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THE RELATIONSHIPS OF QUEMISIA
GRAVIS
(RODENTIA: HEPTAXODONTIDAE)

(WITH ONE PLATE)

By

CLAYTON E. RAY

Associate Curator, Division of Vertebrate Paleontology
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CITY OF WASHINGTON
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The large Hispaniolan caviomorph *Quemisia gravis* was described by G. S. Miller, Jr. (1929a, pp. 22-25; pl. 4, figs. 2, 2a) on the basis of a fragmentary immature right mandibular ramus (the type, U.S.N.M.¹ 253175), a fragment of an upper incisor, and a partial femur, all from caves near St. Michel de L'Atalaye in north-central Haiti. To these Miller added later in the same year (1929b, pp. 10-11, pl. 2, fig. 3) a distal half of a femur and the proximal end of an ulna, both from a cave at Boca del Infierno on the southern shore of Bahia de Samana, Dominican Republic. These five fragments constitute the entire known material of *Quemisia*, and of them only the jaw is of much value in determining the affinities of the genus.

In the initial description and subsequently—insofar as it has been noticed at all—*Quemisia* has been associated closely with *Elasmodontomys*. G. M. Allen, the only author aside from Miller who has done more than incorporate *Quemisia* into a survey or checklist, stated (1942, p. 128) that Schreuder's (1933) specimens of *Amblyrhiza* "indicate that the animal was closely allied to the 'Quemi' of Santo Domingo, with essentially the same enamel pattern of the molars but with a relatively longer rostrum. . . . The animal must have been a giant in comparison with the 'Quemi'." ² How-

¹U.S.N.M. stands for United States National Museum, M.C.Z. for Museum of Comparative Zoology, and A.M.N.H. for American Museum of Natural History.

²The generic name *Quemisia* reflects Miller's supposition that the animal was the "Quemi" of Oviedo, whose brief description of the animal not actually seen by him was quoted by MacLeay (1829, p. 275) and by Miller (1929b,

ever, except for a fragment of a lower incisor 50 mm. in length, Schreuder had only cranial fragments and the upper dentition of *Amblyrhiza*, all of which were mature, whereas, except for the three postcranial scraps and a fragment of an upper incisor 19 mm. in length, *Quemisia* is known only from an immature lower jaw. Obviously, close comparison between *Quemisia* and Schreuder's specimens of *Amblyrhiza* is impossible, and, although mandibular material of *Amblyrhiza* is available, the closely related *Elasmodontomys* can be more usefully compared to *Quemisia* in that the two are known from jaws of comparable ontogenetic age and are similar in size.

In fact, however, in most characters except size and some details of dentition, *Quemisia* is dissimilar to *Elasmodontomys* and similar to the Capromyidae, in particular to *Plagiodontia* (figs. 1, 2). Interestingly, most of the features in which *Quemisia* differs from *Elasmodontomys* were well described by Miller, who nevertheless failed to recognize that these very features seem to ally *Quemisia* with the Capromyidae. Most of the comparisons of *Quemisia* with *Elasmodontomys* and *Plagiodontia* are straightforward and are most readily comprehended in tabular form (table 1).

The interpretation of the enamel configuration of the cheekteeth, however, is more complex and requires some discussion. The occlusal surface of each cheektooth in *Quemisia* is dominated by three deep, narrowly compressed reentrant folds, two lingual (anterior) and one labial (posterior). The lingual reentrants extend to or almost to the opposite, external enamel wall but do not breach it (except very shallowly in the anterior fold of the unworn M_3). The labial reentrant is completely penetrant, producing on the occlusal surface an isolated posterior enamel island. However, the depth of penetration on the lingual wall by this reentrant is very shallow, especially in the first cheektooth, so that with slight additional wear this fold would have assumed the character of the lingual ones. In *Elasmodontomys* the lingual reentrants are completely penetrant apically, as is the labial reentrant, thus generally producing in moderately worn permanent lower cheekteeth a pattern of four obliquely oriented complete enamel ellipses succeeding

p. 13) and Latinized by Fischer (1830, p. 389[=589]) as *C.[=Capromys] quemi*. Allen (1942, p. 128) pointed out that if Miller's supposition were correct, then the scientific name should be *Quemisia quemi*. However, it seems highly improbable that the identity of Miller's *Quemisia* with Oviedo's "Quemi" could ever be established beyond reasonable doubt. Thus, *Quemisia quemi* is best regarded as a nomen dubium.

