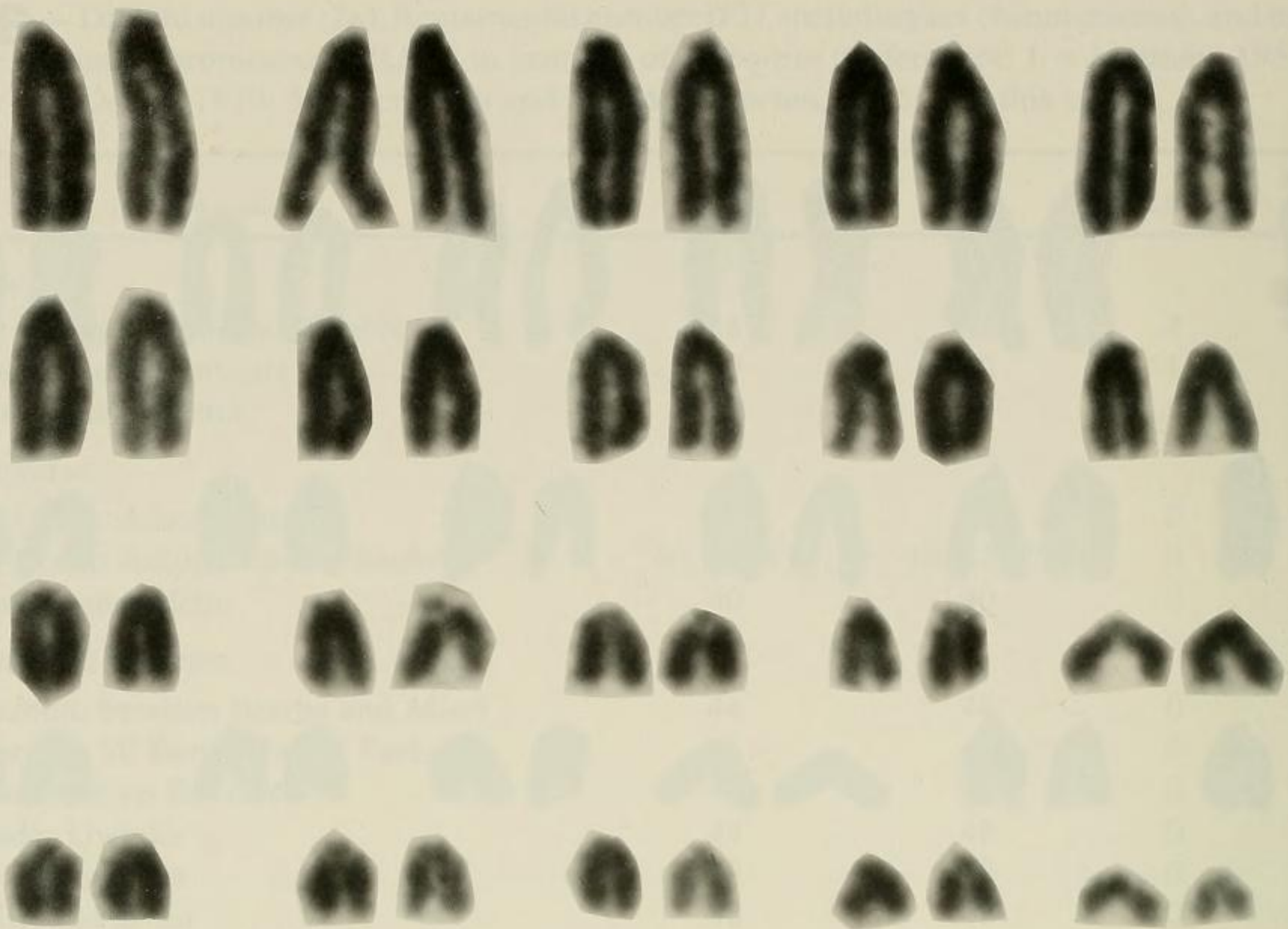
Fig. 11. Karyotype of female *Hybomys trivirgatus* (USNM 463170) from Belebu, Sierra Leone.

calities preclude determination of the sex chromosomes from standard preparations.

Matthey (1959) first published on the karyotype of *univittatus* and described a diploid morphology (2N = 48; all acrocentric) that matches our samples from Gabon and Zaire. Verheyen and Van der Straeten (1985) recently contributed additional chromosomal information for Central and East African *Hybomys* that resembles the variation we encountered, but they attributed their chromosomal variants to different taxa. They identified specimens from Uwinka, Rwanda, having a 2N of 48, as *H. lunaris*; whereas they considered those from between Bimba and Mieri, Cameroon, having a 2N of 44, as *H. univittatus* proper. The latter sample is the only known instance of biarmed chromosomes in the *univittatus* complex, for Verheyen and Van der Straeten (1985) documented a very small pair of metacentrics in their spreads. We shall attempt to reconcile the chromosomal morphologies with the nomenclatural discrepancies apparent in their data and ours in the discussion below.

Discussion

Taxonomy. — The variety of taxonomic opinions advanced for *planifrons* since Miller (1900) diagnosed it have largely reflected the characters emphasized by the systematists who have addressed the question of its status and affinities. Miller himself, who in all probability lacked comparative examples of *trivirgatus,* drew attention to numerous cranial details in recognizing *planifrons* as a species distinct from *univittatus.* His description forcefully asserted the fundamental contrasts in cranial shape exhibited by the two kinds. Yet later authors seemingly attached greater importance to the dorsal striping pattern of the pelage and considered
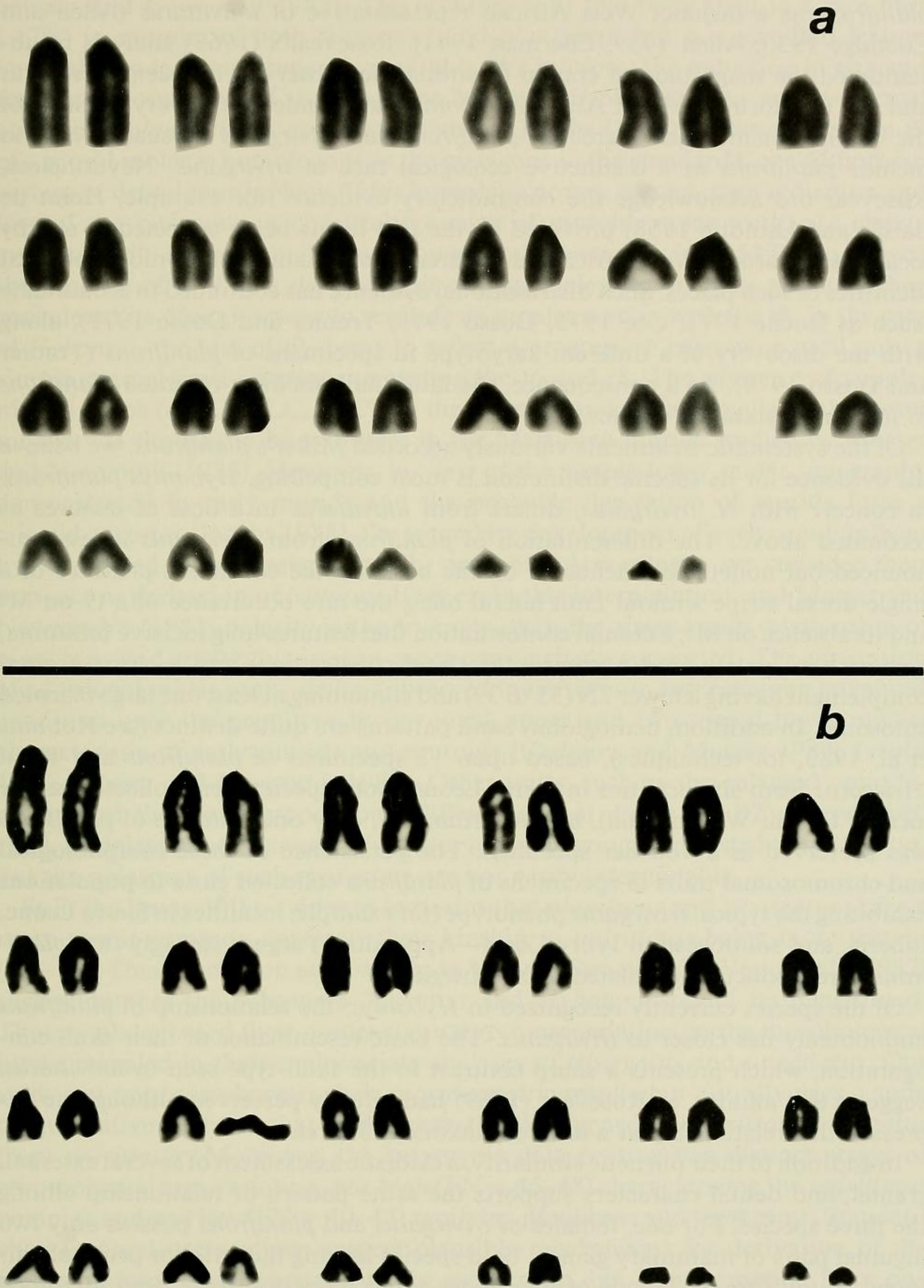
Fig. 12. Karyotypes of *Hybomys univittatus*: a, female (CM 58834) from the vicinity of Eseka, Cameroon; b, male (USNM 537813) from Yalosemba, Zaire.

