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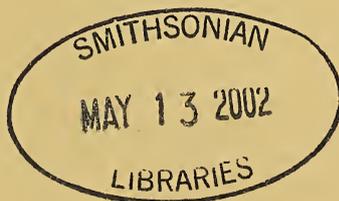
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NEW SPECIMENS OF PICROMOMYIDS
(PLESIADAPIFORMES, PRIMATES) WITH DESCRIPTION OF A NEW
SPECIES OF *ALVEOJUNCTUS*MARY T. SILCOX¹KENNETH D. ROSE²

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ABSTRACT

Two new specimens attributable to the plesiadapiform family Picromomyidae are documented. One, a lower molar, represents a new species here named *Alveojunctus bowni*. This species is the largest and most derived picromomyid currently known, with an extremely simplified molar morphology. The second new specimen is a fragmentary lower jaw attributed to *Picromomys petersonorum*; the specimen includes the first complete lower central incisor known for a picromomyid. This tooth shows none of the derived features seen in microsyopid I₁s, providing no support for a tie to this family. Instead, it is most similar to I₁ in *Tinimomys graybulliensis*, supporting a close relationship between Picromomyidae and Micromomyidae.

KEY WORDS: Incisors, Picromomyidae, Micromomyidae, Plesiadapiformes, Primates, Teeth

INTRODUCTION

In 1996 Rose and Bown recognized a new family of plesiadapiform based on the discovery of associated right and left dentaries representing a new species, *Picromomys petersonorum*. This species is characterized by an enlarged P₄ with a wide, oddly flattened talonid and unusual, cusp-like, mesiobuccal expansions on the trigonids of M₁₋₂. *P. petersonorum* is also exceptional as one of the smallest primate-like animals ever described. The recent description of the “smallest primate” by Gebo et al. (2000) does not discuss *Picromomys*, presumably because the authors do not consider plesiadapiforms to be primates. A comprehensive phylogenetic analysis of dental, cranial, and postcranial features of a wide diversity of plesiadapiforms, euprimates, and other archontans indicates that plesiadapiforms are most appropriately considered primates (Silcox, 2001). The body mass estimates of *P. petersonorum* and the smallest Shanghuang primate discussed by Gebo et al. overlap, so it is unclear which species is actually the smallest described primate.

Rose and Bown (1996) also included a previously described species of plesiadapiform, *Alveojunctus minutus* Bown, 1982, in the Picromomyidae on the basis of similarities in the morphology of the enlarged P₄ and the shared presence of

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low-crowned lower molars with shallow or absent hypoflexids, strongly mesially canted trigonids, twinned entoconid and hypoconulid separated by an entoconid notch, and weak or absent mesiobuccal cingulids. Hooker et al. (1999) challenged the link between *Picromomys* and *Alveojunctus*, suggesting that the relationships of the latter “will remain obscure until more material is found (p. 393).” These authors did not account for the close similarity in P₄ morphology seen in *Picromomys* and *Alveojunctus*, or for the molar characteristics shared by these two genera. Although further material of *Alveojunctus* may suggest a different resolution, the current evidence strongly supports the inclusion of both species in a taxonomic grouping to the exclusion of any other known plesiadapiform.

Rose and Bown (1996) presented a cladistic analysis to elucidate the wider relationships of the Picromomyidae. In spite of some general resemblances to Picrodontidae (e.g., low-crowned molars and strongly mesially canted molar trigonids), the results of the analysis suggested that these similarities are due to convergence and that picromomyids are most closely related to either uintasoricine microsyopids or micromomyids. Although the authors slightly favored the micromomyid tie, they conceded that formalizing this relationship taxonomically was premature given the paucity of the material available at that time. Subsequently, Stafford and Szalay (2000) opined that the Picromomyidae were a group of microsyopids, although this view was not supported by new specimens, a revised cladistic analysis, or a discussion of any character evidence.

This paper documents new specimens of the Picromomyidae, including the description of a new species of *Alveojunctus* based on a single lower molar from the Uintan of California. We recognize that naming a new species based on a single tooth is ordinarily an undesirable practice. In this instance, however, we deem it appropriate because of the extreme scarcity of this group, the diagnostic differences between the new specimen and known picromomyids, and the temporal and geographic separation between this specimen and the rest of the known material of the Picromomyidae. The other species of *Alveojunctus*, *A. minutus*, is known from only a few isolated teeth, and its holotype is also a lower molar, allowing the most appropriate comparisons to be made (Bown, 1982). To date, only nine specimens that can be confidently referred to the Picromomyidae (see below) have been discovered, seven of which are isolated teeth of *Alveojunctus*. This material is known from Wasatchian, Bridgerian, and Uintan deposits, indicating that the family existed for at least six million years. In light of the derived morphology exhibited by known picromomyids, compared to that of their likely closest relatives, the family probably originated significantly earlier. Previous to this report the geographic range of the Picromomyidae was limited to Wyoming—with the description here of a specimen from California the geographic range of this family is significantly increased. All of these indications show that the family is so rare that there can be no guarantee that any better specimens of the new species will ever be recovered.

Dental characteristics of known picromomyids are suggestive of a diet similar to that of the tiny extant marsupial feathertail glider, *Acrobates* (Rose and Bown, 1996), which feeds on a diet of insects, nectar, pollen, and possibly tree exudates (Fleay, 1947; Woodside, 1995; Nowak, 1999), although further study is required to rule out other possibilities (e.g., a diet of soft fruits).

A new specimen of *Picromomys petersonorum* that includes the first complete lower central incisor is also documented here. The morphology of this tooth provides new evidence on the wider relationships of the family.

Abbreviations used in text are as follows: FMNH, Field Museum of Natural History, Chicago, Illinois; SDSNH, San Diego Natural History Museum, San Diego, California; USGS, United States Geological Survey, Denver, Colorado; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington D.C.

SYSTEMATIC PALEONTOLOGY

Order Primates Linnaeus, 1758

Suborder Plesiadapiformes Simons and Tattersall, *in* Simons, 1972

Family Picromomyidae Rose and Bown, 1996

Genus *Alveojunctus* Bown, 1982

Alveojunctus bowni, **new species**

(Fig. 1A)

Holotype.—SDSNH 31788, right M_1 or M_2 . Only known specimen; collected by M. A. Roeder and S. L. Walsh in 1986.

Locality.—San Diego Society of Natural History locality 3373, early Uintan, upper tongue of the Friars Formation, Carmel Mountain Ranch housing development, Unit 15, San Diego Co., California.

Diagnosis.— $M_{1 \text{ or } 2}$ approximately 25–30% larger in linear dimensions than $M_{1 \text{ or } 2}$ in *Alveojunctus minutus*. Lower molar paracristid less well defined than in *A. minutus*. Strong, straight valley present between the protoconid and paraconid/metaconid, missing in *A. minutus*. Contrasts with *Picromomys petersonorum* (but not *A. minutus*) in the lack of cingulids on the lower molar, the buccal cristid obliqua resulting in the absence of a hypoflexid, the poor definition of the buccal cusps, and the absence of a protocristid and postvallid.

Etymology.—For Thomas M. Bown, in recognition of his valuable contributions to knowledge of Paleogene mammals generally, and particularly to the discovery and study of plesiadapiform primates including Picromomyidae.

Description.—The single known isolated tooth cannot be definitively identified as M_1 or M_2 (see Discussion). The lack of a distal expansion associated with an enlarged hypoconulid, present on M_3 of all plesiadapiforms except picrodontids, indicates that it is not likely to be M_3 . It is very low crowned. The tooth has a straight mesial border, associated with a poorly demarcated paracristid and a paraconid that is situated far lingually on the tooth, being positioned just mesial to the metaconid. The paraconid and metaconid, although closely appressed, are separated by a notch, so that each cusp is distinct. A narrow talonid notch separates the metaconid and entoconid. These cusps are closely positioned, compressing the talonid notch, and effectively closing the talonid basin lingually (in spite of the absence of an entocristid). The lingual cusps are better defined than the buccal cusps, although all the cusps are low, broad, and bulbous swellings rather than sharp, pyramidal structures. The broadly swollen bases of the lingual cusps create a scalloped border to the central basin of the tooth (see below).

A chip of enamel is missing on the mesiobuccal margin of the protoconid, but the cusp appears to have been broadly based and displaced mesially, so that it is almost directly buccal to the paraconid. A faint postprotocristid extends down the distal face of the protoconid and merges with the cristid obliqua, which is fully buccal in position. The buccal border of the tooth is convex (although this is accentuated by the minor damage to the protoconid), so there is no sign of an indentation (hypoflexid) distinguishing the trigonid from the talonid. The presence or absence, or precise position, of a hypoconulid is unclear due to slight chipping of the enamel. The lingual cant to the back of the tooth is suggestive of a lingually positioned hypoconulid, but this cannot be confirmed. If a hypoconulid was present it must have been small, because the damage is very limited and there is no evidence of such a feature extending into the talonid basin.

There is no evidence of a protocristid or postvallid, making the trigonid and talonid basins continuous with one another. There is a straight, distinct valley between the protoconid and paraconid/metaconid that extends this composite basin even further mesially, to the front of the tooth. These

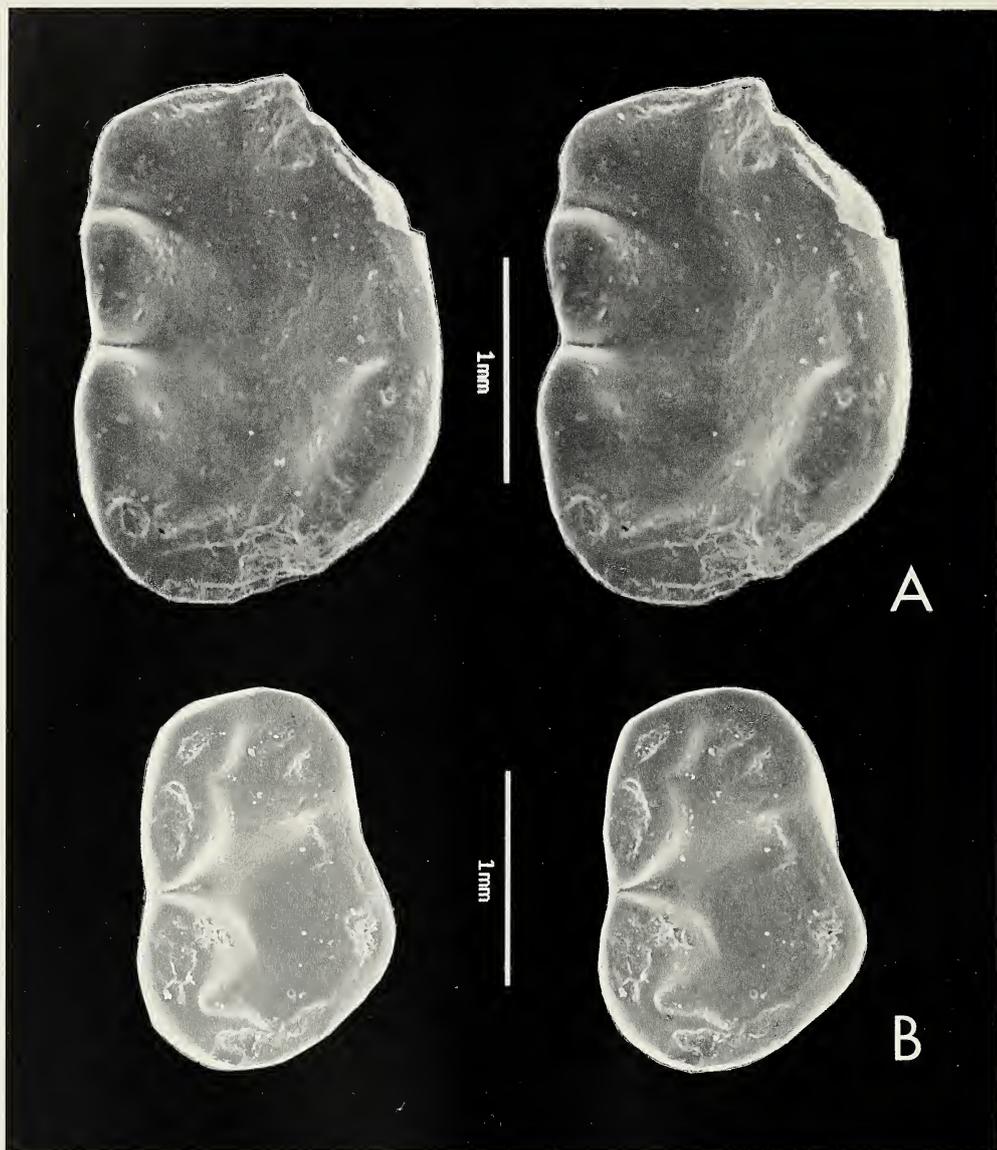


Fig. 1.—A. *Alveojunctus boweni*, new species, SDSNH 31788 (holotype), $RM_{1 \text{ or } 2}$, stereophotograph. B. *Alveojunctus minutus*, USGS 2005 (holotype), $RM_{1 \text{ or } 2}$, stereophotograph. Mesial is to the top of the figure and lingual to the left.

features make the crown of the tooth approximate a single, large, central basin surrounded on the periphery by low cusps and crests.

Measurements (mm) of the Holotype.— $M_{1 \text{ or } 2}$ maximum width = 1.60 mm, maximum length = 2.25 mm. Measured with an ocular micrometer to the nearest 0.05 mm.

Discussion.—SDSNH 31788 was tentatively assigned by Walsh (1996:85) to the ?Palaeonodonta. Its revised identification here as pertaining to a new species

of *Alveojunctus* thus eliminates any record of palaeonodonts from the Uintan of southern California.

SDSNH Loc. 3373 has yielded a diverse assemblage of small mammals of early Uintan age. It was collected by screen-washing approximately 5000 kg of bulk matrix from a 1.2 m thick, caliche nodule-bearing, olive greenish gray siltstone paleosol. Other primate taxa represented at this locality include *Omomys* sp. cf. *O. carteri*, *Washakius woodringi*, and *Uintasorex montezumicus* (see Lillegraven, 1980; Honey, 1990; Walsh, 1996). The stratigraphic and geographic position of SDSNH Loc. 3373 was shown schematically by Walsh et al. (1996: fig. 3).

The identification of SDSNH 31788 as M_1 or M_2 is complicated by uncertainty surrounding the identification of the holotype of *Alveojunctus minutus*, USGS 2005. This tooth was originally identified as an M_1 (Bown, 1982), presumably on the basis of the triangular trigonid that is relatively narrow compared to the talonid. M_2 s in plesiadapiforms tend to have trigonid and talonid regions that are more nearly equal in width. Also, in M_2 the trigonid is generally less triangular than in M_1 as a result of its mesiodistal compression, a flatter mesial border, and a lingually positioned paraconid. These are also distinctions between USGS 2005 and the new specimen. In USGS 2005 there is a shallow hypoflexid, distinguishing the trigonid from the talonid (see Fig. 1B), that is missing in SDSNH 31788 (see Fig. 1A). Also, the flatter mesial border of SDSNH 31788 and more fully lingual position of the paraconid relative to USGS 2005 are consistent with differences between tooth positions (although there are some exceptions to these generalities, as seen in the lower molars of *Purgatorius janisae* and *Palenochtha minor*). Based on this reasoning it seems probable that USGS 2005 is an M_1 and SDSNH 31788 an M_2 .

Rose and Bown (1996) suggested, however, that USGS 2005 is more likely M_2 , based on its similarity to that tooth in *Picromomys petersonorum*. That taxon has a trigonid and talonid of M_1 that are subequal in width, whereas on M_2 the trigonid is clearly narrower than the talonid. *Picromomys* also has a relatively longer trigonid on M_1 than on M_2 . In both of these features USGS 2005 is more similar to M_2 of *Picromomys* than to M_1 . The straighter mesial border and more nearly equal width of the trigonid and talonid in SDSNH 31788 may make this more plausibly an M_1 , based on the comparison with *Picromomys*. It is not clear, however, whether the unusual pattern of differences between M_1 and M_2 in *Picromomys* stems solely from the different expression of the mesiobuccal accessory cusp in this taxon. Particularly, the greater development of this cusp on M_1 , relative to M_2 , makes the mesial border of the tooth appear more squared off, and adds to the length and width of the trigonid. Since this cusp is missing in *Alveojunctus* it might be expected to show the more typical plesiadapiform pattern of differences between M_1 and M_2 . For these reasons, the attribution of the tooth is left open until further material becomes available.

This discussion may prompt the criticism that the differences between USGS 2005 and SDSNH 31788 can be attributed to tooth position alone. The pronounced size disparity between the specimens (we measured USGS 2005 as 1.80 mm long and 1.20 mm wide; SDSNH 31788 is therefore 25% longer and 33% wider than USGS 2005) argues against this. The size difference substantially exceeds that generally seen between tooth positions in plesiadapiforms—in *Picromomys petersonorum*, for example, M_1 is only 10% longer than M_2 , and M_2 is slightly wider (7%) than M_1 . This dental size disparity also translates into a significant

difference in body size. If it is assumed that both molars are M_1 , body mass estimates for *Alveojunctus minutus* range from 50–111 g (Conroy, 1987: all primate or prosimian regressions = 50 g; Gingerich et al., 1982: primate regression = 111 g), whereas the range of estimates for *Alveojunctus bowni* suggests it may have been twice the mass of *A. minutus* (Conroy, 1987: all primate regression = 124 g, prosimian regression = 114 g; Gingerich et al., 1982: primate regression = 238 g). These estimates do not differ significantly if one of the specimens is an M_2 rather than an M_1 .

Additionally, the presence of the deep valley between the protoconid and paraconid/metaconid in SDSNH 31788 (missing in USGS 2005), argues against the view that both of these teeth belong to the same species. The presence or absence of a valley between the protoconid and paraconid/metaconid is not a difference that is seen between tooth positions, and this feature is missing in all related forms. The differences between USGS 2005 and SDSNH 31788 seem to be comprehensible as a further expansion, in the latter, of the broad central basin that is characteristic of *Alveojunctus*. In *A. minutus* this feature is formed because the protocristid and postvallid are absent, allowing continuity between the trigonid and talonid basins. In *A. bowni*, in addition to these features, there is a further expansion forward created by the strong valley between the protoconid and paraconid/metaconid. The reduction in the paracristid allows this valley to extend to the front of the tooth. The mesial displacement of the protoconid in *A. bowni* relative to *A. minutus* is probably also related, since this broadens the part of the trigonid basin that is directly continuous with the talonid basin. In all, the differences between the two species can be explained as an accentuation of the basic adaptive pattern that characterizes *Alveojunctus*, in which the molars became almost flat basins surrounded by weak bulbous cusps and low crests. The geologically younger age of *A. bowni* is also consistent with this view.

Alveojunctus bowni extends both the known temporal and geographic range of the Picromomyidae. To date, the genus *Alveojunctus* is definitively known only from middle Bridgerian and early Uintan deposits. Bown (1982) suggested that FMNH PM28689 might belong to *A. minutus*. This tooth, from the Cathedral Bluff Tongue (early Bridgerian), was attributed to *Niptomomys* sp. by West and Dawson (1973). West and Dawson identified the tooth as a right M_3 , but the molar illustrated is a left M_3 . Unfortunately, the specimen could not be located for study (and may be lost). The larger size of this tooth, relative to *A. minutus*, might suggest that the specimen could belong to *A. bowni*. FMNH PM28689 is unusual in lacking a paraconid, a feature that is present in both SDSNH 31788 and USGS 2005. The paraconid is absent on M_3 of paromomyid plesiadapiforms, and it is indistinct in *Niptomomys doreenae* (see Rose et al., 1993:fig. 1). In *Picromomys* and micromomyids known from serially associated dentitions (*Tinimomys graybulliensis* [Rose et al., 1993:fig. 2] and *Micromomys fremdi* [Fox, 1984:fig. 1]), however, a paraconid is clearly demarcated on M_3 . Since we consider *Alveojunctus* to be more closely related to *Picromomys* and micromomyids than to *Niptomomys* or paromomyids, an indistinct M_3 paraconid would not be expected as a feature of the genus. These indications suggest that this tooth may be attributable to a taxon that is more closely related to *Niptomomys* (as originally indicated by West and Dawson) than to *Alveojunctus*.

Stucky (1982, 1984) referred an additional specimen to *Alveojunctus*. This isolated tooth, a right M_1 , (UCM 44681) was not available for study. Stucky (1982) notes that this tooth has more clearly delineated cusps and a higher trigonid than

Alveojunctus minutus. In light of the fact that *Alveojunctus bowni* differs from *A. minutus* in precisely the opposite ways (i.e., it has a less well defined cusps and a lower trigonid), it seems unlikely that this specimen could be referred to the new species.

Picromomys petersonorum Rose and Bown, 1996
(Fig. 2)

Discussion.—A fragmentary left dentary with a nearly complete I_1 , P_4 talonid, M_1 , and alveoli for $M_{2,3}$ (USNM 494979; Fig. 2) was collected in 1996 by M. T. Silcox from Dorsey Quarry (U.S.G.S. locality D-2035Q; 397m above the base of the Willwood Formation; see Bown et al., 1994, and Silcox and Rose, 2001) in the Bighorn Basin of northwestern Wyoming. Although the I_1 has a break between the root and the rest of the tooth, and the crown is now displaced relative to the dentary, it was found in continuity with the dentary and is clearly part of the same specimen. The morphology of the P_4 talonid and M_1 matches that of the holotype of *Picromomys petersonorum*.

The root of I_1 is enlarged, laterally compressed, and is in a nearly horizontal position in the mandible, as in the holotype (Rose and Bown, 1996). It bears a distinct crest close to the lateral margin of the dorsal surface. Near the base of the crown this dorsal crest crosses from its lateral position to the medial side of the crown, where it descends onto the medial surface and runs distally to a point approximately halfway from the base of the tooth, before fading away. Near the point of this cross-over, another crest begins at the dorso-lateral extent of the crown. The two crests present on the crown of the tooth define a surface that exists in two planes, facing dorsally and medially.

Rose and Bown (1996) noted some basic differences between the morphology of the lower central incisor preserved in the holotype of *Picromomys petersonorum* and that seen in microsyopids. Although the holotype preserves only a part of the root of I_1 , it is clear that I_1 lacks the sharp dorsal border and basal expansion characteristic of microsyopid incisors. Rose and Bown pointed out that the distinctive morphology of microsyopid incisors has resulted from a medial rotation around the long axis of the tooth, so that the homolog of the lateral border of I_1 in most plesiadapiforms forms a sharp dorsal crest in microsyopids. Rose and Bown (1996) argued that such a rotation had not occurred in I_1 of picromomyids. It remained possible, however, that when the rest of the crown became known it would be more microsyopid-like, or else represent a recognizable intermediate stage between the morphology observed in other plesiadapiforms and microsyopids.

The morphology of USNM 494979 does not support this view. The dorsal crest noted by Rose and Bown (1996) on the root is continuous with the medial crest on the crown of the I_1 in USNM 494979. In microsyopids, however, the dorsal crest is homologous with the lateral crest on the crowns of more typical plesiadapiforms (e.g., *Plesiolestes problematicus*; see Bown and Gingerich, 1973). This indicates that the I_1 morphology in *Picromomys* is not an intermediate on the path to the microsyopid condition. Furthermore, the shape of this incisor differs markedly from that observed in microsyopids in lacking a basal expansion of the crown. Also, the portion of the crown that is delimited by crests is not flat, as in microsyopids, but incorporates two distinct planes. In all, the picromomyid I_1 morphology is less consistent with a relationship to microsyopids than that ob-

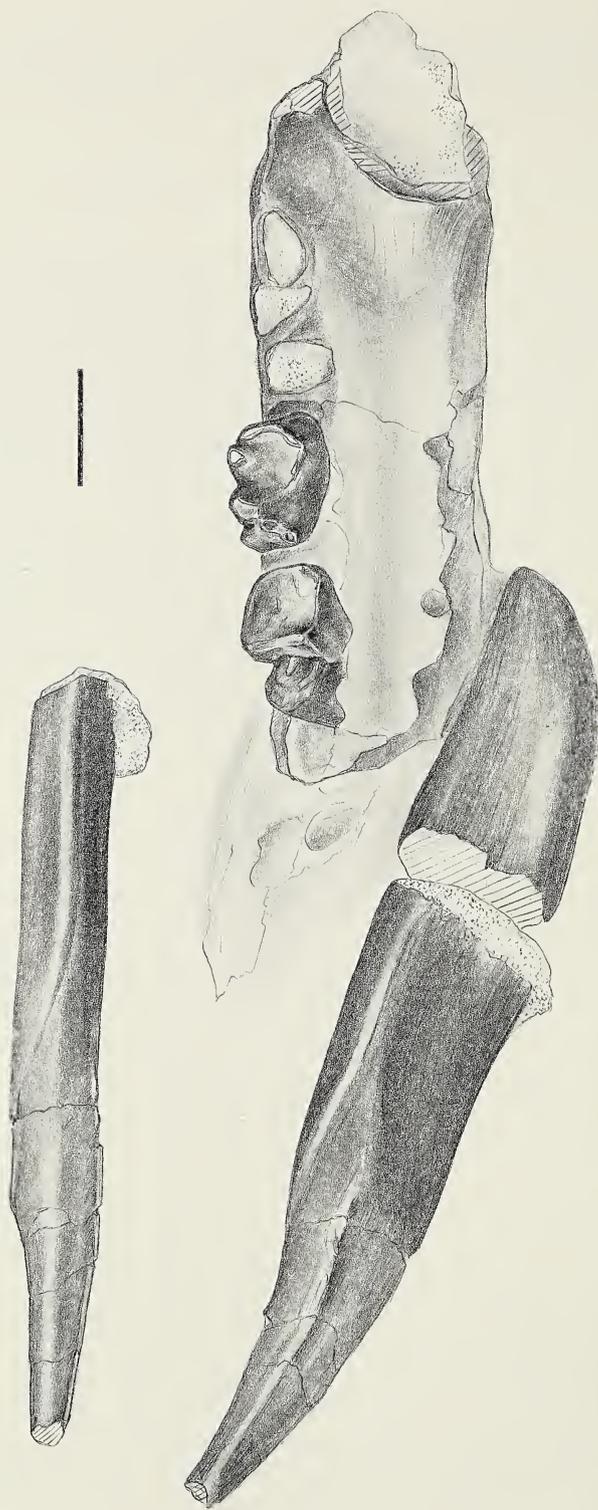


Fig. 2.—*Picromomys petersonorum*. USNM 494979. Incomplete left dentary containing I₁, talonid of P₄, M₁, and alveoli for M_{2.3} in oblique buccal view (below), with occlusal view of I₁ (above). Scale bar = 1 mm.

served in some palaechthonids. Even some primitive plesiadapoids have a more closely comparable incisor morphology (e.g., *Elphidotarsius* sp. cf. *florencae*, in which I_1 is broad at the base but not rotated medially; see Rose, 1975), in spite of the fact that plesiadapoids are not very closely related to microsomyids (Silcox, 2001).

The I_1 of *Picromomys* is similar to this tooth in a number of plesiadapiforms, including *Saxonella*, *Picrodus*, paromomyids, micromomyids, and possibly *Palenochtha minor* (see Gunnell, 1989:fig. 5), in being slender, laterally compressed, and elongate. The evidence available for *Purgatorius* is also consistent with the presence of this morphology, although the tooth itself is still unknown for this basal plesiadapiform (Silcox, 2001). The widespread distribution of this basic morphology suggests that it may be primitive for plesiadapiforms (Silcox, 2001). The lower incisor of *Picromomys* is particularly similar to that of the only micromomyid for which this tooth has been published, *Tinimomys graybulliensis* (i.e., USNM 425583, Beard and Houde, 1989). As in *Picromomys*, I_1 in *Tinimomys* shows a similar reorientation of a dorsolateral crest in the root region to a medial position on the crown. This change in direction in the dorsal crest is not present in any of the other plesiadapiforms examined. When added as a character to the dataset published by Rose and Bown (1996) (see Appendix), an exhaustive search using PAUP* 4.0 β 6 (Swofford, 2001) resulted in a single most parsimonious tree corresponding to their Tree B (length = 73 steps, CI = .49, RI = .537, statistics from PAUP*; see Rose and Bown, 1996:fig. 5). This tree supports a clade including *Picromomys*, *Alveojunctus*, and *Tinimomys*, to the exclusion of *Niptomomys*, and portrays picromomyids as most closely related to micromomyids.

Measurements (mm) of USNM 494979.— P_4 width = 0.80 mm; M_1 trigonid width = 0.70 mm, M_1 talonid width = 0.80 mm, M_1 length = 1.20 mm. Measured with an ocular micrometer to the nearest 0.05 mm.

CONCLUSIONS

This paper documents the eighth and ninth confidently attributed specimens of the Picromomyidae. The type specimen of the new species *Alveojunctus bowni* from the early Uintan of California extends the temporal and geographic range of the family. This specimen demonstrates an even more extreme version of the basic pattern of picromomyid dental structure, leading to an extraordinarily flat and simplified lower molar morphology. This is consistent with an increasingly specialized diet. The second recognized specimen of *Picromomys petersonorum* provides new information on the incisor morphology and suggests a stronger tie to the Micromomyidae than to the Microsomyidae. This may imply that Micromomyidae is a paraphyletic group (Hooker et al., 1999). Specifically, picromomyids and *Tinimomys* may be sister taxa to the exclusion of *Micromomys* (as indicated in Tree B of Rose and Bown, 1996:fig. 5). In light of this, it may eventually be appropriate to make Picromomyidae a subfamily of the Micromomyidae. Making definitive conclusions about the relationships of micromomyids and picromomyids is hampered, however, by the very limited information available for most species of *Micromomys* (Beard and Houde, 1989), and the lack of specimens from the upper dentition of Picromomyidae. Consequently, we prefer to maintain Picromomyidae and Micromomyidae as distinct families, pending further discoveries or additional analyses.

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APPENDIX

New character added to cladistic analysis from Rose and Bown, 1996. 0 = lateral crest (or its homologue) in the root region of I₁ runs straight to the tip of the tooth, without crossing medially; 1 = A dorsolateral crest present in the root region of I₁ becomes re-oriented to lie on the medial side of the crown.

<i>Purgatorius</i>	?
<i>Palaechthon</i>	?
<i>Palenochtha</i>	?
<i>Picromomys</i>	1
<i>Alveojunctus</i>	?
<i>Paromomys</i>	?
<i>Ignacius</i>	0
<i>Navajovius</i>	0
<i>Micromomys</i>	?
<i>Tinimomys</i>	1
<i>Niptomomys</i>	0
<i>Picrodus</i>	0

REVIEW OF THE NEOTROPICAL GENUS *BREDINIA* (TRICHOPTERA:
HYDROPTILIDAE: STACTOBIINI)STEVEN C. HARRIS¹

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ABSTRACT

The Neotropical genus *Bredinia* is reviewed, with descriptions and figures provided for the 16 species presently known, including 13 new species: *B. guanacasteca* n.sp., *B. emarginata* n.sp., and *B. selva* n.sp. from Costa Rica; *B. davenporti* n.sp. and *B. pilcopata* n.sp. from Peru; *B. manabiensis* n.sp. and *B. spangleri* n.sp. from Ecuador; *B. alza* n.sp. from Paraguay; *B. mexicana* n.sp. from Mexico; *B. sucrensis* n.sp. and *B. zulia* n.sp. from Venezuela; *B. espinosa* n.sp. from Brazil, Ecuador, and Venezuela, and *B. venezuelensis* n.sp. from Venezuela, Peru, and Ecuador. New records and illustrations are provided for *B. costaricensis* (Flint), *B. dominicensis* Flint, and *B. appendiculata* Flint and Sykora. A key is provided to separate the males and the associated females.

KEY WORDS: Trichoptera, Hydroptilidae, Neotropics, *Bredinia*, new species, key, systematics

INTRODUCTION

This paper on the genus *Bredinia* represents an addition to a series initiated to describe the microcaddisflies of Costa Rica. However, to place the systematics of the group under review in context, we have expanded the scope of this study to encompass the entire Neotropical region. The genus *Bredinia* was previously thought to be small in terms of species and restricted in distribution (Flint et al., 1999a), but these ideas are revised with this paper. Herein we describe 13 new species from the Neotropical region and provide illustrations and redescriptions of the three species previously described, and a key to the species of males and known females.

The genus *Bredinia* was erected by Flint (1968) for *B. dominicensis*, which was originally collected near the mouth of the Hodges River in Dominica. A second species, *B. appendiculata* Flint and Sykora from Grenada, was added in 1993. More recently, a third species, *B. costaricensis* (Flint), was transferred from *Neotrichia* into *Bredinia* (Flint et al., 1999b). Material examined in this work comes largely from collections at the University of Minnesota and the National Museum of Natural History.

Bredinia is assigned to the tribe Stactobiini, which as currently defined contains ten genera, most of which occur in the Old World. In the New World Stactobiini, there are three genera presently known: *Stactobiella* Martynov in the Nearctic

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region, and *Bredinia* and *Flintiella* Angrisano in the Neotropics (Flint et al., 1999a). Two additional genera from the Neotropics are described and a key provided for the New World Stactobiini in Harris et al. (In Press).

Types of species described in this paper, as indicated by acronyms in the text, are deposited in the collections of the National Museum of Natural History, Smithsonian Institution, Washington (NMNH), University of Minnesota Insect Collection, St. Paul (UMSP), Cornell University, Ithaca (CU), Universidad Nacional Autonoma de Mexico, Mexico City (UNAM), Florida State Collection of Arthropods, Gainesville (FSCA), Academy of Natural Sciences, Philadelphia (ANSP), Carnegie Museum of Natural History, Pittsburgh (CMNH), and Instituto Nacional de Biodiversidad, Heredia, Costa Rica (INBIO). Terminology follows that of Marshall (1979). Length is measured from the tip of the head to the end of the wings and is given as a range within a series of specimens.

SYSTEMATIC ENTOMOLOGY

Bredinia Flint (Fig. 1)

Bredinia Flint, 1968:50. Type species. *Bredinia dominicensis* Flint, 1968, original designation.

Diagnosis.—Adults of *Bredinia* are minute (1–2 mm in length), and typically gray in color, with silvery bands of hairs on the forewings. There are 3 ocelli on the head (Fig. 1A) with simple antenna having 17–19 segments. The mesoscutellum is divided by a transverse suture; the metascutellum is narrow and rectangular, and nearly as wide as scutum. Legs have a tibial spur formula of 0, 2, 4 (Fig. 1B). Wings are narrow, with reduced venation (Fig. 1C). The tibial spur formula and the presence of ocelli serve to separate *Bredinia* from other New World genera. Unique to males in this genus is the presence of an elongate, thickened seta from the posterior of the inferior appendages and elongate apodemes from the anterior of abdominal segment IX. Females of most of the Neotropical stactobiines are unknown, so it is premature at this point to speculate on distinguishing characters. Larvae have been described by Angrisano (In Press), but as with female stactobiines, too few species are known in the larval stage to permit diagnoses.

Male.—Abdominal segment VII annular, without a ventromesal process. Segment VIII annular and complete dorsally, often with anterolateral margins developed as thin apodemes. Segment IX usually reduced ventrally with anterolateral margins developed as apodemes which vary in length. Inferior appendages each with heavy, elongate seta originating on posteroventral margin. Subgenital plate shelflike. Phallus tubular with apex distinctive for the species.

Female.—Abdominal segment VII annular. Segment VIII rectangular, ring of setae on posterior margin, pair of mesal and lateral apodemes. Segment IX narrow and rectangular, pair of lateral apodemes connecting anteriorly with apodemes of VIII. Segment X short and conical, bearing pair of apical papillae. Bursa copulatrix round, rectangular or triangular in ventral aspect, with or without posterior extensions; anteriorly with pair of elongate lateral processes attached to and paralleling narrow mesal process.

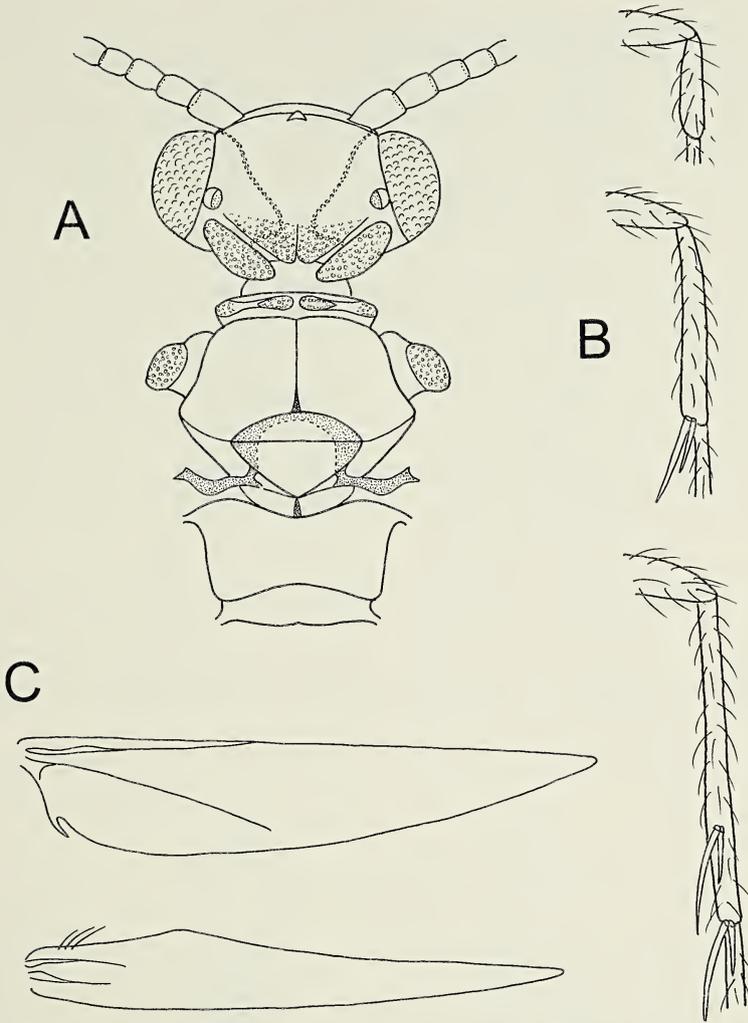


Fig. 1.—*Bredinia costaricensis* (Flint), adult: A. Head and thorax, dorsal. B. Fore, mid and hindleg. C. Fore and hindwing.

Bredinia dominicensis Flint
(Figs. 2, 3)

Bredinia dominicensis Flint, 1968:51.

Diagnosis.—*Bredinia dominicensis*, along with *B. selva* n. sp., and *B. guana-casteca* n. sp., is recognized by the elongate rods extending from the margins of segment IX. *Bredinia dominicensis* is most similar to *B. selva*, but is separated by the acute ventral margin of the inferior appendages in lateral aspect, and the structure of the phallus apex, which has contiguous inner processes. We have records of *B. dominicensis* from Costa Rica, Dominica, Ecuador, Panama, and Trinidad.

Male.—Length 1.5–1.6 mm. Antenna with 18 segments. Silvery gray in color,

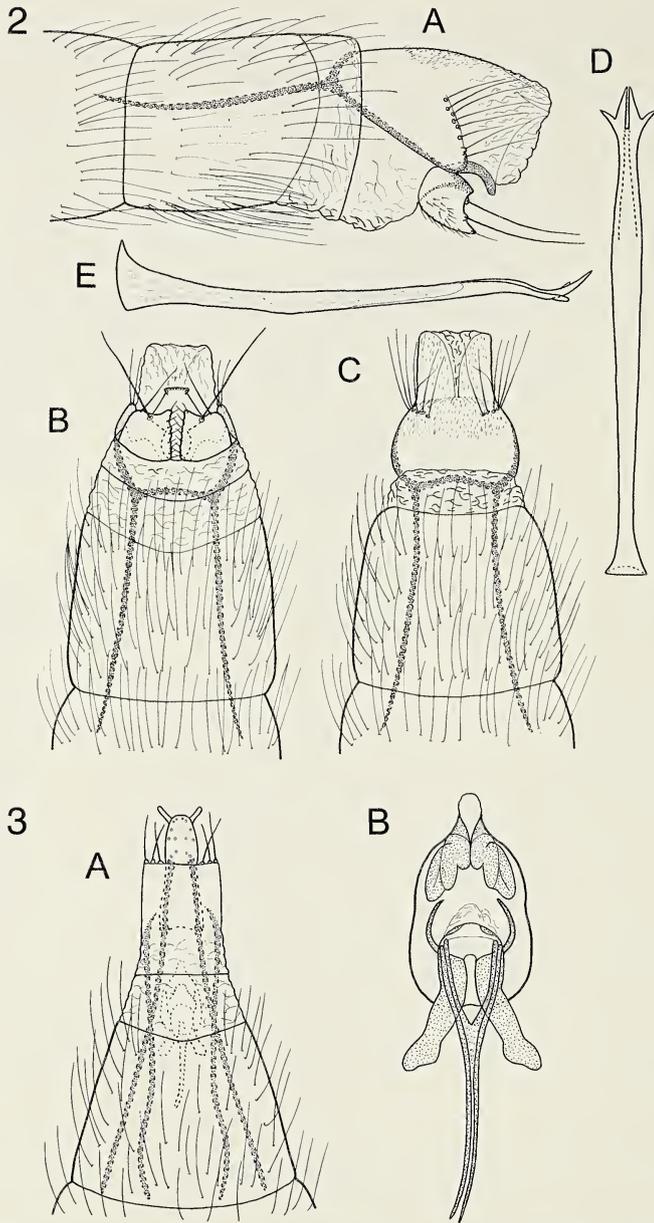


Fig. 2.—*Bredinia dominicensis* Flint, male genitalia, redrawn from paratype: A. Lateral. B. Ventral. C. Dorsal. D. Phallus, dorsal. E. Phallus, lateral.

Fig. 3.—*Bredinia dominicensis* Flint, female genitalia. A. Terminal abdominal segments, ventral. B. Bursa copulatrix, ventral.

forewing with bands of white hair apically and basally. Genitalia as in Fig. 2. Segment VIII annular. Segment IX reduced to narrow bridge ventrally; dorsally round and fused with segment X, anterior margins extended anteriorly as elongate rods which pass through segment VIII. Segment X truncate and membranous. Inferior appendages in lateral view each narrowing to acute apex posteroventrally; in ventral view square. Subgenital plate narrow, shelflike in lateral view; triangular in ventral view. Phallus tubular, apex flattened and tridentate, ejaculatory duct short and triangular.

Female.—Length 1.7 mm. Antenna with 18 segments. Color and features of the head, thorax and wings as in male. Genitalia as in Fig. 3. Segment VII annular. Segment VIII rectangular, ring of setae on posterior margin, pair of mesal apodemes extending into segment VII, second pair of elongate lateral apodemes originating at anterolateral margins and extending into segment VII. Segment IX narrow and rectangular, with pair of lateral apodemes connected anteriorly with mesal apodemes of VIII. Segment X short and rounded apically, bearing pair of apical papillae. Bursa copulatrix rectangular with short posterior extension; anterior with wide lateral processes turned outward at apices, mesal process divided apically.

Material Examined.—**COSTA RICA. Puntarenas:** Quebrada Potrero near Potrero Grande, 5 July 1992, T. Shepard, 1 ♂ (CMNH).

DOMINICA. Hodges River, at mouth, swamp forest, 27 February 1965, W. Wirth, 2 ♂, 2 ♀ paratypes (NMNH).

ECUADOR. Esmeraldas: La Union, 3 February 1979, J. Anderson, 16 ♂ (4♂NMNH, 4♂UMSP, 4♂CMNH). **Pichincha:** Santo Domingo de los Colorados (29 km W), 6 May 1975, P. Spangler, 1 ♂ (NMNH).

PANAMA. Darien: Río Tuira at Río Pucura, 16–17 February 1983, J. Louton, 1 ♂ (NMNH).

TRINIDAD. Tacarigua River, Caura Recreation Area, 10°43' N, 61°17' W, 22 June 1993, O. Flint, N. Adams, 1 ♂, 4 ♀ (NMNH).

Bredinia guanacasteca, new species

(Fig. 4)

Diagnosis.—*Bredinia guanacasteca* is most similar to *B. dominicensis* and *B. selva* n.sp., each having elongate anterior rods from segment IX. The new species is distinguished by the truncate apical margin of the inferior appendages, seen in lateral aspect, and the structure of phallus apex, which terminates in a pair of elongate inner processes. *Bredinia guanacasteca* is known only from the type locality in Costa Rica.

Male.—Length 1.8 mm. Antenna with 18 segments. Brown in alcohol. Genitalia as in Fig. 4. Segment VIII annular, venter emarginate posteriorly. Segment IX reduced to narrow bridge ventrally; dorsally round; anterior margins extended anteriorly as elongate rods passing through segment VIII. Segment X elongate, shelflike in lateral view; dorsum rectangular, slightly emarginate on posterior margin. Inferior appendages nearly square in lateral view, sinuate on posterior margin; square in ventral view, diverging on mesal margin. Subgenital plate narrow, shelflike. Phallus tubular, apex with pair of narrow, elongate inner processes, lateral processes short and contiguous, ejaculatory duct short and wishbone-shaped.

Female.—Unknown.

Type Material.—Holotype ♂. **COSTA RICA. Guanacaste:** Río Tempisque, ca 3 km S route 1, 10.790°N, 85.552°W, el. 75 m, 6 March 1986, Holzenthal and Fasth (NMNH).

Etymology.—Named for the Costa Rican province of Guanacaste.

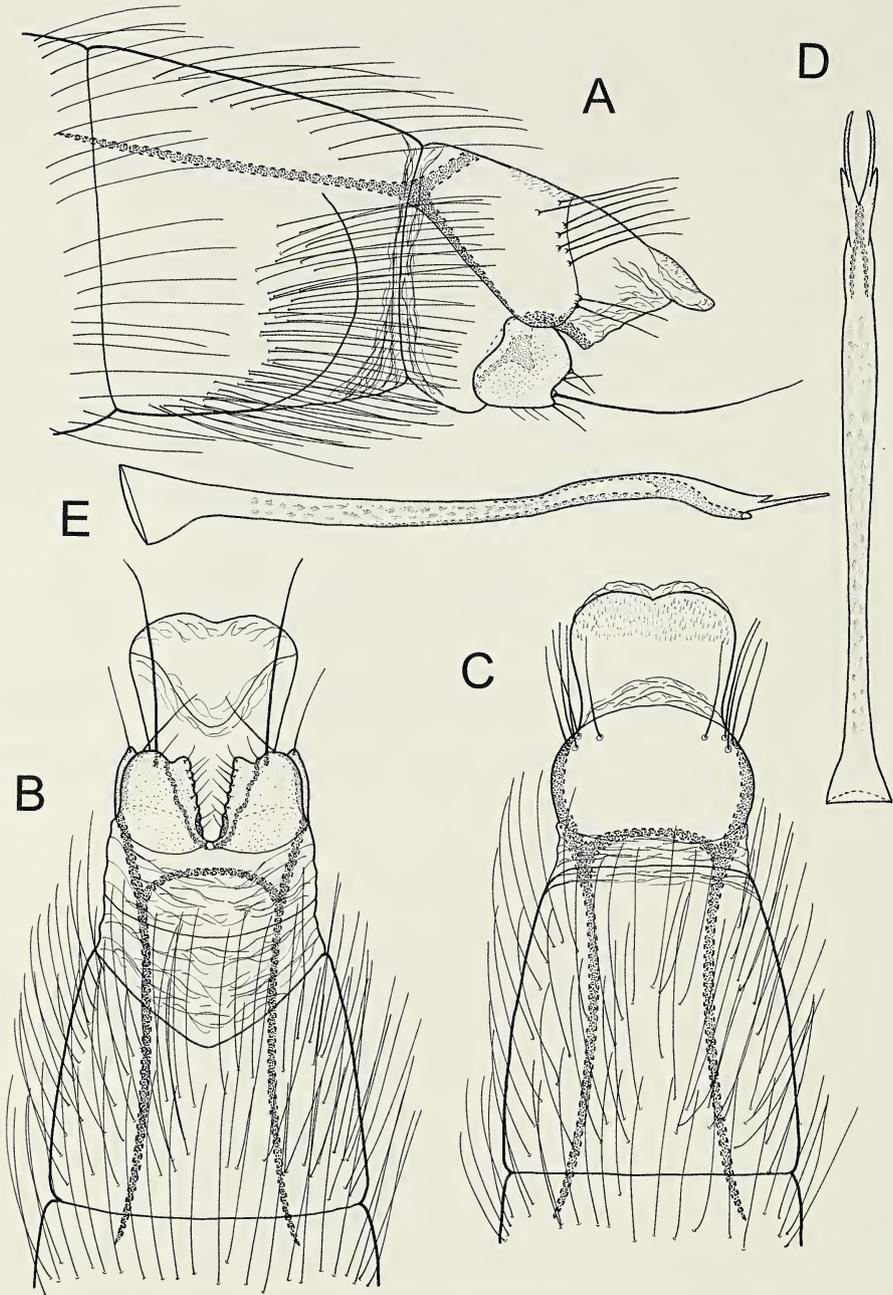


Fig. 4.—*Bredinia guanacasteca* new species, male genitalia: A. Lateral. B. Ventral. C. Dorsal. D. Phallus, dorsal. E. Phallus, lateral.

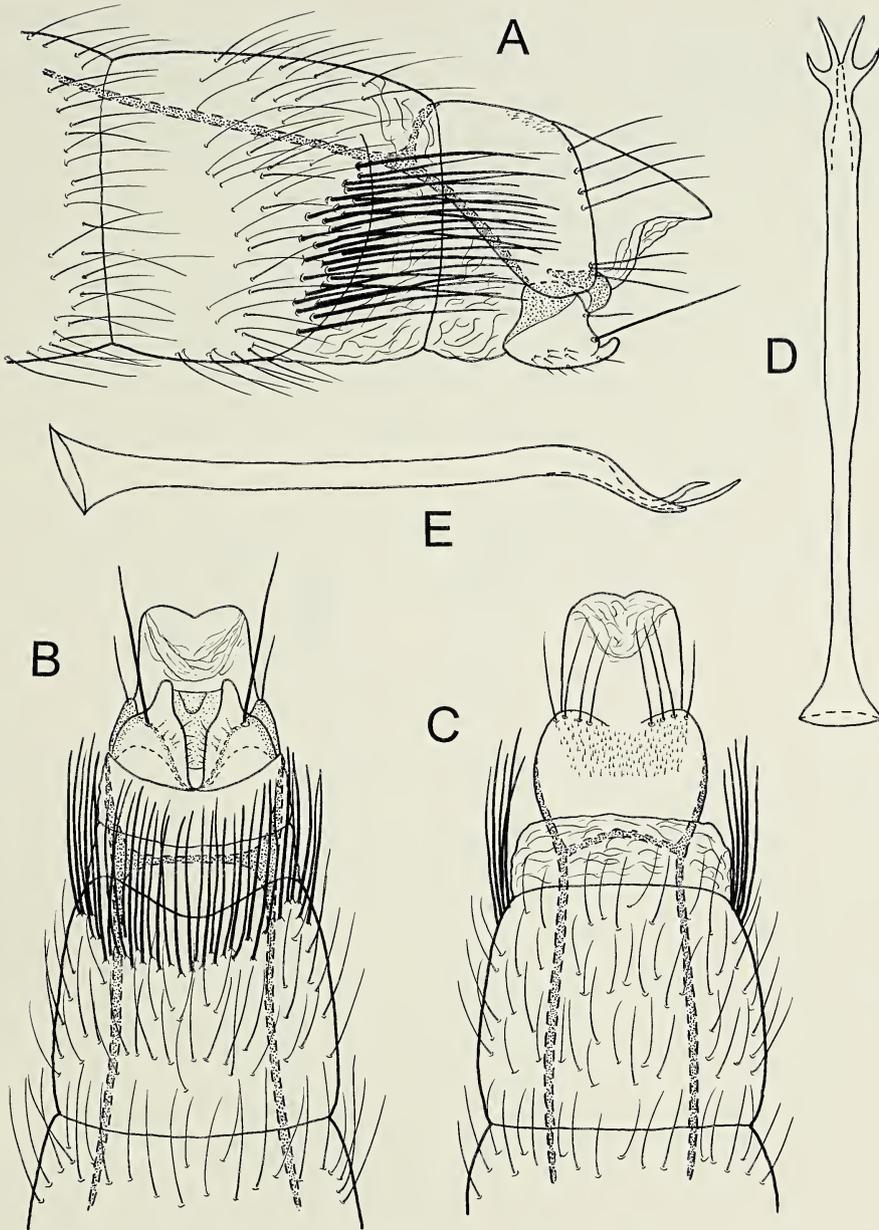


Fig. 5.—*Bredinia selva* new species, male genitalia: A. Lateral. B. Ventral. C. Dorsal. D. Phallus, dorsal. E. Phallus, lateral.