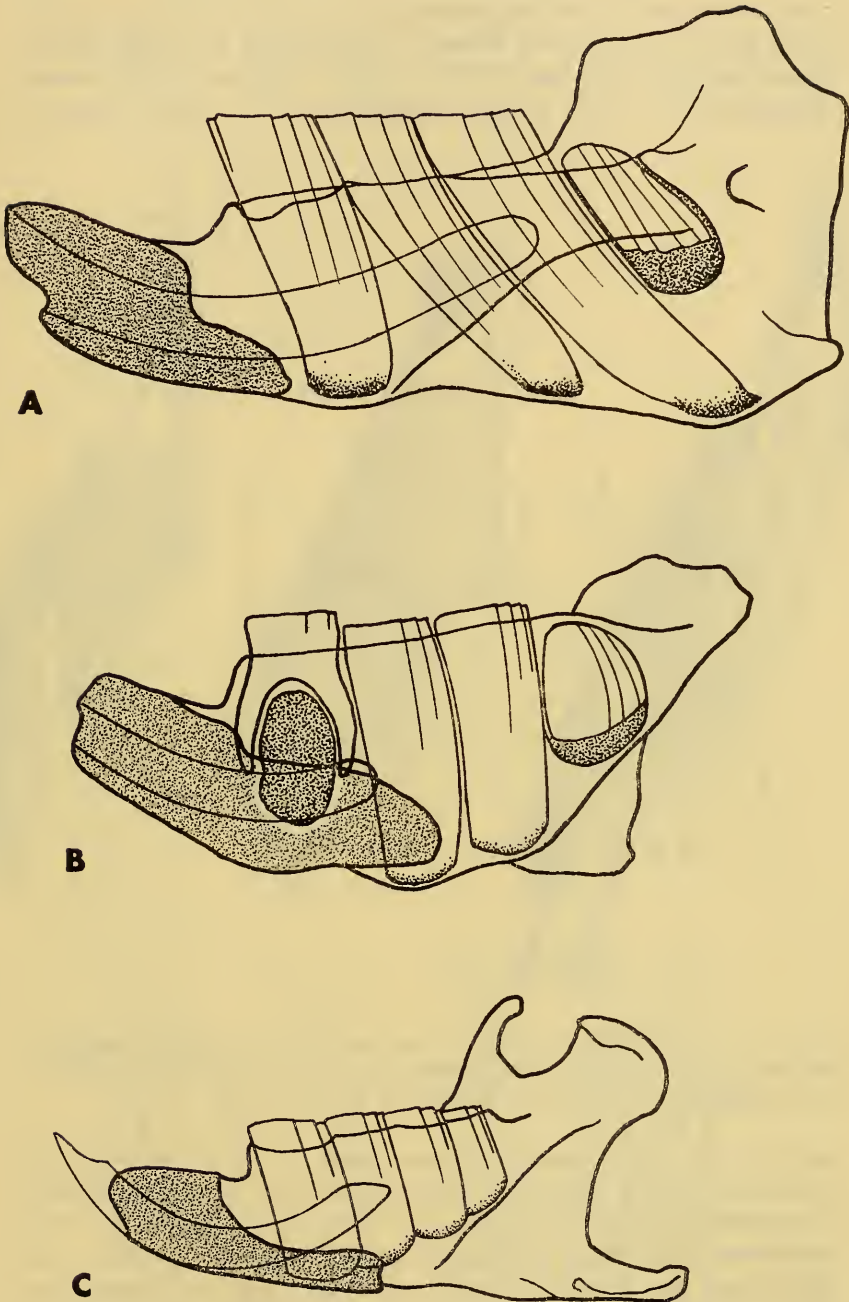


FIG. 1.—Right mandibular rami in lingual aspect of (A), *Elasmodontomys obliquus*, A.M.N.H. 17137h; (B), *Quemisia gravis*, U.S.N.M. 253175 (the type); (C), *Plagiodontia hylaeum*, M.C.Z. 35314. Diagrammatically represented, largely on the basis of X-ray photographs. $1\frac{1}{2} \times$ natural size.