planifrons as a disjunct West African representative of *univittatus* (Allen and Coolidge 1930; Allen 1939; Ellerman 1941). Rosevear's (1969) analysis resubstantiated the magnitude of cranial dissimilarities observed between *univittatus* and the two forms of West African *Hybomys,* and, indeed, the very fineness of the cranial resemblance shared by *planifrons* and *trivirgatus* persuaded him to include *planifrons* as a distinctive ecological race of *trivirgatus.* Nevertheless, Rosevear did acknowledge the contradictory evidence (for example, Heim de Balsac and Lamotte 1958) provided by the two forms being collected at nearby localities in parts of West Africa and apparently maintaining their morphological identities in such places. Such distributional evidence has continued to accumulate (such as Roche 1971; Coe 1975; Dosso 1975; Tranier and Dosso 1979), along with the discovery of a different karyotype in specimens of *planifrons* (Tranier and Dosso 1979). As a consequence, the latter authors have returned *planifrons* to its former status as species.

Of the systematic treatments variously accorded Miller's *planifrons,* we believe the evidence for its specific distinction is most compelling. *Hybomys planifrons,* in concert with *H. trivirgatus,* differs from *univittatus* in a host of features as recounted above. The differentiation of *planifrons* from *trivirgatus* is less pronounced but nonetheless definable on the basis of: the consistent presence of a single dorsal stripe without faint lateral ones; the rare occurrence of a t9 on M^1 and its absence on M^2; a cranial conformation that features long incisive foramina, a short hard palate, and narrow interorbital constriction; and a chromosomal complement having a lower 2N (35 to 39) and containing at least one large biarmed autosome. In addition, hemoglobin band patterns are quite distinct (see Robbins et al. 1983, for techniques), based upon 12 specimens of *planifrons* and 16 of *trivirgatus* from six localities in Sierra Leone. Both species were collected at one locality (10 mi W Panguma), but unfortunately, only one example of *planifrons* was preserved as a voucher specimen. The persistence of these morphological and chromosomal traits in specimens of *planifrons* collected close to populations exhibiting the typical *trivirgatus* phenotype (for example, localities in Sierra Leone, Liberia, and southwestern Ivory Coast—Appendix 1) argues strongly that *planifrons* is reproductively isolated from *trivirgatus.*

Of the species currently recognized in *Hybomys,* the relationship of *planifrons* undoubtedly lies closer to *trivirgatus.* The basic resemblance of their skull configuration, which presents a sharp contrast to the skull-type seen in *univittatus,* suggests this affinity, as Rosevear (1969) had already perceived although he expressed this relationship at a different taxonomic level.

In addition to their phenetic similarity, a cladistic assessment of several external, cranial, and dental characters supports the same pattern of relationship among the three species. For one, females of *trivirgatus* and *planifrons* possess only two inguinal pairs of mammary glands, both species lacking the anterior pectoral pair found in *univittatus.* Trends of mammary gland reduction have been identified in other groups of Muroidea, probably from an ancestral condition of eight mammae (Arvy 1974; Carleton 1980; Neithammer 1972). The presence of a bridge of the alisphenoid bone dividing the masticatory-buccinator foramen from the foramen ovale accessorius is believed to represent a primitive feature of the muroid skull, and its loss, resulting in the formation of a single spacious opening, has been interpreted as a derived condition (Carleton and Musser 1984; Musser 1982;

Musser and Newcomb 1983). The occurrence of this bony strut is a rare trait (<7%) in samples of both *trivirgatus* and *planifrons,* but is a standard feature (>90%) among populations of *univittatus.* We interpret the reduction in size and frequency occurrence of the t9 on the M^1 and M^2 of *trivirgatus* and its virtual absence in *planifrons* as apomorphic states. Jacobs (1978) proposed that the t9 of a murid molar is homologous to the metacone in the standard Cope-Osbornian system of dental terminology. If his homology proves correct, then reduction and loss of the metacone, a constituitive cusp of muroid molar teeth, are clearly evolutionarily derived conditions. Musser and Newcomb (1983:537) also viewed the absence of a t9 as a derived trait among Malaysian murids, although they considered its disappearance to result from amalgamation with the t8. In the case of *Hybomys,* the loss of t9 seems to reflect a progressive narrowing until only a simple enamel crest remains connecting the t6 and t8. The presence of supplemental cusps (AMC, ALC, PLC) on the anterior and labial cingula of the lower molars was thought to be primitive in the Malaysian murids studied by Musser and Newcomb (1983). However, in view of the simple lower molar topography demonstrated in early murids and the probable derivation of murids from a cricetid ancestor (Jacobs 1978), the secondary development of such conulids from hypertrophied cingula seems equally probable. Accordingly, we consider their presence as derived in *univittatus.* If we err in this interpretation, and Musser and Newcomb's (1983) polarity is the true one, then the sister-group relationship of *planifrons* and *trivirgatus* is even more convincingly supported. The possession of additional molar roots, such as observed in *univittatus,* represents an advanced condition over the primitive three-rooted upper and two-rooted lower molars characteristic of early murids and muroids (Carleton and Musser 1984; Jacobs 1978; Musser and Newcomb 1983). Other traits, such as the enlarged optic foramen and the many proportional differences that define the "*Typomys*-type" skull, associate *planifrons* and *trivirgatus* as a pair-group contrasted to *univittatus,* but the polarities of such characters are not easily interpretable.

Still, the brunt of the evidence indicates that *planifrons* and *trivirgatus* share a more recent common ancestor, their kinship to *univittatus* being more distant (Fig. 13). This conclusion adds weight to Van der Straeten and Verheyen's (1982) suggestion that the subgenera *Typomys* and *Hybomys* should be reinstituted. Those authors based their nomenclatural recommendation on the morphological hiatus revealed in their multivariate analyses of *trivirgatus* and *univittatus.* Our study not only corroborates their morphometric results but also divulges a suite of qualitative features that underscore the divergence of *planifrons-trivirgatus* from *univittatus.* Moreover, the karyotypic data portray two distinct arrays of chromosomal arm variation, one high (FN = 46–48) characterizing the *univittatus* complex and one low (FN = 40–42) typifying *planifrons* and *trivirgatus.* Standard chromosomal preparations suggest plausible mechanisms for derivation of the several chromosomal variants within each group, but transformation from one FN level to the other is more complicated and cannot be resolved without banding information and some idea of the distribution of euchromatin and heterochromatin. Whether *Typomys* and *Hybomys* merit generic segregation must await an evaluation of character variation among *Hybomys* and its near relatives.