Bredinia selva, new species
(Fig. 5)

Diagnosis.—*Bredinia selva* is separated from the similar *B. dominicensis* by the shape of the inferior appendages and phallus apex. The inferior appendage of *B. selva* ends in a rounded upturned projection from the ventrolateral margin,

whereas in *B. dominicensis* the ventrolateral margin is acute. The apex of the phallus of both species is similar, but in *B. selva* the inner processes are strongly divergent. *Bredinia selva* is known only from the type locality in Costa Rica.

Male.—Length 1.7 mm. Antenna with 18 segments. Brown in alcohol. Genitalia as in Fig. 5. Segment VIII bearing heavy setae ventrolaterally; venter slightly emarginate posteriorly. Segment IX reduced to narrow bridge ventrally, dorsally rounded and fused with segment X; anterior margins extended anteriorly as elongate rods passing through segment VIII. Segment X shelflike, narrowing distally; in dorsal view rectangular, slightly emarginate posteriorly. Inferior appendages in lateral view each narrowing posteroventrally to rounded, upturned knob; in ventral view triangular in shape with thumb-like process posteriorly, diverging along mesal margin. Subgenital plate in lateral view rounded posteriorly, with downturned distal hook; in ventral view a rectangular plate. Phallus tubular, apex with bifid lateral processes, inner processes strongly diverging, outer processes curved and nearly as long as inner processes; ejaculatory duct narrowly rectangular.

Female.—Unknown.

Type Material.—Holotype ♂. **COSTA RICA**. **Heredia**: Estación Biológica La Selva, 28 April 1989, Agriculture Canada (NMNH). Paratype: **COSTA RICA**. Same locality as holotype, but 21–24 August 1999, D. and M. Davis, 1 ♂ (NMNH).

Etymology.—Named for the type locality, La Selva Biological Station of the Organization for Tropical Studies.

Bredinia espinosa, new species

(Figs. 6, 7)

Diagnosis.—The prominent, spinelike setae from the sides of segment VIII are distinctive and unique for this species. *Bredinia espinosa* is known from Brazil, Ecuador, and Venezuela.

Male.—Length 1.4–1.8 mm. Antenna with 18 segments. Brown in alcohol. Genitalia as in Fig. 6. Segment VIII bearing thickened, spinelike setae laterally; venter emarginate on posterior margin, anterior margins produced into lateral rods extending midway into segment VII. Segment IX reduced to narrow bridge ventrally; dorsally rectangular, rounded apically and emarginate laterally; anterior margins with short lateral rods. Segment X shelflike laterally; rounded lobe in dorsal and ventral views. Inferior appendages round in lateral view; in ventral view spatulate, diverging on mesal margin, emarginate on lateral margins. Subgenital plate in lateral view curving downward and narrowing posteriorly; in ventral view narrowing to mesal beak. Phallus tubular, apex flattened and widened, large lateral flaps with apex of ejaculatory duct mesal and prominent.

Female.—Length 1.8–2.0 mm. Antenna with 18 segments. Color and features of head, thorax and wings as in male. Genitalia as in Fig. 7. Segment VII annular. Segment VIII elongate, ring of setae on posterior margin, pair of elongate mesal apodemes extending through segment VII, second pair of elongate apodemes originating at anterolateral margins and extending into segment VII. Segment IX short, emarginate on posterior margin; pair of lateral apodemes which connect anteriorly with mesal apodemes of VIII. Segment X short and conical, bearing pair of apical papillae. Bursa copulatrix triangular, narrowing posteriorly, pair of sclerotized internal plates posteriorly; lateral anterior processes narrow, sinuate, and membranous apically, inner process originating as oval plate, tapering anteriorly.

Type Material.—Holotype ♂. **ECUADOR**. **Los Ríos**: Quevedo (56 km N), Río Palenque Biological

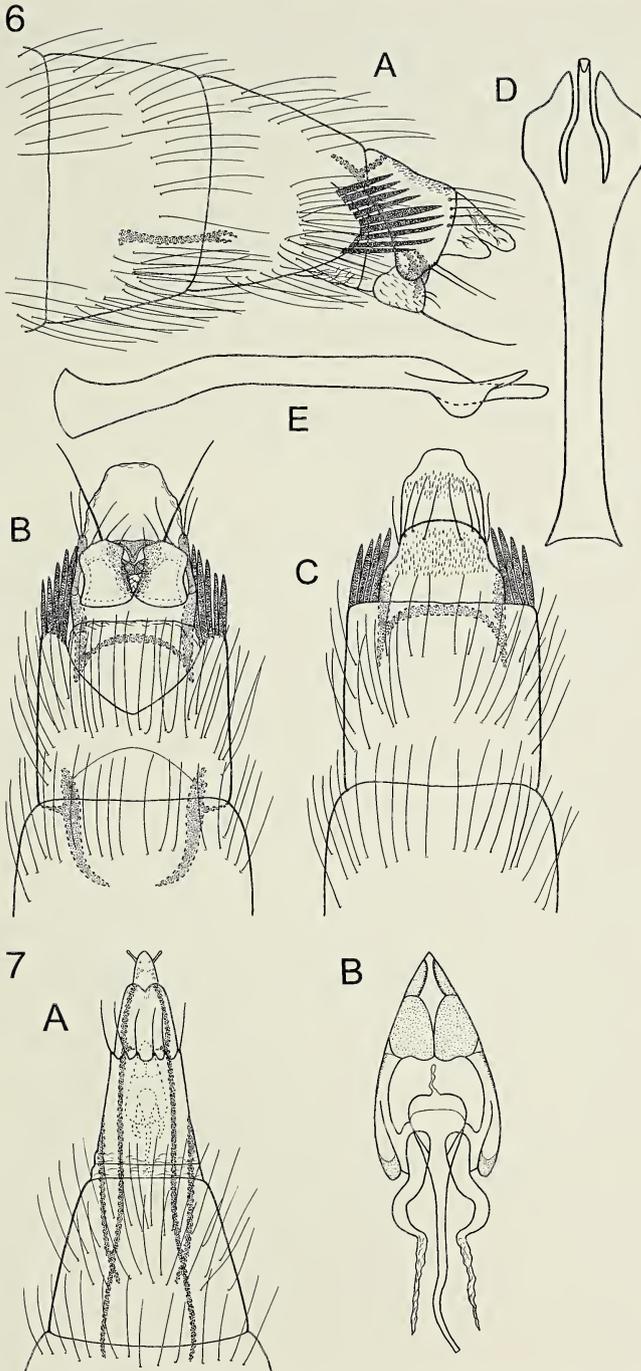


Fig. 6.—*Bredinia espinosa* new species, male genitalia: A. Lateral. B. Ventral. C. Dorsal. D. Phallus, dorsal. E. Phallus, lateral.

Fig. 7.—*Bredinia espinosa* new species, female genitalia: A. Terminal abdominal segments, ventral. B. Bursa copulatrix, ventral.

Station, blacklight at riverbed, el. 250 m, 28–29 July 1976, J. Cohen (NMNH). Paratypes: **ECUADOR**. Same data as holotype, 13 ♂, 1 ♀ (8♂, 1♀NMNH, 5♂CMNH). **Pichincha**: Santo Domingo, (47 km S), 29 July 1976, J. Cohen, 2 ♂, 2 ♀ (UMSP). **Cotopaxi**: Quevedo (36 km NE), el. 1100 m, 21 July 1976, J. Cohen, 8 ♂, 12 ♀ (4♂, 8♀NMNH, 4♂, 4♀CMNH). **Manabi**: Santo Domingo (29 km SW), Rancho Ronald, 6 September 1978, J. Anderson, 4 ♂ (NMNH), same locality, but 20 July 1978, J. Anderson, 1 ♀ (NMNH). **Guayas**: Daule, 23 December 1977, J. Anderson, 9 ♂ (5♂NMNH, 4♂UMSP).

VENEZUELA. Amazonas: San Carlos de Río Negro, 1°56' N, 67°03' W, 13–17 December 1984, R. Brown, 1 ♂, 1 ♀ (NMNH), Cerra de la Neblina, basecamp, el. 140 m, 0°50' N, 66°10' W, 10 February 1985, blacklight in rainforest clearing near Río Baria, W. Steiner, 1 ♂ (NMNH).

BRAZIL. Mato Grosso: bridge on Río Arica, on Cuiaba to Rondonopolis road near km 391 marker, 22 April 1981, D. Wojcik, 1♂ (NMNH). **Rondonia**: creek 8 km S Cacaulandia, 21 November 1991, D. Petr, 1 ♂, 1 ♀ (NMNH).

Etymology.—Derived from the Spanish, “*espina*—bearing spines,” referring to the lateral setae of abdominal segment VIII.

Bredinia appendiculata Flint and Sykora
(Figs. 8, 9)

Bredinia appendiculata Flint and Sykora, 1993:56.

Diagnosis.—*Bredinia appendiculata* is most similar to *B. davenporti* n.sp. Unique to both are the sclerotized dorsal margins of the inferior appendages, which form an acute process extending posteriad, and both have the apex of the subgenital plate downturned. *Bredinia appendiculata* is separated from *B. davenporti* on the basis of having the dorsal process of the inferior appendage elongate, and the more hooklike subgenital plate. Originally described from Grenada, we have also seen specimens of this species from Peru and Venezuela.

Male.—Length 1.5–1.7 mm. Antenna with 18 segments. Brown in alcohol. Genitalia as in Fig. 8. Segment VIII annular; venter deeply emarginate posteriorly, anterior margins produced into short lateral rods. Segment IX reduced to narrow bridge ventrally; dorsally truncate and fused with X; anterior margins with short lateral rods. Segment X shelflike in lateral view; dorsum truncate, with mesal incision posteriorly. Inferior appendages in lateral aspect each with ventral margin crenate, dorsal margin modified into sicklelike process which narrows posteriorly and curves ventrad; in ventral view acute posterior process curving mesad, posteriorly strongly diverging mesally. Subgenital plate in lateral view narrowed posteroventrally into hooklike process. Phallus tubular, apex divided into pair of narrow lobes, with acute apices and inner margins which vary from being crenate to spinose; ejaculatory duct short and triangular.

Female.—Length 1.5–1.8 mm. Antenna with 18 segments. Color and features of the head, thorax and wings as in male. Genitalia as in Fig. 9. Segment VII annular. Segment VIII square, ring of setae on posterior margin, pair of elongate mesal apodemes extending into segment VI, second pair of elongate apodemes originating at anterolateral margins and extending into segment VI. Segment IX short; pair of lateral apodemes connecting anteriorly with mesal apodemes of VIII. Segment X short and conical, bearing pair of apical papillae. Bursa copulatrix triangular, narrowing posteriorly, pair of membranous lobes posteriorly, oval plate anteriorly to which pair of flipperlike processes attach; mesal process elongate and divided apically.

Material Examined.—Holotype ♂, **GRENADA. Parish St. Andrews**: Balthazar Estate, 1 June 1990, J. Frank, A. Thomas (FSCA).

PERU. Madre de Dios: Manu, Pakitza, 12° 7'S, 70° 58'W, el. 250 m., trail 2, first stream, malaise trap, day collection, 14–23 September 1988, O. Flint, N. Adams, 6 ♂, 3 ♀ (4♂, 2♀NMNH, 2♂,

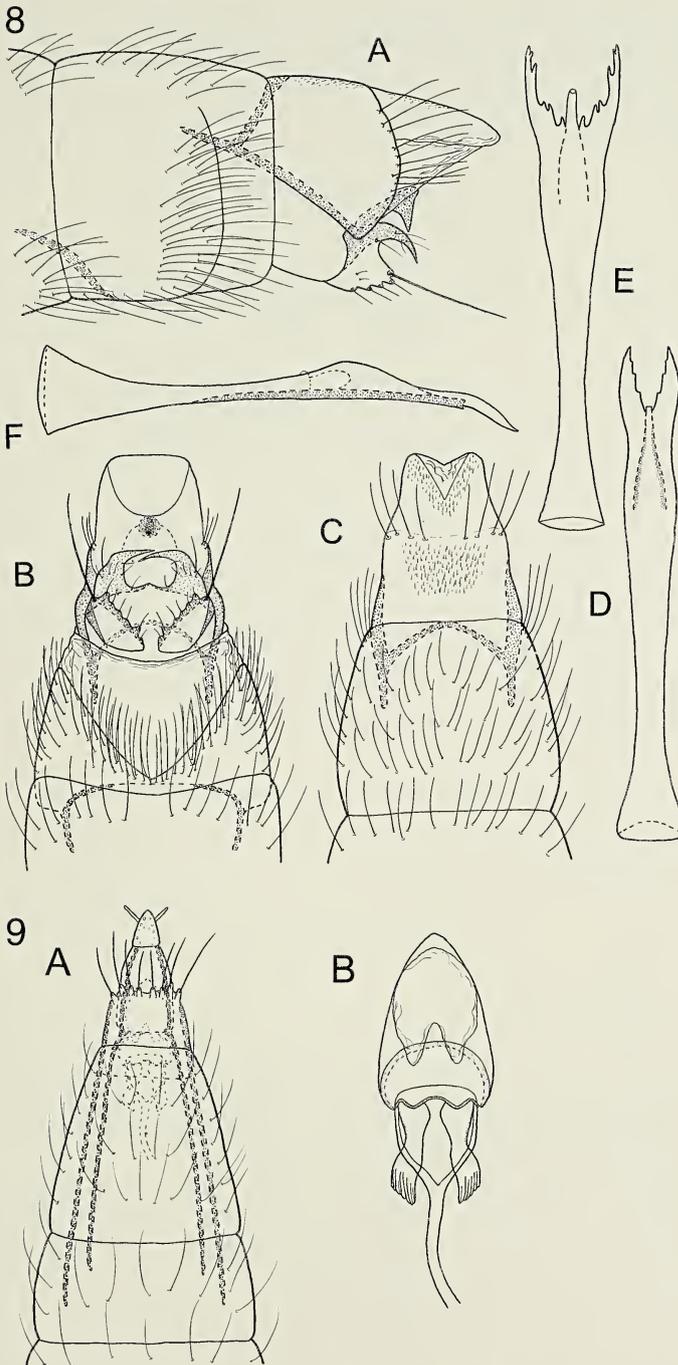


Fig. 8.—*Bredinia appendiculata* Flint and Sykora, male genitalia, redrawn from holotype: A. Lateral. B. Ventral. C. Dorsal. D. Phallus, dorsal. E. Phallus, dorsal (specimen from Peru). F. Phallus, lateral.

Fig. 9.—*Bredinia appendiculata* Flint and Sykora, female genitalia: A. Terminal abdominal segments, ventral. B. Bursa copulatrix, ventral.

1 ♀ CMNH), same locality, but night collection, 2 ♂, 1 ♀ (NMNH), Hostel Erica, near Salvación, 12° 53'S, 71° 14'W, 3 and 5 September 1989, J. Collins, 1 ♀ (NMNH).

VENEZUELA. **Sucre:** Río Cocollar, 1.5 km SE Las Piedras de Cocollar, 10° 09.671'N, 63° 47.605'W, el. 810 m., 7–8 April 1995, R. Holzenthal, O. Flint, 2 ♂, 5 ♀ (UMSP). **Zulia:** Caño Carichuano, 3.4 km SE Carbones del Guasare, 11.002°N, 72.285°W, el 70 m, 12–13 January 1994, Holzenthal, Cressa, Rincón, 2 ♂ (UMSP).

Bredinia davenporti, new species

(Fig. 10)

Diagnosis.—This new species is most similar to *B. appendiculata*, but it differs in having the dorsal process from the inferior appendage shorter, and the ventral process of the subgenital plate smaller and less acute. *Bredinia davenporti* is known only from Peru.

Male.—Length 1.5 mm. Antenna with 18 segments. Brown in alcohol. Genitalia as in Fig. 10. Segment VIII annular; anterior margins produced into very short lateral rods. Segment IX reduced to narrow bridge ventrally; dorsally truncate and fused with X; anterior margins with short lateral rods. Segment X shelflike in lateral view; dorsum truncate, small mesal incision posteriorly. Inferior appendages in lateral aspect each with ventral margin elongate, dorsal margin modified into spinelike process shorter than ventral portion of appendage; in ventral view square, with lateral margin extending posteriorly as fingerlike lobes with elongate posterolateral seta, dorsal process protruding mesally. Subgenital plate in lateral view curving downward posteriorly forming small, acute process. Phallus tubular, apex divided into pair of narrow lobes, with acute apices and crenate outer margins; ejaculatory duct elongate and triangular.

Female.—Unknown.

Type Material.—Holotype ♂. **PERU. Loreto:** Río Sucusari at Explornapo Camp, 3 January 1997, L. Davenport (NMNH).

Etymology.—Named for Dr. Larry Davenport, longtime friend and colleague of the senior author, who collected the type specimen.

Bredinia costaricensis (Flint)

(Figs. 11, 12)

Neotrichia costaricensis Flint, 1967:13.

Bredinia costaricensis (Flint), Flint et al., 1999b:76.

Diagnosis.—This species and *B. venezuelensis* n.sp. are similar in having elaborate branching at the phallus apex. Unlike *B. venezuelensis*, the branches of the phallic apex in *B. costaricensis* are serrate. *Bredinia costaricensis* is commonly collected in Costa Rica and neighboring Panama.

Male.—Length 1.6–2.0 mm. Antenna with 19 segments. Brown in alcohol. Genitalia as in Fig. 11. Segment VIII annular; venter deeply emarginate posteriorly, anteriorly with margins extending into segment VII as short rods. Segment IX reduced to narrow bridge ventrally; dorsally rectangular with posterior margin rounded; anterior margins produced as short, lateral rods. Segment X shelflike in lateral view; dorsum truncate posteriorly. Inferior appendages boot-shaped in lateral view; rectangular in ventral aspect, diverging on mesal margin. Subgenital plate shelflike in lateral view; in ventral view rectangular with mesal hump. Phallus tubular, apex with multibranching lateral processes, anterior branches toothlike, posterior processes elongate and serrate.

Female.—Length 1.8 mm. Antenna with 18 segments. Color and features of

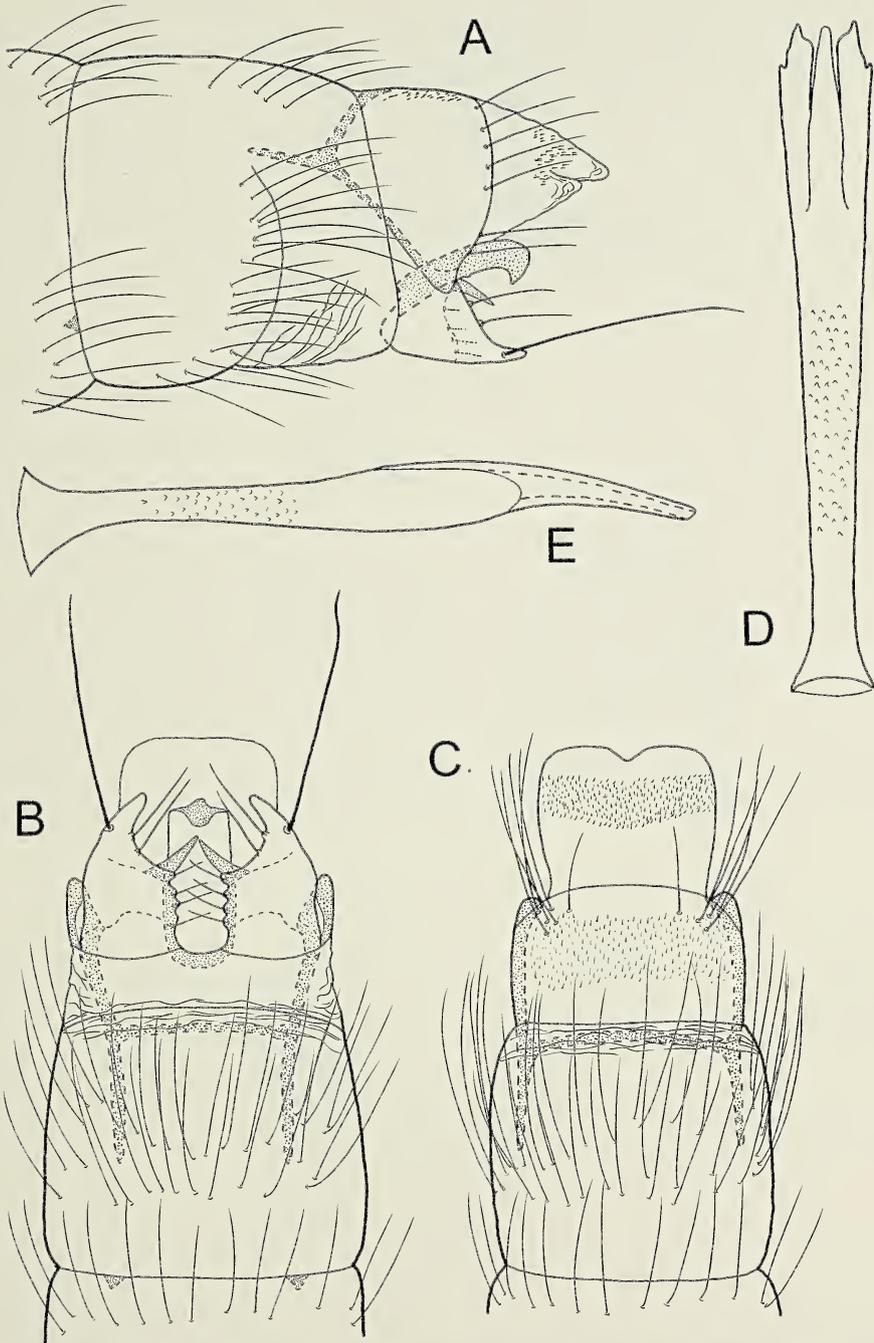


Fig. 10.—*Bredinia davenporti* new species, male genitalia: A. Lateral. B. Ventral. C. Dorsal. D. Phallus, dorsal. E. Phallus, lateral.

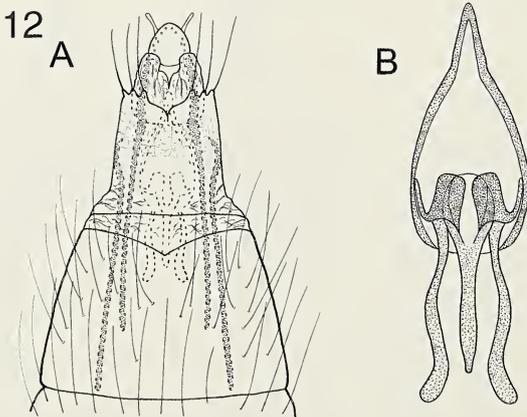
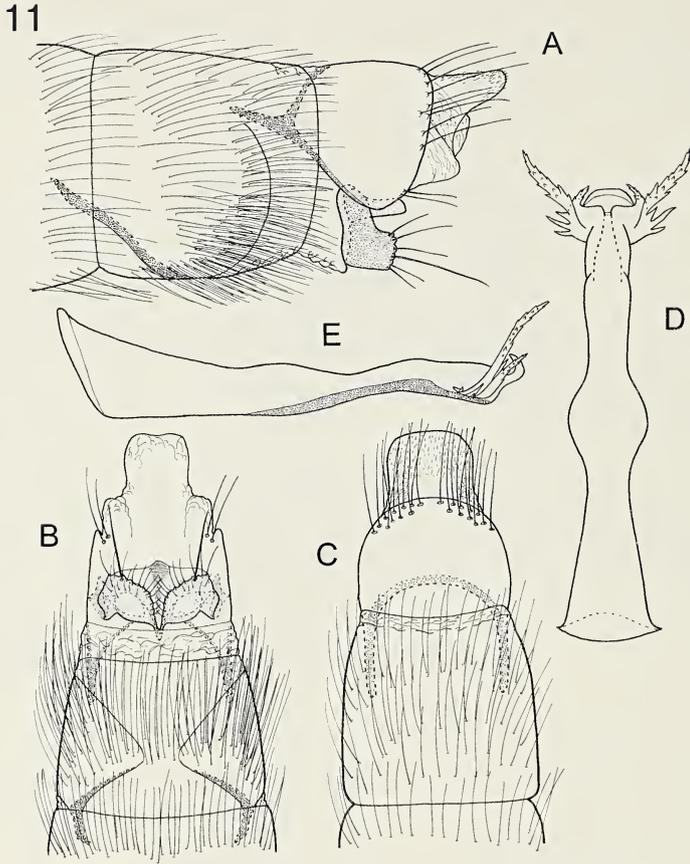


Fig. 11.—*Bredinia costaricensis* (Flint), male genitalia, specimen from Costa Rica: A. Lateral. B. Ventral. C. Dorsal. D. Phallus, dorsal. E. Phallus, lateral.

Fig. 12.—*Bredinia costaricensis* (Flint), female genitalia: A. Terminal abdominal segments, ventral. B. Bursa copulatrix, ventral.

the head, thorax, and wings as in male. Genitalia as in Fig. 12. Segment VII annular. Segment VIII rectangular, ring of setae on emarginate posterior margin; pair of elongate mesal apodemes extending into segment VII, second pair of elongate apodemes originating at anterolateral margins and extending through segment VII. Segment IX short, membranous posteriorly, with pair of lateral apodemes which connect with mesal apodemes of VIII. Segment X short and rounded apically, bearing pair of apical papillae. Bursa copulatrix triangular, anteriorly with pair of lateral processes which are longer than mesal process and originate from square plates.

Material Examined.—**COSTA RICA. Limón:** La Lola near Matina, 11 March 1965, D. Duckworth, 1 ♂ paratype (NMNH), same locality, but 1 May 1957, R. Shenefeld, 1 ♂ paratype (NMNH), Reserva Biológica Barbilla, Río Dantas, 15 km S Pacuarito, 9.994°N, 83.443°W, el. 300 m, 27–30 January 1992, Holzenthal, Munoz, Kjer, 1 ♂ (UMSP), Río Telire and small tributaries, SE Suretka, 9.554°N, 82.892°W, el. 48 m, 1 February 1986, Holzenthal, Morse, Fasth, 2 ♂, 22 ♀ (UMSP), Río Bitey, ca 2.5 km S Pandora, 9.725°N, 82.963°W, el. 15 m, 3 February 1986, Holzenthal, Morse, Fasth, 3 ♂, 6 ♀ (INBIO), Río Barbilla, ca 8 km W B-Line, 10.067°N, 83.369°W, el. 30 m, 31 January 1986, Holzenthal, Morse, Fasth, 29 ♂, 155 ♀ (UMSP), Río Banano, 16 km WSW Bomba, 9.888°N, 83.167°W, 26 March 1987, el. 150 m, Holzenthal, Hamilton, Heyn, 10 ♂ (5♂CMNH, 5♂INBIO), Reserva Biológica Hitoy-Cerere, Río Cerere, 9.671°N, 83.028°W, 23–24 March 1987, el. 90 m, Holzenthal, Hamilton, Heyn, 46 ♂ (NMNH), Río Uatsi, ca 8 km (air) W Bribri, 9.62°N, 82.90°W, 25 March 1987, el. 60 m, Holzenthal, Hamilton, Heyn, 9 ♂ (UMSP). **Cartago:** Río Platanillo, 22 km E. Tayutic, 9.82°N, 83.55°W, el. 730 m, 30 January 1986, Holzenthal, Morse, Fasth, 14 ♂, 4 ♀ (7♂, 2♀CMNH, 7♂, 2♀UMSP), Pejibaye, 22–24 March 1987, W. Steiner, 2 ♂ (NMNH). **Puntarenas:** Río Singrú, ca 2 km (air) S Finca Helechales, 9.057°N, 83.082°W, el. 720 m, 21 February 1986, Holzenthal, Morse, Fasth, 8 ♂ (UMSP), Río Ciebo, route 2, ca 6 km W road to Buenos Aires, 9.149°N, 83.193°W, el. 250 m, 20 February 1986, Holzenthal, Morse, Fasth, 151 ♂, 155 ♀ (50♂, 50♀CMNH, 50♂, 50♀INBIO, 51♂, 55♀UMSP), Quebrada Pita, ca 3 km (air) W Golfito, 8.642°N, 83.193°W, el. 15 m, Holzenthal, Morse, Fasth, 1 ♂ (UMSP), Quebrada Potrero near Potrero Grande, 5 July 1992, T. Shepard, 32 ♂, 47 ♀ (CMNH), Río Guineal, ca 1 km (air) E Finca Helechales, 9.076°N, 83.092°W, 22 February 1986, el. 840 m, Holzenthal, Morse, Fasth, 29 ♂ (INBIO).

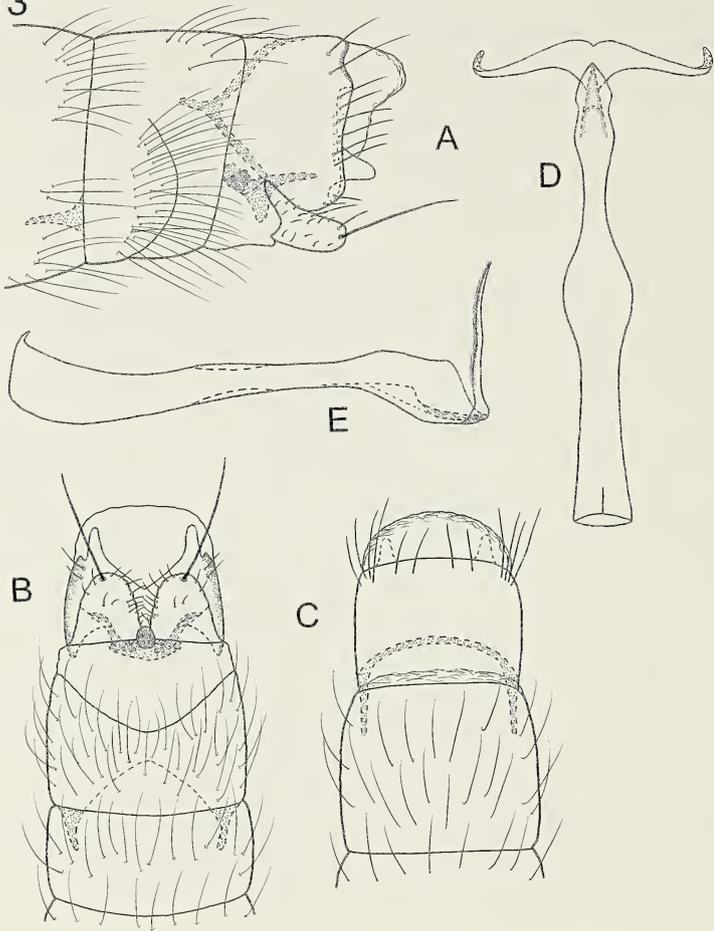
PANAMA. Chiriquí: Dolega, 17 July 1967, O. Flint, 4 ♂, 5 ♀ (NMNH), David, Dolequito, 3 June 1964, A. Broce, 5 ♂, 7 ♀ (NMNH), Río El Pueblo, 27 June 1964, el. 700 m, A. Broce, 4 ♂, 5 ♀ (NMNH). **Bocas del Toro:** Río Changuinola at Zegla, 25 April 1985, R. Flowers, C. Stephens, 1 ♂ (CMNH), Quebrada Canaza at pipeline road, el. 300', 18 May 1985, R. Flowers, 1 ♂, Río Teribe at Zegla, 20 April 1985, R. Flowers, A. Gonzales, 10 ♂ (NMNH).

Bredinia manabiensis, new species
(Figs. 13, 14)

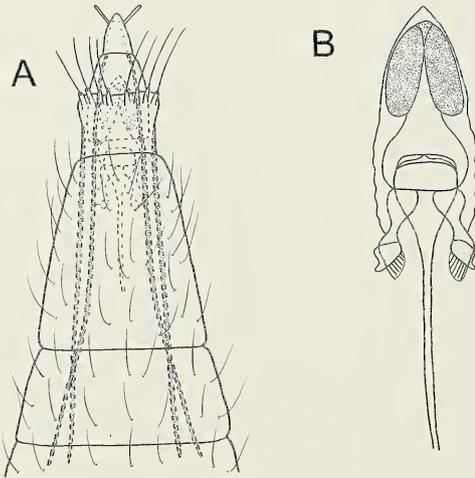
Diagnosis.—*Bredinia manabiensis*, with *B. costaricensis* and *B. venezuelensis* n.sp., shares a similarity in the appearance of the phallic apex, which is T-shaped. In both *B. costaricensis* and *B. venezuelensis*, the lateral processes from the phallic apex are multibranching, whereas in *B. manabiensis*, they are simple. The species has been collected only in Ecuador.

Male.—Length 1.5 mm. Antenna with 19 segments. Brown in alcohol. Genitalia as in Fig. 13. Segment VIII annular; venter shallowly emarginate posteriorly, anteriorly with margins extending into segment VII as short rods. Segment IX reduced to narrow bridge ventrally, anterior margins produced as short anterior rods; dorsally rectangular. Segment X lobate in lateral view; dorsum membranous and rounded posteriorly. Inferior appendages rectanguloid in lateral view; thumb-like in ventral aspect, each with posterior margin rounded. Subgenital plate shelf-like in lateral view, with ventral process at midlength; in ventral view deeply incised mesally with lateral margins produced as fingerlike lobes. Phallus tubular, apex T-shaped with elongate lateral processes; ejaculatory tube short and triangular.

13



14



Female.—Length 1.5 mm. Antenna broken, with at least 15 segments. Color and features of the head, thorax and wings as in male. Genitalia as in Fig. 14. Segment VII annular. Segment VIII square, ring of setae on posterior margin, pair of elongate mesal apodemes extending into segment V, second pair of elongate apodemes originating at anterolateral margins and extending into segment V. Segment IX trianguloid; pair of lateral apodemes connected anteriorly with mesal apodemes of VIII. Segment X short and conical, bearing pair of apical papillae. Bursa copulatrix triangular, narrowing posteriorly, pair of oval, sclerous plates posteriorly, oval plate anteriorly bearing a pair of scalelike processes sclerotized at tips; mesal process elongate and continuous with anterior plate.

Type Material.—Holotype ♂. **ECUADOR. Manabi**: 29 km W Santo Domingo, Rancho Ronald, 20 July 1978, J. Anderson (NMNH). Paratype: **ECUADOR**. Same data as holotype, 1 ♀ (NMNH).

Etymology.—Named for the province in Ecuador where the species was collected.

Bredinia venezuelensis, new species

(Figs. 15, 16)

Diagnosis.—This species is similar to *B. costaricensis*, particularly in the elaborate branching processes of the phallus apex. The structure of the inferior appendages and subgenital plate is also similar in the two species, but the T-shaped phallic apex also bears some similarity to that of *B. manabiensis*. The new species is recognized by arrangement of the multibranching processes at apex of the phallus, which are slender and fingerlike. *Bredinia venezuelensis* is known from Venezuela, Peru, and Ecuador.

Male.—Length 1.4–1.9 mm. Antenna with 17 segments. Brown in alcohol. Genitalia as in Fig. 15. Segment VIII annular; venter deeply emarginate posteriorly, anteriorly with lateral margins produced as short rods. Segment IX reduced to narrow bridge ventrally; dorsally rectangular, anterior margin extending anteriorly as narrow rods to middle of segment VIII. Segment X lobate in lateral view; broadly rounded and membranous in dorsal view. Inferior appendages square in lateral view; in ventral view square with lateral margins narrowing basally, mesal margins slightly diverging. Subgenital plate shelflike in lateral view with dorso-basal projection; in ventral view rectangular with mesal hump. Phallus tubular, apex T-shaped with elongate, fingerlike branches laterally; ejaculatory duct narrowly triangular.

Female.—Length 1.8–2.0 mm. Antenna with 17 segments. Color and features of the head, thorax and wings as in male. Genitalia as in Fig. 16. Segment VII annular. Segment VIII square, ring of setae on emarginate posterior margin, pair of elongate, mesal apodemes extending midway into segment VII, second pair of elongate apodemes originating at posterolateral margins and extending midway into VII; scaly appearance on ventral surface. Segment IX short, pair of membranous lobes ventrally, pair of lateral apodemes connecting anteriorly with mesal apodemes of VIII. Segment X short and conical, bearing pair of apical papillae.

←

Fig. 13.—*Bredinia manabiensis* new species, male genitalia: A. Lateral. B. Ventral. C. Dorsal. D. Phallus, dorsal. E. Phallus, lateral.

Fig. 14.—*Bredinia manabiensis* new species, female genitalia: A. Terminal abdominal segments, ventral. B. Bursa copulatrix, ventral.

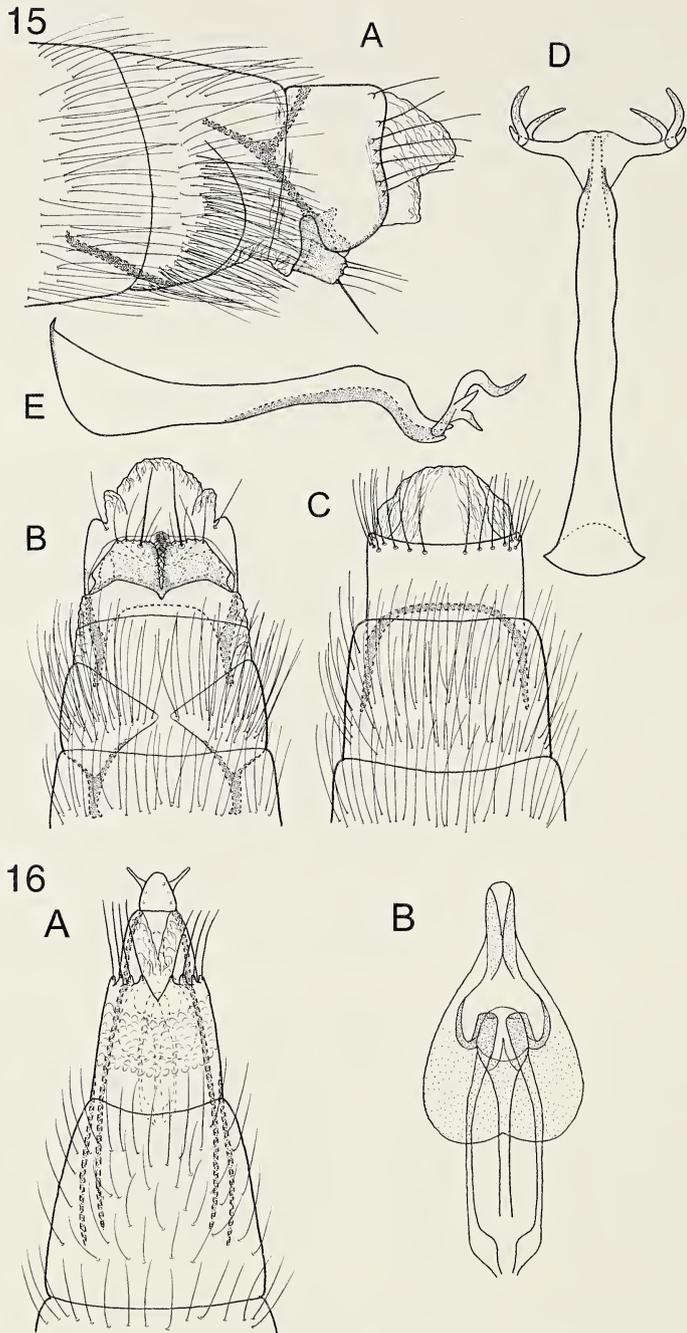


Fig. 15.—*Bredinia venezuelensis* new species, male genitalia: A. Lateral. B. Ventral. C. Dorsal. D. Phallus, dorsal. E. Phallus, lateral.

Fig. 16.—*Bredinia venezuelensis* new species, female genitalia: A. Terminal abdominal segments, ventral. B. Bursa copulatrix, ventral.

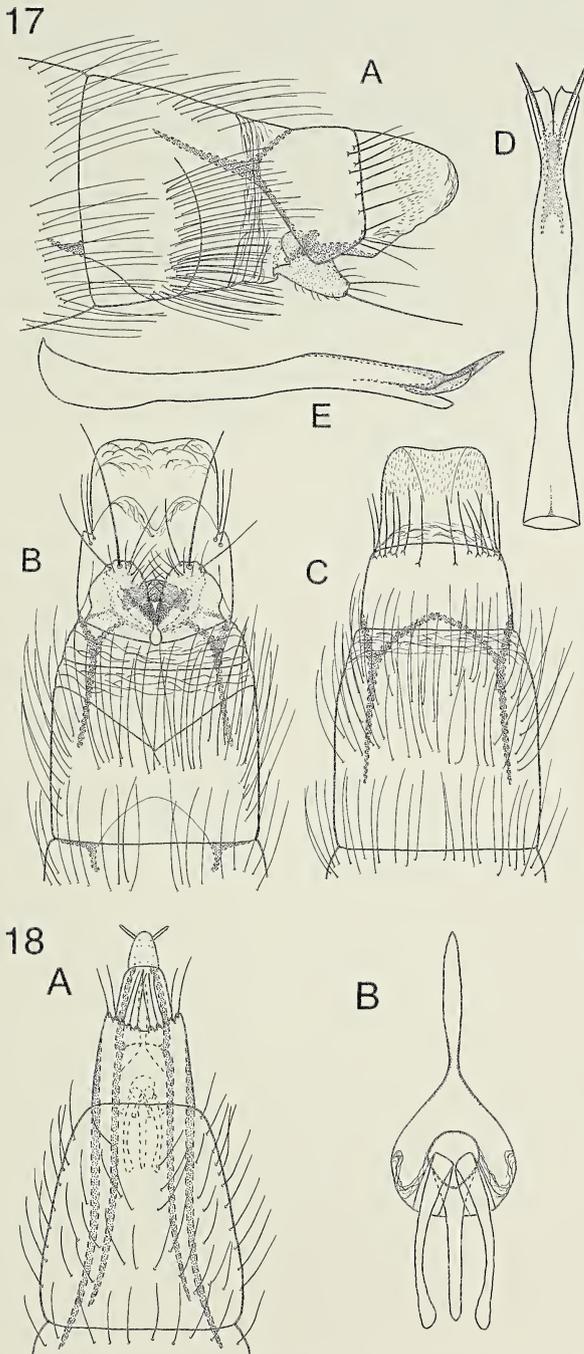


Fig. 17.—*Bredinia pilcopata* new species, male genitalia: A. Lateral. B. Ventral. C. Dorsal. D. Phallus, dorsal. E. Phallus, lateral.

Fig. 18.—*Bredinia pilcopata* new species, female genitalia: A. Terminal abdominal segments, ventral. B. Bursa copulatrix, ventral.

Bursa copulatrix triangular, narrowing posteriorly to form rectanguloid process; anteriorly with pair of thin, elongate lateral processes which originate from square, sclerous plates, mesal process shorter than lateral processes.

Type Material.—Holotype ♂. **VENEZUELA**. **Zulia**: Perija El Tucuco, Mission El Tucuco, Río El Tucuco, 11 km from church, 1–5 October 1979, H. Savage (NMNH). Paratypes: **VENEZUELA**. Same data as holotype, 53 ♂ (33♂NMNH, 20♂UMSP), El Tucuco, Sierra de Perija, montane forest, 28–29 January 1978, blacklight, J. Heppner, 19 ♂ (UMSP), Baralt, Río Pauji at rt 3 between San Juan and San Antonio, 9–11 October 1979, H. Savage, 42 ♂ (20♂NMNH, 12♂CMNH, 10♂UMSP). **Aragua**: Parque Nacional Henri Pittier, Río La Trilla, 22.5 km N Rancho Grande on road, 17–19 September 1979, H. Savage, 124 ♂ (80♂NMNH, 20♂CMNH, 24♂UMSP), Cuyagua, Río Grande, 20–23 September 1979, H. Savage, 7 ♂ (NMNH), Ocumare, 19–20 February 1969, P. and P. Spangler, 7 ♂ (NMNH). **Barinas**: Río Santo Domingo, Barinas, 17 February 1976, C. and O. Flint, 5 ♂ (NMNH). **PERU**. Puerto Bermudez, Río Pichis, 17 July 1961, 2 ♂, 8 ♀ (CU).

ECUADOR. **Pastaza**: Puyo, 27 km N Estación Fluviométrica, 4 February 1976, P. Spangler, 6 ♂ (NMNH), same locality, but 5 May 1977, P. Spangler, D. Givens, 1 ♂ (NMNH), same locality, but 10 May 1977, P. Spangler, D. Givens, 1 ♂, same locality, but 21 May 1977, P. Spangler, D. Givens, 1 ♂ (NMNH), same locality, but 6 May 1977, 1 ♂ (NMNH). **Napo**: Puerto Nuevo (2 km S), 1.5 km W of river, 9 July 1976, J. Cohen, 5 ♂ (NMNH).

Etymology.—Named for the country of Venezuela.

Bredinia pilcopata, new species (Figs. 17, 18)

Diagnosis.—This species is most similar to *B. spangleri* n. sp., in the appearance of the genitalic features, but the two species can be separated by the structure of the phallus. The lateral processes at the phallic apex in *B. pilcopata* are much shorter than those of *B. spangleri*; the apex is divided into a pair of truncate lobes; and the ejaculatory duct is not protruding. *Bredinia pilcopata* is known only from a few localities in Peru.

Male.—Length 1.3–1.4 mm. Antenna with 18 segments. Brown in alcohol. Genitalia as in Fig. 17. Segment VIII annular; venter emarginate posteriorly, anteriorly with margins produced into shortened rods. Segment IX reduced to narrow bridge ventrally; dorsally rectangular with posterior margin truncate, anterior margins extending anteriorly as elongate rods to midlength of segment VIII. Segment X lobate in lateral view; dorsally nearly square. Inferior appendages triangular in lateral view, narrowing posteroventrally; in ventral view nearly square, diverging along mesal margins, lateral margins sinuate. Subgenital plate narrow, shelflike in lateral view with small basal process. Phallus tubular, apex with thin lateral processes originating from truncate lobes, ejaculatory duct triangular.

Female.—Length 1.6–2.0 mm. Antenna with 18 segments. Color and features of the head, thorax and wings as in male. Genitalia as in Fig. 18. Segment VII annular. Segment VIII rectangular, ring of setae on emarginate posterior margin, pair of elongate, mesal apodemes extending into segment VI, second pair of elongate apodemes originating at anterolateral margins and extending through segment VI. Segment IX rectangular, pair of lateral apodemes connecting anteriorly with mesal apodemes of VIII. Segment X short and rounded apically, bearing pair of apical papillae. Bursa copulatrix round with narrow, elongate posterior projection; anteriorly with pair of lateral processes, similar in width and length to mesal process.

Type Material.—Holotype ♂. **PERU**. **Cuzco**: Pilcopata, 8–10 December 1979, el. 600 m, J. Heppner (NMNH). Paratypes: **PERU**. Same data as holotype, 2 ♂ (NMNH, UMSP). **Huanuco**: Río Hualago, Tingo Maria, 14–16 August 1963, W. Peters, 4 ♂, 1 ♀ (3♂, 1♀NMNH, 1♂CMNH), same locality, but 24–27 September 1955, S. Roback, 4 ♂, 8 ♀, (2♂, 4♀ANSP, 2♂, 4♀NMNH), Hotel

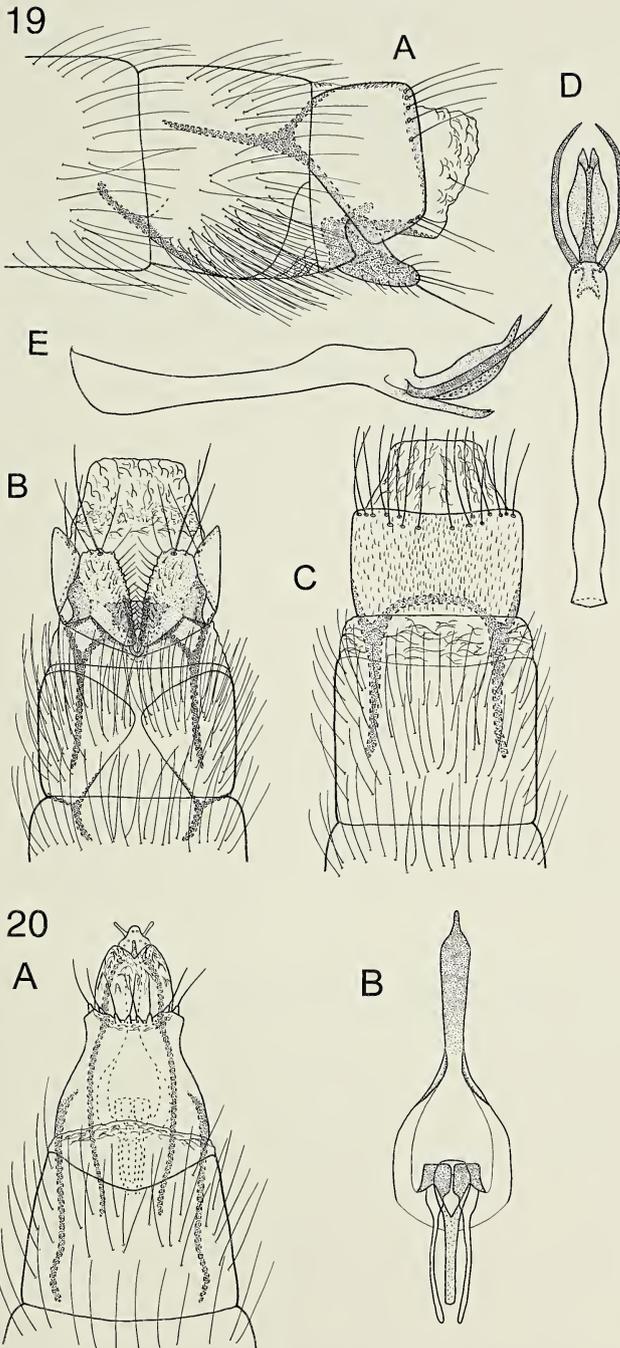


Fig. 19.—*Bredinia spangleri* new species, male genitalia: A. Lateral. B. Ventral. C. Dorsal. D. Phallus, dorsal. E. Phallus, lateral.

Fig. 20.—*Bredinia spangleri* new species, female genitalia: A. Terminal abdominal segments, ventral. B. Bursa copulatrix, ventral.