one another on the occlusal surface, as in P_4 of A.M.N.H. 17137h (fig. 2A). With varying amounts of additional wear the lingual folds generally withdraw from complete penetrance but remain tightly appressed or in close approximation to the external enamel



FIG. 2.—Right mandibular rami in occlusal aspect of (A), *Elasmodontomys obliquus*, A.M.N.H. 17137h; (B), *Quemisia gravis*, U.S.N.M. 253175 (the type); (C), *Plagiodontia hylaeum*, M.C.Z. 35314. $1\frac{1}{2} \times$ natural size.

wall of the tooth through extreme wear, as in M_1 and M_2 of A.M.N.H. 17137h (fig. 2A). The labial reentrant generally remains completely penetrant in deeply worn teeth. The dentition of *Elasmodontomys* in general is discussed in detail by Ray (1964b). One labial and two (major) lingual reentrant folds are present in the lower cheekteeth of *Plagiodontia* and other Antillean capromyids.

TABLE 1.—Comparison of *Quemisia* with *Elasmodontomys* and *Plagiodontia*.

All quoted passages are from Miller (1929a, pp. 22-24). In order to facilitate comparison to specimens not X-rayed, the posterior termination of the mandibular symphysis and of the incisor is expressed in relation to the occlusal plane of the cheekteeth, by projection of the termini perpendicular to that plane, with the line of sight perpendicular to the symphyseal (midsagittal) plane.

<i>Elasmodontomys</i>	<i>Quemisia</i>	<i>Plagiodontia</i>
1. Size large. Occlusal length P_1-M_2 , 27.6 mm.	1. Size large. Occlusal length DP_1-M_3 , 24.5 mm.	1. Size medium. Occlusal length DP_1-M_2 , 15.7 mm. in M.C.Z. 35314, an adult; less in younger individuals.
2. "Mandibular symphysis extending . . . barely to middle of pm_1 ."	2. "Mandibular symphysis extending backward beyond level of middle of m_1 ," actually to posterior margin of M_1 . The great breadth of the symphysis undoubtedly is correlated with large size.	2. Mandibular symphysis extending to posterior edge of DP_4 even in specimens much younger than <i>Quemisia</i> and to posterior margin of M_1 in adults.
3. "Shaft of the incisor extends far beyond the symphysis to terminate beneath middle of m_2 ," actually beneath posterior margin of M_2 .	3. "Shaft of lower incisor not extending behind symphysis, its base lying beneath anterior half of m_1 ," actually beneath middle of M_1 .	3. Shaft of lower incisor extending little or not at all behind symphysis, its base lying beneath middle of M_1 .
4. Angular process not flaring laterad, lying in plane of cheekteeth; denticulous portion of mandible continuous with angular process, which "is so thick that it forms considerably more than half of the entire transverse diameter" of the mandible.	4. Angular process flaring laterad, offset from plane of cheekteeth; denticulous portion of mandible "separated from the base of the angular process by a shallow groove. . . . Anterior base of the angular process . . . laterally compressed . . . so that it forms about one-third of the transverse diameter of the mandible."	4. Angular process as in <i>Quemisia</i> .