Although our study principally focusses on the status and relationships of *planifrons,* some comment is warranted concerning the specific integrity of *univittatus.*
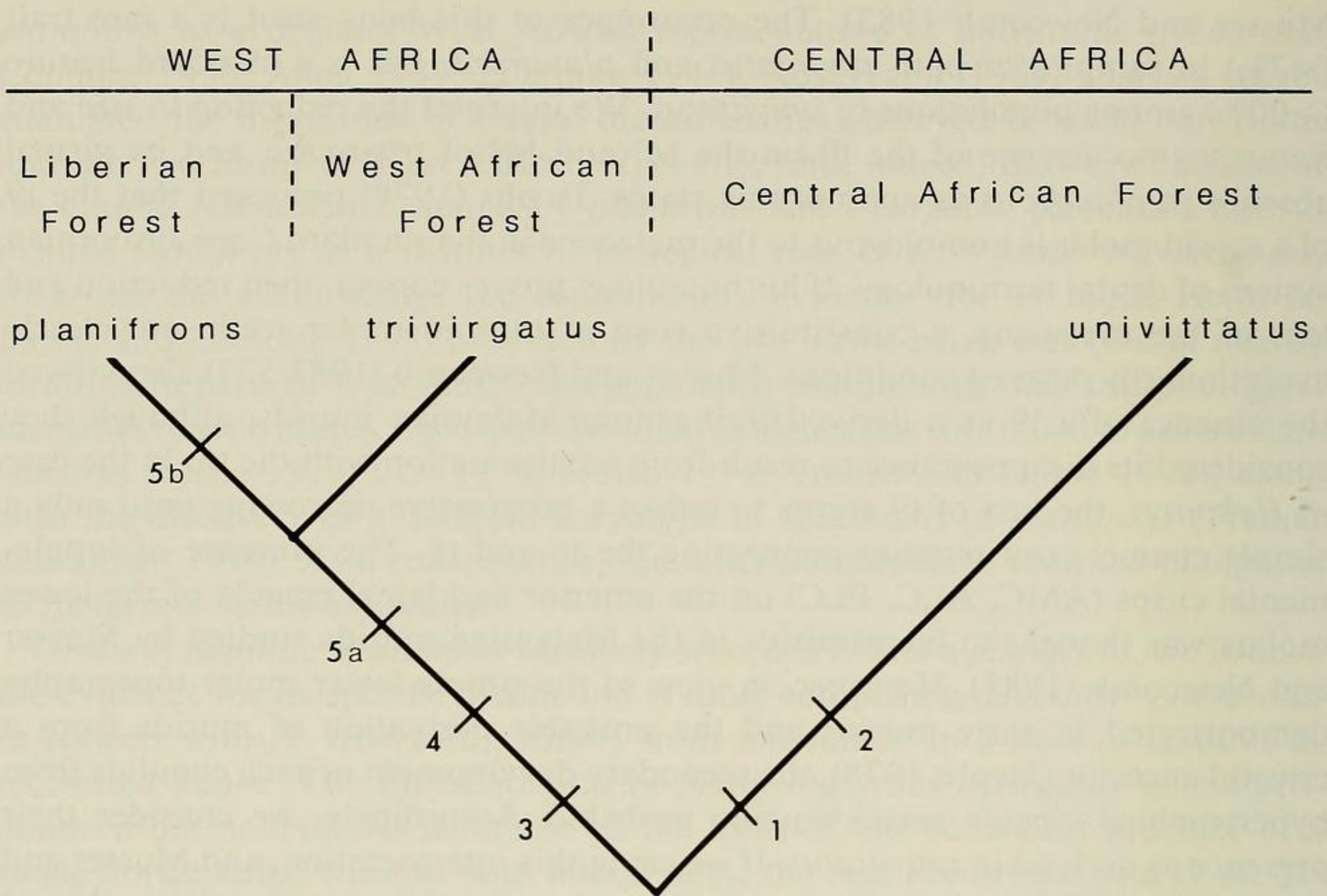
Fig. 13.   Hierarchy of proposed relationship among three species of *Hybomys* and their geographical distribution with regard to major forest zones. Apomorphic character state transformations are: 1) acquisition of accessory molar roots; 2) acquisition of supplemental molar cusps; 3) loss of the pectoral pair of mammae; 4) loss of the alisphenoid strut; 5a) reduction in size of t9; 5b) loss of t9.

The morphological and chromosomal heterogeneity uncovered here and in other recent studies intimates that more than one species is represented among our samples. Several forms have been described, all of them treated as subspecies of *univittatus* until very recently: *Mus univittatus* Peters, 1876, from Dongila, Gabon; *Mus rufocanus* Tullberg, 1893, from Vevaka, Cameroon, considered a synonym of the nominate race; *Mus univittatus lunaris* Thomas, 1906, from Ruwenzori east, Uganda, elevated to species by Verheyen and Van der Straeten (1985); *Hybomys univittatus badius* Osgood, 1936, from Mt. Cameroon; and *Hybomys univittatus basilii* Eisentraut, 1965, from Mocatal, Fernando Poo, raised to a species by Van der Straeten (1985). The evidence for the specific status of *lunaris* derives from chromosomal and morphometric analyses (Van der Straeten 1985; Verheyen and Van der Straeten 1985); that for the recognition of *basilii* on morphological divergence from mainland *univittatus* (Van der Straeten 1985).

Basically two kinds of karyotypes (2N = 44, 46; FN = 46 and 2N = 48; FN = 48) have now been reported for populations of *univittatus*-like forms (Table 5). Verheyen and Van der Straeten (1985) documented such a chromosomal difference between examples from Rwanda (2N = 48) and Cameroon (2N = 44) and considered the former to represent *H. lunaris* and the latter true *H. univittatus*. The 2N = 48 karyotype exactly matches that which we discovered in our specimens from Gabon and Zaire. Since our Gabon sample from Cap Esterias originated from a place just northwest of Dongila, the type locality of *Mus univittatus* Peters, we regard the all-acrocentric, 2N = 48 chromosomal formula as characteristic of

univittatus, not *lunaris.* Verheyen and Van der Straeten (1985) assumed that *lunaris* applied to their Rwandan locality because it was the geographically closest epithet available for easternmost populations of *Hybomys.* Thomas (1906) described *lunaris* from an intermediate elevation on the northeastern slope of Mt. Ruwenzori, the Mubuku Valley, Uganda, and his diagnosis clearly depicts a small, delicate form of *Hybomys.* In fact, our two Ugandan examples (both in age class IV) from Kanyawara, a place near the type-locality, precisely fit Thomas' description in their coloration, delicate skull, and small size (OcNL = 31.6, 31.8; LMax = 5.2, 5.3; IoC = 5.1, 5.3; HFL = 25, 25). These two specimens contrast sharply with the larger robust skulls seen in our examples from Uwinka, Rwanda, the same locality where Verheyen and Van der Straeten obtained karyotypic preparations. Morphologically and chromosomally, the karyotyped *Hybomys* from Gabon, Rwanda, and Zaire, reported herein and by Verheyen and Van der Straeten (1985), conform closely and appear to represent but one species, *univittatus.*

Chromosomal morphologies that depart from the 2N = 48 condition have been described for *univittatus*-like populations inhabiting the forests of Cameroon. Great significance cannot be ascribed to the karyotypic differences we obtained for specimens from Bamenda and Eseka (2N = 46; FN = 46) as compared to that reported by Verheyen and Van der Straeten (1985) for samples from Mieri-Bimba (2N = 44; FN = 46), because a simple Robertsonian-type polymorphism could explain the presence/absence of the small metacentric pair and consequent difference in diploid number. Verheyen and Van der Straeten (1985) considered the chromosomal formula found in the Mieri-Bimba specimens to be characteristic of *univittatus,* but as argued above, we believe that the 2N = 48, all-acrocentric complement applies to true *univittatus.* In addition to the chromosomal difference, Van der Straeten (1985) demonstrated an appreciably larger size for the Cameroon series as compared to specimens from Rwanda. In like manner, considerable morphological heterogeneity, not all of it consonant with a simple interpretation of intraspecific geographic variation, occurs among our OTUs of "*univittatus,*" particularly the three from Cameroon. Specimens from Lolodorf and the vicinity of Eseka, for example, are larger in most cranial dimensions than those from Batanga (Fig. 8, Appendix 2); the latter are phenetically closer to the animals from Gabon that have the 2N = 48 karyotype.