Tingo Maria, Tingo Maria, 6 October 1955, S. Roback, 11 ♂ (5♂ ANSP, 2♂ CMNH, 2♂ NMNH, 2♂ UMSP).

Etymology.—Named for the town of Pilcopata where the species was collected.

Bredinia spangleri, new species

(Figs. 19, 20)

Diagnosis.—Both *B. pilcopata* and *B. spangleri* have elongate anterior rods from segment IX and lateral processes at the phallus apex, however in *B. spangleri* these lateral processes are sclerotized and elongate. The species has been reported only from Ecuador where it is often abundant in blacklight collections.

Male.—Length 1.4–1.9 mm. Antenna with 18 segments. Brown in alcohol. Genitalia as in Fig. 19. Segment VIII annular; venter emarginate posteriorly, anteriorly with margins produced into shortened rods. Segment IX reduced to narrow bridge ventrally; dorsally rectangular with posterior margin truncate, anterior margins extending anteriorly as elongate rods to anterior region of segment VIII. Segment X truncate and membranous. Inferior appendage triangular in lateral view, narrowing posteroventrally; in ventral aspect rectanguloid, diverging on mesal margin. Subgenital plate thin, shelflike in lateral view, with small basal process; thin and squarish in ventral view. Phallus tubular, apex with slender, elongate lateral processes; ejaculatory duct protruding, with oblong lateral lobes.

Female.—Length 1.6–2.0 mm. Antenna with 18 segments. Color and features of head, thorax and wings similar to those of male. Genitalia as in Fig. 20. Segment VII annular. Segment VIII short and wide, ring of setae on posterior margin; pair of elongate, mesal apodemes extending just into segment VII, second pair of elongate apodemes originating at anterolateral margins and extending well into segment VII. Segment IX lobate, pair of lateral apodemes connecting to mesal apodemes of VIII. Segment X short and conical, with pair of apical papillae and with narrow mesal plate anteriorly. Bursa copulatrix round with narrow, elongate posterior projection; anteriorly with thin pair of lateral processes, which are narrower and longer than mesal process, and which originate from small square plates.

Type Material.—Holotype ♂. **ECUADOR. Pastaza:** Puyo, (16 km W) at blacklight, 3 February 1976, P. Spangler et al. (NMNH). Paratypes: **ECUADOR.** Same data as holotype, 1 ♂ (NMNH), same locality, but 8–11 February 1976, P. Spangler et al., 1 ♂ (NMNH), same locality, but 16 May 1977, P. Spangler, D. Givens, 2 ♂ (NMNH), same locality, but 30 January 1976, P. Spangler, et al., 2 ♂ (NMNH), 27 km. N Estación Fluviométrica, February 1976, P. Spangler, et al., 21 ♂, 1 ♀ (NMNH), same locality, but 15 May 1977, P. Spangler, D. Givens, 5 ♂, 2 ♀ (UMSP), riverside at blacklight, 29 May 1975, J. Cohen, J. Langley, 18 ♂, 23 ♀, (UMSP), 3 km W, 15 July 1976, J. Cohen, 14 ♂, 89 ♀ (NMNH), 21 May 1977, P. Spangler, D. Givens, 1 ♂ (NMNH), same locality, but 10 May 1977, 28 ♂, 1 ♀ (CMNH), same locality, but 14 May 1977, 5 ♂ (NMNH), same locality, but 17 May 1977, 9 ♂ (NMNH), same locality, but 11 May 1977, 17 ♂ (CMNH), same locality, but 21 May 1977, 67 ♂, 2 ♀ (UMSP), same locality, but 7 May 1977, 55 ♂ (NMNH), same locality, but 6 May 1977, 65 ♂ (UMSP), same locality, but 21 May 1977, 1 ♂ (NMNH), same locality, but 5 May 1977, 79 ♂ (NMNH), same locality, but 15 May 1977, 2 ♂ (NMNH), same locality, but 1.5 km S 14 May 1977, 15 ♂, 1 ♀ (CMNH), same locality, but 8 May 1977, 66 ♂, 1 ♀ (UMSP), same locality, but 13 May 1977, 15 ♂ (NMNH). **Napo:** Tena (8 km SW), 29 May 1977, P. Spangler, D. Givens, 1 ♂ (NMNH), same locality, but 23 May 1977, 1 ♂ (NMNH), Puerto Nuevo (2 km S) 1.5 km W to River, 9 July 1976, J. Cohen, 1 ♂ (CMNH), Río Jondachi, 30 km N Tena, el. 950 m, 10 September 1990, O. Flint, 30 ♂, 123 ♀ (NMNH). Pano, 580 m, 12 September 1990, O. Flint, 1 ♂, 4 ♀ (UMSP). **Cotopaxi:** Quevedo (36 km NE), 21 July 1976, el. 350 m, J. Cohen, 1 ♂ (NMNH).

Etymology.—Named for Dr. Paul J. Spangler, who collected many of the specimens of this species.

Bredinia alza, **new species**
(Fig. 21)

Diagnosis.—This species is most similar to *B. mexicana* n. sp., with both having the apical structure of the phallus deeply bifurcated. The strongly upturned posteroventral process of the inferior appendages is unique to *B. alza* and serves to differentiate the species. *Bredinia alza* is known from a single locality in Paraguay.

Male.—Length 2.0 mm. Antenna with 18 segments. Brown in alcohol. Genitalia as in Fig. 21. Segment VIII annular; venter deeply emarginate posteriorly, anterior margins produced into short lateral rods. Segment IX reduced to narrow bridge ventrally; dorsally square with lateral margins rounded, anterior margins produced into short, lateral rods. Segment X shelflike, narrowing posteriorly in ventral view; dorsally membranous, rounded laterally and emarginate posteriorly. Inferior appendages square in lateral view, each with elongate extension from posteroventral margin which is strongly turned dorsad, triangular in ventral view with series of thick setae on mesal margins. Subgenital plate appearing as narrow shelf in lateral view; wide and rectanguloid ventrally. Phallus tubular, deeply divided at apex, each side narrowing to acute apex which is turned outward; ejaculatory duct narrowly triangular and protruding within apical incision.

Female.—Unknown.

Type Material.—Holotype ♂. **PARAGUAY. Concepción:** Concepción, 26 August 1989, at black-light, J. Kochalka (NMNH).

Etymology.—From the Spanish “*alzar*—to lift, or raise” referring to the distinctive inferior appendages which are upturned apically.

Bredinia mexicana, **new species**
(Figs. 22, 23)

Diagnosis.—The phallic apex of this new species is structurally similar to that of *B. alza*, and that of *B. espinosa*, but the mitten-shaped inferior appendages, as seen in ventral view, are unique to *B. mexicana*, as are the acute spinal processes of the subgenital plate. The species has been only collected at the type locality in Mexico.

Male.—Length 1.3–1.6 mm. Antenna with 18 segments. Brown in alcohol. Genitalia as in Fig. 22. Segment VIII annular; venter emarginate posteriorly, anteriorly with lateral margins developed as small rods. Segment IX annular, only slightly reduced ventrally; dorsally round and fused posteriorly with X, anterior margin produced into short lateral rods. Segment X shelflike in lateral view; square in dorsal view. Inferior appendages shoe-shaped, elongate posteroventrally in lateral view; in ventral view mitten-shaped with mesal projection, widely separated and narrowing basally. Subgenital plate with dorsal and ventral processes in lateral view; in ventral view, dorsal processes acute and angled inward, ventral process beaklike and angled ventrad. Phallus tubular, deeply incised apically, producing elongate lateral lobes; ejaculatory duct narrowly triangular and protruding distally.

Female.—Length 1.4–1.8 mm. Antenna with 18 segments. Color and general features of head, thorax and wings as in male. Genitalia as in Fig. 23. Segment VII annular. Segment VIII square with ring of setae on posterior margin; pair of elongate, mesal apodemes extending into segment VII, second pair of elongate apodemes originating from anterolateral margins and extending into segment VI.

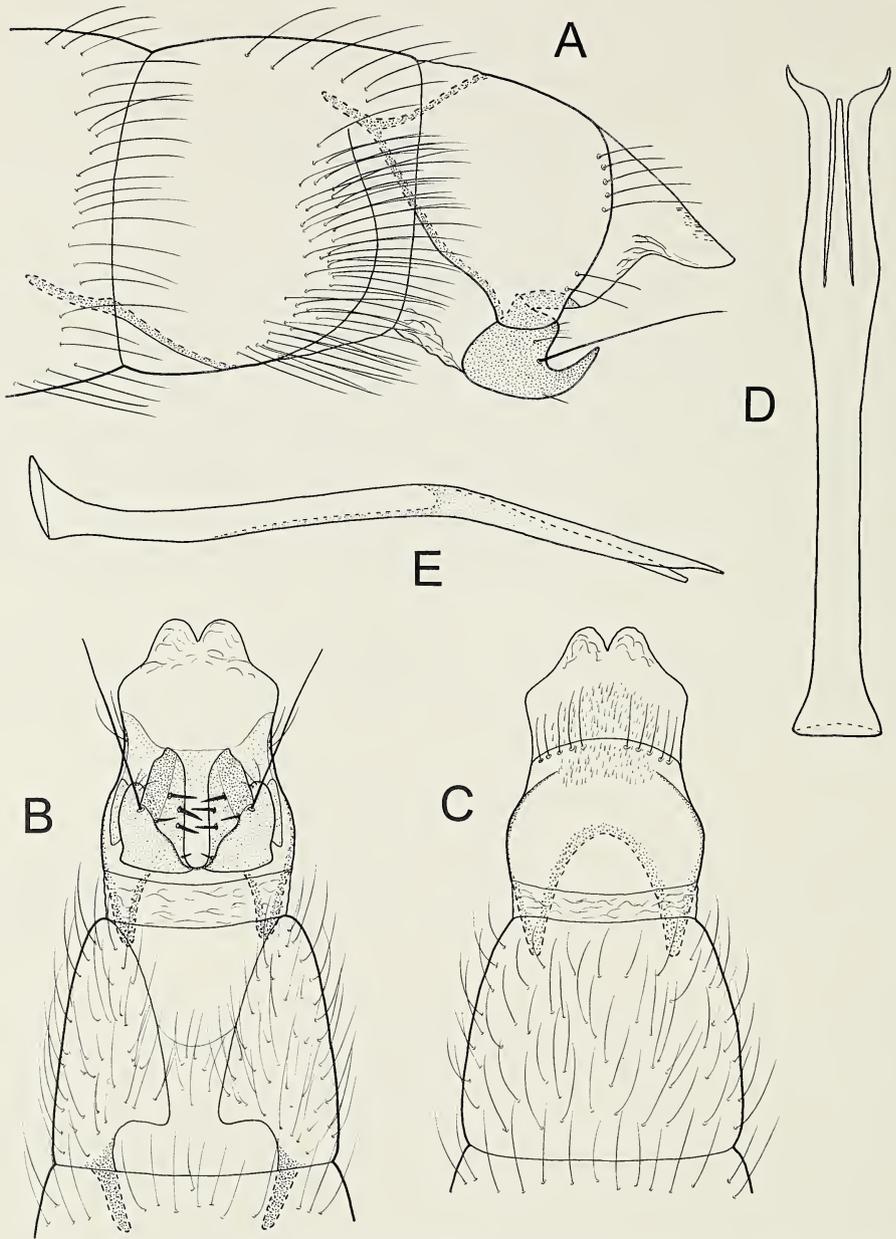


Fig. 21.—*Bredinia alza* new species, male genitalia: A. Lateral. B. Ventral. C. Dorsal. D. Phallus, dorsal. E. Phallus, lateral.

Segment IX rectangular with pair of lateral apodemes connecting with mesal apodemes of VIII. Segment X short and rounded apically, bearing pair of apical papillae. Bursa copulatrix rectangular with broad protrusion posteriorly; anteriorly with lateral processes widening at apices to rounded lobes.

Type Material.—Holotype ♂. MEXICO. Tamaulipas: Río Frio at La Poza Azul near Gómez

Farias, 18 May 1989, S. Harris, A. Contreras (NMNH). Paratypes: MEXICO. Same data as holotype, 12 ♂, 17 ♀ (8♂, 13♀NMNH, 1♂, 1♀UNAM, 2♂, 2♀UMSP, 1♂, 1♀CMNH).

Etymology.—Named for the country of Mexico.

Bredinia sucrensis, **new species**
(Figs. 24, 25)

Diagnosis.—While the phallic apex of *B. sucrensis* is similar to that seen in *B. alza*, the inferior appendages, in lateral aspect, more closely resemble those of *B. mexicana*. However, the inferior appendages of *B. sucrensis* are much more rectangular in ventral aspect than those seen in *B. mexicana*. This species has been only collected from a single location in Venezuela.

Male.—Length 1.6 mm. Antenna with 18 segments. Brown in alcohol. Genitalia as in Fig. 24. Segment VIII annular; venter truncate posteriorly, anteriorly with lateral margins developed as small rods. Segment IX depressed dorsoventrally, anterolaterally extending into segment VIII and narrowing to pair of short, lateral apodemes; dorsally round with posterolateral margins produced as pair of short lobes. Segment X shelflike in lateral view; round posteriorly in dorsal view. Inferior appendages boot-shaped, elongate posteroventrally in lateral view; in ventral view rectangular, with mesal margins undulate and diverging posteriorly. Subgenital plate narrow in lateral view; in ventral view, thin and rectanguloid. Phallus tubular, deeply incised apically producing elongate lateral lobes flaring outward apically; ejaculatory duct narrow and protruding distally.

Female.—Length 1.6 mm. Antenna with 18 segments. Color and overall features of the head, thorax and wings as in male. Genitalia as in Fig. 25. Segment VII annular. Segment VIII square with ring of setae on posterior margin; pair of elongate, mesal apodemes extending midway into segment VII, second pair of elongate apodemes originating from anterolateral margins and extending into segment VII. Segment IX rectangular with pair of lateral apodemes connecting with mesal apodemes of VIII. Segment X short and rounded apically, bearing pair of apical papillae. Bursa copulatrix rectangular with broad protrusion posteriorly; anteriorly with lateral processes widening at apices to rounded lobes.

Type Material.—Holotype ♂. VENEZUELA. Sucre: Parque Nacional Peninsula de Paria, Uquire, Río La Viuda, 1 April 1995, 10° 42.830'N, 61° 57.661'W, el. 15 m, Holzenthal, Flint, Cressa (NMNH). Paratype: VENEZUELA. Same data as holotype, 1 ♀ (NMNH).

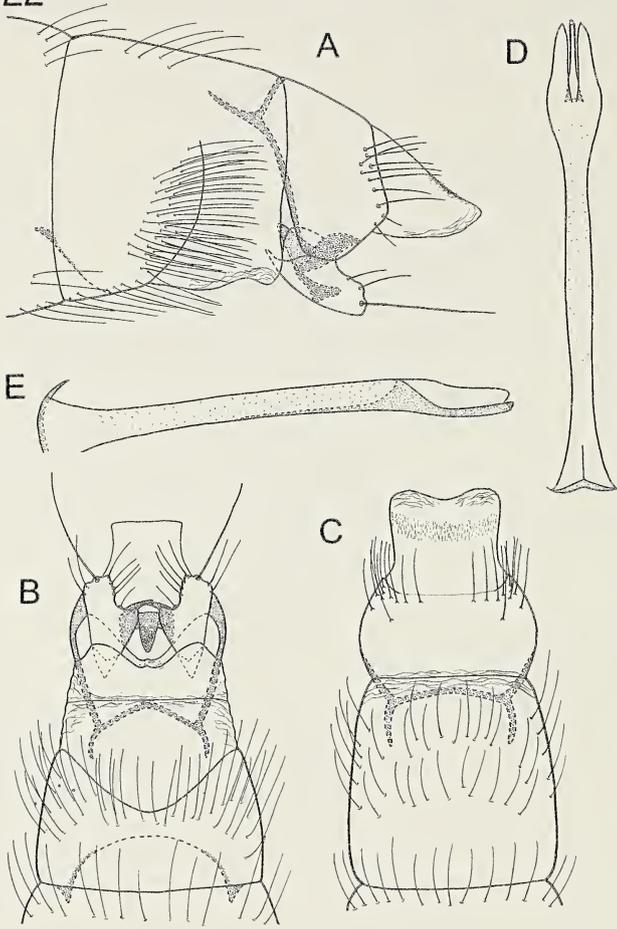
Etymology.—Named for the state in Venezuela where the species was collected.

Bredinia emarginata, **new species**
(Fig. 26)

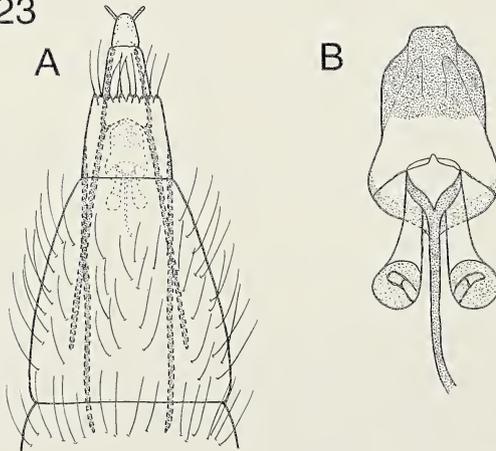
Diagnosis.—*Bredinia emarginata* is distinguished from other members of the genus by the deep dorsal emargination of segment IX and the elongate anterior rods from the lateral margins of segment VIII. The species is known only from the Río Pizote in Costa Rica.

Male.—Length 1.4 mm. Antenna with 18 segments. Brown in alcohol. Genitalia as in Fig. 26. Segment VIII annular; venter slightly emarginate posteriorly, anteriorly with lateral margins produced into elongate rods extending through segment VII. Segment IX reduced to rectanguloid bridge ventrally; dorsally with deep mesal excision, bearing line of setae on inner margins, anterior margin produced into short lateral rods. Segment X lobate, shelflike in lateral view; dorsally rectangular with shallow mesal emargination. Inferior appendages triangular in lateral view, narrowing posteroventrally; in ventral view triangular, diverging on

22



23



mesal margins and narrowing posteriorly, bearing thick seta on mesal margin and elongate seta posteriorly. Subgenital plate rectangular in lateral aspect and oriented dorsoventrally; appearing as narrow, curving band in ventral view. Phallus tubular, apex with shallow excision from which tonguelike ejaculatory duct protrudes.

Female.—Unknown.

Type Material.—Holotype ♂. **COSTA RICA. Alajuela:** Río Pizote, ca 5 km N Dos Ríos, 10.948°N, 85.291°W, 9 March 1986, Holzenthal and Fasth (NMNH).

Etymology.—Named for the distinctive structure of abdominal segment IX.

Bredinia zulia, new species

(Fig. 27)

Diagnosis.—This species has several features in common with *B. emarginata*. Both have a shallow emargination at the phallic apex, and both have short, rounded inferior appendages when viewed in ventral aspect. *Bredinia zulia* is recognizable by the cuplike excision at the apex of the phallus, which creates small lateral “ears” and the dorsum of segment X which is entire rather than incised. *Bredinia zulia* is known only from the type locality in Venezuela.

Male.—Length 1.2–1.6 mm. Antenna with 18 segments. Brown in alcohol. Genitalia as in Fig. 27. Segment VIII annular, venter emarginate posteriorly, anteriorly with lateral margins produced into short lateral rods. Segment IX reduced to narrow bridge ventrally; square dorsally, anterior margins extended anteriorly as slender rods midway into segment VIII. Segment X lobate in lateral view, dorsally forming rounded lobe. Inferior appendages triangular, narrowing posteriorly, in ventral view rounded apically, diverging along mesal margin. Subgenital plate shelflike in lateral view, with dorsoventral projection from base; rectangular in ventral view with mesal lobelike processes. Phallus tubular, apex with rounded incision; ejaculatory duct narrowly triangular.

Female.—Unknown.

Type Material.—Holotype ♂. **VENEZUELA. Zulia:** El Tucuco, Sierra de Perija, 28–29 January 1978, at blacklight, J. Heppner (NMNH). Paratypes: **VENEZUELA.** Same data as holotype, 11 ♂ (8♂NMNH, 2♂UMSP, 1♂CMNH).

Etymology.—Named for the state in Venezuela where the species was collected.

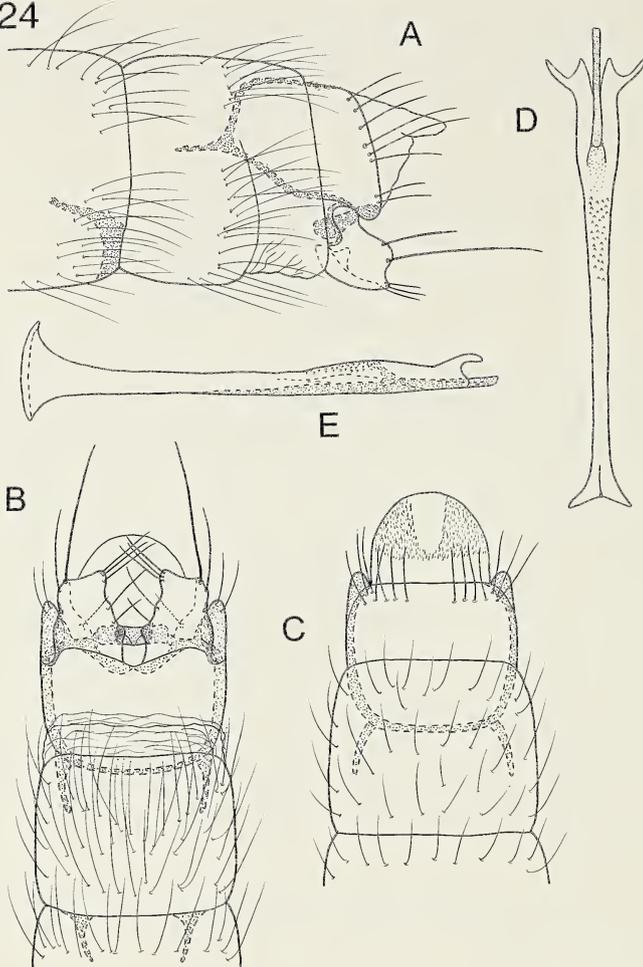
KEY TO *BREDINIA* ADULTS

- | | | |
|--------|---|----|
| 1. | Males | 2 |
| 1'. | Females (excluding females of <i>B. alza</i> , <i>B. emarginata</i> , <i>B. guanacasteca</i> , <i>B. selva</i> , and <i>B. zulia</i> , which are unknown) | 17 |
| 2 (1). | Anterolateral rods of segment IX elongate, extending through segment VIII (Figs. 2A, 4A). | 3 |
| 2'. | Anterolateral rods of segment IX short, not extending through segment VIII (Figs. 10A, 15A). | 5 |
| 3 (2). | Phallus apex with inner processes only slightly longer than lateral processes (Fig. 2D); | |

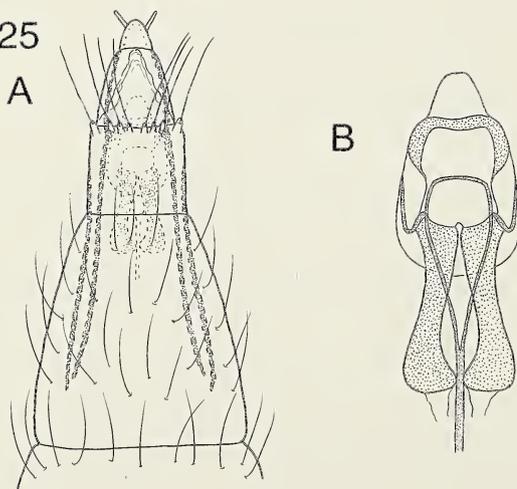
Fig. 22.—*Bredinia mexicana* new species, male genitalia: A. Lateral. B. Ventral. C. Dorsal. D. Phallus, dorsal. E. Phallus, lateral.

Fig. 23.—*Bredinia mexicana* new species, female genitalia: A. Terminal abdominal segments, ventral. B. Bursa copulatrix, ventral.

24



25



inferior appendages each narrowing to acute or upturned apex ventrolaterally (Figs. 2A, 5A). 4

3'. Phallus apex with inner processes thin and much longer than lateral processes (Fig. 4D); inferior appendages each not narrowing to acute apex ventrolaterally (Fig. 4A). *B. guanacasteca*

4 (3). Inferior appendages each narrowing to acute apex ventrolaterally (Fig. 2A), in ventral view nearly square (Fig. 2B); phallus apex with inner bifid processes straight (Fig. 2D). *B. dominicensis*

4'. Inferior appendages each narrowing to rounded, upturned projection (Fig. 5A), in ventral view triangular in appearance (Fig. 5B); phallus apex with inner bifid processes diverging (Fig. 5D) *B. selva*

5 (2'). Segment VIII with thick, spinelike setae on lateral margins (Fig. 6A) *B. espinosa*

5'. Segment VIII without thick, spinelike setae on lateral margins (Figs. 8A, 10A) 6

6 (5'). Inferior appendages each with dorsolateral margin modified as elongate, spinelike process (Figs. 8A, 10A); subgenital plate, in lateral aspect, well developed and extending posteriorly beyond midpoint of inferior appendages (Figs. 8A, 10A) 7

6'. Inferior appendages lacking spinelike processes from dorsolateral margins (Figs. 11A, 19A); subgenital plate in lateral aspect, poorly developed, never extending beyond midpoint of inferior appendages (Figs. 13A, 22A). 8

7 (6). Dorsal process of each inferior appendage elongate, extending beyond ventral lobe (Fig. 8A); subgenital plate with long, acute ventral process (Fig. 8A) *B. appendiculata*

7'. Dorsal process of each inferior appendage shorter than ventral lobe (Fig. 10A); subgenital plate curving downward apically, forming short process (Fig. 10A). *B. davenporti*

8 (6'). Phallus apex with elongate, lateral processes directed laterad, forming T-shape (Figs. 11D, 13D). 9

8'. Phallus apex lacking elongate, lateral processes, or with processes directed apicad, not forming T-shape (Figs. 17D, 19D) 11

9 (8). Lateral processes from apex of phallus multibranching (Figs. 11D, 15D); inferior appendages truncate in ventral view (Figs. 11B, 15B). 10

9'. Lateral processes from apex of phallus simple (Fig. 13D); inferior appendages rounded in ventral view (Fig. 13A). *B. manabiensis*

10 (9). Multibranching lateral processes from phallus apex toothlike and acute, or serrate (Fig. 11D). *B. costaricensis*

10'. Multibranching lateral processes from phallic apex slender and fingerlike (Fig. 15D) *B. venezuelensis*

11 (8'). Posterior of phallus with thin, sclerotized lateral processes, originating subapically and differentiated from shaft of phallus (Figs. 17D, 19D). 12

11'. Phallus apex with sclerotized, lateral processes broad and not differentiated from shaft of phallus (Figs. 22D, 27D). 13

12 (11). Lateral processes from phallic apex short, about one-sixth total phallus length, phallus apex divided into truncate lobes (Fig. 17D) *B. pilcopata*

12'. Lateral processes from phallus apex elongate, about one-third total phallus length, phallus apex not divided into pair of truncate processes (Fig. 19D). *B. spangleri*

13 (11'). Phallus apex deeply incised with lateral lobes flaring outward (Figs. 21D, 24D). 14

13'. Phallus apex shallowly incised with lateral lobes straight (Fig. 22D), or curving inward (Fig. 27D). 15

←
 Fig. 24.—*Bredinia sucrensis* new species, male genitalia: A. Lateral. B. Ventral. C. Dorsal. D. Phallus, dorsal. E. Phallus, lateral.

Fig. 25.—*Bredinia sucrensis* new species, female genitalia: A. Terminal abdominal segments, ventral. B. Bursa copulatrix, ventral.

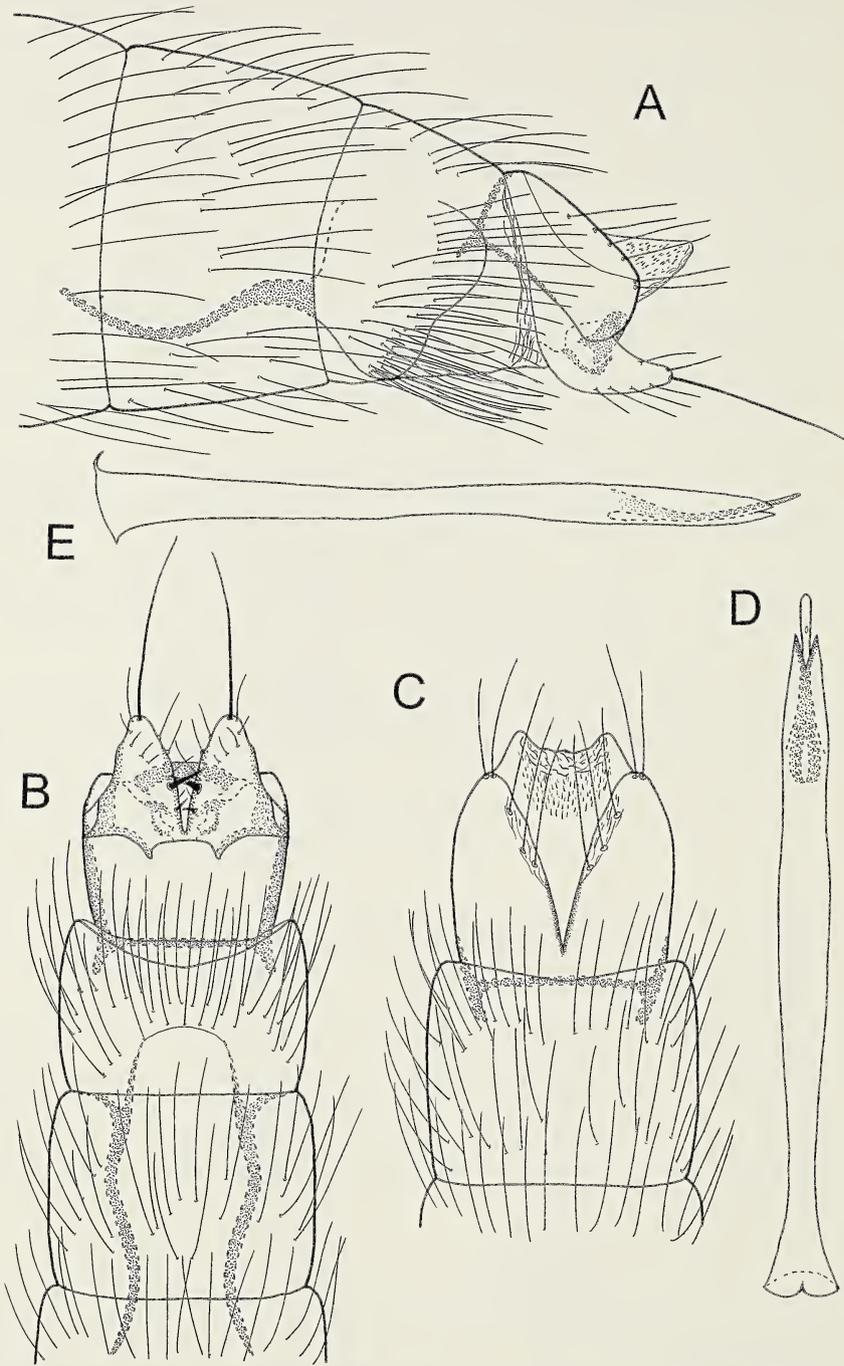


Fig. 26.—*Bredinia emarginata* new species, male genitalia: A. Lateral. B. Ventral. C. Dorsal. D. Phallus, dorsal. E. Phallus, lateral.

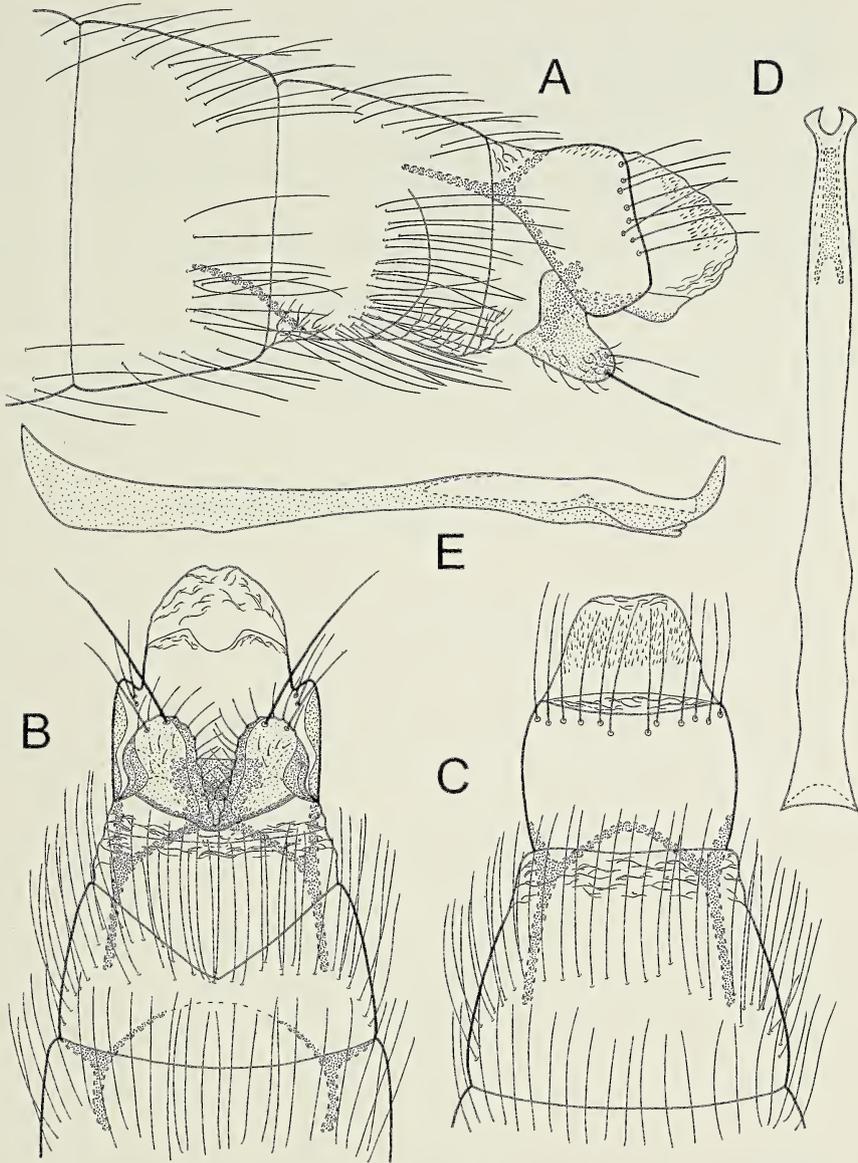


Fig. 27.—*Bredinia zulia* new species, male genitalia: A. Lateral. B. Ventral. C. Dorsal. D. Phallus, dorsal. E. Phallus, lateral.

- 14 (13). Inferior appendages each narrowing posterolaterally to acute upturned hook (Fig. 21A) *B. alza*
- 14'. Inferior appendages each truncate posterolaterally (Fig. 24A) *B. sucrensis*
- 15 (13'). Inferior appendages mitten-shaped in ventral view (Fig. 22B); phallus apex enlarged with mesal incision about one-fifth phallus length (Fig. 22D) *B. mexicana*
- 15'. Inferior appendages rounded in ventral view (Figs. 26B, 27B); phallus apex not enlarged with mesal incision very shallow (Figs. 26D, 27D) 16
- 16 (15'). Segment IX deeply emarginate dorsally (Fig. 26C); phallus apex V-shaped with lateral

- lobes narrowing distally (Fig. 26D); elongate apodeme from posterolateral margin of segment VIII (Figs. 26A, 26B) *B. emarginata*
- 16'. Segment IX not deeply emarginate dorsally (Fig. 27C); phallus apex cuplike or U-shaped, with lateral lobes truncate distally (Fig. 27D); short apodeme from posterolateral margin of segment VIII (Figs. 27A, 27B). *B. zulia*
- 17 (1'). Bursa copulatrix triangular in shape, gradually narrowing posteriorly (Figs. 7B, 9B) 18
- 17'. Bursa copulatrix rounded or truncate in shape, abruptly narrowing posteriorly to form thin (Fig. 18B) or wide (Fig. 25B) process 20
- 18 (17'). Anterolateral processes of bursa copulatrix short and wide, with serrate apices (Figs. 9B, 14B) 19
- 18'. Anterolateral processes of bursa copulatrix elongate and thin, with membranous apices (Fig. 7B) *B. espinosa*
- 19 (18'). Bursa copulatrix with pair of oval sclerites posteriorly (Fig. 14B); anterolateral processes with sclerotized plate apically (Fig. 14B) *B. manabiensis*
- 19'. Bursa copulatrix with membranous lobe posteriorly (Fig. 9B); anterolateral processes without sclerotized plate apically (Fig. 9B) *B. appendiculata*
- 20 (17'). Posterior process of bursa copulatrix short (Figs. 3B, 25B); anterolateral processes wide (Figs. 3B, 25B) 21
- 20'. Posterior process of bursa copulatrix elongate (Figs. 12B, 16B); anterolateral processes narrow (Figs. 16B, 20B) 23
- 21 (20). Posterior process of bursa copulatrix wide (Figs. 23B, 25B); posteriorly with wide (Fig. 23B) or narrow (Fig. 25B) sclerotized region 22
- 21'. Posterior process of bursa copulatrix narrow (Fig. 3B); posteriorly with series of sclerotized lobes (Fig. 3B) *B. dominicensis*
- 22 (21). Posterior sclerotized region of bursa copulatrix wide (Fig. 23B); anterolateral processes flaring outward at apices (Fig. 23B) *B. mexicana*
- 22'. Posterior sclerotized region of bursa copulatrix narrow (Fig. 25B); anterolateral processes curving inward at apices (Fig. 25B) *B. sucrensis*
- 23 (20'). Posterior process of bursa copulatrix more than five times longer than wide (Figs. 18B, 20B); ventral surface of segment VIII smooth (Fig. 18A) 24
- 23'. Posterior process of bursa copulatrix less than five times as long as wide (Figs. 12B, 16B); ventral surface of segment VIII scaly (Fig. 16A) or not (12A) 25
- 24 (23). Posterior process of bursa copulatrix abruptly narrowing apically (Fig. 20B); anterolateral processes originating from sclerotized plates (Fig. 20B) *B. spangleri*
- 24'. Posterior process of bursa copulatrix gradually narrowing apically (Fig. 18B); anterolateral processes not originating from sclerotized plates (Fig. 18B) *B. pilcopata*
- 25 (23'). Posterior process of bursa copulatrix triangular (Fig. 12B); anterolateral processes shorter than body of bursa copulatrix and curving outward at apices (Fig. 12B) *B. costaricensis*
- 25'. Posterior process of bursa copulatrix rectangular (Fig. 16B); anterolateral processes longer than body of bursa copulatrix and curving inward at apices (Fig. 16B) *B. venezuelensis*

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NEW SPECIES OF MICROCADDISFLIES (TRICHOPTERA:
HYDROPTILIDAE) FROM NORTHERN FLORIDASTEVEN C. HARRIS¹

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ABSTRACT

Seven new species of microcaddisflies, *Oxyethira chrysocara*, *Hydroptila eglinensis*, *H. bribriae*, *H. sarahae*, *H. okaloosa*, *H. hamiltoni* and *H. sykora* from northern Florida are described and illustrated. New figures for previously described species, *H. carolae*, *H. circangula* and *H. roberti*, are provided to facilitate identifications of the new species.

KEY WORDS: Trichoptera, Hydroptilidae, microcaddisflies, new species, Florida

INTRODUCTION

Ongoing collecting in spring-fed streams and other aquatic habitats in northern Florida by Manuel Pescador and Andrew Rasmussen of Florida A&M University have yielded several new species of caddisflies. In this paper, seven new microcaddisflies are described, one in the genus *Oxyethira* and six in the genus *Hydroptila*. With these new species, microcaddisflies in Florida now total 60 species (Pescador et al., 1995; Harris et al., 1998). The distribution of most of the new species is apparently restricted to small streams and springs on Eglin Air Force Base, an area of northern Florida noted for several endemic caddisflies (Harris et al., 1982; Gordon, 1984), three of which are microcaddisflies. Several of the new species are very similar to more widely occurring southeastern species, suggesting that this region of northern Florida may have contained isolated relict populations at some point in time. Terminology used in the descriptions follows that of Marshall (1979), with length measured from the tip of head to the wing end. Type material will be deposited at the National Museum of Natural History, Smithsonian Institution (NMNH), Carnegie Museum of Natural History (CMNH), Florida State Collection of Arthropods (FSCA), Illinois Natural History Survey (INHS), Clemson University Arthropod Collection (CUAC), Florida A&M University (FAMU), and Clarion University (CU).

SYSTEMATIC ENTOMOLOGY

Oxyethira chrysocara, new species

(Fig. 1)

Diagnosis.—In many respects, *Oxyethira chrysocara* is very similar to *O. dunbartonensis* Kelley from South Carolina and Georgia. Both species have reduced inferior appendages and elongate processes from the phallus apex, but the two species differ in the details of these structures. In *O. dunbartonensis* the phallic processes are membranous and linear, whereas in *O. chrysocara* they are sclero-

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Submitted 3 October 2001.

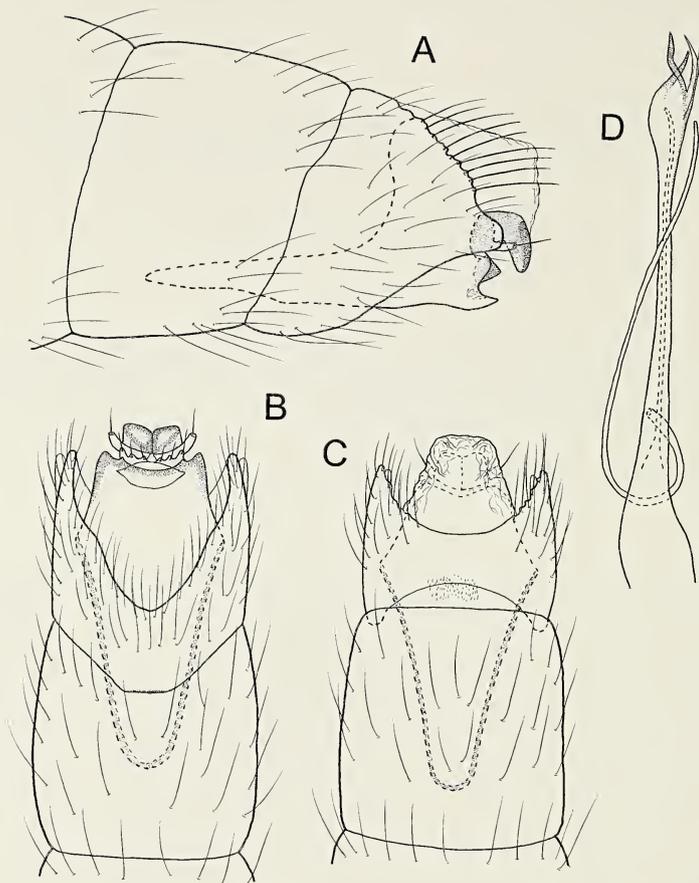


Fig. 1.—*Oxyethira chrysocara* new species, male genitalia: A. Lateral. B. Ventral. C. Dorsal. D. Phallus, lateral.

tized and curving; and the inferior appendages differ in the number of setiferous lobes, two in *O. dunbartonensis*, six in *O. chrysocara*. As well, the new species lacks the ventromesal process from abdominal segment VII, which is present in *O. dunbartonensis*. The species is known only from the type locality, a small headwater stream in Clay County.

Description.—Male. Length 2.4 mm. 25 antennal segments. Brown in alcohol. Abdominal segment VII annular in lateral view; emarginate posteriorly in ventral view, lacking ventromesal process. Segment VIII in lateral view narrowing posteromesally to truncate knob; deeply incised ventrally, shallowly emarginate dorsally. Segment IX in lateral aspect narrowing anteriorly, posterodorsally a thin bridge, posteroventrally narrowing to acute process; in ventral view tapering anteriorly, truncate posteriorly; dorsally fused with X. Segment X rectanguloid in lateral aspect; dorsally a membranous lobe, gradually tapering distally to truncate apex. Inferior appendages reduced to triangular knob on the inner surface of segment IX, thin in ventral view with numerous setiferous lobes along posterior margin. Subgenital plate tongue-like in lateral view and strongly downturned; in ventral view square, fused along mesal margin, narrow bilobed process ventrad. Phallus long and narrow with broad medial constriction; apical portion bulbous with pair of crossing sclerous fingerlike processes, elongate lip ventrally; long paramere at base of medial constriction and encircling shaft.

Type Specimens.—Holotype, ♂ (NMNH): **FLORIDA. Clay County:** Gold Head Branch near old mill crossing, 29°49'56"N, 81°56'45"W, 1 May 1998, A. Rasmussen.

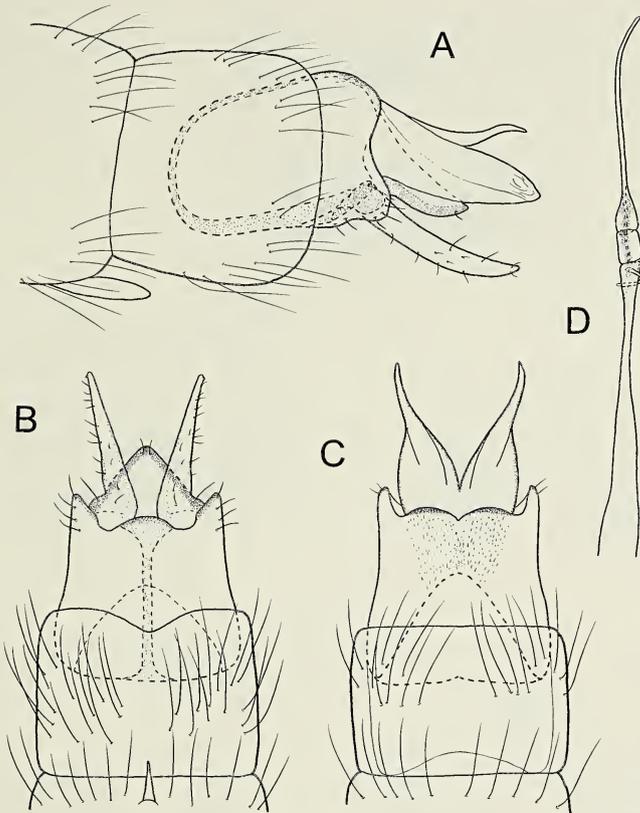


Fig. 2.—*Hydroptila eglinensis* new species, male genitalia: A. Lateral. B. Ventral. C. Dorsal. D. Phallus, ventral.

Etymology.—From the Greek “gold head,” referring to the type locality of the new species.

Hydroptila eglinensis, new species
(Figs. 2, 3A)

Diagnosis.—In many features, *H. eglinensis* is similar to *H. disgalera* Holzenthal and Kelley. Both species lack the eversible scent glands on the heads of the males, and genitalic features are similar. *Hydroptila eglinensis* is readily distinguished by the saberlike inferior appendages, which are clublike in *H. disgalera*. The new species is widely distributed in the coldwater streams on Eglin Air Force Base.

Description.—Male. Length 2.2–2.7 mm. 28 antennal segments. Head lacking eversible glands under the dorsal scent caps. Brown in alcohol. Abdominal segment VII annular with short posteromesal process from venter. Segment VIII annular; ventrally with slight emargination on posterior margin. Segment IX roughly rectangular in lateral aspect, rounded anteriorly, posteriorly with mesal emargination; square in ventral view, truncate anteriorly, posteriorly with wide mesal incision, elongate mesal sclerite internally; dorsum with wide incision on posterior margin. Segment X elongate and tapering distally in lateral view, fingerlike process from dorsum; dorsally with deep mesal excision, lateral lobes abruptly narrowing at midlength. Inferior appendages thin and tapering to slightly upturned apex in lateral view; triangular in ventral view, diverging apically. Subgenital plate triangular in lateral and ventral views, sclerous along posterior margin. Phallus elongate and tubular, composed of three sections; anterior section wide basally, bearing short paramere below juncture with short, tubular median section; distal portion about same length as basal portion, wide at juncture, slender apically.

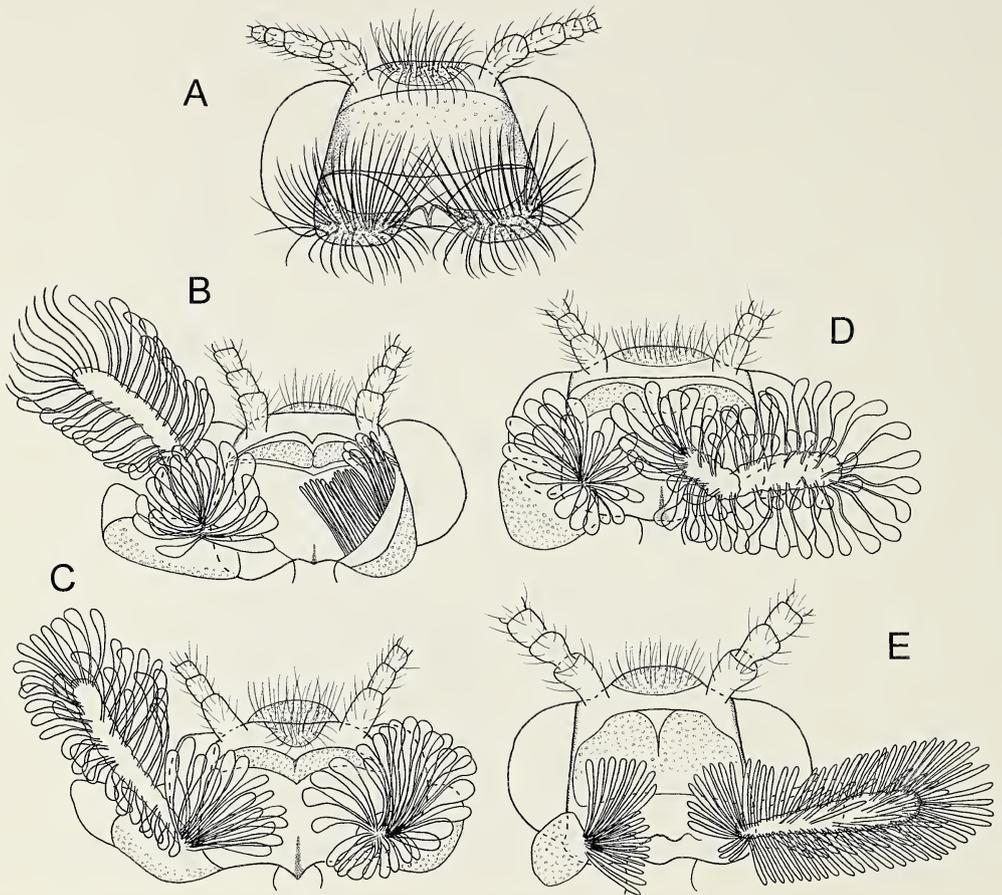


Fig. 3.—Eversible scent glands on heads of male *Hydroptila*: A. *Hydroptila eglinensis* new species. B. *Hydroptila bribriae* new species. C. *Hydroptila carolae* Holzenthal and Kelley. D. *Hydroptila sarahae* new species. E. *Hydroptila circangula* Harris.