TABLE 1. *Continued*

<i>Elasmodontomys</i>	<i>Quemisia</i>	<i>Plagiodontia</i>
5. Horizontal and ascending rami of mandible lying in same plane, lingual surfaces merging over broad area.	5. Horizontal and ascending rami offset, lingual surfaces with bony ridge extending posterodorsad from directly behind the last molar toward the articular process, decreasing in height posterodorsally and merging with ascending ramus.	5. Horizontal and ascending rami as in <i>Quemisia</i> .
6. Mandibular foramen opening on lingual surface of jaw posterior to toothrow, in typical mammalian position.	6. Mandibular foramen opening on dorsal face of horizontal ramus between M_2 and ascending ramus.	6. Mandibular foramen opening as in <i>Quemisia</i> . (Little weight can be attached to this character as the condition in <i>Amblyrhiza</i> is somewhat similar to that in <i>Quemisia</i> .)
7. Molars invading thickened angular process (cf. 4 above), penetrating to its ventral border; extremely hypsodont; forming roots; maximum height of M_2 (38.6 mm.) much greater than occlusal length of P_1-M_2 (cf. 1 above).	7. Molars not invading angular process (cf. 4 above); moderately hypsodont; probably evergrowing; maximum height of M_2 (21.3 mm.) less than occlusal length of DP_1-M_2 (cf. 1 above).	7. Molars as in <i>Quemisia</i> ; cheekteeth definitely evergrowing; maximum height of M_2 (11.6 mm. in M.C.Z. 35314) less than occlusal length of DP_1-M_2 (cf. 1 above). In U.S.N.M. 253155, a younger individual, height of M_2 is 12.0 mm., occlusal length of DP_1-M_2 , 14.7 mm.
8. P_4 locus diphyodont; DP_4 replaced prior to eruption of M_2 .	8. P_4 locus diphyodont; DP_4 replaced subsequent to eruption of M_2 .	8. P_4 locus monophyodont; P_4 probably suppressed.
9. Cheektooth row oblique to sagittal plane.	9. Cheektooth row almost parallel to sagittal plane.	9. Cheektooth row oriented as in <i>Quemisia</i> .

In these forms the labial reentrant lies anterior to the posterior lingual one (*Plagiodontia*, *Capromys*), abuts it (*Isolobodon*), or merges with it (*Aphaetreus*). An isolated posterior enamel island is thus produced in *Aphaetreus*, superficially as in *Quemisia* but actually through the confluence of two folds, not the complete penetration of one. The lingual folds in *Plagiodontia* and the labial fold in *Isolobodon* and *Aphaetreus* approach those of *Quemisia* most closely in compression and depth of penetration, and although the approach is not very close, it is not so remote in this respect as are these genera from *Capromys*.

The posterior enamel wall of each reentrant fold in *Quemisia* is extremely thin and in places not certainly detectable owing to damage to the occlusal surface. Similar, but less radical, thinning is characteristic of *Elasmodontomys* but has been observed in no Antillean capromyid.

Among the most striking features of *Quemisia*, Miller (1929a, p. 24) noted that "the forward turning of the enamel folds so that the anterior portion of each fold is approximately parallel with the main axis of the toothrow is a specialization of high degree and very peculiar kind." This character is especially well shown by a sharp flexure of the posterior (here posterolabial) wall of each tooth, marking the "forward turning." A similar flexure is present on the corresponding face in *Plagiodontia*, but it is not well shown by the reentrants. Differences in enamel configuration between *Quemisia* and *Plagiodontia* appear to be no greater than between the latter and *Capromys*.

The discovery of a new species of capromyid (Ray, 1964a), assigned tentatively to *Plagiodontia* and based unfortunately on a single tooth (DP⁴?), narrows the structural gap between the dentition of *Quemisia* and that of capromyids. The new species has the crown of the tooth compressed perpendicular to the reentrant folds, and the deeply penetrant, much compressed reentrant folds oriented strongly anteroposteriorly.

As part of a general survey of Antillean capromyids, the above comparisons and those presented in table 1 were written in essentially their present form on the basis of the type description of *Quemisia gravis* at a time when the type specimen was temporarily unavailable. Subsequent availability of the type has not materially altered these observations, but X-rays of it have augmented them startlingly (fig. 1B). The first cheektooth is a deeply worn DP₄ with long slender anterior and posterior roots curving about a

large crypt for P_4 . Judging from degree of wear of DP_4 and state of development of M_3 , the latter would have come into use prior to replacement of DP_4 by P_4 . In any case DP_4 was retained relatively much longer in *Quemisia* than in *Elasmodontomys*. In a specimen of the latter with DP_4 and the crypt for P_4 in a condition comparable to that in the type of *Quemisia gravis*, M_2 is just at the point of eruption (cf. Ray, 1964b, fig. 1D) and, in a specimen with M_3 at the point of eruption (as in *Quemisia*), P_4 is already in full use (fig. 1A).

I have examined the fragmentary upper incisor and the fragmentary femur referred to *Quemisia* from the caves near St. Michel de L'Atalaye and find in them no clues to the relationships of the genus. The femur is distinctive in the extreme flattening of the shaft (noted by Miller 1929a, p. 24) and in the relatively large size of the head (pl. 1). The referred specimens from Boca del Infierno could not be located at the time of this writing.