In summary, we see evidence of at least three moieties comprising the population samples traditionally called "*univittatus.*" All of these possess the "*Hybomys*-type" cranial architecture, supplemental molar cusps, accessory roots, and an alisphenoid strut, yet they also exhibit slight but consistent differences in size, proportion, and karyotype that suggest separate biological species. A medium-sized form having a diploid number of 48 seems to range most broadly in Central Africa and, of the three, probably deserves the appellation *univittatus* Peters, 1876. The other two moieties, one smaller and one larger than *univittatus,* are apparently more restricted geographically. The small and delicate form *lunaris* may qualify for species recognition to judge from the distinctive morphology seen in our two Ugandan specimens and their concurrence with Thomas' (1906) description. However, the karyotypic divergence attributed to "*lunaris*" by Verheyen and Van der Straeten (1985) is questionable; in our opinion, *univittatus lunaris* Thomas, 1906, has yet to be examined karyotypically. The larger-bodied animals are represented by series from Cameroon with lower diploid numbers (44, 46), but the level of

their differentiation and what names should be properly attached are presently unclear. Three possibilities are Tullberg's (1893) *rufocanus* from Vevaka, Cameroon, Osgood's (1936) *badius* from Mt. Cameroon, and Eisentraut's (1965) *basilii* from Fernando Poo (recently elevated to species by Van der Straeten, 1985), any of which could prove applicable. Indeed, detailed study of population samples from Cameroon may provide a key to understanding differentiation within the subgenus *Hybomys*. Eisentraut's (1973) analysis of vertebrate distribution in Cameroon and on nearby Fernando Poo pictures a very complex evolution and intermixture of lowland and montane faunal elements, and certainly the number of species uncovered in the few thoroughly reviewed rodent genera in Cameroon corroborates this pattern of complexity (Robbins et al. 1980; Robbins and Schlitter 1981). Whether populations of *Hybomys* experienced similar fragmentation and differentiation in west–central Africa will require additional studies of variation over broader segments of their range and critical association of distinctive morphologies to type-specimens.

Ecology and zoogeography.—Our knowledge of the ecology and behavior of *Hybomys* has been derived primarily from investigations of the Central African form *univittatus*. Such studies have disclosed that these mice are solitary and terrestrial, are generally diurnal in their activity rhythms, and consume mostly insects and fruits and less often seeds (Duplantier 1982; Genest-Villard 1978, 1980; Rosevear 1969). Ecological descriptions of collecting sites consistently associate *univittatus* with the great equatorial rainforest of Central Africa, in both primary and secondary stands with dense understory and lush ground cover (Duplantier 1982; Genest-Villard 1980; Misonne 1963). When available for comparison, information on West African *Hybomys* basically resembles the life history and habitat requirements sketched for *univittatus* (Cole 1975; Rosevear 1969). Still it would be worthwhile to explore whether the apparent contrast in size of the optic foramen (which should first be confirmed quantitatively) noted between *univittatus* and *trivirgatus-planifrons* relates to any behavioral differences. Hooper and Carleton (1976), for instance, demonstrated a contrasting reliance upon olfactory versus visual cues in prey detection and capture corresponding to dietary contrasts in life stages of invertebrates consumed, for a congeneric pair of Middle American insectivorous murids that possess different-sized eyeballs and optic foramina.

Since the distinctiveness of *planifrons* has been obscured by its synonymy under *trivirgatus* or *univittatus,* little attention has been devoted to understanding its specific habitat associations and possible interactions where it seems to coexist with *trivirgatus*. One can conclude that the two species occur sympatrically as indicated by general locality designations (Dosso 1975; Heim de Balsac and Lamotte 1958; Roche 1971; Tranier and Dosso 1979), but it is not readily clear from reading such accounts whether the two kinds inhabit the same microenvironment (that is, were actually taken in the same trap line). Coe (1975) did observe that his examples of *trivirgatus* were restricted to the upper regions of the Nimba range; whereas, specimens of *planifrons* were (p. 537) ". . . limited to high forest and its fringes at low altitude . . ." and (p. 556) were ". . . all trapped in secondary forest and along track sides in dense vegetation."

During a survey of small mammals in northern Sierra Leone, we had the opportunity to collect five specimens of *H. planifrons* and to observe firsthand

the character of their habitat. This area, between 9°35' and 9°55'N, receives a moderately high amount of rainfall (about 2000 mm annually) and supports a mosaic of habitats, including low and high-grass savannahs, seasonally flooded grasslands (bolilands), and invasive forest. Although the dominant vegetation type covering this region is Guinea Savannah, all specimens of *planifrons* were collected at three localities in the high-canopied, semi-deciduous forest, distributed either as a narrow corridor of riverine forest, as forest fringing a small shallow lake, or as an isolated hillside patch enclosing a moist ravine (Fig. 14). No *Hybomys* were collected in forested areas where the understory was sparse and the ground open; instead, each of the three sites contained a luxuriant understory and dense ground cover. A profusion of vines and creepers, the lush growth of ferns and other herbaceous plants, and the presence of some sedges and mosses suggested the wetter character of such microenvironments within the forest. In fact, we came to anticipate the presence of *H. planifrons* where dense stands of one particular herbaceous plant, *Marantachloa* sp. (Marantaceae), grew (Fig. 15). Presumably the association of *planifrons* with *Marantachloa* was only indicative of the existence of a moister, cooler microclimate preferred by the mice. Of the five specimens, three were taken at trap stations on the ground beneath such dense vegetation, and two were collected in the hollow of a rotting log covered with moss and mushrooms. The capture of two animals was between 7:00 and 7:30 and between 8:00 and 10:00 in the morning, suggesting that *planifrons* too is diurnal.

The known distributional limits of *Hybomys* mirror its association with primary or secondary tropical forest, as the range of the genus tightly conforms to the reaches of the great lowland rainforests in Africa (Fig. 16). Collecting sites beyond the perimeter of the major rainforest zone underscore the fidelity of *Hybomys* to high forest habitats, for they include gallery forest (for example, *planifrons* in northern Sierra Leone) or montane forest at intermediate elevations (for example, *univittatus* in Uganda). Populations of the *univittatus* complex occupy the evergreen rainforests of Central Africa and are not known to occur west of the Cross River in eastern Nigeria, a range approximately equivalent to the Congo Forest Block of Booth (1958b) or the Lower Guinea Forest of Moreau (1966, 1969). *Hybomys trivirgatus* is a species of the West African rainforest belt, its eastern frontier terminating at the Niger River and extending westerly to southeastern Sierra Leone. This distribution encompasses all of the Upper Guinea Forest of Moreau (1969), as well as the Western Nigerian Forest, which some have considered a subregion of the Lower Guinea Forest (Booth 1958b; Moreau 1969). The occurrence of *planifrons* is evidently more geographically restricted, our samples only representing Sierra Leone and Liberia, southeastern Guinea around Mt. Nimba, and southwestern Ivory Coast west of the Sassandra River. This distributional pattern approximately corresponds to the Liberian Forest, generally viewed as a discrete subdivision of the West African tropical forest (Booth 1958b; Delany and Happold 1979).

The several forest provinces mentioned above have been distilled from zoogeographic studies of a variety of forest-inhabiting vertebrates, including mammals (Booth 1954, 1958a, b; Grubb 1978, 1982), birds (Marchant 1954; Moreau 1966, 1969; Diamond and Hamilton 1980), rhacophorid tree frogs (Schiotz 1967), and cyprinodont fishes (Clausen 1964). In view of the breadth of these zoogeographic syntheses, the distributional congruence of species of *Hybomys* to pre-

Fig. 14.   Hillside patch of high forest with lush growth of herbaceous ground cover in Outamba-Kilimi National Park, northern Sierra Leone. Specimens of *Hybomys planifrons* were collected on the ground beneath the dense plant cover.