Type Specimens.—Holotype ♂ (NMNH): **FLORIDA, Okaloosa County**: Rogue Creek, 0.6 km S Base Rd. 232, Eglin Air Force Base, 30°33'19"N, 86°34'51"W, 21 May 1998, M. Pescador, A. Rasmussen. Paratypes: **FLORIDA**. Same locality and data as holotype, 28 ♂ (10♂ NMNH, 10♂ CMNH, 4♂ INHS, 4♂ FSCA), same locality, but 28 October 1998, 3 ♂ (CU), Juniper Creek, at Base Rd. 221, Eglin Air Force Base, 1.3 km E State Rd. 85, 30°36'29"N, 86°31'24"W, 21 May 1998, M. Pescador, A. Rasmussen, 1 ♂ (CU), Juniper Creek at head, west side of Base Rd. 231, Eglin Air Force Base, SE Duke Field, 30°36'21" N, 86°30'05" W, 21 May 1998, M. Pescador, A. Rasmussen, 3 ♂ (CUAC), East Turkey Hen Creek at Base Rd. 601, Eglin Air Force Base, 30°39'27" N, 86°34'05" W, 28 October 1998, M. Pescador, A. Rasmussen, 2 ♂ (FAMU), East Turkey Hen Creek at head, 0.3 km W Okaloosa Lookout Tower, 30°38'48" N, 86°33'23" W, 25 May 1998, M. Pescador, A. Rasmussen, 13 ♂ (5♂ NMNH, 5♂ CMNH, 3♂ INHS), unnamed tributary to Turkey Creek at Base Rd. 634, Eglin Air Force Base, 30°35'29" N, 86°35'58" W, 27 October 1998, M. Pescador, A. Rasmussen, 4 ♂ (2♂ CUAC, 2♂ FAMU).

Etymology.—From Eglin, in reference to this species occurring on Eglin Air Force Base.

Hydroptila bribriae, new species

(Figs. 3B, 4A–D)

Diagnosis.—This species and the following can be grouped with *H. carolae* Holzenthal and Kelley and *H. circangula* Harris on the basis of genitalic features.

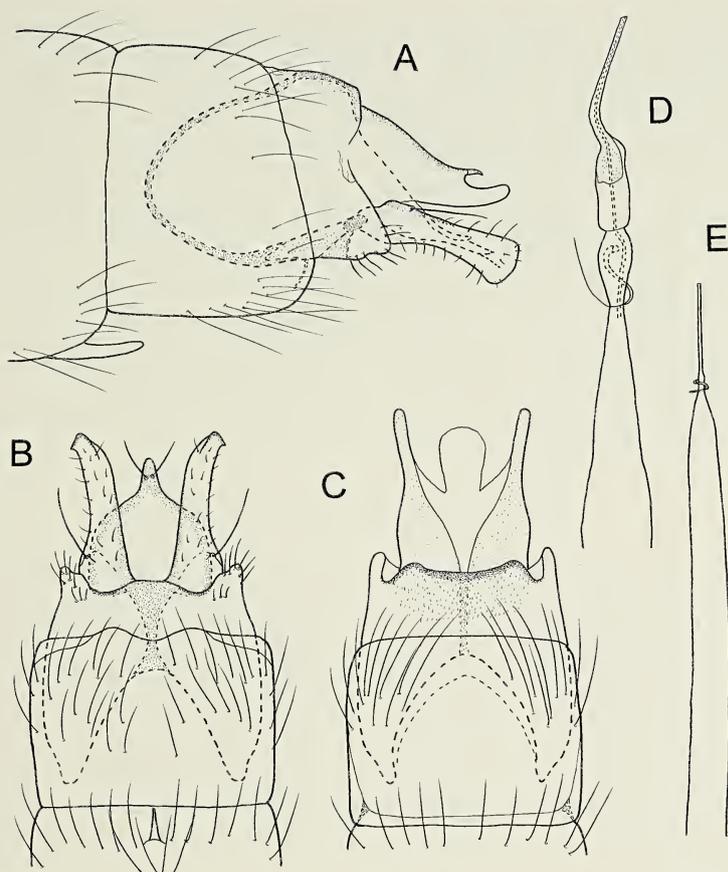


Fig. 4.—*Hydroptila bribriæ* new species, male genitalia: A. Lateral. B. Ventral. C. Dorsal. D. Phallus, ventral. E. *Hydroptila carolæ* Holzenthal and Kelley, phallus, ventral.

All four have the subgenital plate ending in a nipplelike projection; all four have club-shaped inferior appendages; and all have a similar phallic structure. The species are separated by a combination of genitalic structures, and the structure of scent glands on the head. *Hydroptila bribriæ* is separated from *H. carolæ* by phallic structure, which in the latter is much more elongate basally (Fig. 4E), and from both *H. carolæ* and *H. circangula* by the scent glands of the head. The filaments of these glands are pipelike in both *H. bribriæ* (Fig. 3B) and *H. carolæ* (Fig. 3C), and linear in *H. circangula* (Fig. 3E). However, in *H. bribriæ* the filaments at the end of the eversible lobes are replaced by elongate hairs. *Hydroptila bribriæ* was widely distributed across Eglin Air Force Base.

Description.—Male. Length 2.2–2.7 mm. 30 antennal segments. Eversible scent glands of head with elongate pipe-shaped filaments, except at tip where replaced with long hairs. Brown in alcohol. Abdominal segment VII annular with short posteromesal process from venter. Segment VIII annular; ventrally with slight emargination on posterior margin. Segment IX roughly rectangular in lateral aspect, rounded anteriorly, posteriorly with mesal emargination; in ventral view, deeply incised anteriorly, posteriorly with wide, shallow incision mesally, narrow internal mesal sclerite; dorsum with thin lateral lobes posteriorly. Segment X elongate and tapering distally in lateral view, central lobe appearing as short fingerlike process from dorsum; dorsally trifold, with elongate lateral lobes narrowing abruptly at midlength,

mesal lobe membranous and round. Inferior appendages club-shaped in lateral view, widening towards apex; roughly rectanguloid in ventral view, diverging apically, sclerotized point on outer apical margin, elongate seta from basal margin. Subgenital plate triangular in lateral view; in ventral view rounded basally, apex narrowing mesally to nipplelike projection bearing pair of stout setae. Phallus tubular, composed of two sections; anterior section wide basally, bearing short paramere below juncture with posterior section, which is tubular at base, then narrowing abruptly to slender curved apex.

Type Specimens.—Holotype ♂ (NMNH): **FLORIDA. Santa Rosa County:** Indigo Creek, at Base Rd. 213, Eglin Air Force Base, 19 March 1998, M. Pescador, A. Rasmussen. Paratypes: **FLORIDA.** Same locality and data as holotype, 5 ♂ (3♂ NMNH, 2♂ CMNH). **Okaloosa County:** Juniper Creek, at Base Rd. 221, Eglin Air Force Base, 1.3 km E State Rd. 85, 30°36'29"N, 86°31'24"W, 21 May 1998, M. Pescador, A. Rasmussen, 17 ♂ (5♂ CMNH, 3♂ FSCA, 3♂ CUAC, 3♂ CU, 3♂ INHS), same, but 19 March 1998, 2 ♂ (FAMU), Juniper Creek at head, west side of Base Rd. 231, Eglin Air Force Base, SE Duke Field, 30°36'21" N, 86°30'05" W, 21 May 1998, M. Pescador, A. Rasmussen, 1 ♂ (CU), East Turkey Hen Creek at head, 0.3 km W Okaloosa Lookout Tower, 30°38'48" N, 86°33'23" W, 25 May 1998, M. Pescador, A. Rasmussen, 1 ♂ (FAMU). **Walton County:** Rocky Creek, at headwaters, Eglin Air Force Base, 25 April 1979, J. Scheiring, 3 ♂ (2♂ CMNH, 1♂ NMNH).

Etymology.—Named for Briana Kriebel, affectionately nicknamed "bribri" and "bug" by her family, in recognition of the Kriebel family's support of Clarion University.

Hydroptila sarahae, new species
(Figs. 3D, 5)

Diagnosis.—This species appears to be closest to *Hydroptila circangula* Harris, on the basis of genitalic features. The appearance of the inferior appendages and the phallus are nearly identical, but subtle differences can be found. Both have the subgenital plate ending in a nipplelike projection, but this projection is much longer in the new species, and although the inferior appendages are similar in ventral aspect, an elongate seta at midlength is present in *H. sarahae*, but absent in *H. circangula*. The new species can also be separated by the arrangement of the scent glands on the head, which have linear filaments in *H. circangula* (Fig. 3E) as compared to the pipe-shaped filaments of *H. sarahae* (Fig. 3D). As with the previous two species, *H. sarahae* is widely distributed in the streams on Eglin Air Force Base.

Description.—Male. Length 2.0–2.5 mm. 26 antennal segments. Eversible scent glands of head with elongate pipe-shaped filaments. Brown in alcohol. Abdominal segment VII annular with short posteromesal process from venter. Segment VIII annular. Segment IX roughly rectangular in lateral aspect, rounded anteriorly, posteriorly with slight ventral emargination; in ventral view, deeply incised anteriorly, posteriorly with pair of lateral incisions, narrow mesal sclerite; dorsum truncate posteriorly. Segment X elongate and hoodlike in lateral view; dorsally with deep mesal incision posteriorly, lateral margins sclerous. Inferior appendages boat-shaped in lateral view, widening to rounded apex; triangular in ventral view, diverging distally with apices rounded, elongate seta laterally at midlength. Subgenital plate elongate and slender in lateral view; in ventral view triangular, apex narrowing mesally to long nipplelike projection bearing pair of stout setae. Phallus tubular, evenly divided into two sections; anterior section wide basally, bearing short paramere below juncture with posterior section, which is wide and tubular basally, with slender ejaculatory duct protruding apically.

Type Specimens.—Holotype ♂ (NMNH): **FLORIDA. Okaloosa County:** Rogue Creek, 0.6 km S Base Rd. 232, Eglin Air Force Base, 30°33'19"N, 86°34'51"W, 21 May 1998, M. Pescador, A. Rasmussen. Paratypes: **FLORIDA.** Same locality and data as holotype, 15 ♂ (6♂ NMNH, 6♂ CMNH, 3♂ INHS), same locality, but 28 October 1998, 4♂ (CU), Rogue Creek at Base Rd. 233, Eglin Air Force Base, 14 August 1985, B. Armitage, 2 ♂ (CU), Juniper Creek, at Base Rd. 221, Eglin Air Force Base, 1.3 km E State Rd. 85, 30°36'29"N, 86°31'24"W, 21 May 1998, M. Pescador, A. Rasmussen, 1 ♂ (CUAC), East Turkey Hen Creek at head, 0.3 km W Okaloosa Lookout Tower, 30°38'48" N, 86°33'23", 21 May 1998, M. Pescador, A. Rasmussen, 1 ♂ (FSCA), East Turkey Hen Creek at Base Rd. 601, Eglin Air Force Base, 30°39'27" N, 86°34'05" W, 26 October 1998, M. Pescador, A. Rasmussen, 1 ♂ (FAMU), Turkey Creek at Base Rd. 232, Eglin Air Force Base, 30°33'42" N, 86°32'10" W, 27 October 1998, M. Pescador, A. Rasmussen, 2 ♂ (FSCA), Turkey Creek at Base Rd. 232, Eglin Air Force Base, 30°33'42" N, 86°32'10" W, 21 May 1998, M. Pescador, A. Rasmussen, 2 ♂ (CUAC), Turkey Creek at Base Rd. 233, Eglin Air Force Base, 19 August 1983, B. Armitage, 47♂ (14♂ NMNH,

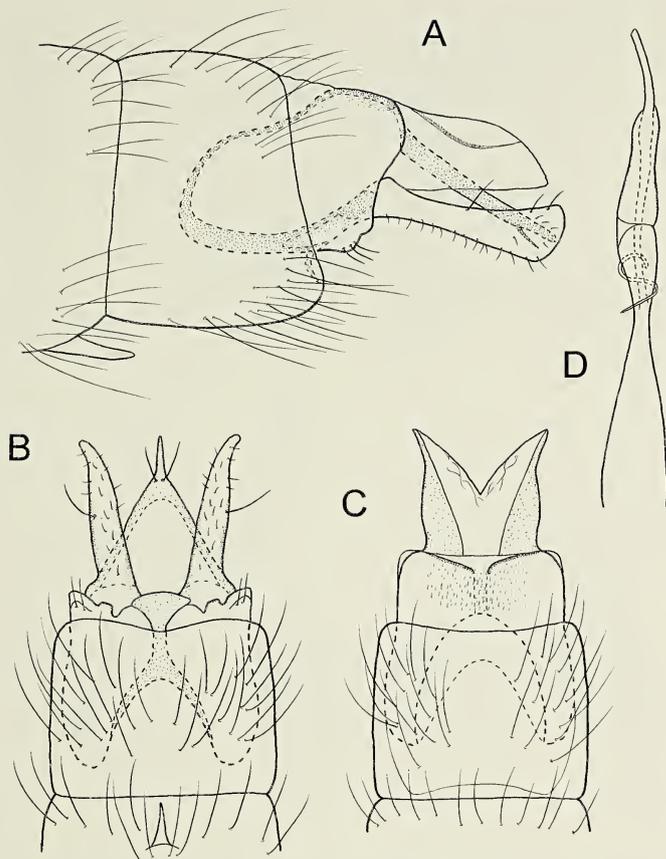


Fig. 5.—*Hydroptila sarahae* new species, male genitalia: A. Lateral. B. Ventral. C. Dorsal. D. Phallus, ventral.

13♂ CMNH, 10♂ INHS, 10♂ FAMU), unnamed tributary to Turkey Creek at Base Rd. 619, Eglin Air Force Base, 14 August 1985, B. Armitage, 11 ♂ (4♂ FSCA, 4♂ CUAC, 3♂ CU).

Etymology.—Named for my daughter Sarah on the occasion of her 21st birthday.

Hydroptila okaloosa, new species

(Fig. 6)

Diagnosis.—*Hydroptila okaloosa* bears some resemblance to *H. pecos* Ross and *H. ajax* Ross in the shape of the downturned inferior appendages, but the large, bulbous segment X is more similar to that of *H. protera* Ross. The new species is quite distinctive, particularly in the appearance of the phallic apex, but the combination of the ventrad curving inferior appendages and deeply incised tenth tergum will also separate *H. okaloosa*. Despite widespread collecting in the streams of Eglin Air Force Base, *H. okaloosa* was only found in Rogue Creek.

Description.—Male. Length 2.9–3.1 mm. 30 antennal segments. Eversible scent glands of head with long pipe-shaped filaments, except at tip where replaced with long hairs (as in Fig. 3B). Brown in alcohol. Abdominal segment VII annular with short posteromesal process from venter. Segment VIII tapering posteroventrally in lateral aspect, setose lobe posterodorsally; ventrally with mesal incision on posterior margin; rectanguloid dorsally. Segment IX short, largely contained within VIII, rounded

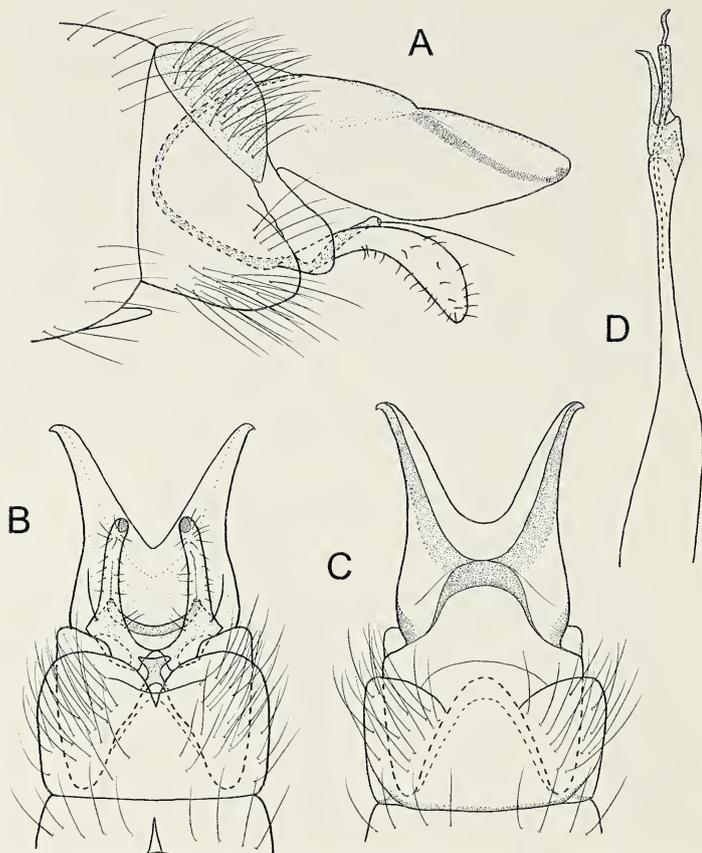


Fig. 6.—*Hydroptila okaloosa* new species, male genitalia: A. Lateral. B. Ventral. C. Dorsal. D. Phallus, ventral.

anteriorly; in ventral view deeply incised anteriorly, posteriorly with wide emargination; dorsum narrowing to rounded lobe which is apparently fused with X. Segment X elongate and bulbous in lateral view, sclerotized band dorsolaterally; in dorsal view deeply emarginate, lateral extensions tapering distally to acute out-turned apices, outer margins sclerous. Inferior appendages enlarged distally and downturned in lateral view; ventrally long and fingerlike, contiguous basomesally, inner margins slightly concave. Subgenital plate long and thin in lateral aspect, bearing elongate seta apically; ventrally a thin, narrow shelf, emarginate and sclerous on posterior margin. Phallus tubular, apex divided into two elongate processes, outer process curved at apex, inner process rectangular and bearing ejaculatory duct which protrudes apically; paramere absent.

Type Specimens.—Holotype ♂ (NMNH): **FLORIDA. Okaloosa County**: Rogue Creek, 0.6 km S Base Rd. 232, Eglin Air Force Base, 30°33'19"N, 86°34'51"W, 21 May 1998, M. Pescador, A. Rasmussen. Paratype: **FLORIDA**. Same locality as holotype, but 7 April 1999, 1 ♂ (CMNH).

Etymology.—Named for the type locality in Okaloosa County.

Hydroptila hamiltoni, new species
(Fig. 7A–D)

Diagnosis.—In overall genitalic features, this new species is nearly identical to *H. roberta* Hamilton and Holzenthal from Georgia. Only the structure of the phallus will serve to separate the two species; in *H. roberta* (Fig. 3E) the basal and apical sections of the phallus are the same length, with the phallic apex

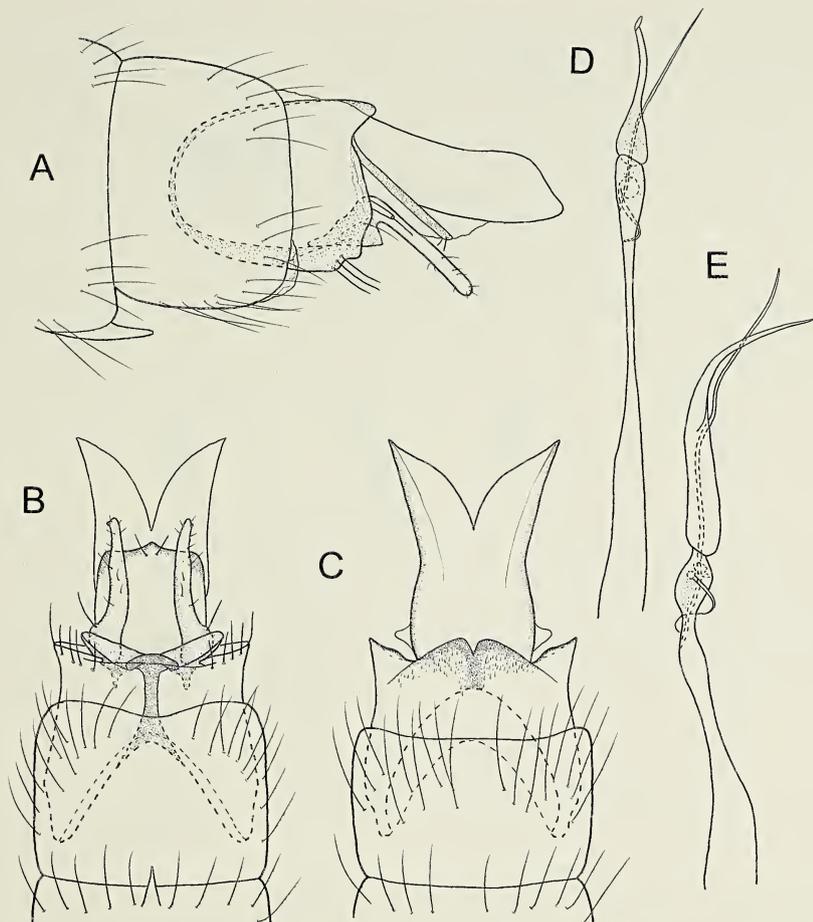


Fig. 7.—*Hydroptila hamiltoni* new species, male genitalia: A. Lateral. B. Ventral. C. Dorsal. D. Phallus, ventral. E. *Hydroptila roberta* Hamilton and Holzenthal, phallus, ventral.

elongate and thin, while in *H. hamiltoni*, the basal section of the phallus is about four times the length of the apical section, with the phallic apex short. The new species was widely distributed in the streams on Eglin Air Force Base.

Description.—Male. Length 2.5–2.8 mm. 27 antennal segments. Eversible scent glands of head with elongate pipelike filaments, except at tips (as in Fig. 3B). Brown in alcohol. Abdominal segment VII annular with short posteromesal process from venter. Segment VIII annular. Segment IX in lateral aspect rounded anteriorly, posteriorly with dorsal protuberance; ventrally with deep mesal incision anteriorly, truncate posteriorly; dorsum lobate posteromesally with narrow incision. Segment X elongate and bulbous in lateral view; narrow dorsally with deep mesal excision posteriorly. Inferior appendages thin and nearly parallel-sided in lateral view, strongly curved at base which bears thin setiferous lobe; in ventral view elongate and narrow, tapering distally with sclerotized lateral point at apex, widely separated basally. Subgenital plate long and slender in lateral view; ventrally a thin, narrow shelf, emarginate and sclerous on posterior margin. Phallus elongate and tubular, distal portion about $\frac{1}{4}$ length of basal portion, widening at juncture, narrowing apically to recurved tip; short paramere encircling shaft below juncture of sections.

Type Specimens.—Holotype ♂ (NMNH): **FLORIDA, Okaloosa County**: Rogue Creek, 0.6 km S Base Rd. 232, Eglin Air Force Base, 30°33'19"N, 86°34'51"W, 21 May 1998, M. Pescador, A. Rasmussen. Paratypes: **FLORIDA**. Same locality and data as holotype, 13 ♂ (5♂ NMNH, 4♂ CMNH,

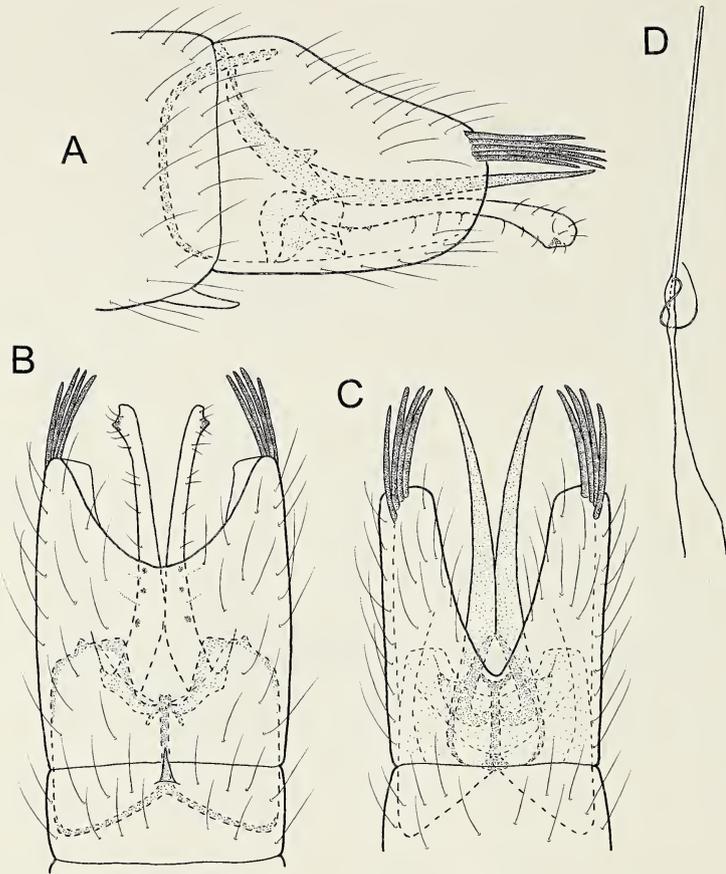


Fig. 8.—*Hydroptila sykorai* new species, male genitalia: A. Lateral. B. Ventral. C. Dorsal. D. Phallus, ventral.

4♂ INHS), Juniper Creek, at Base Rd. 221, Eglin Air Force Base, 1.3 km E State Rd. 85, 30°36'29"N, 86°31'24"W, 21 May 1998, M. Pescador, A. Rasmussen, 6♂ (2♂ FAMU, 2♂ CUAC, 2♂ CU), East Turkey Hen Creek at head, 0.3 km W Okaloosa Lookout Tower, 30°38'48" N, 86°33'23" W, 25 May 1998, M. Pescador, A. Rasmussen, 3♂ (2♂ FAMU, 1♂ FSCA).

Etymology.—Named for Steven W. Hamilton, co-describer of *H. roberta*, in recognition of his many contributions to the study of caddisflies.

***Hydroptila sykorai*, new species**
(Fig. 8)

Diagnosis.—This new species is very similar in overall appearance to *Hydroptila ouachita* Holzenthal and Kelley, which is apparently endemic to Schoolhouse Spring, a small artesian spring, in Louisiana (Holzenthal and Kelley, 1983). Both species have heavy spines from the margins of abdominal segment VIII, but while these spines are short and curved inward in *H. ouachita*, they are much longer and straight in *H. sykorai*. Both species also have abdominal segment X divided distally, but in *H. ouachita* this division is shallow, whereas in *H. sykorai* it is very deep, creating a pair of narrow rods. The locality of this new species is a small, cold, sand-bottom springrun.

Description.—Male. Length 1.9–2.3 mm. 28 antennal segments. Eversible scent glands of head with elongate pipe-shaped filaments (as in Fig. 3B). Brown in alcohol. Abdominal segment VII annular with short posteromesal process from venter. Segment VIII in lateral view elongate and tapering distally; deeply emarginate dorsally, with series of stout elongate spines from posterolateral margins; posterior margin with shallow mesal incision ventrally. Segment IX short, retracted within segments VII and VIII; narrowing dorsally in lateral view; in dorsal and ventral views square, with deep, rounded mesal incision posteriorly and shallow incision anteriorly. Segment X elongate and thin in lateral view; dorsally with deep mesal incision distally, creating acute, sclerous lateral rods. Inferior appendages long and thin in lateral view, widening to rounded apex distally; thin in ventral view, diverging distally with apices rounded and bearing darkened point laterally. Subgenital plate not evident. Phallus very narrow and tubular, with thin paramere encircling shaft near midlength.

Type Specimens.—Holotype male. **FLORIDA, Gadsden County**: headwaters of Quincy Creek, 7 km N Quincy at Florida A&M Research and Extension Center, 30°39'27" N, 84°36'50" W, 7 June 1999, A. Rasmussen, emergence trap (NMNH). Paratypes: **FLORIDA**. Same locality as holotype, but 17 January 1998, 1 ♂ (CMNH), same, but 20 March 1999, 1 ♂ (FAMU), same, but 4 April 1999, 1 ♂ (INHS), same, but 21 June 1999, 1 ♂ (CUAC).

Etymology.—Named for Jan Sykora, friend and colleague, in recognition of his contributions to the study of caddisflies.

ACKNOWLEDGMENTS

Appreciation is expressed to Manny Pescador and Andy Rasmussen of Florida A&M University for allowing me to examine microcaddisflies in their collections from northern Florida and for reviewing the resultant manuscript. John Morse of Clemson University kindly lent paratypes of *Hydroptila roberti*, *H. carolae*, and *H. ouachita* for examination. Brian Armitage of the Ohio Biological Survey and Joseph Scheiring provided some material from their collections on the Eglin Air Force Base. The comments of the anonymous manuscript reviewers and editors at the Carnegie Museum of Natural History are also greatly appreciated.

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*FROM THE ARCHIVES AND COLLECTIONS*A MIOCENE BONE BED FROM AGATE FOSSIL BEDS
NATIONAL MONUMENTW. ORR GOEHRING¹ AND MARY R. DAWSON²

"In 1904 a field party of the Carnegie Museum, the writer in charge, was extremely fortunate in discovering what will undoubtedly prove to be one of the most important quarries of fossils as yet discovered in the Miocene of North America" (Peterson, 1906). So begins former field collector for Carnegie Museum O. A. Peterson's account of the discovery of Agate Spring Fossil Quarry, located on the Upper Niobrara River in Sioux County, Nebraska.

Peterson's claim that the quarry's discovery was "extremely fortunate" is no exaggeration. The quarry may never have been discovered at all had it not been for the curious eye of James H. Cook, owner of the Agate Springs Ranch. In 1885, two years before he purchased the ranch from his father-in-law, Cook spotted some bone fragments scattered under a rock shelf near the ranch house (United States National Park Service, 1980). Not certain of the origin of the bones or their significance, Cook did not report the find until after he and his wife Kate bought the ranch from Dr. Elisha B. Graham in 1887 (United States National Park Service, 1980).

Though he provides a different date for the discovery of the bone fragments, Peterson (1906) gives a similar account of Cook's find, and he goes on to describe the enthusiasm with which he and other members of the Carnegie Museum field party began their initial excavation:

In 1890 Mr. James H. Cook, on whose property the Agate Spring Fossil Quarry is located, discovered many small bones and fragments in the talus from the fossil-bearing stratum from the hills, in which the quarry is located. Very naturally he thought that the bones were those of Indians interred together with their horses. Mr. Cook accompanied me to this place in August, 1904. Realizing that this was a discovery of much paleontological promise we immediately began work on the deposits and resumed work early in the season of 1905.

According to Peterson (1906), Cook began his own excavation of the site in the fall of 1904. Anxious to preserve the specimens using the most modern methods, Peterson wrote Cook a letter asking him to refrain from his work until a party from the Carnegie Museum could return to the site in the spring of 1905. Cook complied with the request, and excavation resumed in April of 1905 (Fig. 1). Peterson (1906) writes:

¹ Managing Editor, Scientific Publications.

² Curator, Section of Vertebrate Paleontology.



Fig. 1.—O. A. Peterson excavating at Carnegie Hill in Agate Fossil Beds, Sioux County, Nebraska, circa 1909. Section of Vertebrate Paleontology photo archives, negative no. 6.

During the season of 1905 the party uncovered an area of 45×20 feet in the quarry. This area was plotted out in squares five feet in dimension, and a diagram was made representing this arrangement. The bones are found mostly disarticulated, much mixed, and thickly distributed through this layer of sandstone. It was soon discovered that the most intelligent way in which to secure this tangled mass of material was to take out blocks of sandstone which contain the fossils.

Fossils of the rhinoceros *Menoceros* were the most abundant in the excavation area that became known as Carnegie Hill, followed by those of the large entelodont *Dinohyus* and the chalicothere *Moropus*. One of the slabs containing this jumble of bones has been kept together as a bone bed, preserving the fossils just as they were found in the sandstone block collected by Peterson and his team.

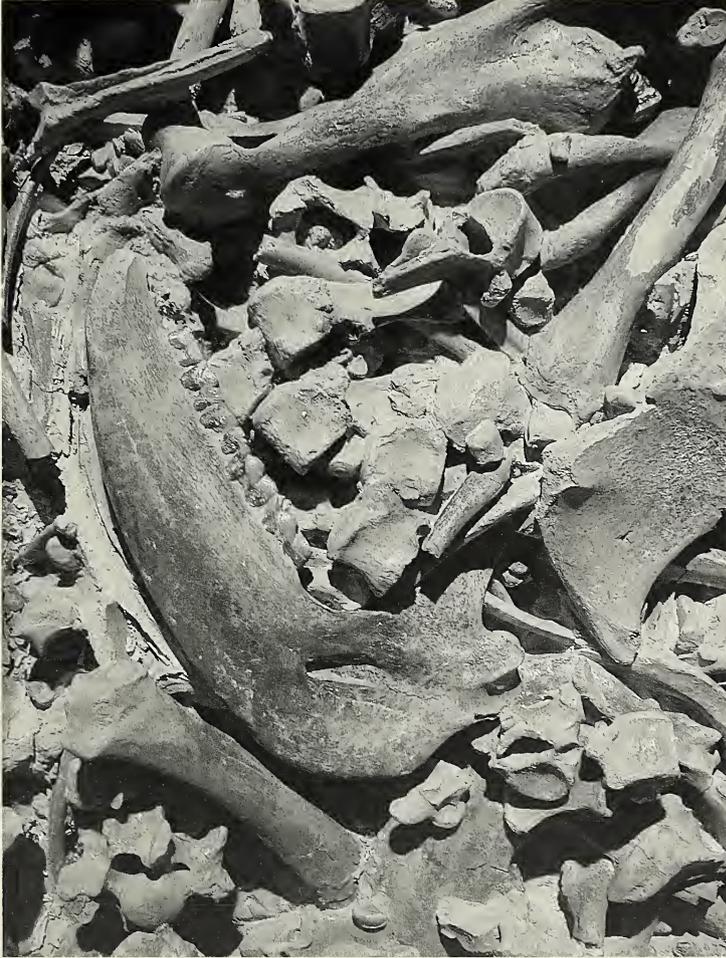


Fig. 2.—A small section of the Early Miocene Bone Bed from Agate Fossil Beds, Sioux County, Nebraska. The bone bed, newly renovated for exhibit in 2001, measures approximately 4 × 8.5 feet. Photograph by Norman Wuerthele, CMNH.

The newly renovated block (Fig. 2), one of the most impressive specimens from the quarry, contains hundreds of dissociated bones, probably carried to their place of deposition by moving water.

The locality that Peterson (1906) described as “one of the most important quarries of fossils as yet discovered” has proven to be just that: in 1965 the United States Congress designated the quarry and the area surrounding it along the Niobrara River Agate Fossil Beds National Monument.

Acknowledgments: Elizabeth A. Hill and Norman Wuerthele, CMNH, contributed to the preparation of figures 1 and 2, respectively.

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COMPARING POTTERY FROM THE PROTO-HISTORIC McKEES ROCKS VILLAGE AND EISIMINGER SITES OF SOUTHWESTERN PENNSYLVANIA

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Staff Archaeologist/Archaeology Collection Manager, Section of Anthropology

ABSTRACT

Comparison of pottery from two Proto-historic sites in southwestern Pennsylvania, McKees Rocks Village and Eisiminger, disclosed important differences. McKees Rocks Village, occupying a prominent Ohio River escarpment in Allegheny County, produced distinctive pottery featuring decorated added rim-strips and simple stamping, while cordmarked Eisiminger pottery had lips that were scalloped or impressed in their interior by cord-wrapped paddle impressions applied perpendicularly to the lip. It is hypothesized that Eisiminger, located on a hill in Greene County, represented remnant Monongahela populations, whereas McKees Rocks Village was established by an intrusive people with affinities to Wellsburg Phase sites in Ohio and West Virginia. It is also suggested that the Wellsburg Phase people may have been of Iroquoian origin, based on discussed artifacts.

KEY WORDS: Proto-historic, rim-strips, Foley Farm Phase, Wellsburg Phase

INTRODUCTION

The McKees Rocks Village site, 36 AL16, and the George Eisiminger site, 36GR2, are Proto-historic sites located 67 km apart in southwestern Pennsylvania (Figs. 1:1&2). Pottery indicates the sites had dissimilar antecedents in spite of their proximity and apparent contemporaneous occupation. The purposes of this paper are to review the archaeological contexts of the two sites, describe and compare their pottery forms in order to illustrate the differences, and discuss the cultural affiliations of the inhabitants of the sites. The McKees Rocks Village site and the George Eisiminger site were occupied at a critical span of time for the Upper Ohio Valley region of North America, which in succeeding years came to be abandoned by Native Americans for almost a century.

THE SITES

The McKees Rocks Village Site

The McKees Rocks Village site was located on the south side of the Ohio River about 4.8 km downstream (northwest) of its origin at the confluence of the Allegheny and Monongahela rivers (Fig. 2). It was situated a short distance from the mouth of Chartiers Creek, a mainly northward flowing stream that drains approximately 834 square km. Anyone traveling down Chartiers Creek and entering the Ohio River would immediately confront Brunot Island, a locality that would have provided the site inhabitants with access to riverine resources since the channel between the island and the mainland was relatively shallow except during early spring flooding. The McKees Rocks Village site was elevated 24 m above the Ohio River, on a high terrace providing a commanding view of the surrounding area.

Submitted 3 September 2001.



Fig. 1.—Map of U.O.V. with archaeological sites referred to in text. 1. McKees Rocks Village, 36AL16. 2. Eisiminger, 36GR2. 3. Foley Farm, 36GR52. 4. Household, 36WM61. 5. Johnston, 36IN2. 6. Georgetown, 36BV29. 7. Lang, 36WH48. 8. Portman, 36AL40. 9. Sony, 36WM151. 10. Throckmorton, 36GR160. 11. Wellsburg, 46BR2. 12. Godwin-Portman, 36AL9.



Fig. 2.—Portion of U.S.G.S. Pittsburgh West Quadrangle (1948) showing location of the McKees Rock Village site, 36AL16.

The area occupied by the McKees Rocks Village site was referred to as “Fort Hill” on a map prepared by George Mercer for the Ohio Company in 1753 (Brown 1959:Pl. 17). Mercer also noted that:

There had been an Indian Fort there some years ago. The ditch is now to be seen. There the Indians always fled upon an Alarm as it was reckoned the strongest Fort they had. Several thousands have lost their lives in the Attack of it but was never taken (Brown, 1959:Pl. 17).

Also located on the same terrace was the McKees Rocks Mound, 36AL6, exca-

vated by Carnegie Museum of Natural History (CMNH) in 1896 (Mayer-Oakes, 1955:145–153).

The ceramic artifacts (and some triangular points) used in this analysis were recovered by William Buker during a 1958–64 salvage excavation of the McKees Rocks Village site. Buker's work was hampered by factors such as vandalism, past disturbance of the general area containing the dwellings and a cemetery, and the lack of excavation continuity stemming from seasonal shutting down of the fieldwork (Buker, 1968:3–4). The important assemblage of artifacts Buker managed to salvage, despite these deterrents, provided the basis for the recent attribution of the McKees Rock Village site to the Wellsburg Phase (Carskadden and Morton, 2000:183). Buker (1968:46–49) recognized that McKees Rocks had affinities to the Wellsburg and Riker sites of Fort Ancient. Buker's (1968:3–49) report in *Pennsylvania Archaeologist* was followed by reports by Lang (1968:50–80) on "The Natural Environment and Subsistence Economy of the McKees Rocks Village Site," and Jones (1968:81–86) on "Corn from the McKees Rocks Village site." Thus, Buker and his colleagues provided important contributions to the prehistory of the Upper Ohio Valley even though much of the site they excavated had been destroyed before their work began.

The sole radiocarbon date for the McKees Rocks Village site was obtained from wood charcoal submitted in 1968 by Don Dragoo to the University of Michigan Radiocarbon Laboratory. A date of 620 ± 100 B.P., Cal. A.D. 1354 (M-2201) was obtained (James B. Griffin, letter to Dragoo, 5/21/69). This assay, from an unknown on-site provenience, is too early for the Wellsburg Phase artifacts herein discussed. The date might relate to an earlier Late Prehistoric occupation since most southwestern Pennsylvania sites were utilized more than once during that period (George, 1983; Buker, 1993; Eisert, 1993).

The genesis of the theory for the Proto-Historic age of the Wellsburg component of the McKees Rocks Village site came from James Morton (personal communication, 1995), who developed his idea while examining comparable pottery from known A.D. 17th century sites in Ohio and West Virginia. After subsequent conversations with Buker, the author re-examined CMNH catalog listings of metal scraps found during the 1958–64 excavation. The results are that one brass bead (Fig. 3A) and four brass scraps (Fig. 3B) were recorded from three units—Features 32, 36 and 41. Further supporting a Proto-historic locus at the McKees Rocks Village site are another piece of scrap brass (Fig. 3C) and a brass arrow point (Fig. 3D) recovered by Donald Tanner from old spoil piles.

CMNH curates a small collection of artifacts from the Wellsburg site, 46Br2, donated by W. Singer in 1954. Among the 51 artifacts are 23 shell tempered rim sherds that feature sub-lip decoration like those found at the McKees Rocks Village site. When viewed by the author in 1993, the Wellsburg site (Fig. 1:11) appeared to be severely impacted by commercial development.

The George Eisiminger Site

The George Eisiminger site, 36GR2, is located at an elevation of 366 m on a hill in Greene County (Fig. 1:2). Originally it was recorded as the Jesse Lapping site. The Eisiminger site occupies the southwestern slope of the hill (Fig. 4), but its extent and exact boundaries are difficult to discern because the field has not been plowed for many years. A spring-head and an unnamed run are situated 25 m to the southeast; Smith Creek, a north-flowing, fourth order stream, lies 1.2

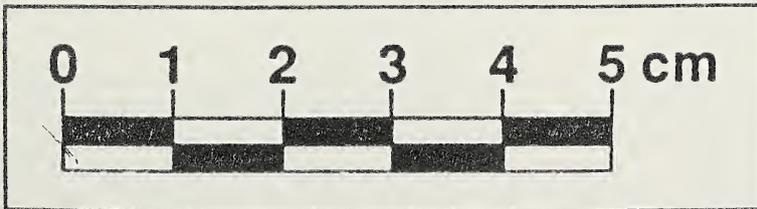
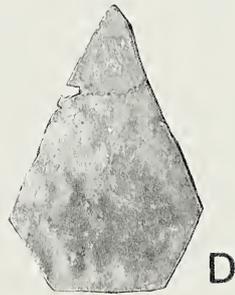
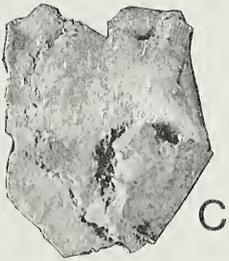
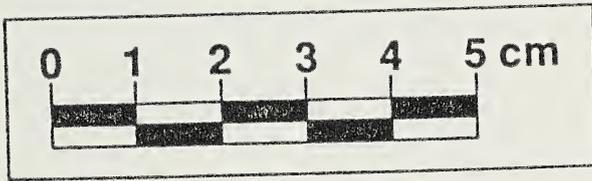
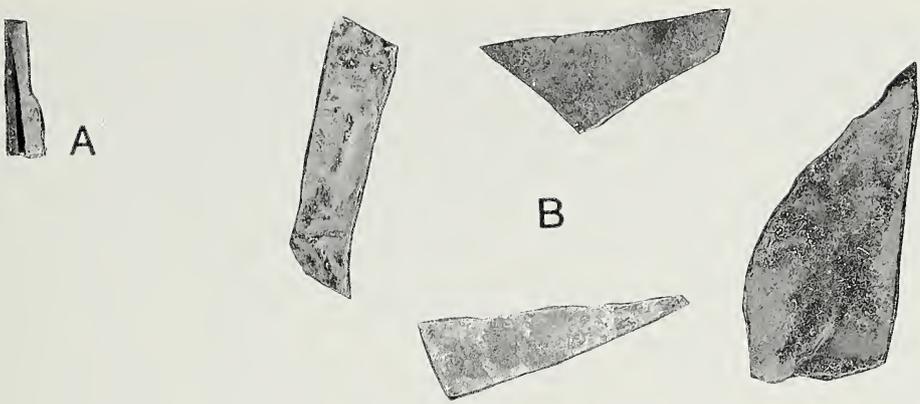


Fig. 3.—Proto-historic artifacts from the McKees Rocks Village site excavated by Buker. A. Brass bead. B. Brass scraps. C. Brass scrap, donated by Tanner. D. Brass arrowhead, donated by Tanner.

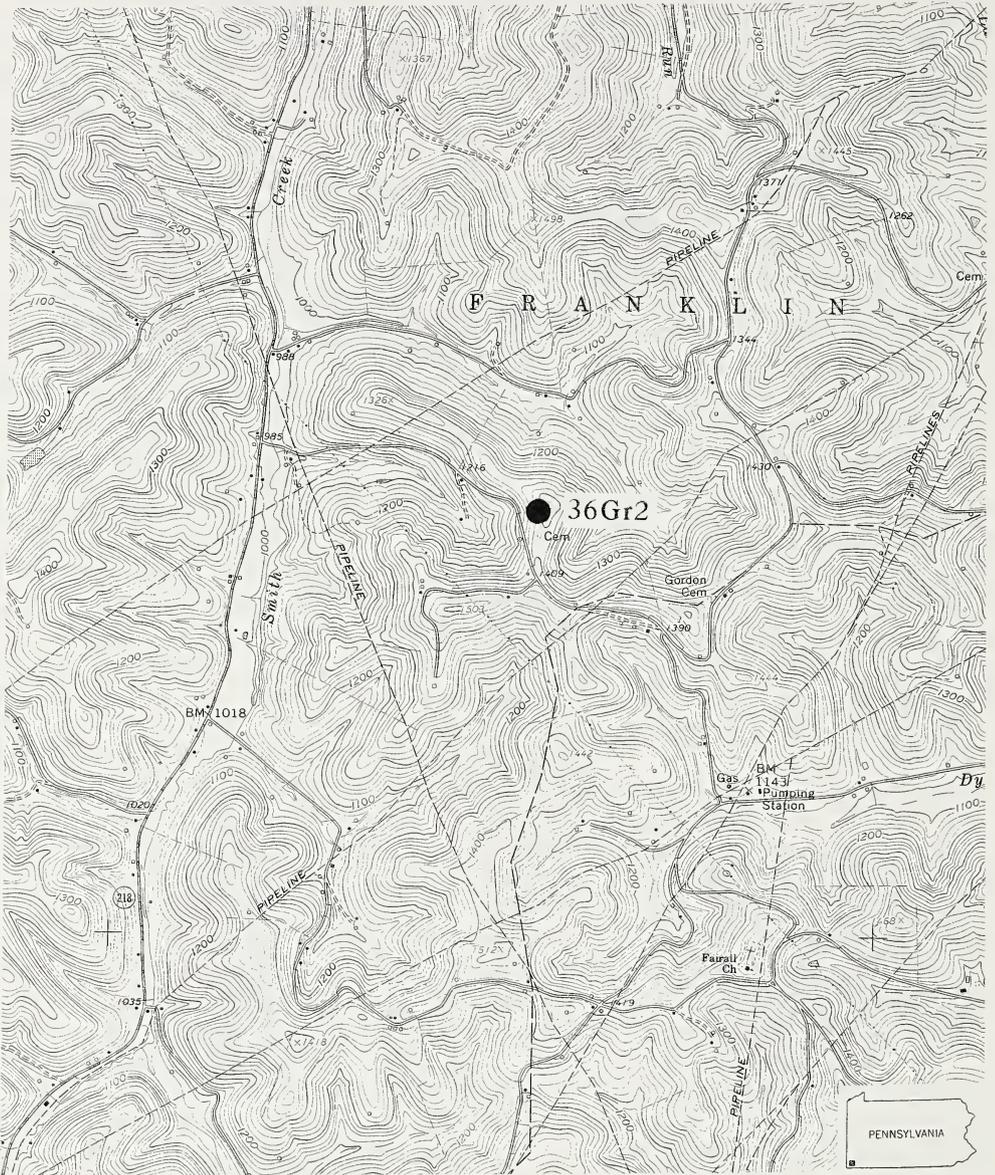


Fig. 4.—Portion of U.S.G.S. Oak Forest Quadrangle (1973) showing location of the Eisiminger site, 36GR2.

km to the west (Fig. 4). Mayer-Oakes (1955:122) first called attention to the Eisiminger site as one of "... at least five sites that are clustered in an area just south of Waynesburg, PA. ..." that produced "... [a] fair amount of European trade material ...". CMNH possesses a small amount of surface collected artifacts from the Eisiminger site; a much larger assemblage is curated at the Paul R. Stewart Museum, Waynesburg College.

The Eisiminger site artifacts at Waynesburg College were excavated by Paul

Stewart in the early 1950s. In an unpublished manuscript entitled "Excavation of Pottery House" (see Appendix), Stewart (n.d.:2) described a structure that "... was approximately 18 feet long by 12 feet wide, almost rectangular, and the main floor almost completely paved with small stones ranging from 2 to 3 square inches to 50 or 50 square inches, the average being approximately 10 square inches." Stewart (n.d.:2-3) also recorded the existence of a "... number of lobes from 2 to 3 inches to as much as 8 or 10 inches below the paved surface." Apparently, there were six of these "lobes" that were "... from two to three feet across and were found ... all around the structure except at the southwest, where presumably the entrance had been established." Stewart (n.d.:2) considered these features to be firepits, but their numbers and positions around the structure suggest instead that this was a "petal house," a structure type originally described as a "Food Warehouse or Big House" by Herbstritt (1983:114-117) at the Throckmorton site, 36GR160 (Figure 1:10). Similar features have been recorded at the Foley Farm site, 36GR52 (Fig. 1:3) (Herbstritt, 1984), and the Sony site, 36WM151 (Fig. 1:9) (Davis and Wilkes, 1997:33-36), but the appendages in these cases were attached to round houses (detected from their circular postmold patterns). Thus, the "Pottery House" at the Eisiminger site, being rectangular, is apparently anomalous in form compared to those of the other sites. Stewart (n.d.:5) states that "... no well-defined post holes were found ..." during his excavation.

Stewart (n.d.:3) noted the "... amazing wealth of potsherds ..." from the structure that, otherwise, had an "... almost complete absence of artifacts except pottery ..." For this study, 61 rim sherds provenienced to the Eisiminger site were borrowed from the Paul R. Stewart Museum, and many of them presumably were recovered during Stewart's excavation of the Pottery House. Mayer-Oakes (1955:127-128) illustrated Waynesburg College pottery from the Eisiminger site that included rim sherds of three bowls, two reconstructed "jars," and a section of a compound vessel (Fig. 5). The larger of the two jars (Mayer-Oakes, 1955:128, Pl. 68, A), has a scalloped rim.

Among the few non-ceramic items found was "the small roughly-rolled bit of copper kettle of settler origin" (Stewart, n.d.:3). Mayer-Oakes (1955:123) listed Proto-historic artifacts as "... blue glass beads, two red beads with a blue core, and several perforated fragments of small copper spheres, perhaps crudely hand-made bell fragments ..." He also alluded to "... a small scrap of silver ..." that was considered, at that time, as providing the best evidence of a Proto-historic artifact (Mayer-Oakes, 1955:122-123). The blue glass beads are a type Lapham (1995:24) designates "Washington Boro Blue." The type is the most commonly found bead on three Pennsylvania and one New York sites dating between A.D. 1600 and 1625 (Lapham, 1995:Fig. 4). Two of these sites, Spragg, 36GR12, and Foley Farm, 36GR52, are Proto-historic sites located in Greene County, Pennsylvania.

COMPARISONS

The McKees Rocks Village and Eisiminger sites are dissimilar in many ways and the data gathering process for each site also differed. The author has analyzed 1,221 rim sherds from 14 Late Prehistoric and Proto-historic Monongahela sites as part of a larger study, and the data from the Eisiminger site reproduced in Table 1 are extracted from that analysis. The McKees Rocks Village site data are derived mostly from Buker's site report, with special attention given his Tables 3



Fig. 5.—Portion of a double pottery vessel from the Eisiminger site.