From the evidence at hand, I find only modest support for inclusion of *Quemisia* with the Heptaxodontinae and much to warrant exclusion. Similar size and geographic proximity afford only peripheral evidence of affinity with *Elasmodontomys*. The similarities noted in occlusal pattern and in enamel thinning constitute perhaps the most compelling evidence for relationship. Diphyodonty at the P_4 locus is of course a primitive eutherian character retained in most other caviomorphs. Dental development at this locus in *Quemisia* differs in detail from that in heptaxodontines in the longer retention of DP_4 in *Quemisia* (presaging suppression of P_4 ?). The differences between *Quemisia* and *Elasmodontomys* in the preserved features of the lower jaw (table 1) indicate more radical divergence in their respective developmental complexes than that observed within caviomorph families.

The uncertain position of *Quemisia* emphasizes the eastern Caribbean distribution of heptaxodontines in that not only Cuba, but now perhaps Hispaniola, is without them. Furthermore, the relationships of the Jamaican *Clidomys*, *Speoxenus*, and *Spirodontomys*, customarily brigaded with the Heptaxodontinae, remain to be established. With regard to *Clidomys*, the best known of the three, Anthony (1920, p. 472) has wisely stated, "it would be premature to indulge in conjecture . . . as to the relationships of this new genus. It is significant, however, that the dentition shows *Clidomys* to be only remotely related to the other large hystricomorphs of the West Indies." In these statements I heartily concur, and, although pro-

nouncements on the detailed affinities of *Clidomys* must await careful study of specimens already available and the collection of supplementary material, there can be no doubt that, even if *Clidomys* should prove to be a heptaxodontid, its relationships to the eastern Caribbean forms are remote. Thus, the Heptaxodontinae at present include with certainty only *Amblyrhiza* on Anguilla and St. Martin, and *Elasmodontomys*³ on Puerto Rico.

If *Quemisia* is not a heptaxodontine, then the only remaining probable relatives among Antillean caviomorphs are the capromyids. Of course, it is possible that *Quemisia* represents a separate invasion from the mainland and thus has no close Antillean relatives. This alternative is in my opinion the more radical and is unsupportable on the basis of present, admittedly meager, evidence. Prior to X-raying the mandible of *Quemisia*, I had confidently placed the genus in the family Capromyidae, comparing it most closely with *Plagiodontia*. Discovery of diphyodonty at the P₄ locus in the specimen makes this assignment untenable at present, but evolutionarily much more interesting if correct. The transfer of *Quemisia* to the Capromyidae would disrupt not only the concept of that family but current superfamilial groupings as well (cf. Schaub, 1953, pp. 396-397; Wood, 1955, pp. 181-182; Wood and Patterson, 1959, pp. 323-327), which is not warranted on the basis of inadequate knowledge of a single genus. Pending discovery of more material, *Quemisia* may be retained, incertae sedis, in the Heptaxodontidae, recognizing that this is a temporary expedient.

Considering *Quemisia* for the moment as a capromyid, the impression is strengthened that Hispaniola has been an important center of capromyid radiation in the Antilles, in terms of both number of forms (five genera and nine species on Hispaniola) and breadth of diversification. The history of Antillean capromyid evolution assuredly is not a simple one of differentiation on and dispersal from Hispaniola or any one island, but *Plagiodontia*, *Isolobodon*, and *Aphaetreus* (with *Quemisia*?) do seem to constitute a natural assemblage (the *Plagiodontia* group), accounting for four genera and eight species on Hispaniola. The importance of this group in the Quaternary fauna of Hispaniola at least suggests origin of *Isolobodon* on that island, followed by eastward dispersal by natural means or human transport (or both) through Mona, Puerto Rico, St. Thomas, and St. Croix. The *Capromys* group (including *Capromys*, *Geo-*

³ *Heptaxodon* is based on juvenile individuals of *Elasmodontomys* and is the junior synonym (Ray, 1964b).

capromys, and *Hexolobodon*), represented on Hispaniola only by the well-differentiated *Hexolobodon phenax*, has its greatest diversity on Cuba with two genera, weakly differentiated, and five species.⁴

Available evidence suggests that the *Plagiodontia* group has undergone a relatively old radiation on Hispaniola but is not known with certainty to have dispersed from the island by natural means, whereas the *Capromys* group has undergone a relatively young radiation on Cuba and has dispersed widely from that island at least in part by natural means.