Fig. 15. Dense stand of *Marantachloa* sp. (Marantaceae) underneath riverine forest in Outamba-Kilimi National Park, northern Sierra Leone. *Hybomys planifrons* were trapped in forested areas where this plant grew in profusion.
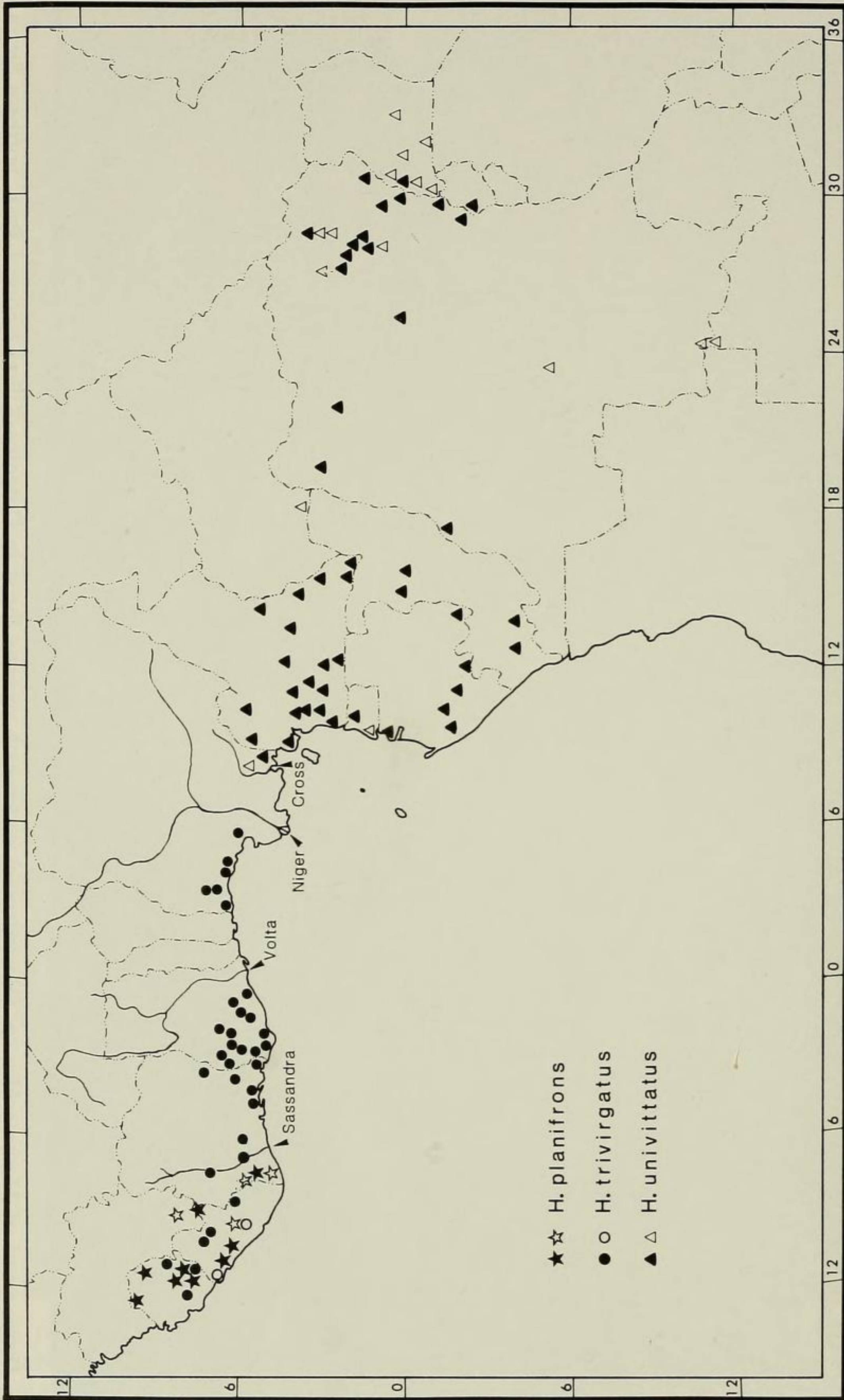
Fig. 16.   Distribution map of western and central Africa illustrating collection localities of mice of the genus *Hybomys*. Closed symbols represent specimens examined by one of us; open symbols signify literature records. The mouths of four West African rivers mentioned in the discussion are indicated by arrows.

viously recognized forest zones, is not unexpected. Numerous workers have cited the Niger River as the probable boundary line or "natural barrier" separating populations of *trivirgatus* and *univittatus,* or *Typomys* and *Hybomys,* those names employed either as subgenera or genera by the various authors (St. Leger 1931; Hayman 1935; Rosevear 1953, 1969; Van der Straeten and Verheyen 1982). However, as remarked by Rosevear (1969), what species inhabits (or inhabited) the interfluvial region between the Niger and Cross remains unknown: localities of *trivirgatus* occur only west of the Niger River and those of *univittatus* only east of the Cross (Fig. 16). Whatever the case, the differentiation of these mice across the Niger-Cross catchment is at least recognizable at the subgeneric level. Other authors have emphasized the pronounced discontinuity in faunal affinities of forest-dwelling vertebrates at the Niger River (Booth 1958b; Diamond and Hamilton 1980; Robbins 1978).

The hiatus in distribution of *trivirgatus* in southern Benin and Togo (Dahomey Gap) and in southeastern Ghana (Accra Plains) corresponds to southern projections of Guinea Savannah, areas whose increased aridity and lack of high forest have been convincingly attributed to recent modifications through human agency (Booth 1958b, 1959; Robbins 1978). Thus, the conspecificity of populations in western Nigeria with those west of the Dahomey Gap suggests a recent distribution of *trivirgatus* across a continuous West African forest belt, a geographic pattern which supports those who have questioned the significance of the gap as an isolating factor (Booth 1958b; Diamond and Hamilton 1980; Robbins 1978).

We have no records of *planifrons* from east of the Sassandra River in southwestern Ivory Coast (Fig. 16). In view of the collecting activity in southern Ivory Coast and Ghana, this distributional terminus does not appear to be an artifact of inadequate sampling, but the presence of *planifrons* should still be sought among samples of *Hybomys* east of the Sassandra. As presently known, the range of *planifrons* conforms to an hypothesized Liberian forest refuge. The past formation of such a refuge has been interpolated from the relatively high endemicity of vertebrate faunas inhabiting this westernmost high forest tract (Diamond and Hamilton 1980; Grubb 1982), from otherwise anomalous breaks in distribution in the vicinity of southwestern Ivory Coast (Booth 1958b; Schiotz 1967), and from the sharp convergence of isohyets (the "Baoule V") toward the coastline and related constriction of the rainforest in this region (Moreau 1969).

The distributional pattern observed in *Hybomys* concords with our interpretation of kinship among the species. That is, the two forms occupying the West African forest belt, or parts thereof, bear closer phylogenetic relationship to one another than to the species (or species complex) inhabiting the Central African forest block.