Table 1.—Comparison of pottery attributes for the McKees Rocks Village and Eisiminger sites.

Trait	McKees Rocks Village ¹	Eisiminger
Shell Tempering	98.8%	98.0%
Exterior Treatment, rim sherds:		
Cordmarked	86.0%	96.0%
Plain	10.0%	2.0%
Simple Stamped	4.0%	0.0%
Striated	0.0%	2.0%
Incidence of Rim Strips	85.0%	3.0%
Final Cordage Twist:		
“Z”	21.0%	70.0%
“S”	79.0%	30.0%
	(N = 34)	(N = 46)
Bowls	Present (not common)	Present (not common)
Loop Handles	Present (not common)	0.0%
Nodes	Present	0.0%
Lugs	Present	
Vertical Compound Vessels	0.0%	2.0% ²

¹ Only shell tempered rim sherds were used for more viable comparisons.

² There are two examples of vertical compound vessel sherds in the Eisiminger sample, but only one was available for study.

and 4 (Buker, 1968:21, 24). The author performed the final twist analysis on 34 rim sherds since that analysis technique was not yet utilized in the 1960s. Buker kindly donated most of the rim sherds used in the analysis.

The McKees Rocks Village site and Eisiminger site samples are comparable in having high percentages of shell tempering and cordmarking, a not unexpected occurrence for Upper Ohio Valley Proto-historic sites, but the samples differ markedly in all other attributes. The Eisiminger vessel sample discloses a ceramic "profile" consisting of a shell tempered, cordmarked vessel with a high percentage (70%) of Final "Z" twist cordage impressions. In addition, the vessel would have an elongated jar shape with a slightly flaring rim (Mayer-Oakes, 1955:128, Fig. 68A). Punctations are present on 16% and one rim sherd exhibits fingernail incising. The McKees Rocks Village vessel sample indicates a vessel that was most often cordmarked, but with a small percentage (4%) being simple stamped. The typical McKees Rocks Village vessel also had a decorated, added rim strip, or filet, and a globular form (Buker, 1968:14–16). The final cordage twist type is usually (79%) Final "S" twist in the McKees Rocks Village sample, a finding that sharply contrasts with the Eisiminger data. The McKees Rocks Village site ceramic inventory includes lugs, nodes, and a few loop handles, although "Loop handles from the site are usually small and poorly made" (Buker, 1968:24).

There is no question that the pottery vessels from the two sites represent two distinct pottery-making traditions. In the following section, these differences will be further discussed.

NOT ALL RIM STRIPS ARE CREATED EQUAL

Differences in Added Rim Strips

There is a significant difference between the frequency of added rim strips for the Eisiminger site (3%) and McKees Rocks Village site (85%) ceramic samples (Table 1). There are qualitative as well as quantitative differences between the rim strips.

Eisiminger

Only four rim sherds incorporate rim strips. Two rim strips exhibit oblique cordmarking. One of the cordmarked rims (Fig. 6A) is decorated with an uneven row of ovate punctations that exist above as well as at the bottom of the rim strip. The second cordmarked rim (Fig. 6B) has a row of crude punctations more or less in the mid-section of the strip. The punctations appear to have been applied with a bifurcated tool. A third rim sherd (Fig. 6C) has punctations applied at the bottom of its wider rim strip. These punctations were done with a circular tool that had a central blade-like middle.

The fourth Eisiminger rim strip (Fig. 7) is represented by two, cross-mended sections of a rim sherd with a single, incipient castellation. The rim strip is thicker, decorated more prominently with a row of punctations, and horizontally cork-marked; the sub-rim strip area is vertically cordmarked. This fourth Eisiminger rim sherd is the most similar in overall appearance and configuration to the McKees Rocks Village site forms.

McKees Rocks Village Site

Buker (1968:13–25) provides detailed descriptions of four varieties of rim strips from the McKees Rocks Village site. Buker's illustrations and descriptions and

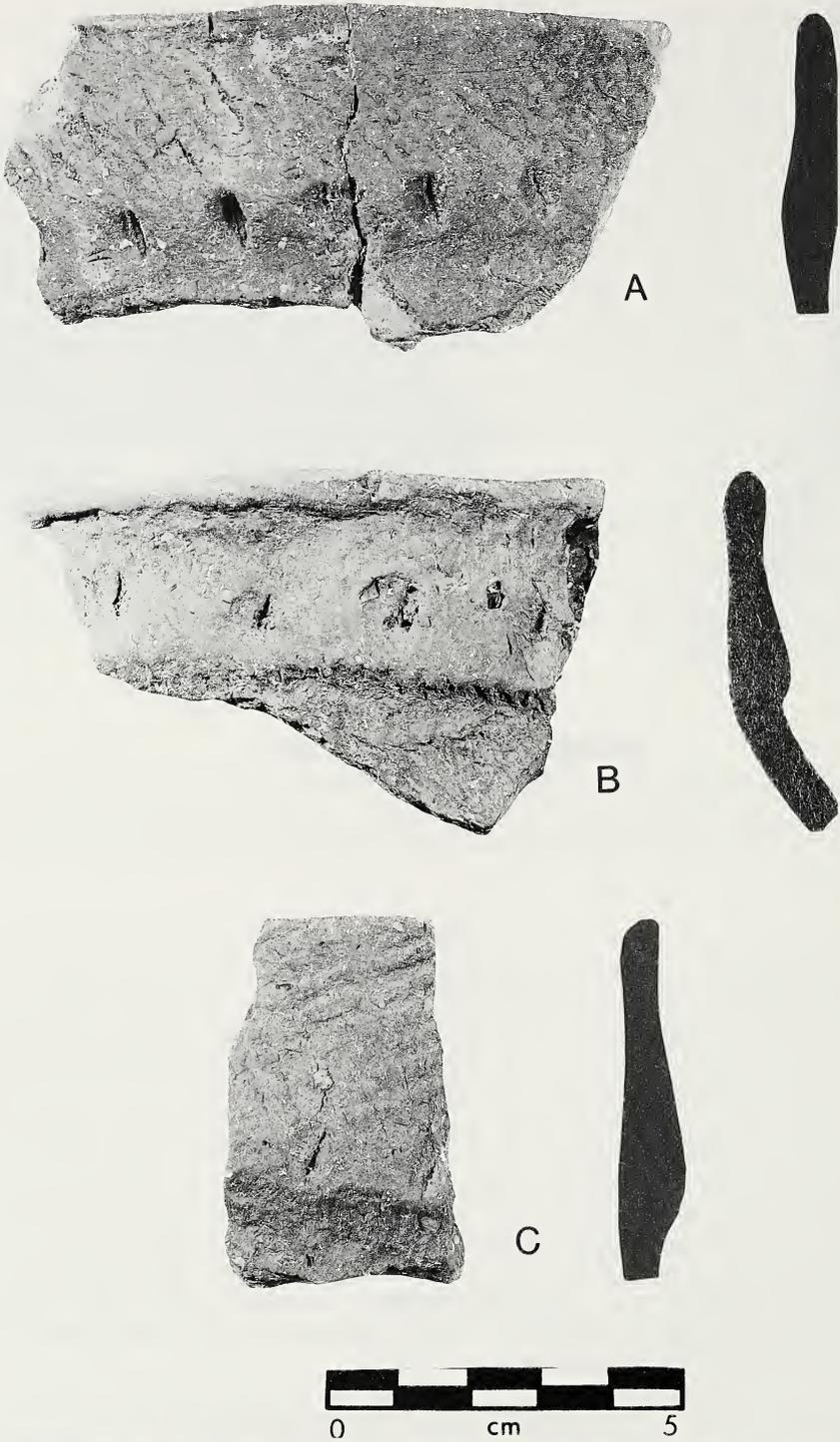


Fig. 6.—Eisinger site rim sherds. A. Uneven row of punctations at bottom of rim strip. B. Crude punctations in central area of narrow rim strip. C. Wide rim strip with crude punctations at bottom.

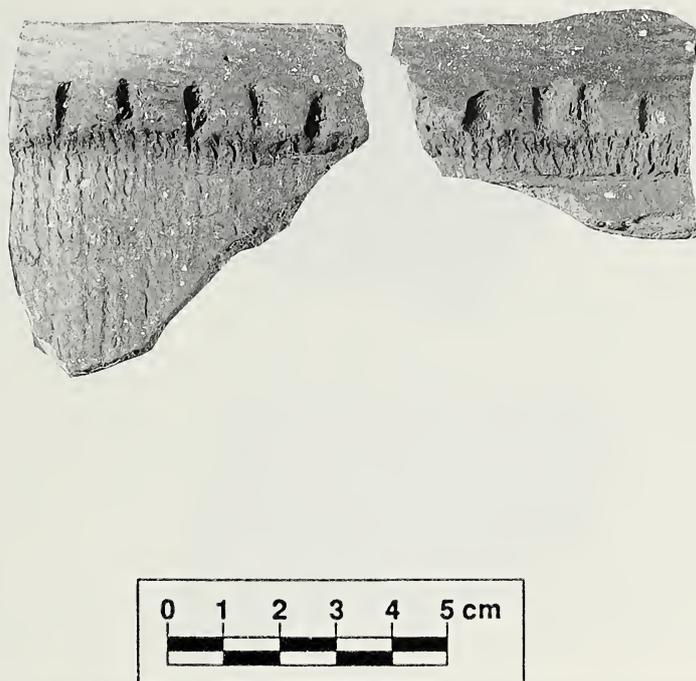


Fig. 7.—Eisiminger site rim sherds from same vessel with prominent punctations on a narrow strip and a low, rounded castellation.

the author's study of McKees Rocks Village site specimens (Fig. 8) leave no doubt that the McKees Rocks Village potters were crafting these decorative and practical additions to their pottery in a much more refined and careful manner, quite possibly for a long time. The contrast between the rim strips from the two sites is striking. Whereas the Eisiminger rim strips are generally unevenly decorated, the McKees Rocks Village samples are the opposite, indicating a well-developed competence. Punctations are prominent and pleasing (Fig. 8), as if the individual potters were "signing" their products with their "maker's marks," in the author's view.

THE POTS, THE PEOPLE, AND THE QUESTIONS OF ORIGINS

Eisiminger Site

The five Proto-historic sites identified by Mayer-Oakes (1955:122) for Greene County have risen to twelve sites, including two reported from West Virginia, one in bordering Monongalia County, and another in Ohio County (Babich et al., 1996). The Eisiminger site is included in these twelve sites. Johnson (1990:9) assigned these sites to the Foley Farm Phase of Monongahela following Herbs-tritt's (1984) popular report descriptions based on the partial excavation of the Foley Farm site, 36GR52 (Fig. 1:3). However, none of these authors have provided a definition of the Foley Farm Phase that entails artifact and settlement pattern trait frequencies for a number of sites. Thus, we are left with an extremely spotty database for, at least, one of the terminal phases of Monongahela.

The data from the Eisiminger site does, however, invite contemplation about

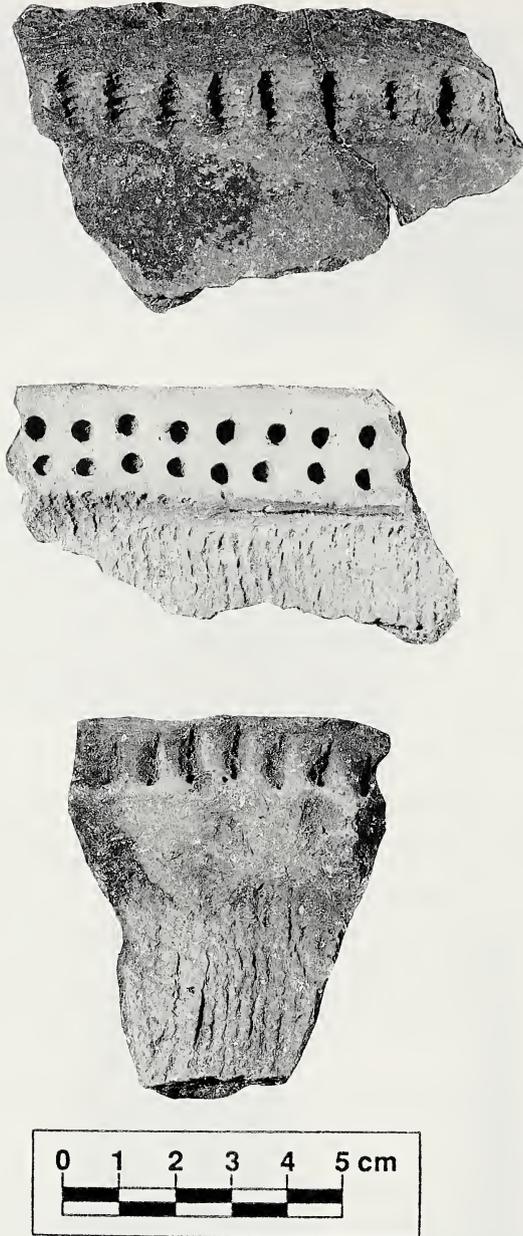


Fig. 8.—Three rim sherds from the McKees Rocks Village site.

the possible cultural make-up of the Foley Farm Phase people. In discussing the results of the Foley Farm site excavation, Herbstritt states that the fieldwork:

... uncovered samplings of the Monongahela's material culture which have, among other things, proven a long tradition of native technology.

There seems to have been very little change in the culture's ceramic, stone, bone and shell industries. (Herbstritt, 1984:30).

Certainly, the validity of Herbstritt's proposition holds true for the ceramic artifacts representing Eisiminger. Although shell tempering and cordmarking are traits that Monongahela shares with Fort Ancient, these attributes are nonetheless typically Monongahela, especially of later components. A general lack of appendages, such as lugs or loop handles, is also characteristic of non-Drew Phase Monongahela ceramic assemblages. A minor incidence of non-decorated castellations occurs in many Monongahela samples, and Eisiminger is no exception.

During the aforementioned study of 1,221 rim sherds from 14 sites, it was determined that 20% of the Eisiminger site's rim sherds were scalloped. What can be considered significant about this figure is the fact that the Late Monongahela Household site, 36WM61 (Fig. 1:4), had a 94% incidence of scalloped, or deep, tool-impressed lips (George et al., 1990:51). These occurred on cordmarked, shell tempered vessels that had slightly flared rims (George et al., 1990:50). The Household site, with a ^{14}C date of 325 ± 80 B.P., Cal. A.D. 1562 (UGA-3453), was occupied just a few years before European trade goods started to appear in the Upper Ohio Valley. Why, then, is there only a small percentage of scalloped lips at Eisiminger? Why, also, are there punctations, added rim strips and castellations in the Eisiminger site sample, whereas none of these attributes were at Household (George et al., 1990:50–51)?

It is here proposed that Eisiminger represents a gathering of remnant Monongahela populations who brought their pottery traditions with them and that the various attributes constitute continuations of these. This would be in agreement with Herbstritt's (1984:30) suggestion that there was "little change in the culture's ceramic . . ." industry. Thus, the tradition of tool-impressed or scalloped lips, present at Eisiminger (Fig. 9A), if not in great numbers, seems to imply that some potters carrying the Household site ceramic mental template were a part of the Eisiminger site population.

Another lip decoration, that of perpendicularly applied, cord-wrapped paddle edge impressions on the inner lip (Fig. 9B), occurs on 15% of Eisiminger rim sherds. This attribute is also present on rim sherds from Foley Farm (32%) and Throckmorton (14%) (Figure 1:10) (Herbstritt, 1983:153–154). On one Eisiminger rim sherd the interior lip notching was deep enough to result in a scalloped lip (Fig. 9C), suggesting, perhaps, that scalloping gave rise to the inner lip, cord-wrapped paddle impressions, that is considered to be a Proto-historic Foley Phase attribute.

The most unusual rim sherds in the Eisiminger sample are portions of vertical compound vessels in which only the lower of two rim sherds are intact (Fig. 5). The larger of these consists of three joined sections, two of which exhibit a flared rim with a perpendicularly notched lip. The lower section of the vessel has almost horizontal cordmarking, whereas the less intact upper vessel has convoluted cordmarking that tends toward vertical. The plain interior, while carinated at the joined area, exhibits no evidence of an intersecting joint. Mayer-Oakes (1955:128, Pl. 68B) illustrated the same compound vessel portion that was attributed to Pottery House at Eisiminger. The second example (Fig. 9D) is a single sherd, with a protruding lip, that exhibits shallow notching. The upper portion of the vessel is not large enough to determine surface treatment, whereas the lower section has



Fig. 9.—Eisiminger site rim sherds. A. Rim sherd with scalloped lip. B. Perpendicular cord-wrapped paddle edge applied to inner lip. C. Same as “B” except that application resulted in scalloped lip. D. Rim sherd of a second double pot.

fine, horizontal cordmarking (Fig. 9D). This rim sherd differs from the one described above (Fig. 5) because the interior is not carinated.

The only other vertical compound vessel that is known for the Upper Ohio Valley is a McFate Incised vessel found associated with an adult female burial at the Johnston site, 36IN2 (Fig. 1:5) (Dragoo, 1955:95, 136). Griffin (1966:137 & Pl. LXIX) discussed two double vessels recovered from the Madisonville site, one of which was associated with a child burial. With the paucity of data available, one can only conclude that compound or double vessels are so rare that there are too few of them known for anyone to undertake a study of this enigmatic yet intriguing artifact type that appears on Proto-historic, and slightly earlier, sites.

McKees Rocks Village Site

In the "Interpretations" section of his site report, Buker (1968:46) states, "If McKees Rocks cannot be placed satisfactorily within the framework of known Monongahela culture, even when all the variations in Monongahela are considered, some of the answers probably lie elsewhere." The question we still ask is where is elsewhere? The author herein makes a few suggestions about the McKees Rocks Village site and its possible relationships, although that question cannot be answered with certainty.

In its present context, McKees Rocks Village site appears to have represented an isolated village far removed from its nearest known affiliate, the Wellsburg site (Fig. 1:11), which is 111 river km downstream on the Ohio River in West Virginia. This might not have been so. A few artifact assemblages are of interest, although the data are limited because the upper Ohio River and Chartiers Creek valleys have been devastated by urbanization and industrialization.

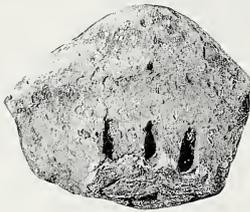
The most significant of these is from the Georgetown site, 36BV29, located on an Ohio River terrace in Beaver County, Pennsylvania, just east of the West Virginia State line (Fig. 1:6). Mayer-Oakes (1955:178) excavated a series of five-foot squares to various levels at Georgetown to help formulate pottery sequences for the Upper Ohio Valley. Among artifacts from the site, donated to CMNH by Emil Alam, are six rim sherds (in two restored sections) of a shell tempered vessel with sub-lip fillet, and a notched lip (Fig. 10A); the extant neck area exhibits faint, vertical cordmarking. The sherds' close resemblance to a McKees Rocks Village site rim sherd (Fig. 10C) implies its Wellsburg Phase affinities.

Another rim sherd from the Georgetown site consists of a shell tempered castellation with three sub-lip vertical punctations (Fig. 10B) on a plain surface. Both the prominent and uniform punctations and the almost pointed castellation, similar to those illustrated by Buker (1968:Fig. 10A, Fig. 12A, and 12D), indicate a Wellsburg Phase origin. Unfortunately, the Georgetown site has been recently devastated by severe flood-induced bank cave-ins as well as uncontrolled looting, so determining the extent of any Wellsburg Phase component is highly unlikely.

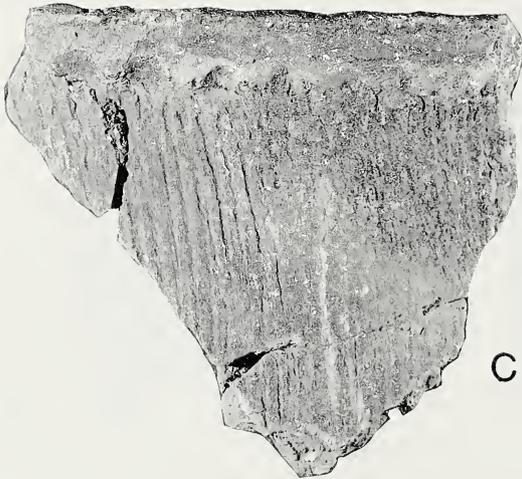
The incidence of simple stamped pottery in the Upper Ohio Valley is very rare, except for the McKees Rocks Village site. In the Chartiers Creek valley, the multi-Late Prehistoric component Lang site, 36WH48 (Fig. 1:7), salvage excavated in 1986-87, produced nine simple stamped body sherds from three features. A single radiocarbon date of 490 ± 110 B.P., Cal. A.D. 1430 (Beta-19,162) is considered to be a valid temporal marker for the Late Monongahela occupation. Shell tempered rim sherds from the Lang site, relating to the Late Monongahela occupation, have sub-lip punctations that are usually oblique, pseudo-collars and protruding cas-



A



B



C



tellations. The Lang site simple stamped body sherds have some resemblance to Wellsburg Phase sherds, but the decorative techniques of rim sherds are not identical.

Another site with similar rim sherds is the Portman site, 36AL40 (Fig. 1:8), partially excavated by Allegheny Chapter, Society for Pennsylvania Archaeology (SPA) members and directed by William Buker in 1968–69. Like the Lang site, Portman had multiple Late Prehistoric occupations (Buker, 1993:13). Two radiocarbon dates of 530 ± 90 B.P., Cal. A.D. 1412 (Uga-1643) and 560 ± 60 B.P., Cal. A.D. 1403 (Beta-57298) document contemporaneity with the Lang site. One simple stamped body sherd is recorded for Portman (Buker, 1993:23). It is believed that the late components of the Lang and Portman sites, separated by only 5.5 km, represent a yet unnamed Late Monongahela phase that, in some ways, is related to the Wellsburg Phase. Its spatial extent is presently unknown.

There are two simple stamped, shell tempered rim sherds recorded from the Godwin-Portman site, 36AL39 (Fig. 1:12), another Chartiers Creek valley locus. A recently obtained radiocarbon assay of 520 ± 60 B.P., with a calibrated intercept date of A.D. 1420 (B-153248), may relate to the simple stamped rim sherds. The site, which is 0.25 km north of the Portman site, was partially excavated by CMNH in 1968 (Dragoo et al., 1969) and salvage excavated in 1978–79 by members of the SPA just prior to its destruction. One of the small rim sherds has shallow punctations on the lip whereas the lip of the other is plain.

Further afield, there are four simple stamped, shell tempered body sherds from the Johnston site, 36IN2 (Fig. 1:5), that are listed in the CMNH Field Catalog (#760) as “simple stamped?”, but are not mentioned in the site report by Dragoo (1955:101–105). Re-examination of the sherds by the author verifies that they are simple stamped. The Johnston site is obviously late, based on its inclusion in the Johnston Phase of Monongahela that, characteristically, produces both Monongahela and McFate pottery (George, 1997).

DISCUSSION

The coming of the Wellsburg Phase people to McKees Rocks Village, probably during the late sixteenth century A.D., to one of the most prominent and defensive locations along the upper Ohio River valley, must have created consternation among indigenous populations. Buker (n.d.) noted that the abundant subsistence remains at McKees Rocks suggest that the village population was large enough to control an adequate sized catchment area. The resource-rich and accessible Chartiers Creek Valley may not have been occupied by indigenous populations when the McKees Rocks Village was settled. It is also especially interesting that the generally upland area north of the site, and away from the river, is devoid of Late Prehistoric village sites, a fact emphasized by Buker (personal communication). This area, now known to Pittsburghers as the “North Hills,” would have provided extensive and accessible hunting grounds necessary for sustaining a large village population.

←

Fig. 10.—Georgetown and McKees Rocks Village sites rim sherds. A. Shell tempered rim sherd with a sub-lip fillet and notched lip from Georgetown. B. Shell tempered castellation with sub-lip vertical punctations from Georgetown. C. McKees Rocks Village site shell tempered rim sherd similar to “A” from the Georgetown site.

Ceramic influences, such as the McKees Rocks-like decorated rims strip at Eisiminger and the curious, but somewhat similar, pottery from Lang and Portman, suggest that there were degrees of cultural integration in force in southwestern Pennsylvania, and elsewhere, slightly before contact, as had been suggested by other archaeologists (Pollack and Henderson, 1992:289). It appears that the McKees Rocks Village potters had some influence on indigenous peoples based on the seemingly random spread of simple stamped wares.

The author also suggests that there is some evidence that the Wellsburg Phase people were Iroquoian. Buker (1968:Fig. 15K) illustrated a portion of an Iroquois acorn-ring pipe from McKees Rocks. An Iroquoian affiliation for the Wellsburg Phase might also be inferred by the lack of biconcave discoidals in the McKees Rocks Village site sample since this artifact type is not present on northern Iroquoian sites (George, 2001:4). The McKees Rocks Village site contained triangular points that are the small Madison forms one would expect from a late Late Prehistoric/Proto-historic site in the Upper Ohio Valley. However, there is also a sample of parallel-sided triangular points (Fig. 11A), the type that Railey (1992:161–163) referred to as “Type 5, Fine Triangular; Straight-Sided” in “Fort Ancient Cultural Dynamics in the Middle Ohio Valley” (Henderson, 1992). The latter is not the triangular point type found at the South Park Village site of Whittlesey origin (Brose, 1994:94–98). A second point sample from McKees Rocks Village (Fig. 11B) is what Railey (1992:156–158) designated “Fine Triangular; Flared Base” and may represent an earlier Fort Ancient involvement with the McKees Rocks Village site, possibly dated by the aforementioned A.D. 14th century radiocarbon date.

CONCLUSIONS

The separate cultural entities that are recognized by two distinct ceramic traditions, herein described, are symptomatic of the upheaval in the Upper Ohio Valley at the beginning of the 17th century. Diminished Monongahela populations occupied upland loci and the floodplains of minor streams well away from major rivers. It is suspected that all of these were relatively small villages with limited population, as exemplified by the Throckmorton site (Herbstritt, 1983). Paradoxically, a much stronger alien population was able to establish and maintain a large defensive-positioned village, on a prominent escarpment, and able to control an extensive catchment area. There is now some evidence that there were Wellsburg Phase settlements between Wellsburg and McKees Rocks. This belies the supposed spatial isolation of the latter. Unfortunately, the heavy industrialization of the upper Ohio River valley may have eliminated other possible Wellsburg Phase sites. The appearance of simple stamped sherds on a few sites, plus the existence of at least one Eisiminger rim sherd with an added rim strip, implies social interchange and, perhaps, a non-belligerent relationship between McKees Rocks villagers and some indigenous people. As always, we have much to learn.

ACKNOWLEDGMENTS

This paper would not have been possible without the substantial efforts of Bill Buker, who, with other volunteers, excavated portions of the McKees Rocks Village site while enduring the most trying of conditions. Such dedication is seldom properly recognized. I also thank Jim Morton of Columbus, Ohio, who prodded us into the recognition of the Proto-historic age of the McKees Rocks Village. James D. (Fuzzy) Randolph, Curator of the Paul R. Stewart Museum at Waynesburg College, loaned me the artifacts and the unpublished report on the “Pottery House” at Eisiminger. Stewart’s unpub-

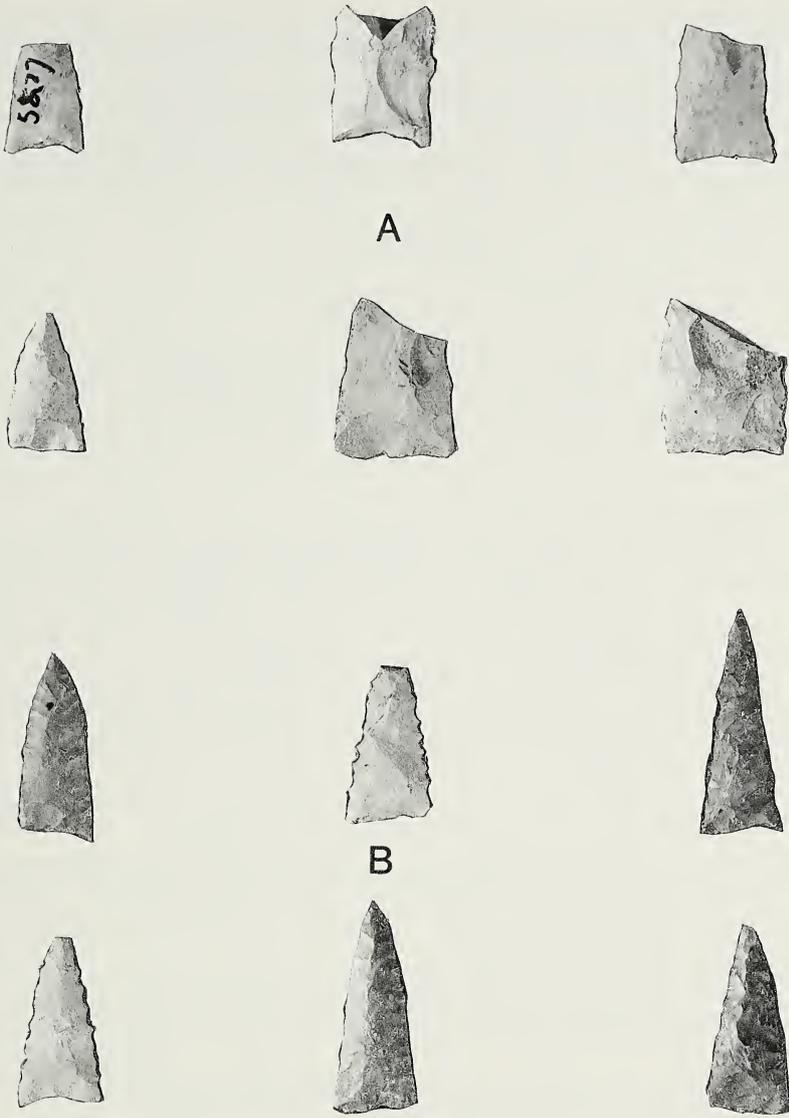


Fig. 11.—McKees Rocks Village site triangular points. A. Straight sided. B. Elongated, flared base type.

lished report deserves wider recognition; it is appended to this article to increase its availability. Randolph's interest and cooperation are greatly appreciated, as is his upbeat attitude. The author is also appreciative of the help in the form of donated collections, provided by long-time Society for Pennsylvania Archaeology members Emil Alam and Donald P. Tanner. I thank Carnegie Museum of Natural History people as follows: Curator-in-Charge David R. Watters for darkroom help and editorial assistance; retired Associate Curator Verna L. Cowin, who made editorial suggestions; and Section Secretary Charmaine C. Steinberg for typing the various drafts of this paper. I express my sincere gratitude to Fuzzy Randolph for permission to include Stewart's "Pottery House" manuscript.

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APPENDIX

While reviewing “Comparing pottery from the Proto-historic McKees Rocks Village and Eisiminger sites of southwestern Pennsylvania,” David R. Watters, Curator of Anthropology and the Anthropology Editor for Scientific Publications, suggested incorporating the following unpublished manuscript, entitled “Excavation of Pottery House” by Dr. Paul R. Stewart, since the information therein contributes significantly to an understanding of the Eisiminger site. Stewart’s early research at the Pottery House assumes even more importance because of James Herbstritt’s excavation of the Proto-Historic site (36Gr160) in 1982, where settlement pattern details seemingly duplicate those at Eisiminger.

The “Excavation of Pottery House” is a part of Stewart’s undated, sixteen-page manuscript entitled “Indian Archaeology,” an important document, completed in the middle 1950s, that is on file at the Paul R. Stewart Museum of Waynesburg College. Permission to publish the “Excavation of Pottery House” portion of the manuscript was granted by James D. Randolph, Director of the Stewart Museum. On the last page of the “Indian Archaeology” manuscript is this statement:

“Unfinished manuscript by Dr. Paul R. Stewart who, with James D. Randolph, made this study. The illustrations referred to in the article were never made. The pottery pieces are in the Waynesburg College Museum.”

The content of the manuscript is reproduced exactly as it appears in the original, including blank spaces (_____) where data or other information were not included in the original.

EXCAVATION OF POTTERY HOUSE

[by Paul R. Stewart]

THE PROBLEM

A village site, which for the present we will call the Eisiminger focus of the Monongahela Woodland culture in harmony with the suggestions made by Mary Butler in Bulletin No. 753 of the Pennsylvania Historical Commission, lies approximately three and one-half miles south of Waynesburg, Pennsylvania, three-fourths of a mile east of the Waynesburg-Blacksville road. The site occupies portions of two fields on what is now known as the George Eisiminger property. Figure 1 shows the contoured map of the village site.

The site was partially plowed in the summer of 1950 and completely plowed

in the summer of 1951. Previous to the year mentioned, a large number of desultory excavations had been made on the south side of the spot marked "Lapping Cemetery." A fence had previously divided the field into a north and south portion just to the south of this cemetery. When the fence was taken away and the entire village site plowed, the author with a number of his students undertook to explore a few pits disclosed by probing just to the northwest of the former Lapping Cemetery.

In the summer of 1950, Mr. William Mayer-Oakes and James Swauger of the Carnegie Museum, had been taken to the site by the author. Mr. Mayer-Oakes continued a superficial examination through the summer of 1950. Our conclusions were that this site represented an occupation of the Monongahela Woodland culture mentioned above. Certain artifacts of brass and copper indicated European settler contact. Fort Ancient culture never seemed definitely to be established. The excavations at the locality mentioned above were for the purpose of further determining the type of culture. [end of page 1 in original]

THE EXCAVATION

Upon the excavation of the first pit probed, it was discovered that we were not exploring a simple firepit, but a complex situation disclosed in Figures 2 and 3, where it will be observed that instead of separate firepits, we were in fact exploring an ancient house which we have been pleased to call "Pottery House."

As will be seen by the drawing, the structure was approximately 18 feet long by 12 feet wide, almost rectangular, and the main floor almost completely paved with small stones ranging from 2 or 3 square inches to 50 or 60 square inches, the average being approximately 10 square inches. These stones for the most part showed no indication of firing, but had evidently been taken from a sandy shale which underlies most of the village site. Here and there among the pavement stones were other stones showing the hematitic red caused by firing. The stones had probably been tramped in between the flatter stones of the main pavement. In a very few places the pavement was double as if certain of the stones had sunk and the inhabitants had tramped a few extras in above them. The entire pavement was laid in wood ashes.

This pavement was approximately level and had obviously been graded back into the slight slope, giving approximately a depth of 2 1/2 [two and one half] feet at the upper end and 1 foot at the lower side.

In addition to what we call the main structure (20 feet by 12 feet) there were a number of lobes of from 2 or 3 inches to as much as 8 or 10 inches below the paved surface. Into these pits the pavement extended downward from the main pavement into the lobes. There were six of these lobes, which were doubtless firepits, the ashes being much deeper in them than over the main structure. These pits were from two to three feet across and were found, as Figure 4 shows, all around the [end of page 2 in original] structure except at the southwest, where presumably the entrance had been established.

Smaller fire pits were found near the structure and were assumed to be related to it. On the upper side of the pavement (See Figure 3) an embankment of excavated fragments of shaly sandstone had been piled and later, presumably after the structure was deserted, had caved in.

ARTIFACTS

One of the noteworthy observations was the almost complete absence of artifacts except pottery. Two arrowheads, one notched and the other triangular, were found (See Figure 5). One small bone awl (animal species undetermined) and another awl made from the bone of an _____ were excavated. One slightly decorated bit of mussel shell was found and one very well-formed flaking implement. Added to these artifacts was the small roughly-rolled bit of copper kettle of settler origin. This was found in such a position that it could possibly have been intrusive.

DESCRIPTION OF THE POTTERY

The outstanding feature of this dwelling was the amazing wealth of potsherds. This led to our naming it the "Pottery House." _____ rimsherds were found in the various pits and scattered over the floor. Usually more or less wood ash was found over the potsherds whether they happened to be in the firepit lobes or on the main floor. Approximately _____ sherds other than rimsherds were found in the dwelling, not counting the sherds which were found in sufficient number to reconstruct vessels. Figure 6 shows a group of the most interesting rimsherds. Attention is called to rimsherds a, b, c, d, e, which were definitely crenate, as were rimsherds used in reconstructing vessel No. _____ shown in Figure _____. In surface discoveries, no crenate rimsherds had been found previously by the author or by Mayer-Oakes.

Most noteworthy of all the sherds were Nos. f, g, h, which neither the author or [sic] Mayer-Oakes had ever seen before in any of the village sites [end of page 3 in original] examined in this area. Evidently a secondary flange was modeled part of the way down from the rim of the pot. Unfortunately, the primary rim could not be discovered in any of these three unusual sherds. From the rapid thinning of the pottery above the secondary ledge, it was estimated that this vessel probably held in the neighborhood of one and a half pints or a quart.

A noteworthy feature of the pottery in Pottery House is the fact that not one of the _____ rimsherds had any notch crease or lip designed for facilitating pouring, although several such devices had been found in the surface finds of the site.

There were sufficient sherds to reconstruct with confidence two complete pottery vessels shown in Figure 7. The left shows interrupted cord shaping with either cylindrical or flat corded paddle. To the right was the most important find of all. A little more than three-fourths of the entire rim was found and was beautifully and rather regularly crenate with a slight twist such as is used by modern housewives in edging a pie crust. The sides of the vessel had been fashioned with rather continuous diagonal strokes of a corded paddle, averaging about _____ degrees departure from the edge of the pot. Toward the bottom of the bulge of this pot, the cording had been changed to cross as well as oblique strokes.

This pot had been extremely well-fired because the potsherds were practically unweathered and when dried made a clinking sound when stroked. This was in contrast with the pot represented by rimsherd No. j, which had almost exactly the same design, but in this case the pot had been very poorly fired so that most of its sherds have weathered beyond the possibility of much reconstruction. [end of page 4 in original]

Note: (Excavation)

No well-defined post holes were found although along the upper side where a trench, possibly for drainage, had been dug, there were lower spots in two of which were there were found fairly large stones which might have been used in wedging saplings in place. The question, of course, arises whether this was a wigwam or hogan type made by bending poles over the structure, and roofing and siding it with bark and latticed branches, or whether advantage had been taken of trees growing in the neighborhood. [end of page 5 in original, except for the "unfinished manuscript by Dr. Paul R. Stewart . . ." quotation that appears before the text in the Appendix of the present paper]

FLEAS (SIPHONAPTERA) FROM ANCASH DEPARTMENT, PERU WITH
THE DESCRIPTION OF A NEW SPECIES, *ECTINORUS ALEJOI*
(RHOPALOPSYLLIDAE), AND THE DESCRIPTION OF THE MALE OF
PLOCOPSYLLA PALLAS (ROTHSCHILD, 1914) (STEPHANOCIRCIDAE)

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ABSTRACT

A collection of 358 fleas representing 6 families, 19 genera, and 21 species was made from eight species of mammals in seven provinces within Ancash Department, Peru. Specimens were also obtained from bank cavities and water flea traps. A new species of flea, *Ectinorus alejoi* (Rhopalopsyllidae) collected from *Lagidium peruana* Meyen, 1833 (vizcacha) is described from Recuay Province, bringing the total number of species belonging to the genus *Ectinorus* to 32. The male of *Plocopsylla pallas* (Rothschild, 1914) (Stephanocircidae) is also described for the first time. *Plocopsylla pallas* (16%), *Neotyphloceras crassispina hemisus* Rothschild, 1914 (14%), and *Cleopsylla townsendi* Jordan, 1936 (9%) comprised 39% of the total number of fleas collected. Three fleas are reported from Peru for the first time (*D. stejnegeri*, *P. achilles*, and *E. alejoi*). Eleven additional species represent new records for Ancash Department (*A. thurmani*, *C. townsendi*, *C. m. minerva*, *E. gallinacea*, *E. claviger*, *N. c. hemisus*, *P. pallas*, *P. d. quitanus*, *S. inca*, *T. bleptus*, and *T. titschacki*).

KEY WORDS: *Ectinorus alejoi*, *Ectinorus claviger*, *Plocopsylla pallas*, flea, Siphonaptera

INTRODUCTION

The flea fauna of South America is drastically understudied and Peru is no exception. Johnson's (1957) monographic work of the South American flea fauna comprises most of the known Peruvian records, which include 59 recognized taxa. Four additional Peruvian taxa were recorded by Hopkins and Rothschild (1966), ten by Smit (1970, 1976, 1978, and 1987), and three by Schramm and Lewis (1987, 1988), providing a total of 76 taxa. Our report provides a record of flea

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taxa recently collected in Ancash Department. Prior to this study, only 10 species (including cosmopolitan species) were recorded in Ancash Department. Miscellaneous fleas were opportunistically collected in September 1998 by Dr. Pat Carney, Uniformed Services University of the Health Sciences (USUHA) during biomedical research studies. They were also collected during a medical entomology training program conducted 2–6 September 1999 by personnel of USUHS, Bethesda, MD in cooperation with the Ministerio de Salud, Hospital de Caraz (USUHS Team). Following the 1999 training program, medical technologists from several provincial hospitals also submitted fleas. During 23–30 March 2000 hantavirus studies were conducted (Hastriter Team) and fleas and tissue samples were collected (results of the hantavirus investigations are published elsewhere). Among our material are a new species of *Ectinorus* Jordan, 1942 (Rhopalopsyllidae) and the undescribed male of *Plocopsylla pallas* (Rothschild, 1914) (Stephanocircidae). A review of the genus *Ectinorus* was provided in Hastriter (2001). The description of one additional species of *Ectinorus* brings the total number of species in this genus to 32. This paper presents and discusses several new records for Ancash Department and examines the current species known to occur in Peru to include three new records for the country.

MATERIALS AND METHODS

During the September 1998 collections and those made during the September 1999 training program, collection activities were confined to agricultural areas along the Santa River near Choquechaca (Hauzlas Province). Vegetation included bamboo thickets in wet areas along the river, and *Agave* sp. and numerous varieties of cacti along the valley floor away from the river. Special emphasis was placed on trapping in and around human dwellings and along rock fences extending through fields (elevation: 2100–2200 m). Habitats selected during the flea and hantavirus research study (March 2000) included the following: 1) Chiquian Province (3600–4000 m)—High elevation grassland known as “puna” consisting of large fescue (*Festuca orthophylla* Pilger, 1898) and needle grass (*Stipa ichu* Kunth, 1829). 2) Huaraz Province (1800–3700 m)—steep rocky slopes with low growing vegetation. 3) Huaylas Province (3300–3700 m)—Parque Nacional Huascarán was characterized by steep rocky slopes, heavily vegetated with low growing shrubs. Region was small plot agriculture and sheep grazing. 4) Recuay Province (3600–4400 m)—the lower elevations were over-grazed by sheep and the upper regions were abundantly covered with *F. orthophylla* and *S. ichu* and small scattered boulders. Habitats in Pomabamba and Huari Provinces were not observed by the authors.

Standard aluminum collapsible Sherman traps baited with oatmeal or oatmeal and peanut butter were used to trap small mammals. Trapped mammals were shaken into cloth or plastic bags at each capture site and transported to a field processing location. Each animal was brushed briskly with a toothbrush over a white bucket to capture the fleas. Fleas were placed in 80% ethanol, returned to the laboratory and prepared by soaking in 10% KOH for a period (~24 hours), dehydrated in serial alcohols (70, 80, 95 and 100%, a minimum of 30 minutes each), cleared in methyl salicylate (maximum of 20 minutes), and xylene (minimum of one hour). Fleas were mounted on glass microscope slides in Canada balsam using 12 mm cover-slips (#1 thickness). Mammals were euthanized by cervical dislocation. Each was weighed, measured, preserved in 10% formalin,

and later identified. Miscellaneous fleas were collected by hand-picking nesting materials or substrates from earthen bank nest cavities. Water flea traps were used to capture fleas in human dwellings. Traps were comprised of a shallow plastic pan (2.5 cm deep \times 45 cm wide) with a kerosene-wicked can set in the middle. Water was added to the pan and the wick lighted. Fleas attracted to the burning lantern were captured in the mote of water. Unless otherwise noted, all specimens were collected in Ancash Department, Peru.

Total body lengths of males and females were measured from the foremost portion of the frons to the apex of the st. VIII in males and to the posterior border of the sensillial plate in females. The measurement of each sex is expressed as the means of the composite number of specimens measured. Illustrations were prepared with the aid of a camera lucida mounted on a Zeiss compound microscope. With exception of the term *processus basimeris ventralis* adopted from Smit (1987), the terminology of flea structures follows those of Rothschild and Traub (1971).

RESULTS

Ceratophyllidae

Dasypsyllus stejnegeri (Jordan, 1937)

Specimens Examined.—**Recuay Province:** 19 km W Recuay (9°44'6"S, 77°30'3"W), 4420 m, ex "soil from nest cavity" of *Colaptes rupicola* Orbigny, 1840 (= Andean flicker) in earth bank, 29 March 2000, Hastriter Team, 3 ♀; and road cut on highway 109 between Chiquian junction and Pavilonica (10°9'36"S, 77°19'43"W), 3980 m, ex *C. rupicola* nest cavity in vertical road cut, 1 April 2000, M. W. Hastriter and R. Soto, 1 ♂.

Remarks.—This flea is distributed from the Bering Straits of Alaska to the southern tip of South America on a wide variety of avian hosts, particularly Passerine land-birds (Smit, 1961). This is the first record of its occurrence in Peru and on a species of *Colaptes*. Since little is known about the bionomics of this flea, it seems prudent to record our observations during its collection. The adult host bird was seen exiting the earth nest cavity (opening: ~18 cm diameter, depth: ~60 cm) on several occasions. A ladder was acquired to access the nest 3.25 m above the ground. Five hatchlings were present and fleas were not noted on them. Approximately one liter of dry, coarse sand was removed from the earthen nest cavity and was protected from the sun until examined. Each of the three female fleas was rather inactive, failing to crawl or jump when probed; however, each became very agitated when placed in alcohol. In comparison, the single male removed from the nest cavity in the road cut along highway 109 was collected from very fine moist soil. There were multiple holes in the road cut that were made by *C. rupicola*, but few were accessible. It should be noted that the localities of the two collection sites (within the same province) were separated by more than 70 km. This would suggest that this flea is established and that *C. rupicola* may be a significant host species throughout high elevations in the South American Andes. Smit (1961) suggested that long-range flying sea birds are responsible for the wide distribution of this flea. This does not seem plausible as there is little association between Passerine birds and sea birds and the species has never been collected from sea birds. Our finding of this species in Peru has great significance in demonstrating an established population between previously disjunct populations in northwestern South America and the Falkland Islands. Its presence in

central Peru supports the theory of distribution by "leap-frogging" by migrating Passerine land birds as proposed by Traub, Rothschild, and Haddow (1983).

Plusaetis dolens quitanus (Jordan, 1931)

Specimens Examined.—**Huaraz Province:** Pariacota (9°33'10"S, 77°35'69"W), ex *Phyllotis andium* Thomas, 1912, 24 March 2000, Hastriter Team, 2♂, 1♀. **Huaylas Province:** Parque Nacional Huascarán (9°30'40"S, 77°28'32"W), 3385 m, ex *Phyllotis amicus* Thomas, 1900, 25 March 2000, Hastriter Team, 2♂, 1♀; Parque Nacional Huascarán (9°30'24"S, 77°27'69"W), 3475 m, ex *P. andium*, 25 March 2000, Hastriter Team, 2♀; Parque Nacional Huascarán (9°30'40"S, 77°28'32"W), 3385 m, ex *Akodon* sp2 cf. *mollis*, 25 March 2000, Hastriter Team, 2♂. **Pomabamba Province:** Huayllan, ex *Mus musculus* Linnaeus, 1758, 17 February 2000, A Lopez, 1♂. **Recuay Province:** 4.6 km W Recuay (9°43'36"S, 77°27'917"W), ~3660 m, ex *Akodon* sp1 cf. *mollis*, 29 March 2000, Hastriter Team, 3♀; 4.6 km W Recuay (9°43'36"S, 77°27'55"W), ~3660 m, ex *P. andium*, 29 March 2000, Hastriter Team, 2♀.

Remarks.—The lateral aspect of t. VIII of males bears an anterior vertical row of two setae and a vertical row of three just posterior to these. The telomere is distinctly rounded along caudal margin opposed to that of *P. equatoris* (Jordan, 1933).

These records represent the most southern distribution of *P. d. quitanus*. Johnson (1957) elaborated on the distribution of earlier records approximately three degrees north in Huancabamba Province, Department of Piura, Peru and material from Ecuador (the type locality for the subspecies). It should be noted that Macchiavello (1948) alluded to *P. equatoris* as an important vector of plague in rural areas of northern Peru, but his specimens probably were *P. d. quitanus*.

Ctenophthalmidae

Neotyphloceras crassispina hemisus Jordan, 1936

Specimens Examined.—**Chiquian Province:** E of Chiquian, (10°9'54"S, 77°19'42"W), 3900 m, ex *Akodon* sp1 cf. *mollis*, 27 March 2000, Hastriter Team, 1♀; E of Chiquian, (10°06'07"S, 77°11'07"W), 4190 m, 27 March 2000, Hastriter Team, 1♀; E of Chiquian, (10°08'06"S, 77°10'22"W), ~3660 m, 27 March 2000, Hastriter Team, 1♀. **Hauzlas Province:** Santa River Valley, Choquechaca (N of Caraz), 2195 m, ex *Oryzomys xanthaeolus* Thomas, 1894, 3–4 September 1999, USUHS Team, 4♂, 5♀; ex *Thomasomys* sp., 4 September 1999, USUHS Team, 1♂, 2♀; ex *P. andium*, 2 September 1999, USUHS Team, 2♂, 7♀; ex *Akodon mollis* Thomas, 1894, 3–4 September 1999, USUHS Team, 1♂, 1♀; ex *O. xanthaeolus*, 27 September 1998, P. Carney, 1♀; ex *A. mollis*, 25 September 1998, P. Carney, 1♀; 9 km N Caraz (9°00'12"S, 77°49'36"W), 2440 m, ex *P. andium*, 30 March 2000, Hastriter Team, 5♂, 3♀. **Huaraz Province:** Pariacota (9°33'27"S, 77°38'82"W), 3630 m, ex *P. andium*, 24 March 2000, Hastriter Team, 1♂, 3♀; Pariacota (9°33'10"S, 77°35'69"W), 3715 m, ex *P. andium*, 24 March 2000, Hastriter Team, 1♀. **Huaylas Province:** Parque Nacional Huascarán (9°30'04"S, 77°25'31"W), 3630 m, ex *Akodon* sp1 cf. *mollis*, 25 March 2000, Hastriter Team, 1♂. **Recuay Province:** 10 km W Recuay (9°43'25"S, 77°29'13"W), 4010 m, ex *P. andium*, 29 March 2000, Hastriter Team, 1♂, 1♀; 19 km W Recuay (9°44'06"S, 77°30'03"W), 4420 m, ex *Akodon* sp1 cf. *mollis*, 29 March 2000, Hastriter Team, 2♀; N of highway 109 between Chiquian junction and Pavilitica (10°9'14"S, 77°19'17"W), 3990 m, ex *P. andium*, 28 March 2000, Hastriter Team, 3♀.