If *Quemisia* is in fact related to the capromyids, then it would suggest that the group has been in the Antilles longer and has undergone more extensive evolution there than previously would have been supposed. It is not impossible that Antillean caviomorphs have arisen from fewer, possibly older, invasions than their current taxonomic separation would imply, and that the descendants of a single invasion could in some cases have diverged to the familial level after invasion. On the basis of present evidence one can speculate at least that *Quemisia*, when better known, will provide an evolutionary bridge between Antillean capromyids and heptaxodontines.⁵ Naturally, since all known forms are of Quaternary age, they must be regarded as collateral members of an adaptive radiation, none of which is ancestral to another, and all of which have evolved at differing rates both in the relation of one lineage to another and of one structure to another in a single lineage. Regarded as divergent products of a single adaptive radiation, the heptaxodontines are relatively highly evolved in terms of hypsodonty and enamel configuration, but conservative in retention of P_4 diphodonty and root formation in P_4 - M_3 , whereas the capromyids are more conservative in degree of hypsodonty and enamel modification, but advanced in the suppression of P_4 and evergrowing cheekteeth. *Quemisia* presents a melange of highly evolved and conservative characters. If the relationships suggested here are real, the waif which gave rise to the Antillean capromyids and heptaxodontines must have dispersed from the mainland prior to the suppression of P_4 . According to the interpreta-

⁴ Schaub (1953, pp. 396-397) distributes the genera discussed in this paragraph among four families, an arrangement which I am wholly unable to accept, but the analysis of which is outside the scope of this paper.

⁵ Wood and Patterson (1959, pp. 325-326) have utilized the lateral process of the supraoccipital in drawing the Echimyidae and Capromyidae together but have pointed out with regret the strong development of the process in *Elasmodontomys*. Is it possible that the lateral process in *Elasmodontomys* is of more profound significance than merely another regrettable instance of rodent parallelism?

tions of Wood and Patterson (1959, pp. 301, 324-326), the invader would necessarily have been an echimyid (or protocapromyid) and the time pre-Colhuehuapian.⁶ Persistence of P_4 in some insular descendants perhaps would not be so startling as in mainland forms.

The above suggestions will remain highly speculative until cranial material of *Quemisia* and of Tertiary caviomorphs is discovered in the Antilles. Nevertheless, it is clear already that *Quemisia* is potentially of great importance in the interpretation of the history of Antillean caviomorphs and has bearing on the arrangement of the Caviomorpha as a whole. Further, it is increasingly clear that the large, high, complex island of Hispaniola will eventually yield the answers to many problems of Antillean faunal history.

I acknowledge with pleasure the assistance of David H. Johnson of the U. S. National Museum, who made available the extensive collections of fossil caviomorphs, including *Quemisia*, from the vicinity of St. Michel de L'Atalaye; Ernest Williams, Karl Koopman, and Bryan Patterson, who read (but did not necessarily fully approve) drafts of the manuscript; Barbara Lawrence, who granted access to the large collection of capromyids in the Museum of Comparative Zoology; James Gavan of the University of Florida Health Center, who provided the X-rays on which figure 1 is based; Sue Hirschfeld who prepared figure 1 and plate 1; the National Science Foundation, which financed these illustrations through NSF GB 178; and Lawrence B. Isham who prepared figure 2. Much of this work was done while the author held the position of assistant curator in the Florida State Museum, University of Florida.

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⁶This age seems inordinately early on the basis of the evidence presented by Wood and Patterson (p. 301). If P_4 was nonfunctional in echimyids after Deseadan time, it seems developmentally improbable that a cryptic P_4 crown (a structure elaborated late in ontogeny) would continue to be produced in a Santacrucian form.

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Fragmentary right femur, U.S.N.M. 253176, of *Quenstedia gracilis* in (A) lateral, (B) medial, (C) anterior, and (D) posterior aspect.
 $\frac{1}{4}$ \times natural size.