Moreover, a similar pattern of relationship and geographical distribution reappears in certain other murines restricted to tropical rainforest (Fig. 17). In particular, the taxonomic history and distribution of *Malacomys* species recall the situation documented for *Hybomys,* in consisting of a broadly distributed Congo forest form, *longipes* (plus the little-known *verschureni*), and two West African species, *edwardsi* and *cansdalei.* Like *Hybomys planifrons, Malacomys cansdalei* had been considered a disjunct race of the Central African species (Rosevear 1969; Rautenbach and Schlitter 1978), but additional study disclosed its distinctiveness and probable cognate affinity to *edwardsi,* another species of the West African
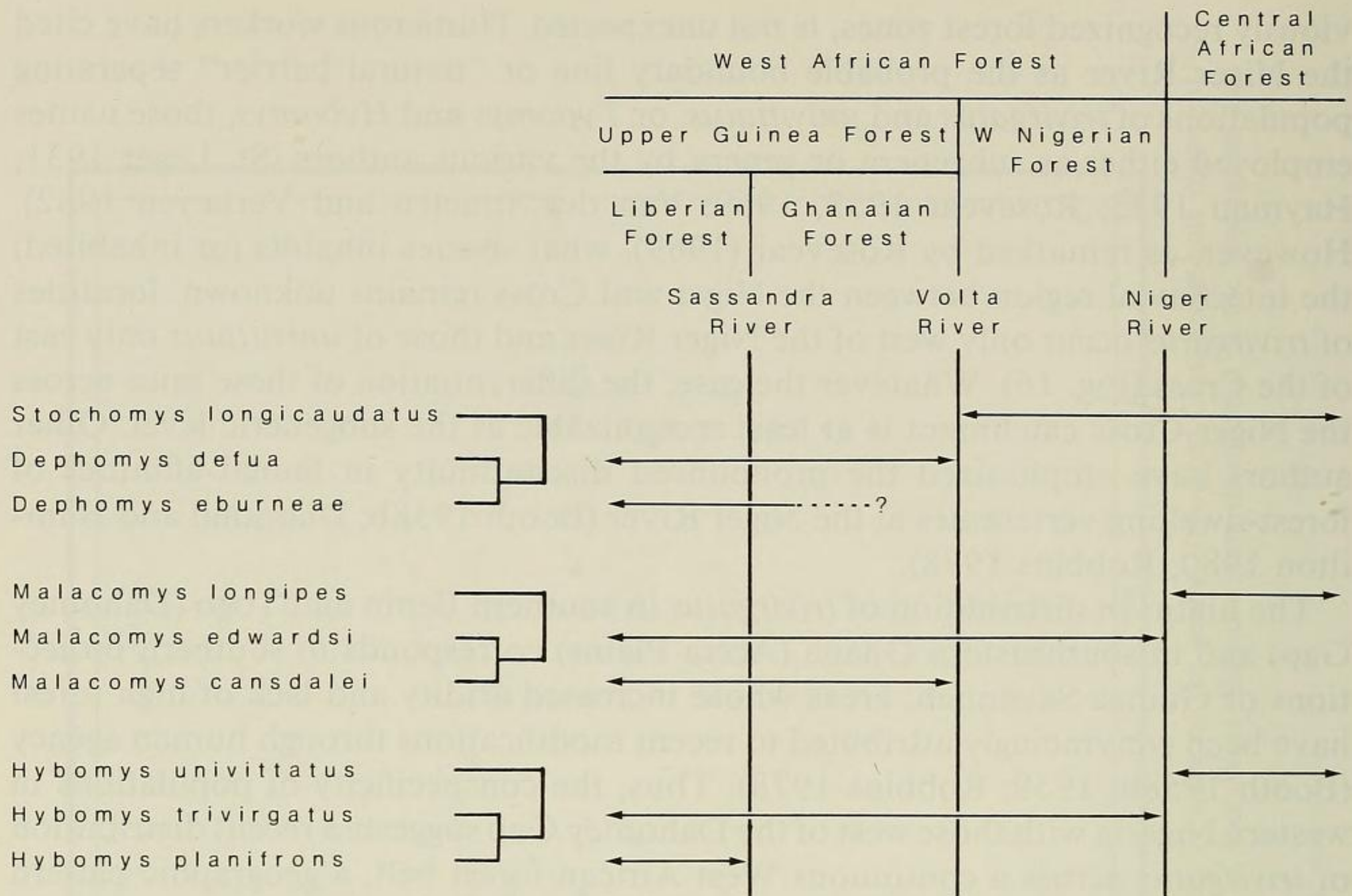
Fig. 17.   Limits of distribution of three vicariant examples of high forest rats in relation to major forest blocks and rivers. Cladograms to the right of the scientific names represent hypothesized relationship within each three-taxon example.

high forest (Van der Straeten and Verheyen 1979). In the case of *Malacomys,* however, the more geographically restricted of the two West African species, *cansdalei,* ranges more widely than *Hybomys planifrons. Dephomys defua, D. eubrneae,* and *Stochomys longicaudatus* are also rats that live primarily in tropical rainforests. Although some systematists have maintained *Dephomys* as a subgenus of *Stochomys* (Heim de Balsac and Bellier 1967; Misonne 1971), others have not (Rosevear 1969; Carleton and Musser 1984). Despite the disagreement over their nomenclatural rank, their near relationship is reasonably established. Based on USNM material, the contiguous pattern of differentiation of *Stochomys* and *Dephomys* resembles that evident in *Hybomys* and *Malacomys,* except that the Central African *Stochomys longicaudatus* penetrates further into West Africa (Fig. 17), having been collected at Agou, Togo.

Assuming an allopatric speciation model for the three examples of high forest rats, the occurrence within each triad of the closest related species pairs in West African forest suggests: 1) the past fragmentation of this forest into at least two West African refugia during dryer climatic periods; 2) the differentiation and genetic divergence of these allopatric stocks during such isolation, and 3) the subsequent range expansion and overlap of the derivative species following climatic amelioration and reunion of the forests. Such a speciation history seems to account more plausibly for the congruent phylogenetic and geographic patterns observed, rather than a speciation history involving multiple dispersals into West Africa from a Central African place of origin. The occurrence of two refugia in West Africa has been postulated in some zoogeographic interpretations (Booth

1958b; Diamond and Hamilton 1980; Schiotz 1967), but firm stratigraphic or palynological evidence demonstrating the existence or location of such refugia remains disturbingly elusive (Livingstone 1975, 1982).

Whether other kinds of forest rats adhere to this pattern, or exhibit yet others, will require further study to refine the number of biological species, the basis of their recognition, and the limits of their distribution. Too few forest-dwelling genera are thusly documented. Fewer still is the number of those genera for which we have reasonably corroborated hypotheses of relationship, either between them or among their constituent species. Nevertheless, the systematic complexity and cosmopolitan forest distribution of genera such as *Praomys* and *Hylomyscus* promise further insight. For instance, Verheyen and Van der Straeten (1981) recently resurrected *Praomys rostratus,* another species Miller (1900) described from Mt. Coffee, from synonomy under *P. tullbergi,* a species having a broader distribution throughout western and westcentral forests.

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Appendix I

The preparation of the distributional map (Fig. 16) relied primarily upon specimens examined by us and to a lesser extent locality records gleaned from the literature. Both kinds of distributional sources are documented below under the headings of Specimens Examined and Additional Records. The locality information appears essentially as stated on specimen tags or as given by authors. To aid verification where necessary and to assist location of obscure collecting sites, we generally consulted the gazetteers provided by Davis and Misonne (1964), Rautenbach and Schlitter (1978), and Rosevear (1965).

Specimens Examined

Hybomys planifrons. IVORY COAST: Niebe, 5°21′N, 7°22′W, 3 (USNM). LIBERIA: Du River, 4 (MCZ); Duside, 2 (AMNH); Gunyon Bassa, 5 (BMNH); Mount Coffee, 2 (USNM, holotype and paratype); Mount Nimba, near Granfield, 1 (BMNH); Nimba Ridge, Mt. Alpha, 1 (BMNH); S Nimba Ridge, 7°44′N, 8°28′W, 5 (BMNH); Parinari Forest, Nimba, 1 (BMNH). SIERRA LEONE: Bintamane Mountain, 13 (BMNH); 10.3 km SE Fintonia, 9°38′N, 12°9′W, 2 (USNM); 10.1 km E Fintonia, 9°45′N, 12°10′W, 2 (USNM); Kenema, 1 (BMNH); Konia 8°07′N, 11°01′W, 1 (USNM); Meema, 8°07′N, 11°00′W, 2 (USNM); Niahun, 8°01′N, 11°02′W, 1 (USNM); 10 mi N Panguma, 8°17′N, 11°16′W, 1 (USNM); 5.2 mi W Sainya, 9°48′N, 12°27′W, 1 (USNM). Total = 48.

Hybomys trivirgatus. GHANA: Adamso, 6°05′N, 1°45′W, 1 (USNM) Ankasa, 40 mi W Axim, 3 (BMNH); Axim, 1 (BMNH); 1 mi N Berekuso, 5°46′N, 0°13′W, 15 (USNM) Bibianaha, 1 (BMNH); Bunsu, 6°19′N, 0°27′W, 2 (BMNH); Goaso, Ashanti District, 4 (BMNH); 6 mi NW Kade, 6°06′N, 0°51′W, 11 (USMN); Kumasi, 9 (BMNH); Mapong, Ashanti District, 7 (BMNH); Oda, 4 (FMNH), 1 (MCZ); Pampramase, 6°40′N, 2°55′W, 2 (BMNH); 32 mi W Prestea, 5°23′N, 2°28′W, 8 (USNM); Tano River, Tano Lodge, 5 (BMNH); W of Sefwi Wiawso, 4 (BMNH). IVORY COAST: 17 km W Abidjan, 5°19′N, 4°08′W, 8 (CM); Adiopodoume, 5°19′N, 4°08′W, 8 (AMNH), 1 (CM), 2 (USNM); Blekoum, 6°23′N, 3°31′W, 3 (USNM); Ehania, 5°17′N, 3°04′W, 5, (USNM); Jacqueville, 5°12′N, 4°24′W, 1 (USNM); 15 km N Lakota, 6°00′N, 5°43′W, 5 (AMNH); Sassandra River, 7°00′N, 7°03′W, 2 (USNM); Soubre, 5°49′N, 6°45′W, 2 (USNM); Yabrasso, 7°26′N, 3°28′W, 3 (USNM). LIBERIA: Banga, 1 (MCZ); Peahtah, 1 (MCZ); Wiersn, 1 (AMNH); Tars Town, 25 km N Zwedru, 6°13′N, 8°08′W, 12 (USNM). NIGERIA: 6 mi N Ago Shasha, 4 mi S Ilashe, 1 (USNM); 30 mi W Benin, 6 (USMN); Gambari, S of Ibadan, 2 (BMNH); Ibadan, 1 (USNM); Ijii Waterworks, near Lagos, 1 (BMNH); Lagos, 5 (BMNH, inc. holotype of *T. t. pearsei*); Federal District, University of Lagos, 10 (USNM); Mamu Forest Reserve, near Ibadan, 1 (BMNH); Nikrowa, W of Benin, 1 (BMNH); Sapoba, 1 (USNM). SIERRA LEONE: Bambawo Forest Reserve, 5 (BMNH); Belebu, 7°47′N, 12°00′W, 1 (USNM); 4 mi S Lalehun, Gola Forest Camp, 7°54′N, 10°58′W, 2 (USNM); Sandaru, 1 (BMNH). Total = 171.