Remarks.—This ubiquitous species is found on a variety of hosts throughout its range and occurred at low (2195 m) and high (4420 m) elevations in all areas sampled in Ancash Department. The apex of the basimere has been used as the major feature to distinguish between the various subspecies of *Neotyphloceras*. This character is variable and unreliable. Males of this subspecies may readily be distinguished from *N. c. chilensis* Jordan, 1936, and *N. rosenbergi* (Rothschild, 1904) by the presence of spicules adorning the surface of the anterior sclerite connecting the left and right basimeres. These structures become visible when

focusing beyond the outer surface of the base of the basimere. They are also present in specimens of *N. c. crassispina* Rothschild, 1914 from Concepción, Chile. *Neotyphloceras c. hemisus* may be a synonym of the nominate subspecies, but the genus requires a comprehensive study for a definitive conclusion.

Leptopsyllidae

Leptopsylla segnis (Schönherr, 1811)

Specimens Examined.—**Hauzlas Province:** Santa River Valley, Choquechaca (N of Caraz), 2195 m: ex *M. musculus*, 2 September 1999, USUHS Team, 1♀; ex *M. musculus*, 4 September 1999, USUHS Team, 4♂, 6♀. **Pomabamba Province:** Huayllan, ex *M. musculus*, 17 February 2000, A. Lopez, 5♂, 5♀.

Pulicidae

Ctenocephalides felis felis (Bouché, 1835)

Specimens Examined.—**Hauzlas Province:** Santa River Valley, Choquechaca (N of Caraz), 2195 m, ex domestic dog, 5 September 1999, USUHS Team.

Remarks.—Hundreds of *C. f. felis* were hand-picked from domestic dogs by the students during the training program and countless others were trapped with water flea traps. An account of the number of specimens was not maintained.

Echidnophaga gallinacea (Westwood, 1875)

Specimens Examined.—**Hauzlas Province:** Santa River Valley, Choquechaca (N of Caraz), 2195 m, water flea trap, 3 September 1999, USUHS Team, 3♂, 2♀.

Remarks.—It is interesting that these stick-tight fleas were actively ambulatory and possibly attracted to the light of the water flea traps.

Hectopsylla suarezi C. Fox, 1929

Specimens Examined.—**Huari Province:** Progreso, ex *Cavia porcellus* (Linnaeus, 1758), 14 April 1999, D. Jodulhe, 1♀.

Remarks.—Most common hosts include caviid rodents, *C. porcellus* and *Cavia aperea* Erxleben, 1777. Hückinghaus (1961) considered *C. porcellus* as a synonym of *C. aperea*. This flea may support that conclusion, since it parasitizes both taxa and peridomestic rodents associated with these caviids. Although this flea is not often collected, its broad distribution is probably attributed to the common transport and trade of *C. porcellus* throughout the Andes.

Pulex irritans Linnaeus, 1758

Specimens Examined.—**Hauzlas Province:** Santa River Valley, Choquechaca (N of Caraz), 2195 m, water flea trap, 3 September 1999, USUHS Team, 3♂, 1♀.

Remarks.—Johnson (1957) recognized only *P. irritans* in South America, whereas Smit (1958) provided morphological justification that both *P. irritans* and *P. simulans* Baker, 1895 occur in North America. The senior author has examined material from localities adjacent to Lima (not reported in this study) which includes specimens comparable to North American *P. simulans*. Species belonging to *Pulex* are common around human habitations throughout Peru and

have been implicated in plague transmission in the highlands of northcentral Peru, particularly in the high Andean valleys in the Department of Cajamarca. Detailed studies of large series of this genus from diverse areas in South America are needed to determine if the complex is comprised of *P. irritans*, *P. simulans*, and possibly undescribed species, as alluded to by Smit (1958).

Tunga penetrans Linnaeus, 1758

Specimens Examined.—**Hauzlas Province**: Santa River Valley, Yuracota, (near brick making bat cave, N of Caraz), 2225 m, ex domestic dog, 20 March 2000, P. Lima, 1♂, 1♀. **Pomabamba Province**: Pomabamba, “in abandoned house,” 9 January 1999, J. Valverde, 4♂, 6♀.

Rhopalopsyllidae

Ayshaepsylla thurmani (Johnson, 1957)

Specimens Examined.—**Huaraz Province**: (9°32'32"S, 77°47'50"W), 1860 m, ex *P. andium*, 23 March 2000, Hastriter Team, 1♀.

Remarks.—*Ayshaepsylla* was erected as a subgenus of *Polygenis* by Smit (1987) and later elevated to genus by Linardi and Guimarães (1993). Accordingly, the genus *Ayshaepsylla* is distinct from all other genera within the subfamily Rhopalopsyllinae by the vestigial nature of the posterodorsal extension of the metasternal furca that does not extend more than one-half the length of the metapleural ridge. Smit (1987) incorrectly changed the spelling to “thurmanni” in all reference to this species. To avoid future perpetuation of this error, the correct species designation is *A. thurmani*, after Deed C. Thurman, Jr. (Johnson, 1957).

Several features of our female differ from those of *A. thurmani* illustrated by Johnson (1957). The dorsal lobe along the caudal margin of st. VII is longer and more acute and the subtending sinus much deeper. Sternum VII has 5 setae per side instead of 4 and the ventral margin of the spermatheca is angular rather than smoothly concave. Johnson (1957) reports the length of the allotype as 3.0 mm, whereas our specimen is about half that length (1.6 mm). Based on these variations, our specimen may prove to be a new species; however, a series to include accompanying males is needed to evaluate this taxon.

This rarely-collected flea has been reported only from two disjunct localities in southwestern Colombia (8♂, 7♀) and southern Peru (4♂, 6♀). Since our new record lies about half way between these localities, additional collecting will probably yield additional specimens throughout intermediate elevations (1465–1920 m) in Peru and Ecuador. Data are insufficient to establish host preferences for this species; however, Linardi and Guimarães (1993) consider Cricetine rodents to be the primary hosts.

Ectinorus (Ectinorus) alejoi Hastriter, **new species**
(Fig. 1A–H, 2A)

Type Material.—**Recuay Province**: W of highway junction 3 and 109 (~10°03'S, 77°22'W), ~4115 m, ex *Lagidium peruanum* Meyen, 1833, 29 March 2000, T. Alejo, 12♂, 2♀. The holotype, allotype, and 5 paratypes (5♂) are deposited in the Carnegie Museum of Natural History (CMNH), Pittsburgh, Pennsylvania, and 7 paratypes (6♂, 1♀) are deposited in the senior author's collection.

Diagnosis.—For those species that have no marginal spinelets on t. I, it most closely resembles *E. viscachae* (Wagner, 1937) in the male by details of the clasp-

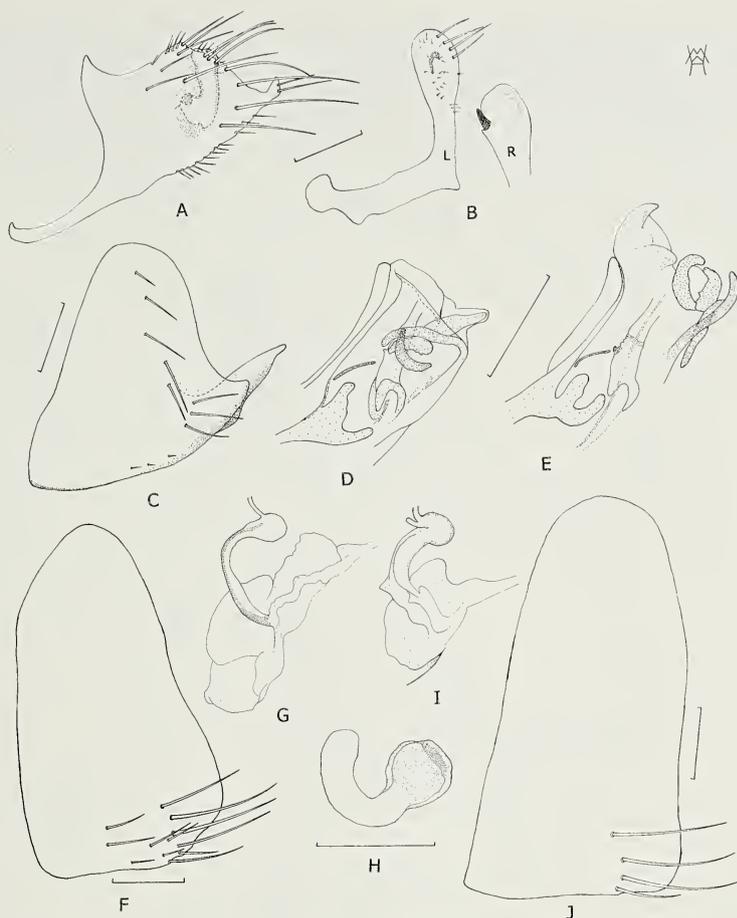


Fig. 1.—*Ectinorus alejoi* n. sp. A. Male clasper (basimere and telomere), holotype. B. Male ninth sternites, (L=left side, R=right side). C. Male eighth sternum, paratype. D. Apex of aedeagus, retracted, paratype. E. Apex of aedeagus, protracted, holotype. F. Female seventh sternum, allotype. G. Bursa copulatrix, allotype. H. Spermatheca, allotype. *Ectinorus claviger*. I. Bursa copulatrix. J. Female seventh sternum. Scale = 100 μ .

er, st. VIII, and st. IX and in the female by the modified abdominal segments and the shape of the spermatheca. It may be distinguished in the male by the presence of a processus basimeris ventralis (Fig. 1A), the caudal margin of the telomere is convex throughout and the apex is only slightly broader than body of telomere, an extended lobe (heel) is absent at the juncture of the proximal and distal arms of st. IX, and the posterior apical margin of st. IX has only 3–4 stout setae (Fig. 1B). Females may be separated from *E. viscachae* by the presence of an isolated lateral patch of 5–6 small setae on st. II (*E. viscachae* has a patch of many setae merging with the ventral setae) and the perula of bursa copulatrix is strongly reflexed and globular (Fig. 1G). Females also differ from those of *Ectinorus claviger* (Rothschild, 1914) by the presence of more than 20 trichobothria on the sensillum.

Description.—Head, male holotype (Fig. 2A): Frontal tubercle close to oral angle by less than its

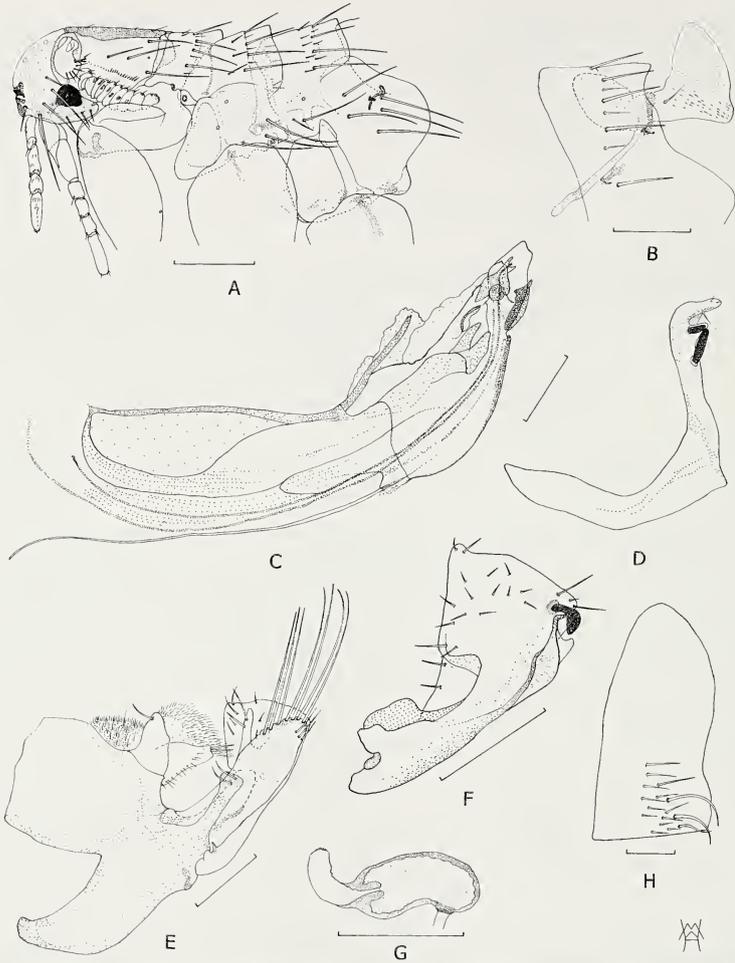


Fig. 2.—*Ectinorus alejoi* n. sp. A. Head and thorax, holotype. *Plocopsylla pallas*. B. Male seventh and eighth tergites. C. Aedeagus. D. Male ninth sternum. E. Male clasper (basimere and telomere). F. Enlargement of telomere, mesal view. G. Spermatheca. H. Female seventh sternum. Scale = 100 μ .

vertical width. Two placoid pits along frontal margin. Ocular setae 3, with single seta anterior to eye (single seta lacking in female). Eye large and darkly pigmented with sclerotized ridge extending to margin of gena associated with visible arch of tentorium. Three setae along lower margin of genal lobe and 2 minute setae at apex. Postantennal area with 3 rows of setae per side (1, 1, 5), intercalaries in posterior row. Occipital groove as deep as width of first maxillary palpus. Third segment of maxillary palpus only half length of other segments. Labial palpus of 5 segments extending to apex of fore coxae, each of the 3 middle segments less than half the length of either segment 1 or 5; maxillae sharply pointed apically. Antennal fossa bordered above by row of 21–22 minute setae. Scape with apical fringe of 7 setae, pedicel with 2 very short setae, and clavus long, extending well onto prosternosome. Thorax (Fig. 2A): notal segments each with 2 rows of setae (anterior row of pronotum of only 2 dorsal setae per side). Mesonotal collar with 6–7 pseudosetae per side (variable in number in some paratypes). Mesopleuron with 5 setae; mesosternum vestigial. Lateral metanotal area with 2 setae (1 large, 1 small). Pleural arch well developed. Metepisternum with single seta. Dorsal margin of metasternum inconspicuous, ventral lobe not extending downward. Metepimeron with anterior vertical row of 2 setae and posterior row of 3 setae, all below level of the foot-shaped spiracular atrium. Legs: Fore coxa with 18–20 lateral setae, mid and hind coxae with numerous setae on mesal surface of

anterior margins and lateral sulcus of mid coxa at most indicated by notch at posterior apical margin. Pair of setae guarding femoral-tibial joint of fore femur about equal in length, lateral setae shorter of pair on mid and hind femora. A single seta present over femoral pit. Surface sculpturing absent on all femora. Mid and hind femora each with single lateral row of 5–6 setae. Tibiae each with 6 dorsal notches and each with corresponding vertical row of 5–6 setae (female with 7 dorsal notches on hind femur). Second segment of fore tarsus longer than each of segments 1, 3, and 4. Two apical bristles of second segment of hind tarsus extending well beyond base of distitarsomere. Four lateral plantar bristles on each segment, 2 preapical plantar bristles of fore and mid distitarsomeres spiniform but less so on hind distitarsomere (1 spiniform and 1 hair-like seta on all distitarsomeres of female). Unmodified Abdominal Segments: Tergum I with 2 rows of setae, anterior comprised of 1–2 setae per side, t. II–VII each with single row of setae with intercalaries (female with 2 rows on each tergite). Each row with one seta below level of very small spiracles (female has 1 or 3 below level of each spiracle). Single marginal antensensilial bristle borne on tubercle. Lateral patch of 2–4 setae on st. II and single seta per side on main row (female with lateral patch of 5–6 setae and 3 per side in main row); st. III–VII each with 2–3 setae per side (female with two rows of 4–5 setae per side on st. III–IV, two rows of 1 and 5 setae per side on st. V–VII). Modified Abdominal Segments, male (Fig. 1A–C): Tergum VIII reduced, without setae. Sensillum with 24–26 trichobothria per side. Manubrium of t. IX narrow, parallel-sided, and turned upward at apex. Basimere nearly square with processus basimeris ventralis (see remarks) at ventral-caudal margin bearing 2 apical setae. Acetabular bristle single; numerous long setae along periphery of basimere. Telomere slightly extending beyond basimere, parallel-sided, and slightly convex along posterior margin (Fig. 1A). Sternum VIII bilobed, with lateral lobe bluntly rounded and medial lobe acutely pointed; lateral portion with 5–6 setae (Fig. 1C). Distal lobe of st. IX club-shaped; lobe of each side asymmetrical. The right distal arm bears a sclerotized tooth on mesal side of apex not present on left side (Fig. 1B). Caudal margin with 4 slender setae and lateral area with scattered setae. Sternum IX lacks tendon. Aedeagus (Fig. 1D–E): Aedeagal apodeme broadly spatulate, bluntly rounded at apex, and with narrow neck preceding fulcral medial and lateral lobes. Penis rods extend around apex of aedeagal apodeme. Orifice of sclerotized inner tube oblique in lateral view; ringed at basal $\frac{1}{2}$. Median dorsal lobe hooked apically with short blunt disto-lateral lobes. Alpha portion of Ford's sclerite "C"-shaped, heavily sclerotized. Securifer of Ford's sclerite claw-like with small tooth on anterior margin. Crochet sclerotized and rod-like. Paired ventral lobes narrow and hook-like. Modified Abdominal Segments, female (Fig. 1F–H): Tergum VIII with 4 setae above spiracle, lateral curved row of 5 long setae and 12 scattered lateral setae. Dorsal caudal lobe of t. VIII conical with group of many setae both mesally and laterally. Conical lobe subtended by broad sinus with 4 evenly spaced marginal setae. Caudal margin of st. VII with rounded lobe; 5–6 lateral setae per side and anterior group of 5–6 smaller setae (Fig. 1F). Sternum VIII broad, apically rounded lobe without setae. Bursa copulatrix sclerotized anteriorly, strongly reflexed caudally; perula globular (Fig. 1G). Bulga of spermatheca nearly spherical; duct emerging at apex. Hilla nearly twice length of bulga; slightly wider distally than proximally. Cribriform area expanded over half of bulga (Fig. 1H).

Length (slide mounted specimens).—Male: 2.0 mm (n=7, range=1.9–2.2 mm); Female: 2.9 mm (n=2, range=2.7–3.0 mm).

Etymology.—This species is named after the collector, Teophilo Alejo, a local hunter and respected conservationist in Recuay Province.

Remarks.—Specimens of *E. alejoi* collected from a single host animal were found in association with a series of *T. titschacki*. The rarity of *T. titschacki* in collections may be a reflection of the infrequent examination of its preferred host, *L. peruanum*. It is predictable that *E. alejoi* occurs throughout the narrow high elevation range of this chinchillid rodent, just as that of *T. titschacki*.

The use of the term processus basimeris ventralis in the key provided by Smit (1987) describing some taxa within the genus *Ectinorus* may be misleading and requires some explanation. As the term would imply, it includes a process that arises from the basimere on its ventral margin. Among those species considered to have a processus basimeris ventralis, the position of the process on the basimere varies considerably from an extreme ventral position forming a deep cleft, or sinus between the basimere and the process [*E. claviger*, *E. budini* (Jordan and Rothschild, 1923), etc.] to a more caudal position that includes a process without

the presence of a cleft, or sinus (*E. ineptus* Johnson, 1957, *E. sentus*, and *E. uncinatus* Beaucournu and Gallardo, 1991). Nonetheless, any process along the ventral or caudal margin of the basimere should be considered the processus basimeris ventralis.

Ectinorus (Ectinorus) claviger (Rothschild, 1914)
(Fig. 11–J)

Specimens Examined.—**Recuay Province:** W of highway junction 3 and 109 (~10°03'S, 77°22'W), ~4115 m, *L. peruanum*, 29 March 2000, T. Alejo, 1♀. This specimen is deposited in the Carnegie Museum of Natural History.

Remarks.—This female was collected from the same host species as *E. alejo* (described above). A very closely related species (if not conspecific), *Ectinorus sentus* (Rothschild, 1914) was also reported from vizcacha (*Lagidium* Meyen, 1833 or *Lagostomus* Brookes, 1828) from the adjacent province of Junin. Wilson and Reeder (1993) indicates that the monotypic genus *Lagostomus* does not occur in Peru. Consequently, the Junin record was assuredly also from *L. peruanum*. Neither *E. claviger* nor *E. sentus* possess marginal spinelets on t. I, and the sensillum of each has fewer than 20 trichobothria per side. The latter character separates them from the closely allied taxon, *E. viscachae* (Wagner, 1937). Females of *E. sentus* are unknown. Our female was compared with the female description of *E. claviger* provided by Wagner (1937) and found to be conspecific. The female is unknown for three additional species within this group [*E. budini* (Jordan and Rothschild, 1923), *E. nomisis* Smit, 1987, and *E. pearsoni* (Johnson, 1957)], but their distributions are extralimital. Smit (1987), in couplet 19 of his key to the species of the subgenus *Ectinorus*, overlooked the description of *E. claviger* females by Wagner (1937). A brief description of the female of *E. claviger* is provided to supplement that of Wagner (1937).

Description.—**Head:** Frontal tubercle well developed. Ocular row of 3 setae, ventral seta the larger. Labial palpus of 5 segments, extending to middle of trochanter. Genal lobe with marginal ventral row of 5 small setae. Eye with deep ventral sinus. Occipital area with single minute seta dorsal to antennal fossa and 3 setae per side along posterior main row. Scape with 5 marginal setae, pedicel with dorsal lobe bearing several small setae and a single seta extending about ½ length of antenna. **Thorax:** Pronotum with single row of setae, mesonotum with two rows of setae and 17–18 pseudosetae under mesonotal collar, metanotum with two rows of setae. Dorsal portion of prosternum arched upward forming depression and shield for terminal segments of antenna. Meso- and metasterna not extending downward. Furca hair-like and pleural arch well developed. Metepimeron with single vertical row of 4 setae and single seta anterior to row. **Legs:** Mid coxa with lateral sulcus incomplete. Hind coxa with fringe of setae mesally from base to apex. Lateral setae guarding femoral-tibial joint shortest on fore femur and longest on mid and hind femora. A single seta extending over anterior pit on each femur. Six dorsal notches on all tibiae with two minute setae between the fourth and fifth notches. Four lateral plantar bristles on each of the distitarsomeres. Unmodified abdominal segments: Tergites lacking marginal spinelets. Two rows of setae per tergite. One antesensillial seta per side set on small tubercle. Patch of 12–13 small setae on st. II isolated from single basal seta per side. Sternum III with 6–7 setae per side, preceded by 5–6 scattered setae. Sternites IV–VI with 4–5, 3, and 4 per side, respectively. Modified abdominal segments: Tergum VIII with 5–7 setae per side dorsal to atrium of spiracle. Atrium with obvious expansion at base. Caudal margin of t. VIII rounded with 8 marginal setae, patch of 6 setae anterior to these, and 10–12 short, stout setae mesally at apex. Caudal margin of st. VII entire (Fig. 1J). Sternum VIII broad and obliquely rounded dorsally. Sides of anal stylet parallel, four times as long as wide, bearing one long seta and 2 minute setae ventral to base of long seta. Ventral anal lobe convexly arched ventrally with numerous stout marginal setae. Spermatheca slightly askew but cribriform area appears to extend from surface to deep within bulga. Perula of bursa copulatrix spherical, not ovoid (Fig. 1I).

Length (single slide mounted specimen).—2.5 mm

Polygenis (Polygenis) litargus (Jordan and Rothschild, 1923)

Specimens Examined.—**Hauzlas Province:** Santa River Valley, Choquechaca (N of Caraz), 2195 m, ex *O. xantheolus*, 2–3 September 1999, USUHS Team, 3♂, 4♀; ex *A. mollis*, 3–4 September 1999, USUHS Team, 2♀; ex *P. andium*, 2 September 1999, USUHS Team, 1♂; ex *Thomasomys* sp., 4 September 1999, USUHS Team, 1♂.

Remarks.—This flea was collected from inside a human dwelling from a water trap and from sylvatic rodents. Macchiavello (1957) reported that *P. litargus* was the principal vector of plague among *Sciurus stramineus* Eydoux and Souleyet, 1841 in Lancones and Cazaderos, Piura Department, Peru. This flea should be considered a potential link in transferring plague from wild rodent populations to commensal, or peridomestic rodents such as *O. xantheolus*.

Tetrapsyllus (Phylliver) bleptus (Jordan and Rothschild, 1923)

Specimens Examined.—**Huaraz Province:** Pariacota (9°33'27"S, 77°38'82"W), 3630 m, ex *P. andium*, 24 March 2000, Hastriter Team, 3♀; Pariacota (9°33'10"S, 77°35'69"W), 3715 m, ex *P. andium*, 24 March 2000, Hastriter Team, 1♀.

Remarks.—Females of this species were collected from two adjacent sites from three specimens of the same host species, *P. andium*. Known only from high elevations (2745–4880 m), it has previously been reported from Junin Department, Peru, south to Parincota Province, Chile and Catamarca (type locality) and Jujuy Provinces, Argentina. Records from Ancash Department establish the most northern account for *T. bleptus*.

Tiasmastus cavicola (Weyenbergh, 1881)

Specimens Examined.—**Hauzlas Province:** Santa River Valley, Choquechaca (N of Caraz), ex *C. porcellus*, January 2000, P. Lima, 5♂, 20♀.

Remarks.—This flea is common on the domestic guinea pig, which is a staple food source for the indigenous people of Peru. Little effort was expended in collecting fleas from these hosts or in human habitations, although they are known to occur in large numbers on *C. porcellus*.

Stephanocircidae

Cleopsylla townsendi Rothschild, 1914

Specimens Examined.—**Chiquian Province:** E of Chiquian (10°03'48"S, 77°19'27"W), 4180 m, ex *P. amicus*, 27 March 2000, Hastriter Team, 1♂ 2♀; E of Chiquian (10°06'07"S, 77°11'07"W), 4180 m, ex *Akodon* sp2 cf. *mollis*, 27 March 2000, Hastriter Team, 4♂ 1♀; E of Chiquian (10°08'06"S, 77°10'22"W), ~3995 m, ex *P. andium*, 27 March 2000, Hastriter Team, 1♀; E of Chiquian (10°09'14"S, 77°19'17"W), 3990 m, ex *P. andium*, 27 March 2000, Hastriter Team, 1♂, 2♀. **Huaraz Province:** Pariacota (9°33'10"S, 77°35'69"W), 3715 m, ex *P. andium*, 24 March 2000, Hastriter Team, 4♂. **Huaylas Province:** Parque Nacional Huascarán (9°30'04"S, 77°25'31"W), 3630 m, ex *Akodon* sp1 cf. *mollis*, 25 March 2000, Hastriter Team, 1♂; Parque Nacional Huascarán (9°30'27"S, 77°26'13"W), 3935 m, ex *Akodon* sp1 cf. *mollis*, 25 March 2000, Hastriter Team, 2♂, 4♀; Parque Nacional Huascarán (9°30'39"S, 77°27'69"W), 3475 m, ex *P. andium*, 25 March 2000, Hastriter Team, 1♂, 2♀; and Parque Nacional Huascarán (9°30'04"S, 77°25'31"W), 3630 m, ex *Akodon* sp2 cf. *mollis*, 25 March 2000, Hastriter Team, 1♀. **Recuay Province:** 4.6 km W Recuay (9°43'36"S, 77°27'55"W), ~3660 m, ex *P. andium*, 29 March 2000, Hastriter Team, 2♀; 19 km W Recuay (9°44'6"S, 77°30'03"W), 4420 m, ex *Akodon* sp1 cf. *mollis*, 29 March 2000, Hastriter Team, 1♀; N of Santos River (10°03'48"S, 77°19'27"W), 4180 m, ex *P. amicus*, 27 March 2000, Hastriter Team, 1♂, 2♀.

Remarks.—The bulga of the spermatheca of *C. townsendi* extends well onto

the hilla, giving the false impression that the hilla is extended into the bulga. This is not apparent in figures of the spermatheca illustrated by Hopkins and Rothschild (1956) and Johnson (1957). The species has been reported from Chimborazo, Ecuador (type locality) and Parincota, Chile, and in four Peruvian Departments (Table 1). It was commonly collected on species of *Phyllotis* and *Akodon* in Ancash Department, although it has been reported from a variety of hosts in other high elevation regions (3660–4880 m).

Craneopsylla minerva minerva (Rothschild, 1903)

Specimens Examined.—**Hauzlas Province:** Santa River Valley, Choquechaca (N of Caraz), ex *P. andium*, 2 September 1999, USUHS Team, 1♂. **Huaraz Province:** Pariacota (9°32'32"S, 77°47'50"W), 1860 m, ex *P. andium*, 23 March 2000, Hastriter Team, 1♀. **Huari Province:** Yungilla, ex *Rattus* "silvestre", 15 April 1999, J. Cisamaro, 1♀. **Huaylas Province:** Parque Nacional Huascarán (9°30'40"S, 77°28'32"W), 3385 m, ex *P. amicus*, 25 March 2000, Hastriter Team, 1♀; Parque Nacional Huascarán (9°30'40"S, 77°28'32"W), 3380 m, ex *Akodon* sp2 cf. *mollis*, 25 March 2000, Hastriter Team, 1♂, 2♀; Parque Nacional Huascarán (9°30'39"S, 77°28'69"W), 3475 m, ex *Akodon* sp1 cf. *mollis*, 25 March 2000, Hastriter Team, 3♂, 1♀. **Recuay Province:** 10 km W Recuay (9°43'25"S, 77°29'13"W), 4010 m, ex *P. andium*, 29 March 2000, Hastriter Team, 1♂, 2♀; 10 km W Recuay (9°43'25"S, 77°29'13"W), 4010 m, ex *P. amicus*, 29 March 2000, Hastriter Team, 2♂, 1♀.

Remarks.—Specimens of *Craneopsylla minerva wolffhuegeli* (Rothschild, 1909) referenced by Macchiavello (1948) from Ecuador, Peru and northern Chile, undoubtedly belong to the nominate subspecies. Although the two subspecies are sympatric in northern Argentina, *C. m. wolffhuegeli* probably does not occur in Peru. Neither species have been reported in Bolivia.

Plocopsylla achilles (Rothschild, 1911)

Specimens Examined.—**Chiquian Province:** E of Chiquian (10°9'54"S, 77°19'42"W), 3900 m, ex *Akodon* sp1 cf. *mollis*, 27 March 2000, Hastriter Team, 1♂, 1♀. **Huaylas Province:** Parque Nacional Huascarán (9°30'27"S, 77°26'13"W), 3935 m, ex *Akodon* sp1 cf. *mollis*, 25 March 2000, Hastriter Team, 2♂, 1♀; Parque Nacional Huascarán (9°30'04"S, 77°25'31"W), 3630 m, ex *Akodon* sp1 cf. *mollis*, 25 March 2000, Hastriter Team, 1♀. **Recuay Province:** 10 km W Recuay (9°43'25"S, 77°29'13"W), 4010 m, ex *P. andium*, 29 March 2000, Hastriter Team, 1♂; 19 km W Recuay (9°44'06"S, 77°30'03"W), 4420 m, ex *Akodon* sp1 cf. *mollis*, 29 March 2000, Hastriter Team, 2♂, 4♀.

Plocopsylla pallas (Rothschild, 1914), male description
(Fig. 2B–H)

Material Examined.—**Huaraz Province:** Pariacota (9°33'10"S, 77°35'69"W), 3715 m, ex *P. andium*, 24 March 2000, Hastriter Team, 1♂; Pariacota (9°33'27"S, 77°38'82"W), 3630 m, ex *P. andium*, 24 March 2000, Hastriter Team, 5♂, 7♀. **Recuay Province:** N of Santos River (10°03'48"S, 77°19'27"W), 4180 m, ex *P. amicus*, 27 March 2000, Hastriter Team, 2♀; road cut on highway 109 between Chiquian junction and Pavilolica (10°9'36"S, 77°19'46"W), 3980 m, ex "Berlese nest from cavity in earth bank," 1 April 2000, M.W. Hastriter and R. Soto, 1♂; N of highway 109 between Chiquian junction and Pavilolica (10°09'14"S, 77°19'17"W), 3990 m, ex *Akodon* sp2 cf. *mollis*, 28 March 2000, Hastriter Team, 1♂; N of highway 109 between Chiquian junction and Pavilolica (10°9'14"S, 77°19'17"W), 3990 m, ex *P. andium*, 28 March 2000, Hastriter Team, 1♂, 8♀; 10 km W Recuay (9°43'25"S, 77°29'13"W), 4010 m, ex *P. andium*, 29 March 2000, Hastriter Team, 10♂, 12♀; 10 km W Recuay (9°43'25"S, 77°29'13"W), 4010 m, ex *P. amicus*, 29 March 2000, Hastriter Team, 3♂, 5♀. Specimens of this series are deposited in the CMNH (2♂, 2♀), the National Museum of Natural History, Washington, D.C. (2♂, 2♀), and the Robert E. Lewis collection (2♂, 2♀). The remaining specimens remain in the senior author's collection.

Remarks.—In his original description of *P. pallas*, Rothschild (1914) provided only a brief description based on two females collected from a "rat" in Junin

Department. His description of the female is herein supplemented (based on 34 ♀) and a description of the male is provided for the first time based on a large series of 22 ♂. Our records would indicate that *P. andium* is the preferred host. This flea was not collected in other provinces (also high altitude sites), although *P. andium* was prevalent.

Diagnosis.—Both sexes resemble *P. viracocha* Schramm and Lewis, 1987 and *P. enderleini* Wagner, 1933 by the lack of basally notched helmet spines and a genal comb consisting of 6 spines (the genal spine being smaller than the others and separated by a space roughly the width of the spines). Schramm and Lewis (1988) assigned these two species to Species Group A, Subgroup A-3. The males of *P. pallas* can now be assigned to this grouping. The male can immediately be distinguished from those of *P. viracocha* by the presence of a slender mesal lobe projecting well beyond the dorsal margin of the basimere (Fig. 2E) and the apex of st. IX bent caudad at a 90° angle (Fig. 2D). The absence of an acutely angled dorso-anterior projection of the telomere (Fig. 2E–F) separates it from *P. enderleini*. Separable from males of both species by the presence of a conspicuous dorsally expanded wing-like sclerite that extends upwards between t. VII and sensillum (Fig. 2B). Females may be separated from *P. enderleini* in having a prectenidial helmet width that is more than one and one-half the length of the longest helmet spine and from *P. enderleini* (5–6 well-separated bristles) and *P. viracocha* (4 well-separated bristles) in having only 3 well-separated marginal bristles below the lobe of t. VIII.

Description, Male.—Head: Anterior helmet consisting of 14 spatulate spines without notched bases. Prectenidial width of helmet more than 1.5 times length of longest helmet spine. Line of minute marginal setae along anterior margin of helmet; single large seta near base of ventral-most helmet spine. Two placoid pits along dorsal margin of helmet. Helmet striations absent above dorsal spine. Gena with 8–9 minute setae along anterior margin; two large lateral setae in vertical row. Genal comb of 6 spatulate spines; dorsal-most spine less than ½ length of others. Genal lobe extending beyond dorsal genal spine and truncate. Maxillary palpus of 5 segments; basal segment very short. Maxilla slightly rounded apically; labial palpus of 5 segments, apex reaching ⅔ length of fore coxa. Postantennal region with anterior group of 18–20 setae per side and 4 rows (4, 5, 8 and 8–9 setae per side); posterior row with intercalaries. Occiput with dorsal tuber. Antennal scape with 5 apical setae extending onto pedicel; pedicel with 10 long slender setae extending beyond 9-segmented clavus. The latter appears compressed and fused, extending far short of antennal fossa. Thorax (Fig. 2A): Pronotum with two anterior irregular rows of setae and a third posterior row; comb composed of 22 spines. Large dorsal notch in prosternum for cervical link plate. Mesonotum with anterior group of setae; posterior row of 6 setae per side with intercalaries and single pseudoseta per side under mesonotal collar. Metapleuron with 9 lateral setae. Mesosternum lobed ventrally downward between pro- and meso-coxae. Metanotum with irregularly arranged anterior row of setae and posterior row of 6 setae per side with intercalaries. The dorso-posterior margin of metanotum barely discernible. Lateral metanotal area with 3 setae. Pleural arch well developed. Metepisternum with single lateral seta; squamulum present. Metasternum lobed antero-ventrally extending downward between mid and hind coxae. Metepimeron with two vertical rows of 4 setae each; atrium of spiracle larger than abdominal spiracles. Legs: Numerous lateral setae on fore coxa. Fore femur with 9–10 lateral setae, no mesal setae. Setae guarding femoral-tibial joint subequal. Dorsal margin of fore tibia with 5 notches bearing setae (2, 2, 3, 3, 3), apical setae arranged in a false comb of 7 setae. Lateral surface of fore tibia with vertical row of 7 setae. Lateral sulcus of mid coxa complete. Anterior femoral pit of mid femur with long outer seta and shorter inner seta; 6 setae each on posterior lateral margin and single mesal seta. Lateral seta guarding femoral-tibial joint of mid femur larger than mesal seta; mesal seta larger than lateral seta on hind femur. Hind tibia with 10 lateral setae, 6 dorsal notches (2, 2, 3, 3, 3, 3 setae), and apical false comb of 9–10 setae. Mid and hind coxae, each with fringe of setae extending about ⅓ from apex to base. Dorsal margin of mid and hind femora with short, stout setae. Hind femur with 8–9 lateral setae arranged toward posterior. Hind tibia with 15 lateral setae, 7 dorsal notches (2, 2, 3, 3, 3, 3, and 4 setae); apical setae interrupted and not forming a false comb as on fore and mid tibiae. The lowest seta in each notch bearing 3 setae separated from adjacent 2 setae by space less than width

Table 1.—A listing of fleas of Peru by political departments (A = new record for Ancash Department; C = species found in current study; P = new record for Peru; X = species recorded in literature; and ? = doubtful occurrence).

Flea species	Ancash	Apurimac	Arequipa	Ayacucho	Cajamarca	Cuzco	Huan-cavelica
<i>Adoratopsylla intermedia coph</i>							
<i>Adoratopsylla intermedia intermedia</i>							
<i>Agastopsylla hirsutior</i>							
<i>Agastopsylla nilotica nilotica</i>							
<i>Agastopsylla pearsoni</i>							
<i>Ayshaepsylla thurmani</i>	AC						
<i>Cediopsylla spillmanni</i>							
<i>Ceratophyllus titicacensis</i>							
<i>Cleopsylla townsendi</i>	AC					X	
<i>Craneopsylla minerva minerva</i>	AC						
<i>Craneopsylla minerva wolffhuegeli?</i>			X				
<i>Ctenidiosomus spillmanni</i>							
<i>Ctenocephalides canis</i>	X				X		
<i>Ctenocephalides felis felis</i>	CX						
<i>Dasypsyllus plumosissimus</i>						X	
<i>Dasypsyllus stejnegeri</i>	PC						
<i>Delostichus phyllotis</i>			X				
<i>Delostichus xenurus</i>	X						
<i>Echidnophaga gallinacea</i>	AC						
<i>Ectinorus alejoi</i> n. sp.	PC						
<i>Ectinorus claviger</i>	AC			X			
<i>Ectinorus disjugis</i>			X				
<i>Ectinorus hecate</i>			X				
<i>Ectinorus hertigi</i>							
<i>Ectinorus ineptus</i>							
<i>Ectinorus pearsoni</i>							
<i>Ectinorus sentus</i>							
<i>Ectinorus simonsi</i>			X				
<i>Ectinorus viscachae</i>				X			
<i>Euhoplopsyllus andensis</i>							
<i>Euhoplopsyllus manconis</i>							
<i>Gephyropsylla klagesi klagesi</i>							
<i>Gephyropsylla klagesi samuelis</i>							
<i>Hectopsylla eskeyi</i>			X				
<i>Hectopsylla psittaci</i>							
<i>Hectopsylla pulex</i>						X	
<i>Hectopsylla suarezi</i>	CX						
<i>Hormopsylla egena</i>							
<i>Hormopsylla trux</i>							
<i>Leptopsylla segnis</i>	CX						
<i>Myodopsylla setosa</i>						X	
<i>Neotyphloceras crassispina chilensis?</i>							
<i>Neotyphloceras crassispina crassispina</i>	X	X					
<i>Neotyphloceras crassispina hemisus</i>	AC						
<i>Neotyphloceras rosenbergi</i>					X		
<i>Nonnapsylla rothchildi</i>							
<i>Nosopsyllus fasciatus</i>							
<i>Nosopsyllus londiniensis londiniensis</i>					X		
<i>Parapsyllus cedei</i>							
<i>Plocopsylla achilles</i>	CP						
<i>Plocopsylla endertieini</i>			X				
<i>Plocopsylla hector</i>							
<i>Plocopsylla inti</i>							
<i>Plocopsylla kilya</i>							

Table 1.—Continued.

Flea species	Ancash	Apurimac	Arequipa	Ayacucho	Cajamarca	Cuzco	Huan-cavelica
<i>Plocopsylla pallas</i>	AC						
<i>Plocopsylla viracocha</i>							X
<i>Plusaetis equatoris?</i>							
<i>Plusaetis dolens quitanus</i>	AC						
<i>Polygenis bohlsi bohlsi</i>							
<i>Polygenis brachinus</i>					X		
<i>Polygenis impavidus</i>						X	
<i>Polygenis litargus</i>	CX				X		
<i>Polygenis litus?</i>							
<i>Polygenis rimatus?</i>	X						
<i>Polygenis roberti beebei</i>		X					X
<i>Polygenis roberti roberti</i>							X
<i>Pulex irritans</i>	CX				X		
<i>Rhopalopsyllus australis tupinus</i>							
<i>Rhopalopsyllus cacicus</i>							
<i>Rhopalopsyllus lugubris lugubris</i>							
<i>Sphinctopsylla inca</i>	AC						
<i>Sternopsylla distincta speciosa</i>						X	
<i>Tetrapsyllus bleptus</i>	AC						
<i>Tetrapsyllus comis</i>							
<i>Tetrapsyllus elutus</i>							
<i>Tetrapsyllus tristis</i>							
<i>Tiamastus cavicola</i>	CX		X		X		
<i>Tiarapsylla bella</i>							
<i>Tiarapsylla titschacki</i>	AC						
<i>Tunga penetrans</i>	CX				X		
<i>Xenopsylla cheopis</i>					X		

of base of same setae. Femoral pits on all three femora with long outer seta and shorter inner seta. The fifth segment of each tarsus with 5 pairs of plantar bristles, the proximal pair placed on plantar surface between second pair, preapical plantar bristles small, paired, and broadly spaced on apex of plantar surface. Unmodified abdominal segments: Number of marginal spinelets variable on t. I–VII (5–6, 3–4, 4, 2–3, 0, 0, and 0 spinelets per side). Tergites I–VI with 2 rows of setae (anterior short setae, posterior long setae with intercalaries). Tergum VII with single row of setae, antesensilial bristles lacking. Single seta of main row below level of pointed spiracular fossa. Notable sclerotized apodemes on basal st. II, bearing single seta per side, st. III–VI with 3 setae per side, st. VII with 1–2 small setae per side. Modified abdominal segments (Fig. 2B, D–F): Tergum VIII greatly expanded into wing-like processes that extend dorsad between t. VII and sensilium, mesal surface spiculose (Fig. 2B). Basimere of t. IX with mesal process along dorsal margin bearing 2 setae, apex with row of 8–9 long marginal setae (Fig. 2E). Apex of telomere nearly twice as wide as near point of articulation with basimere; bearing a scattered group of minute setae on the mesal surface and a large spiniform on the apical-posterior mesal surface. Membranous dorsal anal lobe with single dorsal seta; ventral anal lobe with two ventral setae. Sensilium with 16 sensilial pits per side. Sternum VII extending upward covering st. VIII and aedeagus. Apex of st. IX strongly bent caudad, bearing a single hair-like seta and two highly modified spiniform bristles (Fig. 2D). Aedeagus (Fig. 2C): Lateral lamina narrow at neck broadening toward apex; median lamina broader than lateral lamina. Lateral lamina projecting dorso-caudad above fulcrum. Apodemal rod extending from well differentiated ventral floor of the girdle. Penis rods slightly longer than lateral/median lamina. Dorsal median lobes membranous and somewhat squared apically with sclerotized crochet. Sclerotized inner tube covered laterally by dorsal armature. Modified abdominal segments, female (Fig. 2G–H): Dorsal portion of t. VIII with two stout setae just above spiracular fossa; dorsal margin beneath sensilium strongly concave with well developed lobe along upper caudal margin lacking setae. The dorsal caudal lobe subtended by a shallow sinus with three long marginal bristles equally spaced; anterior and nearly contiguous to these is a shorter subspiniform seta extending obliquely upward. Among a lateral group of 36–38 setae are 2 stout setae. Caudal margin of st. VII with slight concavity, group of 16–18 setae per side of which 2

Table 1.—Continued. Extended.

Ica	Junin	La Libertad	Lambayeque	Lima	Loreta	Moquegua	Pasco	Piura	Puno	San Martín	Tacna	Tambo	Tumbes	Peru Islands
	X								X					
								X						
								X						
	X							X						
X	X	X	X					X	X				X	X
								X						
X		X	X	X				X					X	
	X							X						
	X			X				X						
								X						
	X							X						
X		X	X	X		X		X					X	
	X	X						X						
X		X	X	X				X					X	
		X	X	X				X					X	

are strongly curved ventrad (Fig. 2 H). Sternum VIII without setae. Dorsal anal lobe dorsally enclosed with fringe of 7–8 long setae; anal stylet more than three times as long as wide with 2 short and 1 long setae. Ventral anal lobe inconspicuous with several fine setae along ventral portion. Bulga of spermatheca about twice length of hilla; lumen deeply inserted into bulga and distinctly narrowed at apex of internal orifice. Spermatheca strongly concave ventrally and convex dorsally; lumen of duct enters bulga ventrally (Fig. 2G).

Length (slide mounted specimens).—Male: 2.9 mm (n=20, range=2.6–3.1 mm); Female: 2.9 mm (n=20, range=2.4–3.2 mm).

Sphinctosylla inca (Rothschild, 1914)

Specimens Examined.—**Chiquian Province:** E of Chiquian (10°08'06"S, 77°10'22"W), ~3660 m, ex *P. andium*, 27 March 2000, Hastriter Team, 1♀. **Huaylas Province:** Parque Nacional Huascarán (9°30'04"S, 77°25'31"W), 3630 m, ex *Akodon* sp1 cf. *mollis*, 25 March 2000, Hastriter Team, 2♀; Parque Nacional Huascarán (9°30'27"S, 77°26'13"W), 3630 m, ex *Akodon* sp1 cf. *mollis*, 25 March 2000, Hastriter Team, 1♂.

Tiarapsylla titschacki Wagner, 1937

Specimens Examined.—**Recuay Province:** W of junction highways 3 and 109 (~10°03'S, 77°22'W), ~4115 m, ex *L. peruanum*, 29 March 2000, T. Alejo, 3♂, 7♀.

Remarks.—Three type specimens (1♂, 2♀) were collected on “vizcacha” in the adjacent Department of La Libertad (4000 m) (Wagner, 1937). Additional records include one female each from *L. puruanum*, Department of Puno (ele-

vation unknown) and Department of Junin (~4875 m) (Johnson, 1956). A female was also reported from a feline host in the Department of Puno (Hopkins and Rothschild, 1956). The latter record is undoubtedly a predator-related association. *Lagidium puruanum* seems a preferred host for this species, occurring only at high elevations from central to southern Peru.

DISCUSSION

Very common species (*Pulex irritans* complex, *L. segnis*, *E. gallinacea* and *T. cavicola*) found on peridomestic animals were not aggressively sought except to establish records for Ancash Department. Trapping statistics were kept only for the March 2000 collecting period and an analysis follows. During eight trap nights, 844 traps were set yielding 67 small mammals [*Akodon* sp1 cf. *mollis* (n=16, 23.9%), *Akodon* sp2 cf. *mollis* (n=5, 7.5%), *M. musculus* (n=5, 7.5%), *P. andium* (n=38, 56.7%) and *P. amicus* (n=3, 4.5%)] for a catch rate of 7.9%. *Phyllotis andium* harbored 57% of the total fleas collected. *Plocopsylla pallas* was found on 13 of the 38 (34%) *P. andium* surveyed. The average number of *P. pallas* occurring on *P. andium* that were positive for this flea was 3.4. *Phyllotis andium* was trapped at the same locations as *P. amicus* and *Akodon* sp2 cf. *mollis*, but *P. pallas* was found only once on each of these hosts. One can only speculate as to why *P. pallas* was not collected in provinces other than Recuay, since *P. andium* was present in all provinces at similar elevations and habitats. Fleas most commonly collected on sylvatic mammals during all collection periods included the following: *Plocopsylla pallas* (16%), *Neotyphloceras crassispina hemisus* (14%), and *Cleopsylla townsendi* (9%). These three species comprised 39% of the total number of fleas collected.

The total number of species of fleas currently reported in Peru is 81 (Table 1); however, this may be misleading. Several species listed in Table 1 are probable misidentifications. They include the following: *C. m. wolffhuegeli*, *N. c. chilensis*, *P. equitoris*, *Polygenis rimatus* (Jordan, 1932), and *Polygenis litus* (Jordan and Rothschild, 1908). The latter species reported from Piura Department by Macchiavello (1948) is doubtful, since only three females (localities unknown) of *P. litus* have been reported in the literature (Jordan and Rothschild, 1908, 1923) and can easily be confused with *P. litargus*. Populations of *C. m. wolffhuegeli* flourish much farther south in northern Argentina and southern Bolivia. *Neotyphloceras c. chilensis*, difficult to distinguish from other subspecies, occurs along montane and coastal Chile from Santiago south. *Plusaetis equatoris* may be found in the Andean valleys of northwestern South America as far south as Ecuador. The latter three species probably represent *C. m. minerva*, *N. c. crassispina* or *N. c. hemisus*, and *P. d. quitanus*, respectively. Literature records of *P. rimatus* were reported on the same hosts (*O. xantheolus* and *A. mollis*) on which we found *P. litargus* and likely represents this species. *Polygenis rimatus* is common in lowland areas of Argentina, Brazil, and Paraguay, but not in montane regions. Considering these five species as extralimital to Peru, the total number of recognized taxa that occur in Peru is 76.

The distribution of several species reported in the literature are of special interest. Populations of *Gephyropsylla klagesi samuelis* (Jordan and Rothschild, 1923) and *P. litargus* on the Isla Metapalo (Table 1, Peru Islands) were possibly transported by commerce on their common peridomestic host, *O. xantheolus*, or associated commensal rodents. Although both subspecies of *Adoratopsylla inter-*

media have been reported in Junin and Piura Departments, neither were collected during our studies. This species is harbored by various marsupial species of *Didelphis* Linnaeus, 1758 and *Monodelphis* Burnett, 1830. The distribution of these hosts in diverse habitats throughout the Andean valleys and the lowlands of Peru should support a much broader distribution than the records would indicate for this flea species. We were surprised that *Neotyphloceras rosenbergi* (Rothschild, 1904) was not collected, since it was reported in the departments of Cajamarca and Piura from hosts we commonly collected (*A. mollis* and *O. xantheolus*). Three fleas are reported from Peru for the first time (*D. stejnegeri*, *P. achilles*, and *E. alejoi* n. sp.). Eleven of the 21 species herein reported are new records for Ancash Department (*A. thurmani*, *C. townsendi*, *C. m. minerva*, *E. gallinacea*, *E. claviger*, *N. c. hemisus*, *P. pallas*, *P. d. quitanus*, *S. inca*, *T. bleptus*, and *T. titschacki*).

Future emphasis for flea faunal studies should include departments that have received little attention. Most notably are the departments of the eastern slope of the Andes (Amazonas, Cuzco, Huanuco, Junin, Pasco, and San Martin), the lowland departments (Loreto and Madres de Dios), the southern coastal departments (Arequipa, Moquegua, and Tacna), and the south central montane departments (Apurimac, Ayacucho, Huancavelica).

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REVIEW OF *LEPTOMERYX* (ARTIODACTYLA, LEPTOMERYCIDAE)
FROM THE ORELLAN (OLIGOCENE) OF NEBRASKAWILLIAM W. KORTH^{1,2}

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ABSTRACT

Several hundred specimens were examined of the artiodactyl *Leptomeryx* from the Orellan of North America. The dental morphology used to distinguish Chadronian species of the genus were examined for consistency in the Orellan sample. Based on the consistent dental characters established, three distinct species are recognized from the Orellan: *L. evansi* Leidy, *L. exilis* Cook, and *Leptomeryx ellissae* new species. Additional material of *Leptomeryx* from the Whitneyan was also examined and suggests that *L. minimus* Frick and *L. lenis* Cook may be junior synonyms of *L. exilis* and *L. evansi*, respectively.

Two distinct lineages of *Leptomeryx* are recognized that range from the Chadronian through the Whitneyan and possibly Arikareean, the *L. yoderi*-*L. mammifer*-*L. exilis*-*L. obliquidens* lineage and the *L. speciosus*-*L. evansi* lineage. It is likely that the Arikareean leptomerycid *Pronodens* Koerner is derived directly from the *L. evansi* lineage.

KEY WORDS: *Leptomeryx*, Chadronian, Orellan, Oligocene, Artiodactyla

INTRODUCTION

Historical Review

Leidy (1853) first named *Leptomeryx evansi* as a new genus and species from what is now known to be the Orellan Brule Formation in South Dakota. Since that time, 16 species of *Leptomeryx* have been named, ranging in age from Duchesnean to Hemingfordian (Cope, 1886, 1889; Douglass, 1903; Lambe, 1908; Lull, 1922; Cook, 1934; Frick, 1937; Wilson, 1974). The majority of these species were Chadronian in age (see Webb, 1998 for review). The only Orellan species named, other than the type species, was *L. exilis* from Sioux County, Nebraska (Cook, 1934). In his review of the White River artiodactyls, Scott (1940) cited only a single species from the Orellan, the type species, *L. evansi*.

Heaton and Emry (1996) reviewed the Chadronian species of *Leptomeryx* and followed Scott (1940) in concluding that there was only a single species of leptomerycid from the Orellan, *L. evansi*, and that the other nominal species from the Orellan were merely synonyms of *L. evansi*. Galbreath (1953) recognized only *L. evansi* in his Orellan fauna from northeastern Colorado, but cited a single specimen as *Leptomeryx* sp. The latter specimen was a maxillary fragment with upper cheek teeth that were smaller than referred specimens of upper dentitions of *L. evansi*. In the most recent review of the Leptomerycidae, Webb (1998) also agreed that only a single species of *Leptomeryx* existed in the Orellan and sug-

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gested several synonymies for the known Chadronian to Arikareean species of *Leptomeryx*.

Black (1978) named a new Duchesnean genus of leptomerycid, *Hendryomeryx*. He distinguished *Hendryomeryx* from *Leptomeryx* by its more primitive, lower crowned cheek teeth. He referred a species previously identified as *Leptomeryx* to it, *H. defordi*, from Texas (Wilson, 1974). Storer (1981) also referred one of Cope's Chadronian species, *L. esulcatus*, to *Hendryomeryx*. Webb (1998:fig. 31.6) listed *Hendryomeryx* from the Orellan of Montana without a citation and figured *Hendryomeryx* as surviving into the Whitneyan. However, several authors have considered *Hendryomeryx* as a junior synonym of *Leptomeryx* (Heaton and Emry, 1996; McKenna and Bell, 1997).

In all, as many as three species of leptomerycid or as few as one species may be present in the Orellan of North America. No review of Orellan *Leptomeryx* has ever been made at the species level. With the large samples of *Leptomeryx* now available, such a study is warranted.

Fossil Material

Extensive collections of Orellan *Leptomeryx* are available in several institutions in North America. The bulk of the material studied was from the Orella Member of the Brule Formation, Sioux County, Nebraska. However, comparative samples from the Orellan of North Dakota, South Dakota, Colorado and Wyoming were also studied (see Appendices 1 and 2). The institutions providing the sample were as follows: American Museum of Natural History (AMNH), Carnegie Museum of Natural History (CM), National Museum of Natural History, Smithsonian (USNM), University of Nebraska State Museum (UNSM) and Yale-Peabody Museum (YPM). Many of these samples were collected as early as the early 1900s and no distinction was made as to horizon other than "Oreodon beds" or "Lower Brule" (=Orella Member, Brule Formation). A large, stratigraphically controlled sample was available from the UNSM. The stratigraphic divisions of this sample were based on the divisions of the Orella Member defined by Schultz and Stout (1955): Orella A, Orella B, Orella C, and Orella D (from lowest to highest). A smaller stratigraphically controlled sample from the White River Formation of Niobrara County, Wyoming, from AMNH was also included in this study. Small samples of Whitneyan *Leptomeryx* from the collections of the AMNH and UNSM were also examined and measured for comparison.

Methods

Morphology.—Heaton and Emry (1996) used several features of the lower cheek teeth to distinguish the Chadronian species of *Leptomeryx*. Each of these is explained below and was identified on the Orellan sample of *Leptomeryx* in an attempt to establish its usefulness in separating species (Fig. 1).

1) entoconulid on M_3 —The posterolingual cusp on the talonid of M_3 (entoconulid) is a cylindrical cusp with a deep valley posterior to it, separating it from the hypoconulid on specimens of *L. speciosus* and *L. evansi* (abbreviated S/E). The entoconulid on these teeth is also subequal in height to the hypoconulid. On specimens of *L. yoderi* and *L. mammifer* this cusp is more conical (triangular in lingual view) and slopes more gently posteriorly, eliminating the deep valley between it and the hypoconulid (Y/M). The entoconulid on these teeth is lower in height than the hypoconulid.

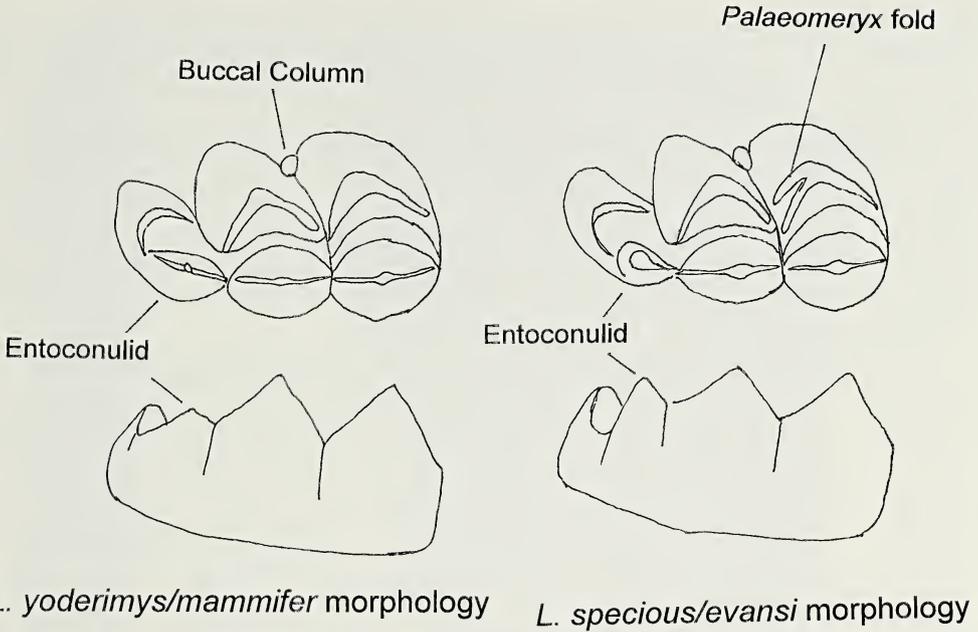


Fig. 1—Schematic diagrams of left M_3 of *Leptomeryx* (occlusal view above, lingual view below) indicating features discussed in text and variation of morphology of entoconulid. Modified from Heaton and Emry (1996:fig. 9).

2) *Palaeomeryx* fold—A small loph that originates from the protoconid on the lower molars and runs down the posterior slope of that cusp is lacking in Chadronian species of *Leptomeryx* but is present on *L. evansi*.

3) enamel wrinkling—Primitively, the enamel of the cheek teeth is smooth as in the Chadronian species of *Leptomeryx*; however, in *L. evansi* it is highly rugose.

4) position of protoconid loph on P_3 —Heaton and Emry (1996) found the major loph running posteriorly from the apex of the protoconid on P_3 (although highly variable) generally ran along the lingual side of the tooth in Chadronian species, but along the buccal edge of the tooth in *L. evansi*.

5) buccal column—The styler cusp between the buccal cusps of the lower molars, if present, is usually a tall column. Its height and presence is variable.

Measurements.—Size has been shown to distinguish species of *Leptomeryx* with similar dental morphology (Heaton and Emry, 1996). Measurements of all cheek teeth of the specimens examined in this study were taken. Maximum widths and lengths of each tooth and alveolar lengths of the molar tooth rows were taken on all specimens. All measurements were taken to the nearest 0.1 mm.

RESULTS

Characters Used to Distinguish Species

Of the characters observed, the most reliable is the morphology of the entoconulid on the talonid of M_3 . The difference between the *L. evansi*/*L. speciosus* morphology and the *L. yoderi*/*L. mammifer* morphology (Heaton and Emry, 1996: fig. 9) is consistently distinguishable. In addition to the differences in the entoconulid cited and figured by Heaton and Emry (1996), it is also evident that in

the Y/M morphology the cusp is lower than both the hypoconulid and the entoconid and does not show signs of wear until the latter two cusps are moderately worn. In specimens with the S/E morphology, the entoconulid is as tall as the adjacent cusps.

The presence of the *Palaeomeryx*-fold on the lower molars is fairly consistent. The *Palaeomeryx*-fold is absent from all specimens with the Y/M entoconulid morphology. Specimens referred to *Leptomeryx evansi* nearly always have this feature present, but there is some variability. In specimens of *Leptomeryx evansi* containing all of the molars, this feature is present on all M₁s, 90% of the M₂s, and 83% of the M₃s. Therefore, the absence of this character was less diagnostic on isolated M₃s.

The degree of enamel crenulation on the molars is generally consistent between the recognized species of *Leptomeryx*, but the range of variability has nearly a complete overlap. The amount of crenulation of the enamel was subjectively recorded numerically from 0 (smooth enamel) to 2 (most crenulated) in increments of 0.5. Specimens of *L. evansi* ranged from 0.5 to 2.0, with a mean of 1.5, meaning that the teeth were generally fairly strongly wrinkled. The specimens with the Y/M entoconulid were generally much smoother, ranging from 0 to 1.5 with a mean of 0.5. It is evident, looking at a large population, that there is a general trend for more highly wrinkled enamel in *L. evansi*, but the overlap is quite large and could not easily be applied to a very small sample of specimens. Similar results were found with the upper cheek teeth as well.

As indicated in Tables 1–4, the teeth of these species differ in size. With approximately 40% overlap, however, large samples with good provenience are needed to distinguish species. Lower dentitions referred to *L. evansi* were generally larger than those with the Y/M entoconulid. Similar results were found with the upper dentitions.

The remainder of the characters analyzed by Heaton and Emry (1996) for the lower dentitions did not appear to be consistent enough to separate species of *Leptomeryx*. For example, presence and size of buccal column on lower molars and posterior protoconid loph on P₃ were extremely variable. The posterior lophid from the protoconid on P₃ of all specimens was directed along the buccal side of the tooth; none of the Orellan specimens has this lophid on the lingual side of the tooth. The buccal column is present on nearly all the specimens from the Orellan and is highly variable in size, ranging from a small cuspule to a distinct column. No general trend in this morphology can be used to separate the Orellan species of *Leptomeryx*.

No features of the upper cheek teeth were examined by Heaton and Emry (1996). However, in the present study there are two features of the upper dentition that appear distinguishable between species. First is the amount of enamel wrinkling, which is reflective of this character in the lower dentition, and the second is the development of a mid-lingual column (protostyle). This cusp is generally large and columnar on most specimens, but is entirely lacking in others. Species are also separable on size of the upper dentitions as noted above. In general, the upper molars of the smaller species are also distinguishable from those of *L. evansi* by their proportions. In *L. evansi*, the upper molars are nearly square (width equal to length), whereas in the smaller species, the upper molars are generally wider than long except M³ (Tables 1 and 4).

There appear to be differences between species based on morphology of the mandible, but the features are known only on a few specimens, so their consis-

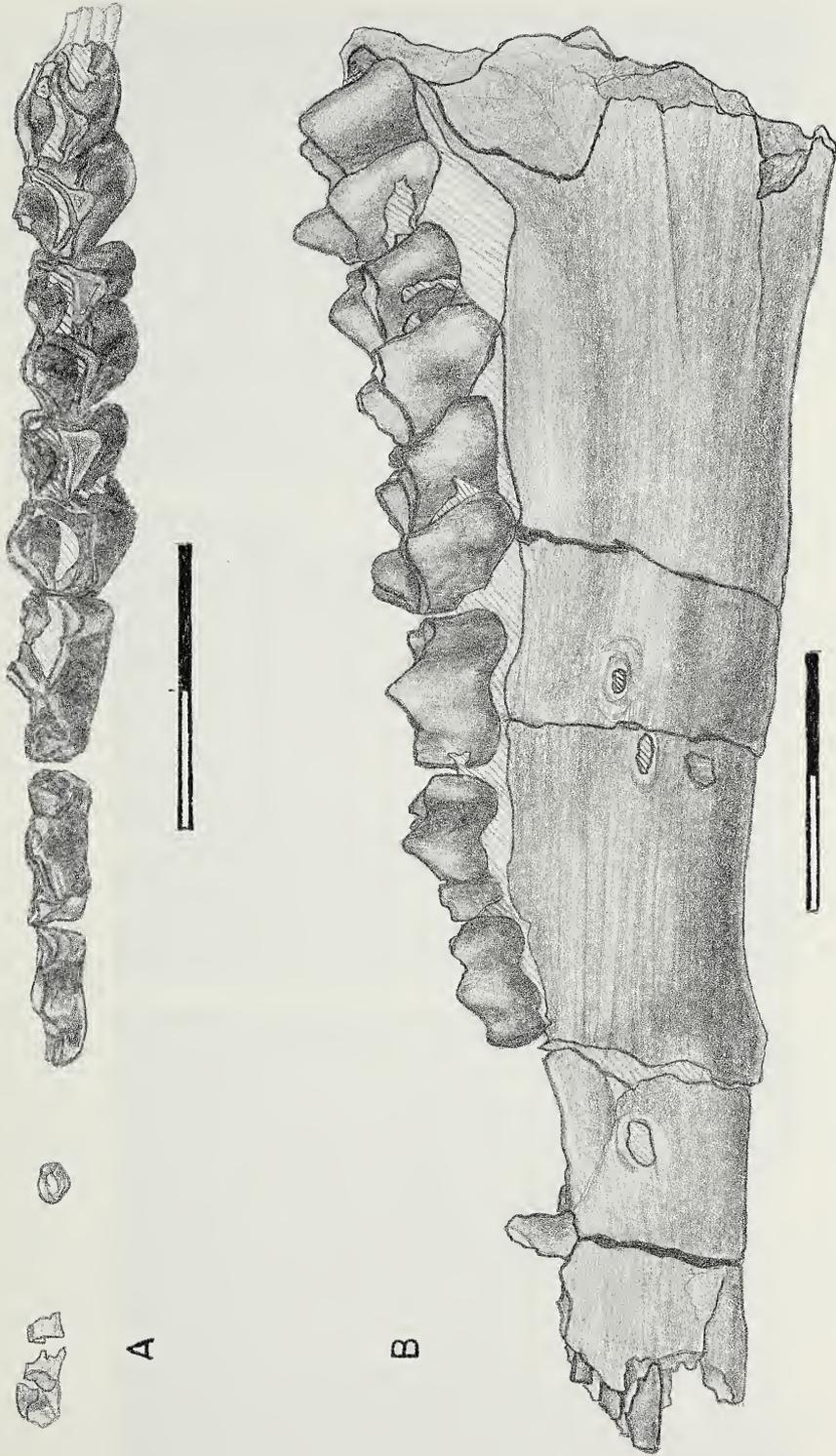


Fig. 2—Mandible and lower cheek teeth of *Leptomeryx evansi*, CM 512A. A. Occlusal view, P₁–M₃. B. Lateral view of mandible. Bar scale = 1 cm.



tency is not known. On mandibles of *Leptomeryx evansi* (Fig. 2) there are one or more accessory mental foramina. They are always below P_4 . This is also true of an intermediate-sized species with the *L. evansi*-type of M_3 morphology (described below). In the known mandibles of the smallest species, there are also accessory mental foramina. One is always ventral to P_3 , and if there is more than one, the second is below P_4 (Fig. 6), as in *L. evansi*.

Another mandibular difference is in the position of P_1 . In all species of *Leptomeryx* there is a diastema between P_1 and P_2 . The main mental foramen is below this diastema. In *L. evansi* P_1 is dorsal to the anterior margin of the mental foramen (Fig. 2). In the smallest species, the alveolus for P_1 is 2.4 mm anterior to the mental foramen. Because of the low number of complete mandibles in the fossil sample, these differences are not included in the diagnoses of the species listed below.

Species Recognized

Three species of *Leptomeryx* can be recognized from the Orellan of Nebraska and the northern Great Plains. *Leptomeryx evansi*, the type species of the genus, is separable from the other species by its larger size, more highly crenulated enamel on the cheek teeth, presence of a protostyle on the upper molars, and S/E morphology of the entoconulid on M_3 .

A second species with the S/E-type of entoconulid morphology of M_3 is also recognizable. It is generally smaller than *L. evansi* with less wrinkling of the enamel and lacks the *Palaeomeryx*-fold on the lower molars.

The third species is the smallest. It lacks a protostyle on the upper molars, has less crenulated enamel on the cheek teeth, has the Y/M morphology of the entoconulid, and lacks a *Palaeomeryx*-fold on the lower molars.

SYSTEMATIC PALEONTOLOGY

Leptomeryx Leidy, 1853

Leptomeryx evansi Leidy, 1853

(Fig. 2, 3; Tables 1 and 2)

Type Specimen.—USNM 157, partial skull and associated mandible.

Referred Specimens.—See Appendix 1.

Horizon and Locality.—Holotype from Orellan White River Group, South Dakota. Referred specimens from the Orellan of the northern Great Plains.

Emended Diagnosis.—Intermediate-sized species; enamel on cheek teeth highly crenulated; *Palaeomeryx*-fold present on lower molars; entoconulid on M_3 cylindrical with deep posterior valley, separating it from the hypoconulid; protostyle present on upper molars.

Discussion.—*Leptomeryx evansi* is, by far, the most common of any of the Orellan species of the genus, outnumbering the other species as much as 50 to 1 in some collections. This species shows little variation throughout its chronological and geographic range. There is virtually no difference in size of the samples

←

Fig. 3—Cheek teeth of *Leptomeryx evansi*. A. Occlusal (above) and lingual view of M_1 – M_3 , CM 175. B. Occlusal view of M^1 – M^3 , UNSM 119726. Bar scale = 1 cm.

Table 1.—Dental measurements of *Leptomeryx evansi* from the Orellan (all horizons and localities combined). Abbreviations: L, length; W, width; N, number of specimens; M, mean; OR, observed range of size; sd, standard deviation; CV, coefficient of variation. All measurements in mm.

	M ₁ -M ₃	LM ₁	WM ₁	LM ₂	WM ₂	LM ₃	WM ₃
N	53	51	48	80	79	129	128
M	22.0	6.2	4.5	6.6	4.9	9.3	4.7
OR	19.8-24.2	5.3-7.2	3.8-5.2	4.2-7.5	4.1-5.4	8.0-10.7	3.7-5.5
sd	1.1	0.4	0.3	0.5	0.3	0.6	0.3
CV	5.0	6.5	6.0	7.5	6.0	6.4	7.1
	M ¹ -M ³	LM ¹	WM ¹	LM ²	WM ²	LM ³	WM ³
N	24	66	66	60	59	41	41
M	19.0	6.3	6.3	6.7	6.8	6.7	6.4
OR	17.8-20.6	5.4-7.0	5.1-7.5	5.8-7.5	5.2-8.4	6.0-7.7	5.4-7.6
sd	0.8	0.3	0.5	0.4	0.7	0.4	0.6
CV	4.2	5.2	8.1	5.4	9.9	6.1	8.8

from Orella A through Orella D (Table 2). Geographically, the only sample that shows any variation is that from Wyoming. The Wyoming sample of *L. evansi* has a slightly longer M₃ than all of the other samples. However, the overlap of the size ranges with other samples is nearly 100% and the difference in the mean is less than 10% of the length of the tooth. This larger size of M₃ is also reflected in the measurement of the molar row (M₁-M₃). Heaton and Emry (1996) also measured a sample from the lower part of the Orellan in Wyoming and produced measurements similar to those of our sample, slightly larger than the remainder of the samples. This is not viewed as enough difference to suggest a separate species with the Wyoming material, only a slight geographic variation in the Wyoming population.

Leptomeryx elissae, new species

(Fig. 4, 5; Table 3)

Type Specimen.—UNSM 119638, mandible with left P₃-M₃.

Referred Specimens.—CM 73416; UNSM 119636, 119637, 119639, 119640; AMNH 53626A, 606-25868, 606-25873 (all mandibles with cheek teeth).

Horizon and Locality.—Holotype from UNSM locality Sx-8, Orella Member (Orella C), Brule Formation, Sioux County, Nebraska. All referred specimens from the Orella Member (Orella C and D), Brule Formation, Sioux County, Nebraska (Orellan).

Diagnosis.—Smaller than *L. evansi*; enamel of cheek teeth smooth (less crenulated than in *L. evansi*); S/E-type of entoconulid on M₃; *Palaeomeryx*-fold lacking on lower cheek teeth.

Etymology.—Named for a daughter of one of the authors (MED).

Discussion.—A small group of specimens that share the S/E-type of entoconulid on M₃ with *Leptomeryx evansi* are distinguishable from the latter by their slightly smaller size, less crenulated enamel on the molars, and lack of a *Palaeomeryx*-fold on the lower molars. This species is intermediate in size between the two other Orellan species of *Leptomeryx* (Table 3), and slightly closer to the smaller species. However, the amount of overlap in the size range with *L. evansi* is large, nearly 50%. The average amount of wrinkling on the molars is 0.7, more

Table 2.—Dental measurements of lower molars of Orellan *Leptomeryx evansi* separated stratigraphically and geographically. Abbreviations as in Table 1.

	M ₁ -M ₃	LM ₁	WM ₁	LM ₂	WM ₂	LM ₃	WM ₃
Nebraska (all levels)							
N	41	39	38	66	65	112	112
M	21.8	6.2	4.5	6.6	4.9	9.2	4.7
OR	19.8-24.2	5.3-7.0	3.8-4.9	4.2-7.5	4.1-5.4	8.0-10.7	3.7-5.5
sd	1.0	0.4	0.2	0.5	0.3	0.6	0.3
CV	4.8	6.5	5.5	7.8	6.1	6.3	6.9
Nebraska (Orella A)							
N	1	1	1	3	3	14	14
M	20.8	5.7	3.8	6.4	4.4	9.0	4.6
OR	—	—	—	6.0-6.9	4.1-4.7	8.1-9.6	3.7-5.3
sd	—	—	—	0.5	0.3	0.4	0.5
CV	—	—	—	7.0	7.0	4.7	10.1
Nebraska (Orella C)							
N	3	3	3	6	6	15	15
M	21.7	6.2	4.4	6.8	4.9	9.0	4.7
OR	20.5-22.5	6.1-6.4	4.1-4.6	6.4-7.2	4.4-5.1	8.1-9.9	4.1-5.2
sd	1.1	0.2	0.3	0.4	0.3	0.6	0.3
CV	5.0	2.5	6.0	5.3	5.6	6.2	6.4
Nebraska (Orella D)							
N	—	—	—	2	2	10	10
M	—	—	—	6.7	4.5	9.2	4.6
OR	—	—	—	6.5-6.8	4.2-4.7	8.1-9.9	4.4-5.2
sd	—	—	—	—	—	0.5	0.2
CV	—	—	—	—	—	5.5	5.1
North Dakota							
N	4	4	4	5	5	7	7
M	21.7	6.1	4.5	6.5	4.8	9.3	4.6
OR	20.7-23.7	5.7-6.4	4.0-5.2	6.2-6.9	4.4-5.3	8.5-10.6	4.1-5.3
sd	1.4	0.3	0.6	0.3	0.4	0.8	0.5
CV	6.4	4.9	12.4	4.2	7.7	8.1	10.4
Wyoming							
N	7	7	5	8	8	8	7
M	22.8	6.4	4.4	6.9	5.0	9.7	4.7
OR	21.6-24.2	5.8-7.2	4.1-4.6	6.5-7.4	4.6-5.4	9.0-10.1	4.6-5.4
sd	1.1	0.4	0.2	0.4	0.2	0.4	0.2
CV	4.6	6.9	4.4	5.2	4.9	4.5	5.0

than the smaller species, less than in *L. evansi*, but with a range of from 0 to 1, less than in the smaller species (0 to 1.5).

Leptomeryx exilis Cook, 1934

(Fig. 6, 7, 8; Table 4)

Type Specimen.—AMNH 81012, partial right mandible with M₂-M₃.

Referred Specimens.—See Appendix 2.

Horizon and Locality.—Holotype from "the Brule (Middle Oligocene) beds about two miles north of Chadron, Nebraska" (Cook, 1934:154). Referred material from Orellan of the White River Group, northern Great Plains.



Fig. 4—Occlusal (above) and lingual view of M_1 – M_3 of *Leptomeryx elissae*, UNSM 119638 (holotype). Bar scale = 1 cm.

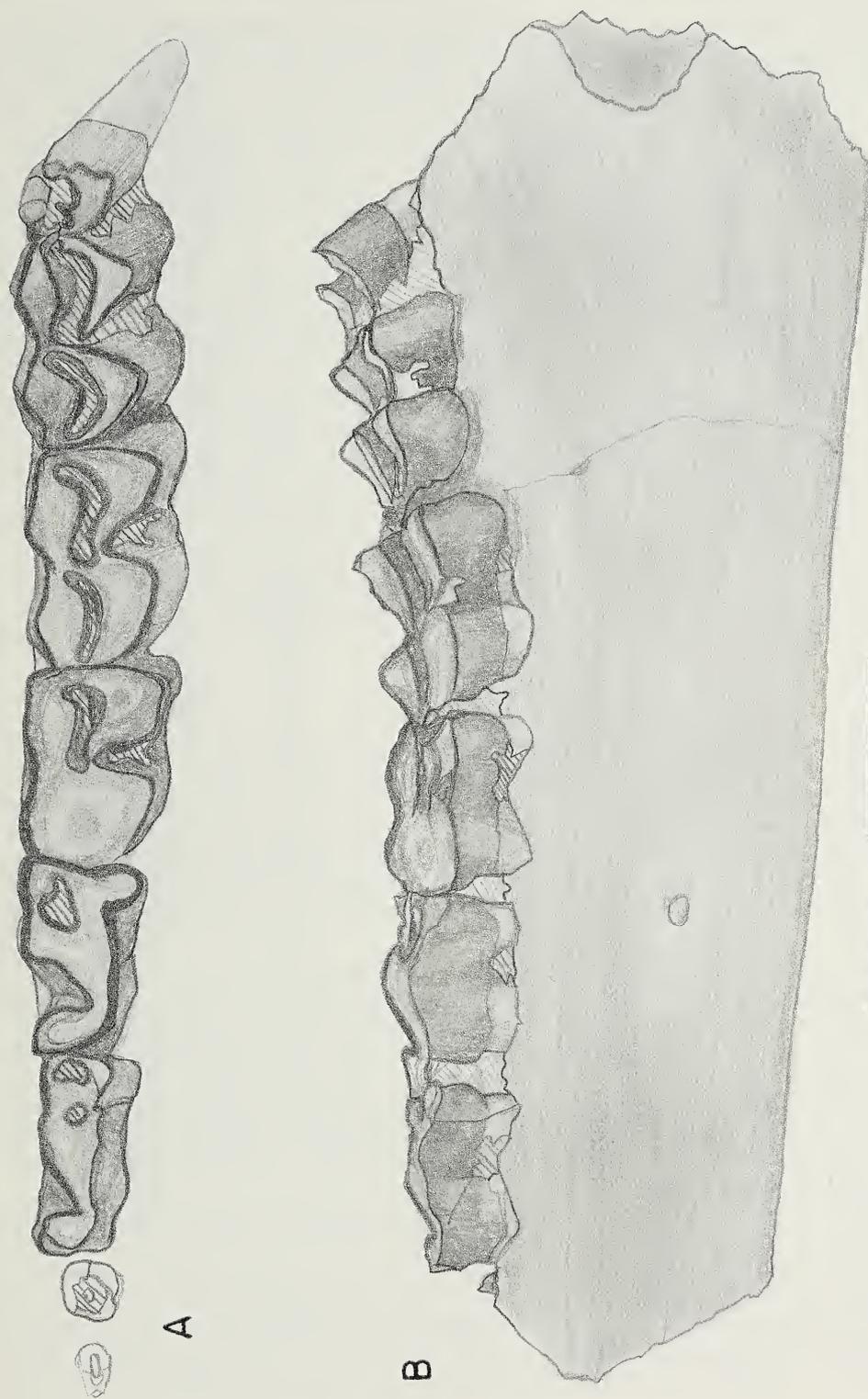


Fig. 5—Mandible and lower cheek teeth of *Leptomeryx elissae*, CM 73416. A. Occlusal view, P₃–M₃ (alveolus for P₂). B. Lateral view of mandible. Bar scale = 1 cm.

Table 3.—Dental measurements of *Orellan Leptomeryx elissae*. Abbreviations as in Table 1.

	M ₁ -M ₃	LM ₁	WM ₁	LM ₂	WM ₂	LM ₃	WM ₃
N	4	3	3	5	5	6	6
M	19.8	5.6	4.3	6.4	4.6	8.6	4.4
OR	19.4-20.4	5.1-6.0	4.0-4.6	6.0-6.7	4.4-4.9	8.0-9.2	4.2-4.6
sd	0.5	0.5	0.3	0.3	0.2	0.4	0.1
CV	2.6	8.4	7.0	4.3	4.6	4.5	3.4

Emended Diagnosis.—Smallest species of the genus; cheek teeth with little or no wrinkling of the enamel; *Palaeomeryx*-fold lacking on lower molars; Y/M type of morphology of entoconulid on M₃; upper molars wider than long (subequal in dimensions in *L. evansi*) and lacking a protostyle.

Discussion.—Specimens of *Leptomeryx exilis* are easily distinguishable from those of the other Orellan species by their smaller size and construction of the entoconulid on M₃ (Y/M-type). This species differs from *L. evansi* in lacking crenulations on the enamel of the molars, and lacking a *Palaeomeryx*-fold on the lower molars. Specimens referred to *Leptomeryx elissae* also have the S/E-type of entoconulid on M₃. The upper molars are proportioned slightly differently from those of *L. evansi* and lack a protostyle.

There appears to be no difference in size or morphology between samples of *L. exilis* from the various horizons within the Orella Member in Nebraska.

CONCLUSIONS

Orellan Leptomeryx

Contrary to recent authors (Heaton and Emry, 1996; Webb, 1998), three distinct species of *Leptomeryx* are recognizable from the Orellan of the Great Plains: *L. evansi*, *L. exilis* and *Leptomeryx elissae*. They are easily distinguishable by size and morphology of the lower third molar. All of the species of *Leptomeryx* from the Orellan are markedly smaller than the species reported from the Chadronian (see Heaton and Emry, 1996). The Chadronian species also lack crenulations of the enamel on the cheek teeth and the *Palaeomeryx*-fold found on Orellan *L. evansi*.

Heaton and Emry (1996) recognized two lineages of *Leptomeryx* in the Chadronian based predominantly on the morphology of the lower molars. One lineage consisted of *L. mammifer* and *L. yoderi* that were relatively large species with the primitive, conical entoconulid on M₃ (Y/M-type). The other lineage consisted only of *L. speciosus* in the Chadronian that was distinguished from the other species by the columnar entoconulid on M₃ (S/E-type) and slightly different size. Heaton and Emry (1996) viewed the *L. mammifer*-*L. yoderi* lineage as ending in the Chadronian, whereas the lineage represented by *L. speciosus* continued into the Orellan with *L. evansi*.

The recognition of three Orellan species demonstrates that the radiation of *Leptomeryx* in the Orellan is not as simple as previously believed. The morphology of M₃ of Orellan *L. exilis* is the same as in *L. yoderi* and *L. mammifer*, making it a likely member of the same lineage, and thus extending this lineage into the Orellan. *Leptomeryx exilis* differs from the former Chadronian species only in its much smaller size. *L. exilis* could easily be derived from late Chadronian *L. mammifer* simply by reducing its size. There appears to be no mor-

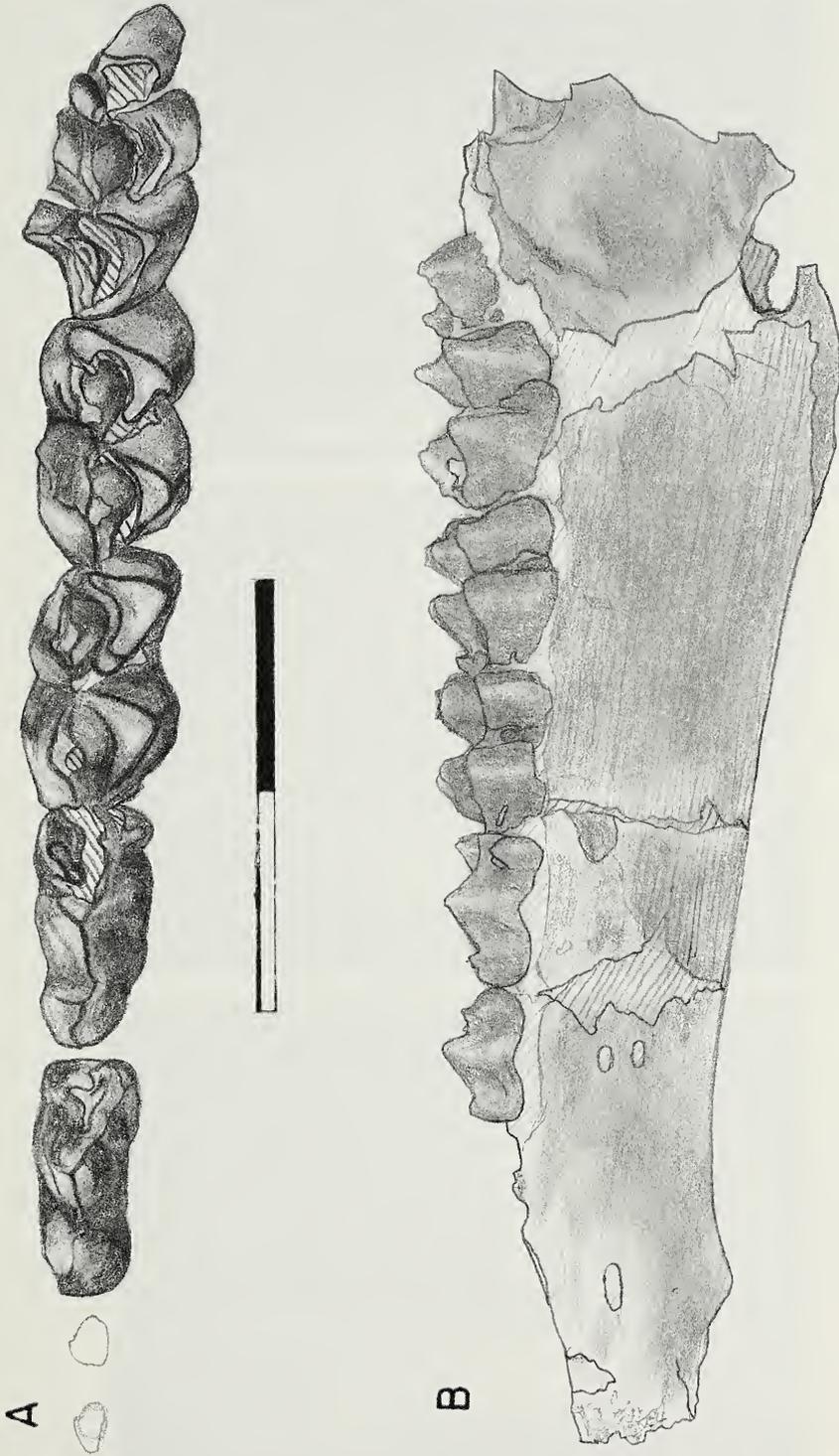
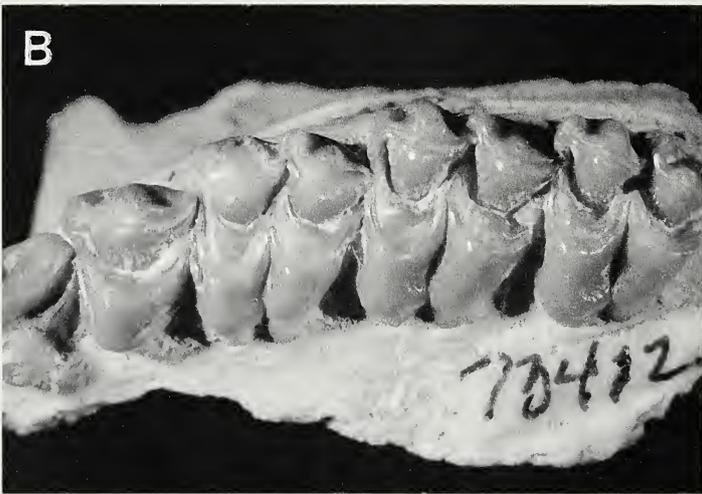
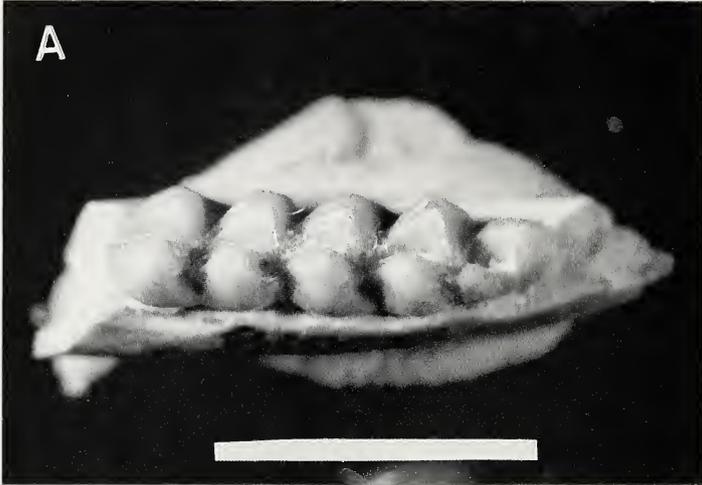


Fig. 6—Mandible and lower cheek teeth of *Leptomeryx exilis*, CM 9109. A. Occlusal view, P₃-M₃ (alveolus for P₃). B. Lateral view of mandible (alveolus for P₁). Bar scale = 1 cm.



phology that would bar *L. mammifer* from an ancestral position with respect to *L. exilis*.

Heaton and Emry (1996) viewed the Chadronian *L. speciosus* as ancestral to the Orellan *L. evansi*, the latter differing in its smaller size, more crenulate enamel on the molars, and presence of a *Palaeomeryx*-fold on the lower molars. The only difference suggested here in this *L. speciosus*–*L. evansi* lineage proposed by Heaton and Emry is the addition of another species from the Orellan. Specimens referred here to *Leptomeryx elissae* are closer to the Chadronian *L. speciosus* in morphology than to Orellan *L. evansi*, lacking the crenulations and *Palaeomeryx*-fold of the latter (primitive characters shared with *L. speciosus*). *Leptomeryx elissae* is even smaller than *L. evansi*, and thus easily distinguishable from *L. speciosus*. It appears that this lineage, characterized by the S/E-type of entoconulid on M₃, splits in the Orellan into a smaller species with simpler cheek tooth morphology (*Leptomeryx elissae*) and a larger species with more complex cheek tooth morphology (*L. evansi*). As with the other lineage of *Leptomeryx*, it is quite likely that the Chadronian *L. speciosus* is ancestral to both of the Orellan species of the genus recognized here.

Whitneyan *Leptomeryx*

Several species of *Leptomeryx* have been named from the Whitneyan: *L. lenis* Cook (1934), *L. minimus* Frick (1937), and *L. obliquidens* Lull (1922). Small samples of Whitneyan *Leptomeryx* are present in the collections of the AMNH, mainly from South Dakota, and were compared to the holotypes of these species.

The holotype of *L. lenis* (AMNH 87013) contains both upper and lower dental elements. The cheek teeth of *L. lenis* are highly crenulated, have distinct *Palaeomeryx*-folds on the lower molars and have the S/E-type of entoconulid on M₃. They are also within the size range of *L. evansi*. The holotype of *L. lenis* is indistinguishable from specimens of the Orellan *L. evansi*. Several specimens of similar size and morphology from the Whitneyan were present in the AMNH collections, and likewise, could not be separated from the Orellan samples of *L. evansi*. It appears likely that *L. lenis* is a junior synonym of *L. evansi*. This synonymy would extend the known record of *L. evansi* into the Whitneyan.

Among the Whitneyan specimens present in the AMNH collections are several that are similar to *L. evansi* in morphology (Fig. 9), but are beyond its range of size (both smaller and larger). These specimens may well represent additional species of *Leptomeryx* from this horizon.

The holotype (AMNH 1347a) and paratype (AMNH 1347) of *L. minimus* from the Whitneyan of South Dakota are small in size, have the Y/M-type of M₃, lack crenulations on the cheek teeth, and lack the *Palaeomeryx*-fold on the lower molars (Fig. 10). In size and morphology, these specimens do not differ from those referred to *L. exilis* from the Orellan. The additional Whitneyan specimens of similar size and morphology in the AMNH collections are also indistinguishable from those of *L. exilis* (Fig. 11). As with *L. evansi* and *L. lenis*, it appears that *L. minimus* is a junior synonym of *L. exilis*, thus extending the record of the latter from the Orellan into the Whitneyan.

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Fig. 7—Cheek teeth of *Leptomeryx exilis*. A. Occlusal (above) and lingual view of M₂–M₃, AMNH 81012 (holotype). B. Occlusal view, P³–M³, CM 73412. Bar scale = 1 cm.

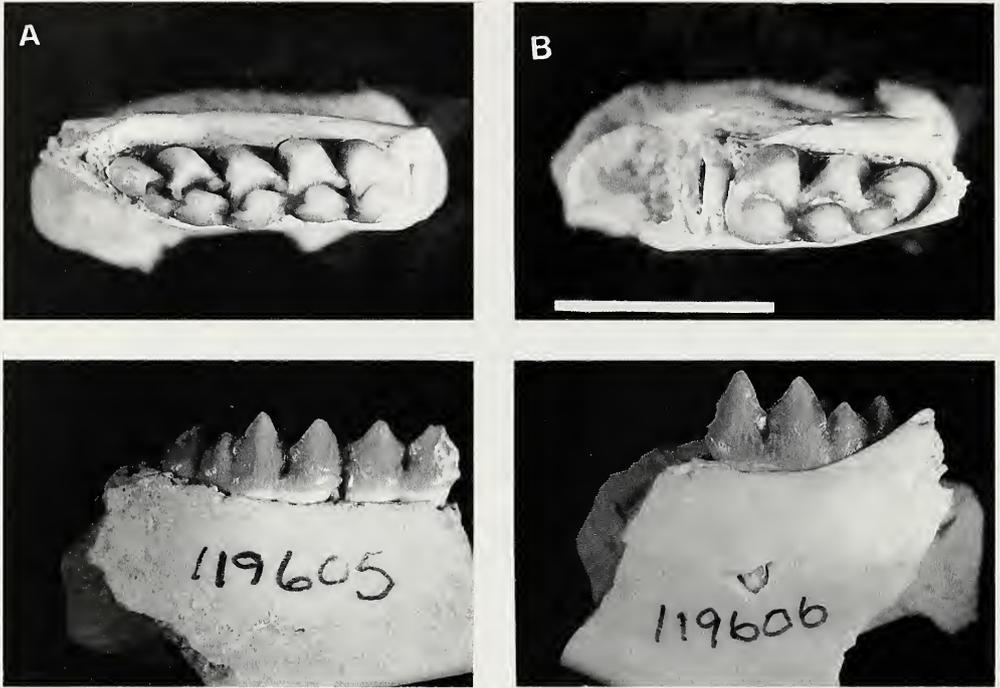


Fig. 8—Occlusal (above) and lingual views of M_3 s of *Leptomeryx exilis*. A. UNSM 11605. B. UNSM 119606. Bar scale = 1 cm.

Leptomeryx obliquidens was also described from the Whitneyan of South Dakota (Lull, 1922). It is much larger than any of the other species of the genus, nearly twice the size of *L. exilis*. It is known only from the holotype (YPM 10541) and one referred specimen (YPM 2248). It has a unique combination of morphologies. The lower molars lack the *Palaeomeryx*-fold and have the Y/M-type of entoconulid on M_3 (as in *L. exilis*), but the cheek teeth are highly crenulated, as in *L. evansi* (Fig. 12). The upper molars, although heavily worn, show no signs of a protostyle. No additional specimens referable to this species could be found

Table 4.—Dental measurements of Orellan *Leptomeryx exilis*. Abbreviations as in Table 1.

	M_1-M_3	LM_1	WM_1	LM_2	WM_2	LM_3	WM_3
N	19	17	17	41	40	68	68
M	19.8	5.4	4.1	6.0	4.5	8.3	4.4
OR	18.0–21.0	4.8–5.8	3.6–4.5	5.1–7.0	3.9–5.2	6.7–9.3	3.4–5.3
sd	0.7	0.3	0.2	0.4	0.3	0.5	0.4
CV	3.7	4.8	6.0	6.4	7.1	6.3	8.0
	M^1-M^3	LM^1	WM^1	LM^2	WM^2	LM^3	WM^3
N	3	4	4	5	5	4	4
M	16.9	5.7	6.0	6.0	6.5	6.1	6.1
OR	16.6–17.2	5.4–5.9	5.8–6.4	5.9–6.2	5.9–7.1	5.9–6.4	5.4–6.5
sd	0.3	0.3	0.3	0.1	0.5	0.2	0.5
CV	1.8	3.9	4.5	2.0	7.3	3.6	7.9

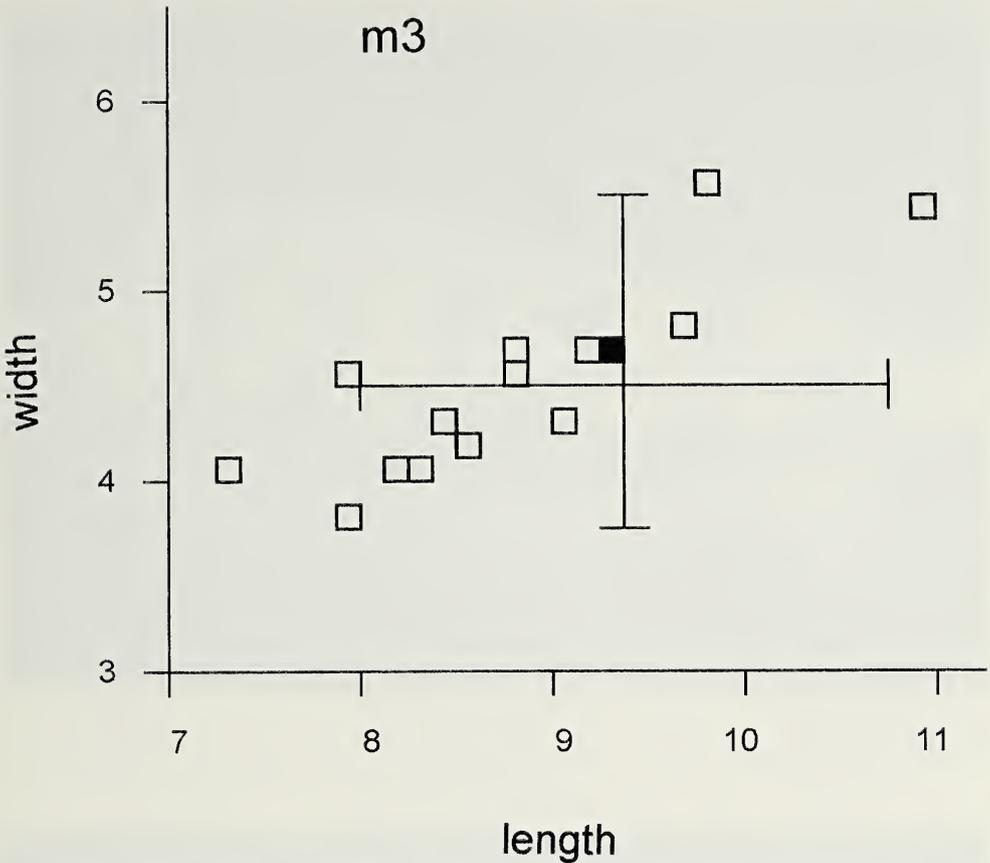


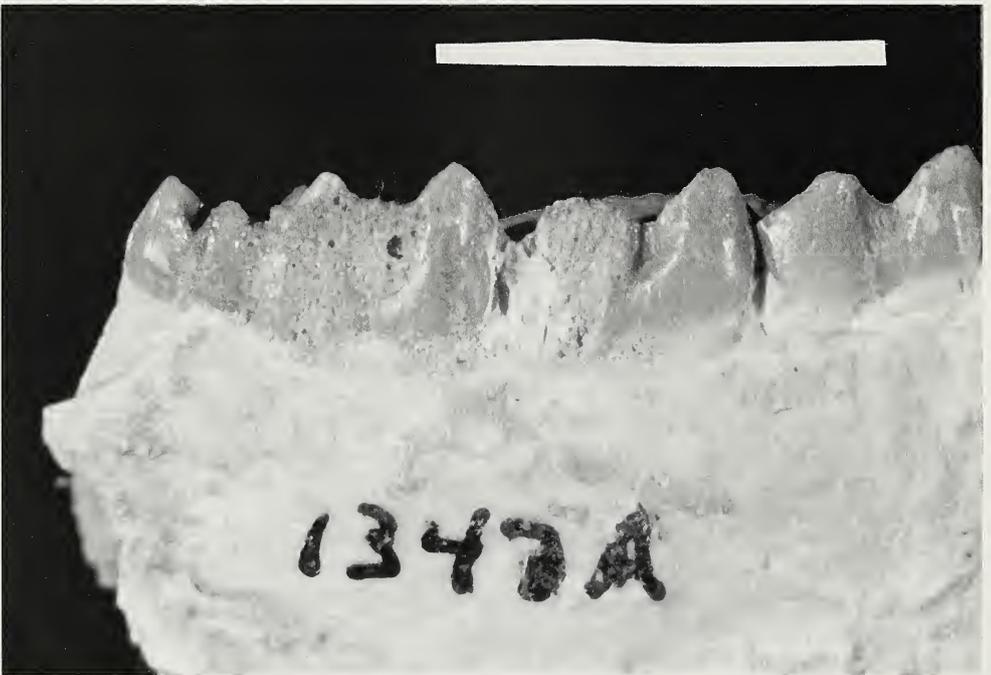
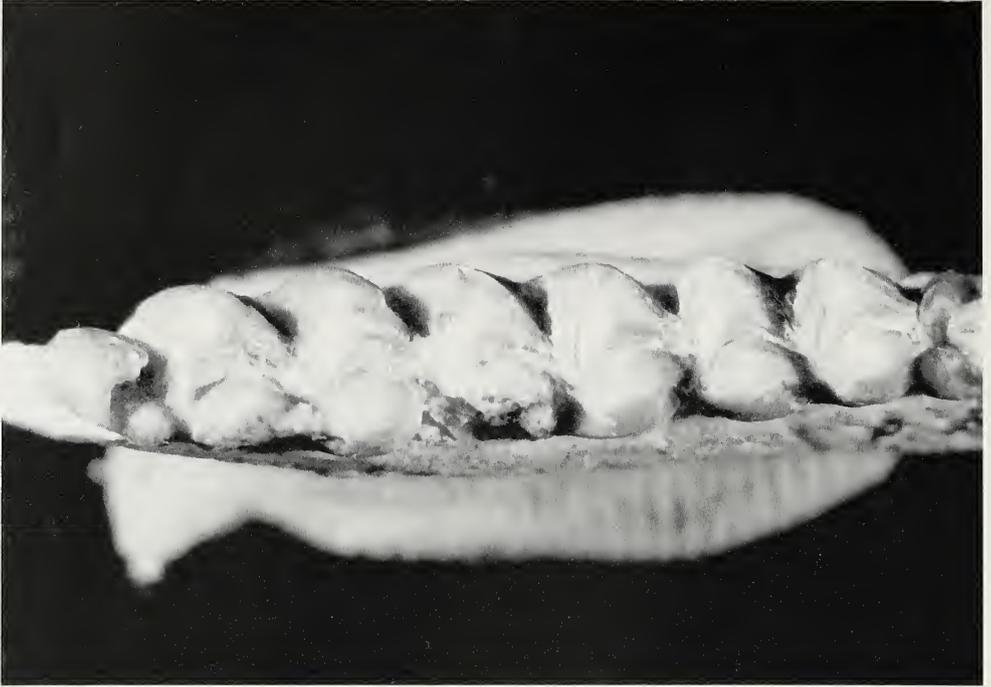
Fig. 9—Scatter diagram of length vs. width of M_3 of *Leptomyerx evansi*-like specimens (S/E-type entoconulid) from the Whitneyan. Crossed lines indicate range of size of Orellan *L. evansi*. Darkened square represents holotype of *L. lenis* (AMNH 81013). Scales in mm.

in any collections. It appears most likely that *L. obliquidens* is part of the *L. yoderi*–*L. mammifer*–*L. exilis* lineage, but that it has attained crenulated molars separately from those of *L. evansi*.