Hybomys univittatus. CAMEROON: Alum, 20 mi E Efulan, 1 (CM); 11 km S, 1 km E Bamenda, 5°51′N, 10°10′E, 1900 m, 2 (CM); Batanga, 26 (CM); Boumba Ngoko, vicinity of Bateka Malen, 2°09′N, 15°11′E, 2 (USNM); 30 km W Bertoua, 8 (AMNH); Bipindi, 13 (AMNH); 4 km N Buba-Bokwai Rd., 1 (FMNH); Mount Cameroon, 5800 ft, 1 (FMNH, holotype of *H. u. badius*); Campo, 1 (CM); Ebolowa, 4 (CM), 1 (FMNH); Efulan, 2 (CM), 4 (USNM); Efulan-Kribi, 1 (AMNH); Eseka, 3°38′N, 10°47′E, 1 (AMNH); 5 km SW Eseka, 3°37′N, 10°45′E, 2 (AMNH); 6 km SE Eseka, 3°35′N, 10°48′E, 2 (AMNH), 1 (CM); 8 km SW Eseka, 3°35′N, 10°44′E, 1 (AMNH), 2 (CM); Kribi, 2 (CM); Lolodorf, 39 (CM), 5 (MCZ); 12 km SE Mamfe, 2 (AMNH); Mengama, 80 mi SE Ebolowa, 1 (CM); Metet, 7 (CM), 6 (MCZ); 20 km E Minta, 3 (AMNH); Moloudou, 2 (CM); 30 km E Nanga-Eboko, 3 (AMNH); 5 km E Ndokayo, 2 (AMNH); Sakbayeme, 3 (FMNH); Sangmelima, 12 (CM); Sonsak, 1 (MCZ); Tisongo, 1 (USNM); Yaounde, 1 (CM); Yokadouma, 5 (CM). CONGO: Dolisie, 4 (AMNH); Etoumbi, 66 (AMNH); Makoua, 1 (AMNH); Mouyondzi, 3 (AMNH). EQUATORIAL GUINEA: Benito River, 15 mi from mouth, 3 (USNM). GABON: Anguanamo Ngovi, 22 (USNM); Estuaire Prov., 1 km SE Cap Esterias, 9 (CM); Mperi, Fernan Vaz, 2 (USNM); Fougamou, 4 (AMNH); Labamba, 1 (FMNH); Mount Tandou, Mouila, 1 (FMNH); Ogouma, Reni Nkami, 4 (USNM); Yombi, 5 (FMNH). NIGERIA: 14 mi S Oban, 2 (USNM). RWANDA: Uinka (=Shangugu), 5 (USNM). UGANDA: Kanyawara, 0°34′N, 30°21′E, 2 (USNM). ZAIRE: Avakubi, 12 (AMNH); Bafwasende, 4 (AMNH); Bogomanda, Lemera, 9 (USNM); Gamangui, 1 (AMNH); Irangi, 30 (USNM); Irumu, 2 (FMNH); Ituri Forest, 3 (FMNH); Kisiki, 36 km N Beni, 2500 ft, 2 (MCZ); Lukolela, 8 (AMNH); Kivu, Tshibati,

near Lwiro, 6400 ft, 9 (AMNH); SW Lake Kivu, Falls of Lwiro River, 6800 ft, 6 (AMNH); Medje, 5 (AMNH); Ngayu, 1 (AMNH); Niangara, 4 (AMNH); Niapu, 3 (AMNH); Stanleyville, 1 (AMNH); Equatorial Region, Gemena Zone, Tandala, 3°02′N, 19°21′E, 1 (USNM); Bumba Zone, Yalosemba, 2°35′N, 21°51′E, 1 (CM), 1 (USNM). TOTAL = 398.

Additional Records

Hybomys planifrons. GUINEA: Boola (Heim de Balsac and Lamotte 1958); Ziela, Mt. Nimba (Rosevear 1969). IVORY COAST: Grabo; Soubre; Tai (Dosso 1975; Tranier and Dosso 1979). LIBERIA: Mount Barclay; Deaple; Freemantown; Harbel (Rosevear 1969).

Hybomys trivirgatus. IVORY COAST: Lamto (Heim de Balsac and Bellier 1967); Tai (Dosso, 1975). LIBERIA: Grand Cape Mount (Jentink 1888); Gonyon (Rosevear 1969); S Nimba Ridge (Coe 1975).

Hybomys univittatus. CAMEROON: Foulassi, 6 km NNW Sangmelima (Perret and Aellen 1956); Mamfe, 400 ft; Fineschang, 650 ft; Tinta Assumbo Mts., 2300 ft (Sanderson 1940); CENTRAL AFRICAN REPUBLIC: la Maboke (Petter and Genest 1970). EQUATORIAL GUINEA: Cabo San Juan (Cabrera 1929). NIGERIA: Nko, 450 ft; Okoiyong, 450 ft (Sanderson 1940); Oban (Rosevear 1969). UGANDA: Kalinzu Forest, Ankole; Maramagambo Forest, Ankole; Bugoma Forest, Bunyoro; Impenetrable Forest, Kigezi; Malabigambo Forest, Masaka; Mbanga Forest, Mubuku Valley, Toro; Mayanja Forest, West Mengo; Mpanga Forest, West Mengo (Delaney 1975). ZAIRE: Fundi Mambaka; Philipili (Dollman 1914); Tingasi; Stat. Gadda; Poko, 20–30 mi NW Medje; Inkongo, Sankuru River (Thomas 1888, 1915, 1916). ZAMBIA: Mwinilunga District, Harr (Ansell 1974, 1978).

Appendix 2

Cranial and External Measurements (in mm) of Selected
Samples of *Hybomys*

Species and locality	n	x̄	1 SD	Range
		Occipitonasal length		
H. planifrons				
All	14	32.9	0.71	31.9–34.2
H. trivirgatus				
Ghana	16	33.6	0.90	32.3–35.1
Ivory Coast	22	33.6	1.23	31.0–36.0
Nigeria	10	33.4	0.62	32.5–34.4
H. univittatus				
Cameroon: Eseka and vic.	15	34.7	0.96	32.7–36.5
Cameroon: Lolodorf	23	33.6	1.21	31.3–36.1
Gabon: Cap Esterias	9	32.6	0.81	31.7–34.0
Zaire: Kivu Prov.	21	33.6	1.30	31.5–35.6
		Rostral length		
H. planifrons				
All	14	12.3	0.44	11.5–13.0
H. trivirgatus				
Ghana	16	12.6	0.52	11.6–13.5
Ivory Coast	22	12.6	0.70	11.0–13.5
Nigeria	10	12.5	0.24	12.2–12.9
H. univittatus				
Cameroon: Eseka and vic.	15	12.0	0.41	11.3–12.7
Cameroon: Lolodorf	23	12.0	0.55	11.2–13.2
Gabon: Cap Esterias	9	11.6	0.53	10.9–12.4
Zaire: Kivu Prov.	21	11.7	0.61	10.5–12.6
		Greatest zygomatic breadth		
H. planifrons				
All	14	15.3	0.47	14.7–16.4
H. trivirgatus				
Ghana	16	15.6	0.66	14.6–16.8
Ivory Coast	21	15.3	0.77	13.7–16.4
Nigeria	10	15.2	0.32	14.7–15.8
H. univittatus				
Cameroon: Eseka and vic.	15	16.6	0.45	15.9–17.2
Cameroon: Lolodorf	23	16.0	0.57	14.8–17.0
Gabon: Cap Esterias	9	15.8	0.58	15.1–16.8
Zaire: Kivu Prov.	18	16.0	0.60	14.9–17.0
		Width of zygomatic plate		
H. planifrons				
All	14	2.6	0.17	2.3–2.8
H. trivirgatus				
Ghana	16	2.6	0.24	2.2–3.2
Ivory Coast	22	2.8	0.28	2.1–3.3
Nigeria	10	2.4	0.18	2.1–2.7

Appendix 2

Continued

Species and locality	n	$\bar{x}$	1 SD	Range
H. univittatus				
Cameroon: Eseka and vic.	15	4.0	0.33	3.3–4.7
Cameroon: Lolodorf	23	3.9	0.29	3.4–4.4
Gabon: Cap Esterias	9	3.5	0.25	3.3–4.0
Zaire: Kivu Prov.	21	3.5	0.29	3.1–4.4
Least interorbital width				
H. planifrons				
All	14	6.0	0.25	5.5–6.4
H. trivirgatus				
Ghana	16	6.4	0.33	5.7–6.9
Ivory Coast	22	6.3	0.36	5.9–7.1
Nigeria	10	6.4	0.26	6.0–6.7
H. univittatus				
Cameroon: Eseka and vic.	15	5.9	0.29	5.3–6.2
Cameroon: Lolodorf	23	5.8	0.57	5.3–6.7
Gabon: Cap Esterias	9	6.1	0.22	5.8–6.4
Zaire: Kivu Prov.	21	5.8	0.31	5.1–6.5
Postpalatal length				
H. planifrons				
All	14	11.1	0.41	10.4–11.8
H. trivirgatus				
Ghana	16	11.3	0.36	10.7–11.9
Ivory Coast	22	11.2	0.50	10.1–12.1
Nigeria	10	11.4	0.39	10.7–12.1
H. univittatus				
Cameroon: Eseka and vic.	15	11.6	0.59	10.7–12.9
Cameroon: Lolodorf	23	11.0	0.62	9.9–12.2
Gabon: Cap Esterias	9	10.4	0.60	10.0–11.7
Zaire: Kivu Prov.	21	11.1	0.53	10.1–12.0
Length of hard palate				
H. planifrons				
All	14	5.6	0.29	5.0–6.1
H. trivirgatus				
Ghana	16	6.2	0.39	5.5–6.9
Ivory Coast	22	6.1	0.33	5.6–6.9
Nigeria	10	6.4	0.29	5.9–6.7
H. univittatus				
Cameroon: Eseka and vic.	15	6.0	0.29	5.5–6.5
Cameroon: Lolodorf	23	5.8	0.33	5.2–6.6
Gabon: Cap Esterias	9	5.6	0.20	5.2–5.8
Zaire: Kivu Prov.	21	5.7	0.38	5.0–6.5
Length of incisive foramen				
H. planifrons				
All	14	5.7	0.33	5.0–6.3

Appendix 2

Continued

Species and locality	n	x̄	1 SD	Range
H. trivirgatus				
Ghana	16	5.3	0.36	4.8–5.9
Ivory Coast	22	5.5	0.37	4.9–6.3
Nigeria	10	5.0	0.19	4.5–5.2
H. univittatus				
Cameroon:·Eseka and vic.	15	6.8	0.35	6.3–7.7
Cameroon: Lolodorf	23	6.8	0.43	6.1–7.6
Gabon: Cap Esterias	9	6.6	0.25	6.1–7.0
Zaire: Kivu Prov.	21	6.8	0.34	6.1–7.6
Diastemal length				
H. planifrons				
All	14	8.2	0.38	7.7–8.7
H. trivirgatus				
Ghana	16	7.9	0.28	7.4–8.4
Ivory Coast	22	8.1	0.55	7.1–9.1
Nigeria	10	8.0	0.27	7.7–8.5
H. univittatus				
Cameroon: Eseka and vic.	15	8.2	0.28	7.7–8.8
Cameroon: Lolodorf	23	8.5	0.49	7.5–9.2
Gabon: Cap Esterias	9	8.3	0.26	7.9–8.6
Zaire: Kivu Prov.	21	8.1	0.51	7.4–9.1
Alveolar length of maxillary toothrow				
H. planifrons				
All	14	5.6	0.17	5.3–5.9
H. trivirgatus				
Ghana	16	5.4	0.24	5.0–5.9
Ivory Coast	22	5.4	0.28	4.8–5.8
Nigeria	10	5.3	0.17	5.1–5.6
H. univittatus				
Cameroon: Eseka and vic.	15	6.1	0.17	5.7–6.4
Cameroon: Lolodorf	23	5.7	0.20	5.2–6.0
Gabon: Cap Esterias	9	5.4	0.16	5.2–5.7
Zaire: Kivu Prov.	21	5.6	0.14	5.3–5.9
Breadth across upper molars				
H. planifrons				
All	14	6.8	0.22	6.5–7.2
H. trivirgatus				
Ghana	15	6.8	0.32	6.1–7.2
Ivory Coast	22	6.7	0.31	6.2–7.4
Nigeria	9	6.7	0.16	6.6–7.1
H. univittatus				
Cameroon: Eseka and vic.	15	7.1	0.27	6.7–7.5
Cameroon: Lolodorf	23	6.9	0.25	6.5–7.3
Gabon: Cap Esterias	9	6.9	0.23	6.5–7.3
Zaire: Kivu Prov.	21	6.7	0.19	6.2–7.1

Appendix 2

Continued

Species and locality	n	$\bar{x}$	1 SD	Range
Depth of mandible				
H. planifrons				
All	14	7.2	0.38	6.7–8.0
H. trivirgatus				
Ghana	16	7.0	0.36	6.6–7.6
Ivory Coast	22	6.9	0.43	5.9–7.7
Nigeria	10	7.1	0.27	6.7–7.5
H. univittatus				
Cameroon: Eseka and vic.	15	8.8	0.46	7.9–9.4
Cameroon: Lolodorf	22	8.4	0.54	7.0–9.6
Gabon: Cap Esterias	9	8.3	0.29	7.9–8.8
Zaire: Kivu Prov.	20	8.5	0.44	7.4–9.4
Total length				
H. planifrons				
All	14	219.4	9.35	201–234
H. trivirgatus				
Ghana	15	222.4	12.30	200–248
Ivory Coast	20	224.0	10.11	199–243
Nigeria	10	218.8	6.05	210–226
H. univittatus				
Cameroon: Eseka and vic.	14	254.5	13.36	233–280
Cameroon: Lolodorf	3	243.7	—	237–254
Gabon: Cap Esterias	5	236.2	5.76	228–243
Zaire: Kivu Prov.	12	238.7	13.68	214–259
Tail length				
H. planifrons				
All	14	96.3	6.39	85–107
H. trivirgatus				
Ghana	15	98.7	9.05	82–120
Ivory Coast	20	101.2	5.71	90–111
Nigeria	10	99.1	6.49	90–115
H. univittatus				
Cameroon: Eseka and vic.	14	121.3	8.21	107–135
Cameroon: Lolodorf	4	119.5	—	109–136
Gabon: Cap Esterias	5	113.8	5.07	106–120
Zaire: Kivu Prov.	12	118.1	7.22	103–126
Hindfoot length				
H. planifrons				
All	14	30.7	1.07	28–32
H. trivirgatus				
Ghana	16	31.6	1.36	30–34
Ivory Coast	22	32.7	1.16	30–35
Nigeria	10	33.2	1.23	31–35

Appendix 2

Continued

Species and locality	n	$\bar{x}$	1 SD	Range
H. univittatus				
Cameroon: Eseka and vic.	15	32.3	1.35	30–35
Cameroon: Lolodorf	4	32.5	—	31–34
Gabon: Cap Esterias	5	30.0	1.00	29–31
Zaire: Kivu Prov.	13	30.9	0.76	30–32