Arikareean Leptomeryx

Although several isolated and fragmentary specimens of *Leptomeryx* have been reported from the Arikareean (see Webb, 1998:471), only a few species have been named. Douglass (1903) named *L. transmontanus* from Montana. However, in an unpublished dissertation, Rasmussen (1977) demonstrated that this species was referable to the more derived genus of leptomerycid, *Pronodens* Koerner, 1940 (also see Taylor and Webb, 1976).

The only other Arikareean species referred to *Leptomeryx* is *L. agatensis* from Sioux County, Nebraska (Cook, 1934). This species is known only from the holotype, a maxilla with upper cheek teeth (AMNH 81505). In size and morphology, this specimen is not separable from upper dentitions of *L. evansi*. Due to the poor record of this species it is impossible at present to recommend the synonymy of



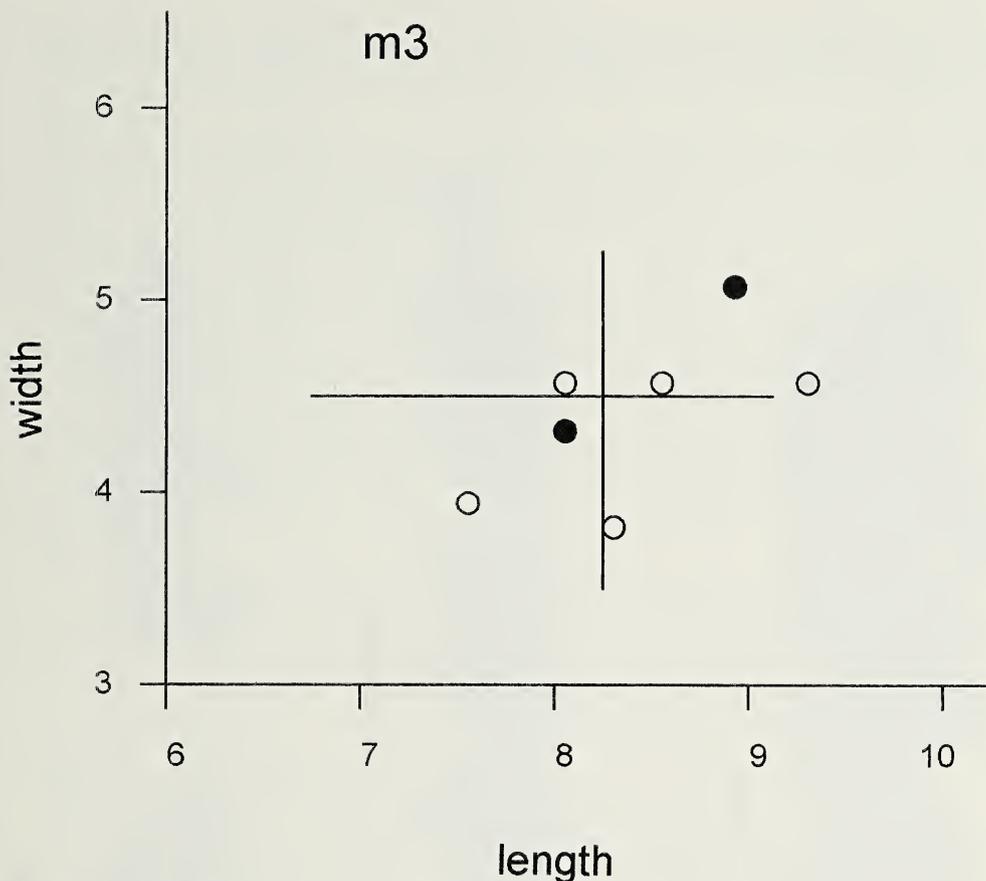


Fig. 11—Scatter diagram of length vs. width of M_3 of *Leptomeryx exilis*-like specimens (Y/M-type entoconulid) from the Whitneyan. Crossed lines indicate range of size of Orellan *L. exilis*. Darkened circles represent holotype and paratype of *L. minimus* (AMNH 1347a and AMNH 1347). Scales in mm.

these two species. It is equally as likely that *L. agatensis* is referable to a species of the Arikareean leptomerycid *Pronodens*, the latter differing from *Leptomeryx* mainly in the morphology of the anterior dentition which is not preserved in the holotype of *L. agatensis*. Webb (1998) listed *L. agatensis* as a synonym of *L. obliquidens*. The marked difference in size of these species makes it very unlikely that they are synonyms.

Relationships of North American Leptomeryx

Two distinct lineages of *Leptomeryx* can be recognized from the Chadronian to the Whitneyan of North America. One contains the Chadronian species *L. yoderi* and *L. mammifer*; the Orellan species *L. exilis*, and the Whitneyan *L.*

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Fig. 10—Occlusal (above) and lingual views of M_1 – M_3 *Leptomeryx minimus*, AMNH 1347A (holotype). Bar scale = 1 cm.

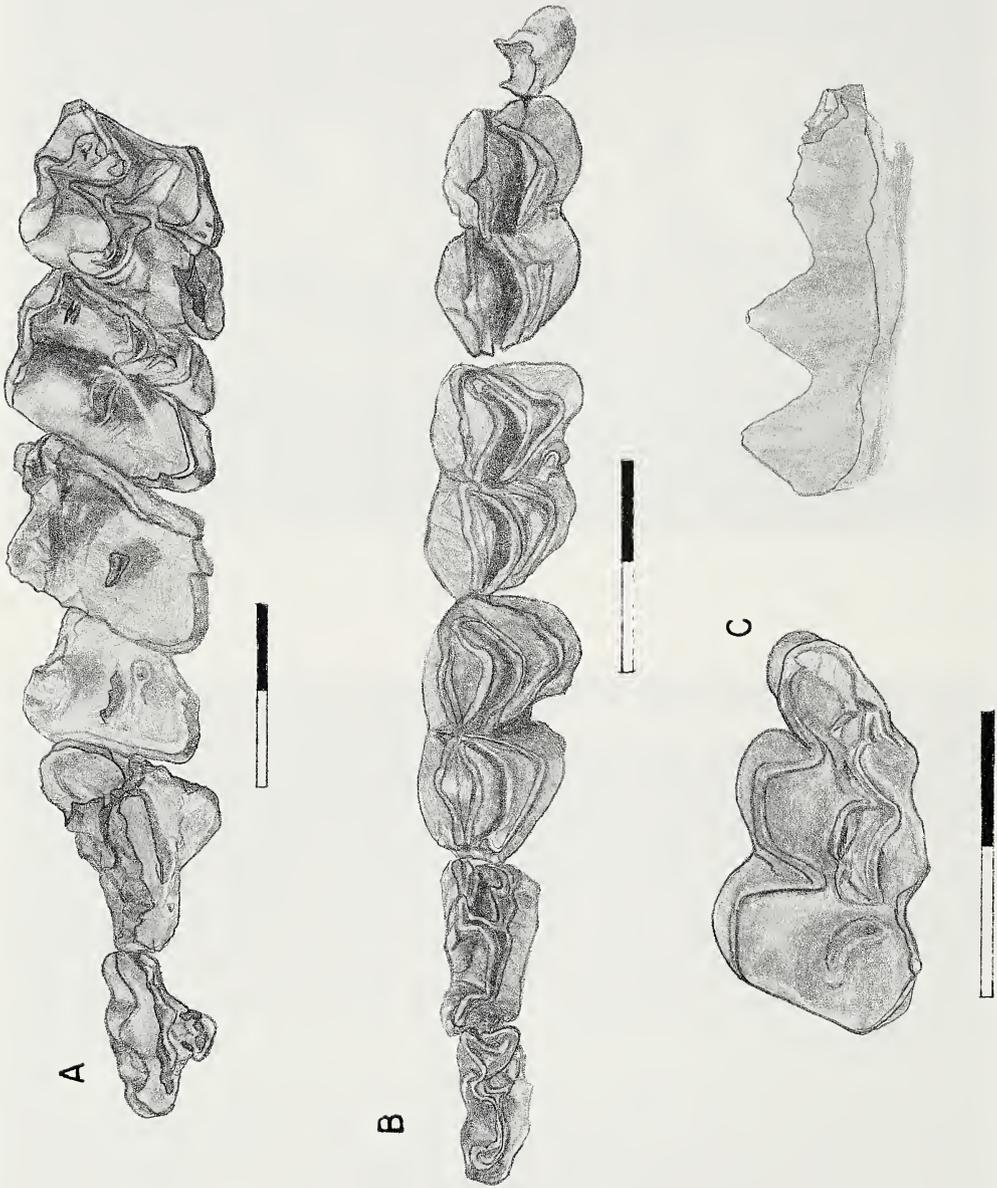


Fig. 12.—Cheek teeth of *Leptomeryx obliquidens*. A. P₂-M₃, YPM 10541 (holotype). B. P₃-M₃, YPM 2248. C. Occlusal view (left) and lingual view M₃, YPM 10541 (holotype). Bar scale below each figure = 1 cm.

obliquidens and *L. minimus* (?=*L. exilis*). The other lineage includes the Chadronian *L. speciosus*, Orellan *L. elissae* and *L. evansi*, the Whitneyan *L. lenis* (?=*L. evansi*) and additional species similar to *L. evansi*, and possibly the Arikarean *L. agatensis*.

The only consistent character that separates these two groups throughout their known record is the morphology of the entoconulid on M_3 . The *L. yoderi*–*L. mamnifer*–*L. exilis*–*L. obliquidens* lineage is characterized by a conical entoconulid that is triangular in lingual view, and is lower than the hypoconulid and strongly connected to it. In the *L. speciosus*–*L. evansi*–*L. elissae* lineage, the entoconulid on M_3 is cylindrical, equal in height to the hypoconulid, and separated from it by a deep, distinct valley (see Heaton and Emry, 1996:fig. 9).

In the first lineage, there is little morphological change through time except in size. There is increase in size during the Chadronian, from *L. yoderi* to *L. mamnifer*, then a marked reduction in size at the Orellan boundary with *L. exilis* which persists into the Whitneyan (?=*L. minimus*). Also in the Whitneyan there is a marked increase in size with the appearance of *L. obliquidens*. The latter also shows the first change in morphology with the crenulation of the enamel on the cheek teeth.

The *L. speciosus*–*L. evansi*–*L. elissae* lineage shows an increase in the occurrence of the *Palaeomeryx*-fold on the lower molars and increased crenulations on the cheek teeth from *L. speciosus* to the Orellan *L. evansi* along with a reduction in size. However, the second Orellan species, *L. elissae*, lacks these derived features of *L. evansi*, and is nearly identical to *L. speciosus* except for its smaller size (even smaller than *L. evansi*). The Whitneyan and later species of this group appear closely related to *L. evansi* with the presence of the *Palaeomeryx*-fold and crenulations on the cheek teeth.

The only Arikarean or later leptomerycids that may have been derived from either of these lineages is *Pronodens*. The latter has slightly higher crowned cheek teeth than *Leptomeryx* and a reduction and modification of the anterior dentition (Taylor and Webb, 1976; Webb, 1998). However, the *Palaeomeryx*-fold is more prominent than in *L. evansi* and the entoconulid has the S/E-type of morphology of the *L. evansi* lineage as well. It is likely that *L. evansi* or a similar species in that lineage was directly ancestral to *Pronodens*.

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APPENDIX I

Referred specimens of Orellan *Leptomeryx evansi* examined in this study.

Nebraska (unspecified level in Orella Member)

CM 175 (3 specimens), 185 (2 specimens), 205 (3 specimens), 226 (5 specimens), 362, 442 (3 specimens), 455 (2 specimens), 472, 458, 2497, 3674 (2 specimens), 3679, 3680 (4 specimens). AMNH 53572 (2 specimens), 53573 (9 specimens), 53621, 53627 (3 specimens), 53626 (3 specimens), 330-726, 330-729, 546-24643, 570-24857, 602-25441, 602-25485, 606-25836, 606-25861, 606-25869, 606-25874, 606-25879, 606-25882, 606-25937, 606-25946 (3 specimens), 611-26636, 611-26638, 611-26642, 611-26653, 611-26658, 611-26670, 611-26676, 611-26677, 616-27214 [Lower dental elements]. CM 205 (7 specimens), 226 (6 specimens), 542, 2497, 3670, 3678, 3682, 3683, 3674 (2 specimens), 3675 (2 specimens), 3676, 3824, 9143, 9144, 9148, 9689 [Upper dental element].

Orella A (Nebraska)

UNSM 119625 through 119630, and 119641 through 119648 [Lower dental elements]. UNSM 119649 through 119660 [Upper dental elements].

Orella C (Nebraska)

UNSM 119634 and 119661 through 119677 [Lower dental elements]. UNSM 119678 through 119698 [Upper dental elements].

Orella D (Nebraska)

UNSM 119699 through 119706 and 119712, 119713 [Lower dental elements]. UNSM 119714 through 119726 [Upper dental elements].

North Dakota

CM 2010a, 28800, 28803a; USNM 78-5, 78-8, 78-22 [Lower dental elements]. CM 2010, 28645 [Upper dental elements].

South Dakota

USNM 9426c (holotype).

Wyoming

AMNH 0-75-1525, 0-81-1611, 0-94-1883, 0-120-2228, 0-442-2044, 058-1379, 088-1691a, 088-1699 [Lower dental elements].

APPENDIX 2

Referred specimens of Orellan *Leptomeryx exilis* examined in this study.

Nebraska (unspecified level in Orella Member)

CM 1289, 73403, 73405, 73407, 73411, 73415, 73419, 73420, 73421; AMNH 53572 (2 specimens), 042-973q, 540-24592a, 606-25946 (3 specimens), 606-25875, 611-26678, 615-27163, 616-27220, 616-27252 [Lower dental elements]. CM 73412 [Upper dental element].

Orella A (Nebraska)

UNSM 119617, 119631, 119632 [Lower dental elements]. UNSM 119621 [Upper dental elements].

Orella C (Nebraska)

UNSM 119600 through 119615, 119618 through 119620, and 119633 [Lower dental elements]. UNSM 119623, 119624 [Upper dental elements].

Orella D (Nebraska)

UNSM 119616 [Lower dental element]. UNSM 119622 [Upper dental element].

South Dakota

AMNH 38838a, 90281, 208-3596-3, 208-3596-7, 230-4183, 230-4276, 230-4277 [Lower dental elements]. CM 9121; AMNH 25858, 53582a, 53596, 606-25840, 606-25857, 611-26647 [Upper dental elements].

Colorado

AMNH 6652, 6664, 9002 [Lower dental elements].

Wyoming

AMNH 0-142-2983g [Lower dental element].

FROM THE ARCHIVES AND COLLECTIONS

W. J. HOLLAND'S SPEECH AT THE INTERNATIONAL CONGRESS OF AMERICANISTS, 13TH SESSION, IN 1902

DAVID R. WATTERS¹

THE CONTEXT OF THE ADDRESS

W. J. Holland, Director of Carnegie Museum, attended the 13th Session of the International Congress of Americanists (13th ICA) which convened at the American Museum of Natural History in New York City from October 20–25, 1902. Holland's participation in the 13th ICA can be tracked through entries in its Proceedings volume published three years later (International Congress of Americanists, 1905). The volume indicates he was a Member of the General Commission of Organization (p. xi), Delegate of the United States (p. xiv), Subscriber (p. xvii), and Member of the Council (p. xxii).

Holland twice addressed the Congress on Monday, October 20, the day the 13th Session opened. In his initial address, which is the subject of this paper, he spoke to the Congress regarding the status of Carnegie Museum. Later that afternoon he read his paper entitled "The Petroglyphs at Smith's Ferry, Pennsylvania." His speech and paper (Holland, 1905*a*, 1905*b*) were published in the Proceedings.

Holland was invited to the dais by the preeminent American anthropologist of the time, Frederic Ward Putnam, who was chairing the Monday session in his role as a Vice President (representing the United States) of the 13th ICA. Holland was the second speaker. He was preceded by W. J. McGee of the Bureau of American Ethnology, Smithsonian Institution, and succeeded by Stewart Culin (Archaeological Museum of the University of Pennsylvania), George A. Dorsey (Field Columbian Museum), Edward S. Morse (Peabody Academy of Science), Frederick Starr (University of Chicago and Davenport Academy of Sciences), and Putnam (Peabody Museum of Harvard University and the American Museum of Natural History), each of whom reviewed the anthropological work conducted by his institution (International Congress of Americanists, 1905:xxvi–xliv). Although Holland's scientific work was in entomology, not anthropology, he shared the lectern that day with some of the major figures in the emerging discipline of anthropology. Holland became acquainted with many prominent North American, Latin American, and European anthropologists during the 13th ICA.

THE CONTENT OF THE ADDRESS

Holland's speech makes it clear that he regarded the 13th ICA as a fine venue for informing Americanists, anthropologists, and museologists about the efforts being made in the field of anthropology by the "infant" Carnegie Museum.

Reproduced below in their entirety are Putnam's introductory remarks, Hol-

¹ Curator, Section of Anthropology

land's speech, and Putnam's closing comments made in 1902, as published in 1905 in the 13th ICA Proceedings:

[Vice President F. W. Putnam speaking] I call upon Dr. W. J. Holland, the director of one of the younger museums (that is, younger in the sense that it has only recently done anything in anthropology) to briefly outline the work of the Carnegie Institute of Pittsburg.

W. J. Holland, of the Carnegie Museum, in responding to the call of the Chair, said:

Mr. President, Ladies and Gentlemen.—The Carnegie Museum is in its infancy, but it is a strong and vigorous infancy. It has already outgrown its swaddling clothes and the manger in which it has been lying. It is now waiting patiently for a decision from the Supreme Court of Pennsylvania, a decision which will undoubtedly allow the manger to be transformed into a bed. There are four or five millions of dollars, thanks to the generosity of the founder, at the service of the Museum for enlarged buildings, but the money cannot be expended until the ground is obtained upon which to put these buildings, and a lawsuit now pending prevents this. Meanwhile we are at work gathering up collections which are to be placed in the halls of the future edifice. We are hiring storerooms. We are, to a certain extent, in the "cold storage" business. Good storage is cold, and should be kept cold for the preservation of collections which are made. Like some very religious people, we are afraid of fire.

Our archaeological work has largely been thus far confined to the valleys of the Monongahela and the Allegheny, which unite at Pittsburg to form the Ohio. We here find mounds, shell-heaps, sites of ancient villages, and sculptured rocks, and we are attempting to map out the location of these memorials of the primitive peoples who once inhabited these portions of western Pennsylvania, and to preserve, so far as possible, the scanty records which relate to the aboriginal inhabitants.

We are also receiving from other places a great deal of interesting material. We are under obligations to the Honorary President of the present meeting [13th ICA], the Duke of Loubat, for notable gifts, and we are under obligations to Mr. [Andrew] Carnegie, the founder, for grants of money which have enabled us to purchase things that are desirable for exhibition in order to illustrate the archaeology of the country at large. We have recently secured considerable sums of money to aid the work of exploration in Egypt, and we have received in return from the Egypt Expedition Fund some very interesting collections. From Colombia, Mexico, India, Japan, and indeed from all parts of the world we have obtained material, which we are classifying. Ultimately we hope to have a large and representative museum in which the student of archaeology will be able to work with satisfaction. We wish to make our work thorough, scholarly, and complete.

Referring again to our immediate neighborhood, I may say that there is not very much of surpassing archaeological interest left for us there. The forefathers shot the Indians, or poisoned them with bad whiskey. They were poor people, who did not have much in the way of goods

and chattels, and all that remains of them are the few tools and stone implements which they carried, and which we find in their graves.

I have the honor, sir, on behalf of the Carnegie Museum, to extend to this Congress an invitation to visit the institution a week from the coming Wednesday. I understand that you will be with us at that time. We have provided for the accommodation of the delegates. We will give you your breakfast, your luncheon, and your dinner. We will speed you as parting guests to "Fort Ancient," somewhere in the "howling wilderness" of southern Ohio, to which point Professor Putnam will probably conduct you. When you come to visit us you shall see for yourselves what we are doing in our museum, the youngest institution of its kind in America. The great works of the United States Steel Corporation, through the courtesy of its president, will be open for inspection, and a train will be provided to take you there and bring you back to dinner.

Vice-President Putnam: We thank Dr. Holland for the information he has given us, and for the cordial invitation to the delegates to meet at Pittsburg and make that one of the stopping-places on the excursion which will follow the meeting of the Congress. (International Congress of Americanists, 1905:xxxix–xxxii).

Putnam referred to Carnegie Institute in his introduction, whereas Holland spoke of Carnegie Museum. In 1902 Carnegie Museum was one of the components of Carnegie Institute, the parent organization; the other components were the Department of Fine Arts and the Music Hall. Also, Pittsburg was the officially sanctioned spelling, the "h" having been dropped by the U.S. Geographic Names Board in 1890 (a decision rescinded in 1911 after protest), but both spellings were in use at the time (e.g., Carnegie Institute, 1907). Holland's allusions to "... swaddling clothes and the manger ..." and "... very religious people ..." in the first paragraph seem peculiar until one realizes that he was an ordained minister, having served as pastor of the Bellefield Presbyterian Church in the Oakland section of Pittsburgh from 1874 until 1891 (Van Trump, 1966:219–220). Holland subsequently served as Chancellor of the Western University of Pennsylvania (now the University of Pittsburgh) from 1891 to 1901.

THE SIGNIFICANCE OF THE ADDRESS

At the time W. J. Holland (Fig. 1) attended the 13th ICA, he had been Director of Carnegie Museum for only four years, having accepted that position in 1898 at the behest of his friend Andrew Carnegie (Avinoff, 1933). Between 1898 and 1901, he concurrently served as the Director of Carnegie Museum and Chancellor of the Western University of Pennsylvania. He succeeded the first director, archaeologist Frank H. Gerrodette, who had resigned in 1896 following a public brouhaha over his excavation of the McKee's Rocks Mound near Pittsburgh (Richardson, 1980:13). A letter in the Carnegie Museum of Natural History Archives, written by Herbert H. Smith (1897), who identified himself as "Curator" but seems to have been serving as the acting director, states that Gerrodette had been elected to the directorship in May, had excavated the McKee's Rocks Mound in July, August, and early September, and resigned in September 1896. Gerrodette, who had been F. W. Putnam's student at Harvard University, arranged for Putnam to visit the excavation at McKee's Rocks Mound during the controversy in 1896.

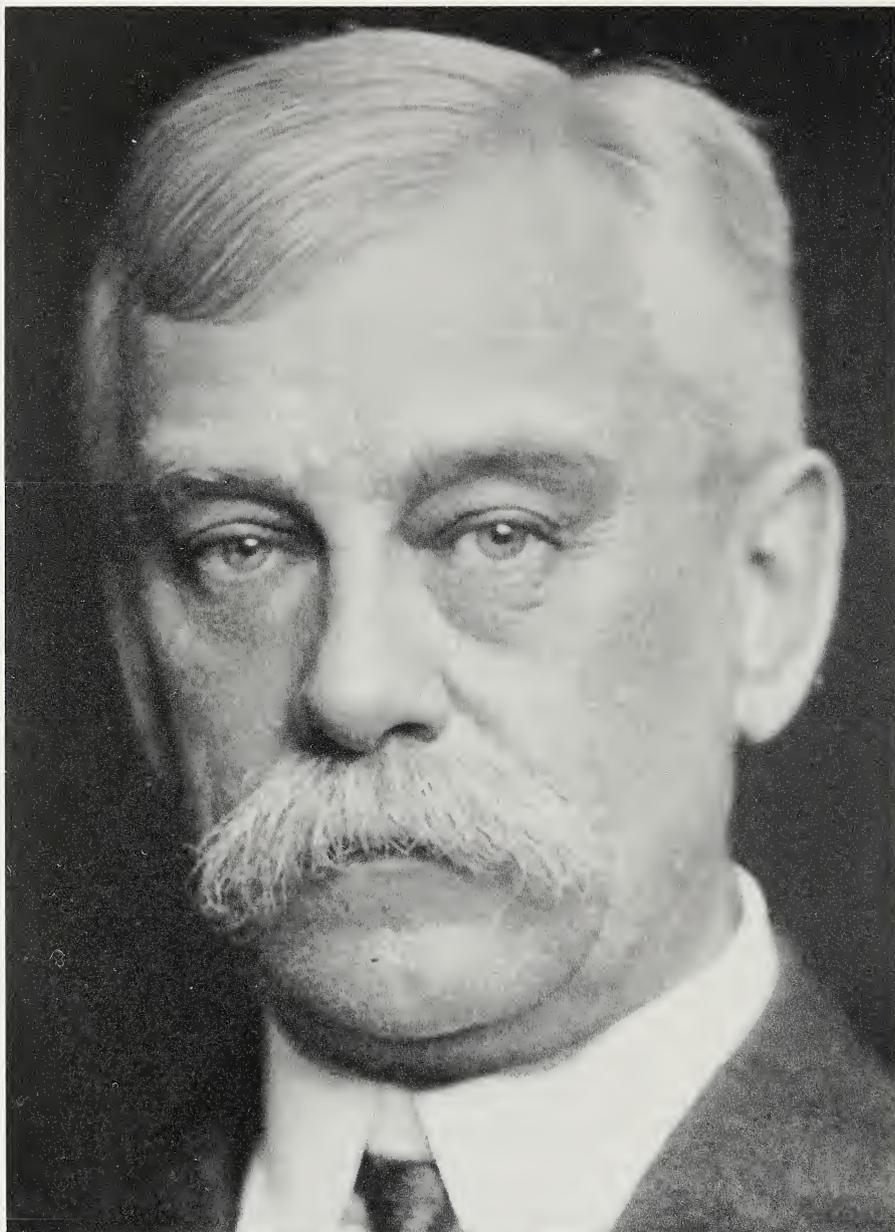


Fig. 1—William Jacob Holland, Director of Carnegie Museum, c. 1910. (Carnegie Museum of Natural History Archives)

Ironically, it was Putnam who introduced Holland when he spoke to the 13th ICA six years later.

Holland's comment about "... enlarged buildings ..." in the first paragraph of his speech refers to the planned addition to the original 1895 building. The settling of the lawsuit to which Holland refers opened the way for the completion

of the addition, with the new building being dedicated in 1907 (Carnegie Institute, 1907). Carnegie Museum collections held formerly in “. . . cold storage . . .” thus finally were displayed in fitting exhibition spaces.

The second and fourth paragraphs relate to the archaeological work carried out in the vicinity of Pittsburgh. Holland’s comment regarding Carnegie Museum’s efforts to map the “. . . mounds, shell-heaps, sites of ancient villages, and sculptured rocks . . .” was a fairly accurate representation, for the time, of the state of knowledge about the range of archaeological sites in the region. Despite Holland’s allusion to Carnegie Museum’s early research efforts, almost a half-century would pass before an intensive program of systematic archaeological research was inaugurated in 1950 through the Upper Ohio Valley Archaeological Survey, directed by Curator James L. Swauger with the fieldwork being carried out initially by William Mayer-Oakes and Donald W. Dragoo (Richardson, 1980:15–16). Holland’s characterization of the local Native Americans as “. . . primitive peoples . . .” and “. . . poor people . . .” who left behind “. . . not very much of surpassing archaeological interest . . .” reflects the prevailing attitude of his times. He acknowledges the forefathers’ role in the decimation of these peoples, although his comment seems to be simply a factual statement without any clear indication of regret.

The third paragraph discloses the areas of the world from which anthropological collections then were being obtained. Acquisition of collections for eventual exhibition in the enlarged building clearly was a priority for Holland, and it was a task that was very much in line with the needs of the “infant” Carnegie Museum. His comment about Carnegie Museum having received Egyptian collections from the Egypt Exploration Fund (EEF) in return for “. . . sums of money . . .” refers to that organization’s Pittsburgh chapter, whose formal charter dates to 1901, although it existed even earlier (Watters and Patch, 1986:32–33). Interest in creating this chapter can be tracked to 1898, when the Museum Committee passed the following resolution:

EGYPTIAN EXPLORATION. Resolved: That the Trustees express their gratification that it is contemplated to establish a centre [sic] of the Egyptian Exploration Fund, here in Pittsburgh, and that so far as practicable the authorities of the Museum will cooperate and offer the Museum as a depository for such objects as may be obtained by this center. (Carnegie Museum, Minutes of the Museum Committee [for October 31, 1898], vol. II, January 3, 1898 to April 1, 1905).

Holland documents his involvement in the founding, recruitment of new members, and fund-raising efforts of the Pittsburgh EEF chapter in six of his monthly reports to the Museum Committee (Holland 1899, 1901*a*, 1901*b*, 1901*c*, 1901*d*, 1902*b*). Other collections that Holland mentions include H. H. Smith’s archaeological collection from Santa Marta, Colombia; a robe donated by the Maharajah of Benares, India; casts of Mexican sculptures donated by Andrew Carnegie, who arranged for their reproduction through the Duke of Loubat; and loans of various Japanese items. Facsimile publications of Mexican codices were the “. . . notable gifts . . .” presented by the Duke of Loubat.

The speech’s final paragraph invites the Congress participants to visit Carnegie Museum. The 13th ICA Proceedings volume (p. lxxvii) discloses that the post-Congress excursion included visits to Philadelphia, Washington, D.C., Pittsburgh,

Fort Ancient in southern Ohio, Cincinnati, and Chicago. Holland tendered this invitation with the approval of the Museum Committee:

INTERNATIONAL CONGRESS OF AMERICANISTS. The Director presented a letter from M. H. Saville, General Secretary of the International Congress of Americanists, stating that about forty members of this society desired to come to Pittsburgh about October 29th and that they would like to be invited to visit the Carnegie Museum and Institute. The Director was, on motion, requested to invite the members accordingly and to arrange for their entertainment. (Carnegie Museum, Minutes of the Museum Committee [for September 29, 1902], vol. II, January 3, 1898 to April 1, 1905).

The delegation toured Carnegie Institute and other points of interest in Pittsburgh on October 29, and Holland took advantage of that opportunity to once again expound upon his ideas for a new Carnegie Museum. Holland's invitation to visit the United States Steel Corporation works (they visited the Homestead plant) seems somewhat incongruous until one realizes that this formerly was the Carnegie Steel Company, the foundation of Andrew Carnegie's wealth and his financial support of Carnegie Museum. Pittsburgh newspaper accounts of the event provide a means of identifying the foreign delegates and some of the institutions and countries they represented (Table 1). One newspaper even published a photograph of the delegates (Fig. 2). According to the newspapers, the delegation's itinerary, after the stop in Chicago, had been expanded to include visits to St. Louis (hosted by the Louisiana Purchase Commission), New York City, and finally Boston and Cambridge.

Holland's speech to the 13th ICA is a valuable document because it is one of the few records yet discovered on the status of anthropology at Carnegie Museum during the early years of his directorship. Although brief, the speech nonetheless provides important insight into Holland's perception of local archaeological resources, intentional acquisition of anthropological collections from around the world in preparation for their installation in the new building, and reliance upon Andrew Carnegie for the financial means to obtain collections and expand the facility. Holland readily used opportunities afforded him by his speeches at the 13th ICA and to the visiting delegation the following week to promote his vision of a new Carnegie Museum to international, national, and local audiences.

THE SIGNIFICANCE OF HOLLAND'S ATTENDANCE

Holland attended the 13th Session of the International Congress of Americanists for several reasons. The Museum Committee had formally endorsed his participation:

CONGRESS OF AMERICANISTS. On motion, Dr. W. J. Holland was appointed to represent the Carnegie Museum at the Thirteenth Annual Meeting of the International Congress of Americanists, to be held in New York in 1902. (Carnegie Museum, Minutes of the Museum Committee [for July 30, 1901], vol. II, January 3, 1898 to April 1, 1905).

The 13th ICA was the first session convened in the United States; all previous sessions had been held at European locations (except for the 11th Session, a special meeting in Mexico in 1895). At the 12th ICA in Paris in 1900, it was

Table 1.—13th ICA foreign delegates visiting Carnegie Museum on October 29, 1902.

Argentine Republic	Señor Juan B. Ambrosetti
Costa Rica	Professor Henri Pittier de Fabrega Professor Juan Fernández Ferraz [incorrectly listed as Juan H. Ferraz]
France	Professor Leon Lejeal, College de France, Paris Señor M. Gonzalez de la Rosa, Paris [misspelled as Gongalez]
Germany	Dr. Eduard Seler, German Government [misspelled as Edward] Professor Karl von den Steinen, University of Berlin
Great Britain	Professor John H. Biles, University of Glasgow, Scotland A. P. Maudslay, Anthropological Institute of Great Britain and Ireland [misspelled as Mandslay]
Honduras	Señor N. Bolet Peraza
Italy	Signor Giovanni Branchi
Mexico	Señor Alfredo Chavero Señor Francisco Belmar, State of Oaxaca
The Netherlands	Professor J. L. van Panhuys
Paraguay	Señor Alonzo M. Criado
Russia	Professor Waldemar Bogarras
Sweden	Professor C. V. Hartman, Swedish Anthropological Society, Stockholm Professor Hjalmar Stolpe, Royal Ethnological Museum, Stockholm
Venezuela	Señor Genera Garcia

Notes:

- (1) The 19 foreign delegates are listed identically in six local newspapers (*Leader*, *Times*, *Dispatch*, and *Chronicle-Telegraph* from October 29, and *Post* and *Gazette* from October 30); the list probably was derived from a Carnegie Museum press release since errors in spelling are consistent in the newspapers.
- (2) Most newspapers state that 31 persons formed the delegation; the twelve individuals not named may have been spouses of delegates and/or American delegates.
- (3) The *Leader* of October 29 mentions five women among the delegation; at least two women are visible in the photograph; the *Times* of October 30 mentions Miss Adela Breton (an Englishwoman) and the unnamed wife of Dr. Seler.

decided to alternate future sessions between venues in Europe and the Americas, and the 13th ICA in New York City inaugurated that scheme. The International Congress of Americanists, the premier anthropological meeting of the times, brought together participants from throughout the Americas and Europe, and the 13th ICA thus afforded Holland an opportunity to meet many eminent anthropologists. Holland also expanded his contacts in the museum field since many of the 13th ICA participants were employed by or otherwise associated with major museums of the day, serving either as anthropologists or administrators on their staffs.

Holland was acquainted with some major figures in American anthropology even before he attended the 13th ICA. In June 1902, only four months before the



Delegates From All Over the Continent Caught by The Dispatch Staff Photographer in Front of Hotel Schenley

Fig. 2—Photograph from the *Dispatch* (October 30, 1902 edition, p. 8) of the visiting delegation of the International Congress of Americanists at the Schenley Hotel in Oakland. (Carnegie Museum of Natural History Archives, Holland newspaper clipping scrapbook)

13th ICA, the founding meeting of the American Anthropological Association (AAA) convened in the Oakland section of Pittsburgh (McGee, 1902*a*, 1902*b*). The founding meeting was held in conjunction with the American Association for the Advancement of Science's (AAAS) annual meeting, which was being attended by anthropologists from its Section H (Anthropology). It was announced beforehand that the AAA founding meeting would be held in the "... audience room of the Bellefield Church, on Monday, June 30, at 2 o'clock" (McGee, 1902*a*:353), which must have referred to the Bellefield Presbyterian Church (there being no other Bellefield church in Pittsburgh), the same church where Holland had served as pastor until 1891 and remained a member. However, McGee (1902*b*:464) afterwards reported the "... Oakland Church ..." to have been the venue of the June 30 meeting. He did not mention the denomination of the church in either article.

I initially thought McGee's use of "Oakland Church" simply was a generalized reference to the Bellefield Presbyterian Church located in Pittsburgh's Oakland section, an assumption that seemed logical and warranted given Holland's personal ties to that church. However, a newly discovered document brings the validity of that assumption into question. Holland, when referring to room arrangements being made for the entire AAAS meeting (not specifically the AAA founding meeting), stated:

The Trustees of the Bellefield Presbyterian Church and of the Oakland Methodist Episcopal Church have kindly tendered the use of their respective buildings for the coming [AAAS] meeting, and I have secured an option upon the Music Hall and the small lecture room of the Institute. (Holland, 1902*a*).

McGee's use of the term "Oakland Church" has an equally plausible chance of having referred to the Oakland Methodist Episcopal Church as the venue for the AAA founding meeting.

McGee (1902*b*:477) did establish one definite link between Holland and the visiting anthropologists when he acknowledged Holland's courtesy in arranging for Carnegie Museum to exhibit a Mexican sculpture discussed by archaeologist Marshall Saville during the Section H scientific sessions. That Holland is identified as one of the founders of the American Anthropological Association (Anonymous, 1903:191) provides additional evidence of his early connections with anthropologists. Thus, in the audience listening to Holland's speech and paper at the 13th ICA were some of the same anthropologists with whom he had interacted in Pittsburgh only four months before.

Holland attended the 13th ICA for another reason. He was interested in exploring the possibility of hiring an anthropologist to become Curator of the Section of Ethnology and Archaeology at Carnegie Museum, and the meeting provided him the opportunity to meet possible candidates. In late January 1903, three months after the 13th ICA ended, Holland offered the curatorship to Stewart Culin. Culin, representing the Archaeological Museum of the University of Pennsylvania, had spoken immediately after Holland at the 13th ICA. He declined Holland's offer in early February.

Holland then entered into negotiations with Carl Vilhelm Hartman for the curator position, and Hartman accepted the offer on February 28 (Watters and Fonseca Zamora, 2001). Hartman had attended the 13th ICA as a representative of the Swedish Society for Anthropology and Geography, and he was one of the delegates visiting Pittsburgh on the post-Congress excursion (Table 1). Having twice heard Holland expound upon his vision for Carnegie Museum, Hartman was aware of the Director's desire to acquire collections. Hartman made it a point in his letters to Holland to emphasize his personal knowledge about collections of antiquities available for purchase in Costa Rica, where he previously had conducted archaeological research in 1896–1897 on a Swedish expedition (Brunius, 1984). Hartman reported for duty on March 17, 1903. Two weeks later, Holland sent him to Costa Rica on his second expedition. Two Costa Rican delegates, Henri Pittier de Fabrega and Juan Fernández Ferraz, with whom Holland became acquainted at the 13th ICA through Hartman and during their subsequent visit to Pittsburgh (Table 1), facilitated the Carnegie Museum expedition. Hartman presented letters of introduction, written by Holland, to both of them when he arrived in Costa Rica. Thus, Holland's attendance at the 13th ICA led not only to the hiring of an anthropology curator, but also resulted in the acquisition of collections from Costa Rica for the "infant" Carnegie Museum.

There are other connections between Carnegie Museum and the 13th ICA. C. C. Mellor, Chairman of the Museum Committee, is listed in its Proceedings volume (p. xviii) as a "Subscriber," although whether he actually attended the Congress is uncertain. Four months later, Mellor's committee approved Holland's recommendation to hire Hartman (Watters and Fonseca Zamora, 2001). In his Monthly Report to the Museum Committee, delivered at its February 28, 1903 meeting (the same day Hartman was hired), Holland wrote:

Dr. C. V. Hartmann [sic], whose acquaintance I formed at the recent Congress of Americanists, is in the building, and I shall take pleasure in presenting him to you at sometime this evening. He has had experience in Museum work, having been associated with Dr. Stolpe, the celebrated Swedish ethnologist, whose assistant he was at Stockholm. He was for a long time with Dr. Lumholtz in Mexico and has written

extensively upon the ethnology of Costa Rica. It may be that he is the man, for whom we are looking. He produces excellent testimonials. (Holland, 1903).

Holland refers to Dr. Hjalmar Stolpe, the person responsible for mentoring Hartman in museum work (Watters and Fonseca Zamora, 2001). Stolpe had attended the 13th ICA, serving as the Vice President representing Sweden (as Putnam did for the United States), and during the excursion thereafter he visited Carnegie Museum (Table 1). Stolpe was Director of the Ethnological Section of the Museum of Natural History of Sweden, and he was one of the contacts made by Holland among the museologists at the Congress.

The 13th ICA was the only session Holland ever attended. However, he retained an interest in the organization and is listed as a subscriber in the Proceedings of some of its later sessions. The final Proceedings volume in which his name appears is from the 23rd Session, which lists him as Director Emeritus of Carnegie Museum but specifies he was "Not in attendance" (International Congress of Americanists, 1930:xxvii). Holland died December 13, 1932 (Avinoff, 1933). The Library of the Carnegie Museum of Natural History holds the Proceedings from most sessions of the International Congress of Americanists convened between the 12th ICA in Paris in 1900 and the 23rd ICA in 1928 in New York City. Appropriately, the Duke of Loubat donated the 12th Proceedings volume while the 23rd Proceedings came from the Estate of W. J. Holland. The Library's preservation of the ICA Proceedings serves as a fitting tribute to Holland's participation in the 13th Session of the International Congress of Americanists one hundred years ago, when the "infant" Carnegie Museum was beginning its vigorous growth under his directorship.

Acknowledgments: Throughout Holland's tenure as Director, the institution was known as Carnegie Museum, only being changed in 1973 to the Carnegie Museum of Natural History. I discovered Holland's association with the 13th ICA during my research on the life of C. V. Hartman, supported by a grant graciously awarded by the Adrienne and Milton Porter Charitable Foundation. I am indebted to CMNH Research Associates Hazel Johnson for obtaining newspaper accounts about the delegation visiting Pittsburgh, researching the churches related to the AAA founding meeting, and tracking biographical information about W. J. Holland, and Oscar Fonseca Zamora (University of Costa Rica) for providing information about Henri Pittier de Fabrega and Juan Fernández Ferraz. I am grateful to CMNH Librarian Bernadette Callery for access to archival resources, Anthropology Collection Manager Deborah Harding for information about the collections mentioned by Holland, Anthropology Secretary Charmaine Steinberg for assisting in manuscript preparation, and Staff Photographer Mindy McNaugher for photographing the newspaper clipping of the visiting delegates.

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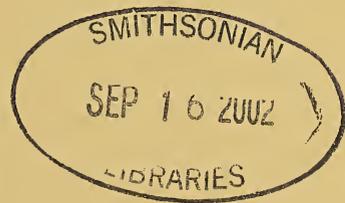
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REVISION OF THE NEW WORLD ABARIFORM GENERA
NEOTALUS N.GEN. AND *ABARIS* DEJEAN
(COLEOPTERA: CARABIDAE: PTEROSTICHINI (AUCTORUM))

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ABSTRACT

New World ground beetles (Coleoptera: Carabidae) in the abariform genus-group are classified into three genera, *Pseudabarys* Chaudoir, *Neotalus* new genus and *Abaris* Dejean. Species of the clade *Neotalus* + *Abaris* are revised. Based on the cladistic analysis of adult characteristics, a preferred hypothesis groups species of *Abaris* into clades that are designated as two subgenera and four species-groups: *Abaris sensu stricto* containing three clades designated as species-groups; *A. striolata*, *A. aenea*, and *A. picipes*-groups and subgenus *Abaridius* Chaudoir (type species *Abaris tachypoides*) comprised of the *A. tachypoides*-group and two species placed *sedes mutabilis* within the subgenus. Seventeen new species are described in the genus *Abaris*: *A. napoensis*, *A. bicolor*, *A. nitida*, *A. nigra*, from Ecuador; *A. franiai*, *A. inflata*, *A. convexa*, *A. inaequaloides*, *A. wardi*, from Bolivia; *A. impunctata*, *A. nobilis*, from Brazil; *A. metallica* from Venezuela; *A. retiaris*, from Colombia and Venezuela; *A. erwini* from Peru and Bolivia; *A. opaca*, from Peru, Bolivia and Brazil; *A. mina*, from Argentina, Brazil, Bolivia, and Paraguay; and *A. aquilonaria* from Central America and Mexico. *Abaris darlingtoni* Straneo and *A. aenea* Dejean are synonymized, the latter is the senior, and hence valid name of the species. The genus *Neotalus* is described to include *N. portai* (Straneo); the species was originally included in *Bothynoproctus* Tschitschérine. Descriptions, distributional information, illustrations of morphological structures, and a key to *Neotalus* and *Abaris* species are provided. Distributional patterns show differences between the *A. picipes*-group species and their sister clade the *A. aenea*-group, with the former being more eurytopic and generally adapted to drier habitats. Biogeographical analysis of biotic zones, using items of error as the optimality criterion, relative to the phylogenetic hypothesis for *Neotalus* + *Abaris*, suggests South American diversification and restriction until at least the Pliocene. *Abaris* species have probably moved into Central America and Mexico four to five times since the development of the land connection with South America in the Pliocene. This contrasts against the biogeographical pattern for *Coptodera* Dejean species (Lebiini), which appear to have basally diverged among the northern areas of Mexico versus South America.

KEY WORDS: New species, systematics, biogeography, classification

INTRODUCTION

Members of the Neotropical genera *Neotalus* new genus and *Abaris* Dejean are small ground beetles (Coleoptera: Carabidae), most individuals are brilliantly metallic with very prominent eyes (Fig. 1). *Abaris* species are uniquely characterized among all Pterostichine grade taxa by pectinate claws (Fig. 2A). These characteristics give them a unique look that is approached in *Pseudabarys* Chaudoir, 1873 and *Prosopogmus* Chaudoir, 1865, both presumed to be closely related genera. I discovered from examination of museum specimens that many more species than the nine named forms of *Abaris* existed. The captivating form and unstudied diversity were the starting points for an interest in revising this group.

A small body of literature treats the abariform species. Straneo (1939) published a key to the eight then named species of *Abaris* and Bousquet (1984) added a

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Submitted 10 October 2001.



Fig. 1.—Photograph of living *Abaris splendidula* (LeConte). Collected in Cochise County, Arizona.

ninth species when he discovered that LeConte's *Pterostichus splendidulus* belonged in the genus *Abaris*. Bousquet and Liebherr (1994) summarized what little had been published on the relationships of the genus *Abaris* and covered nearly all the genera included herein. The complex of genera thought to be closely related and/or associated in published classifications (Bates, 1882; Blackwelder, 1944; Straneo, 1977, 1979; Csiki, 1930; Reichardt, 1977) includes the Nearctic-Neotropical genera *Abaris*, *Abaridius* Chaudoir, *Ophryogaster* Chaudoir, 1878, *Pseudabarys*; the northern African-Palearctic genus *Orthomus* Chaudoir, 1838; and the Australian genus *Prosopogmus*. My previous analysis of both adult and larval characters (Will, 2000) supports a close relationship of these genera, as well as *Blennidus* Motschulsky, 1866, *Oribazus* Chaudoir, 1874, *Dyschromus* Chaudoir, 1835, *Abacillius* Straneo, 1949 (referred to in Will, 2000 as "genus E"), and *Argutoridius* Chaudoir, 1876. These genera form, in part, a clade centering on the subtribe *Euchroina* (auctorum) and the *setalis* series (Moore, 1965).

An exceedingly short or absent coronal suture in the larva was considered by Bousquet and Liebherr (1994) as a potential synapomorphy for *Abaris* and *Orthomus* species. This condition is also found in *Pseudabarys* (Will, 2000) and is a significant character for a clade including some or all of the taxa above.

The combination of large eyes, pectinate claws, and metallic luster suggests that *Abaris* species may have peculiar life histories or behaviors relative to related genera that have characteristics more typical for pterostichine grade taxa. However, the limited field observations for these species do not provide incontrovertible evidence for any adaptive significance for this suite of characteristics. In fact, observations of any sort exist for very few of these beetles. Specimens of these species are uncommon in collections. In addition to my own field work, some recent efforts by carabid collectors such as T. L. Erwin (USNM) and G. E. Ball (UASM) have resulted in the collection of large numbers of specimens from a few locations in Central and South America. I hope this monograph will provide researchers and students, particularly those in South America, with the tools to

identify and study species of *Abaris* so that a greater understanding of their life history and ecology can be obtained.

MATERIALS, METHODS, AND TERMS

Taxonomic Materials

Material examined in the course of this study included 1025 adults specimens of *Abaris* and *Neotalus* species. A number of these were examined in detail including dissection of various internal systems. Material was taken on loan from collections listed below. Museum codens are used in the text and the names listed here are the individuals I corresponded with to obtain material and/or those who processed the loans for me.

Museums and Codens.—AMNH: Department of Entomology, American Museum of Natural History, New York, New York (L. H. Herman).

BMNH: Department of Entomology, British Museum, London (Natural History) (S. Hine).

BORD: C. Bordon collection, Maracay, Venezuela (C. Bordon).

BPBM: Bishop Museum, Honolulu, Hawaii (G. A. Samuelson).

CASC: Department of Entomology, California Academy of Sciences, San Francisco, California (D. H. Kavanaugh, R. Brett).

CMNC: Entomology, Canadian Museum of Nature, Ottawa, Ontario.

CMNH: Section of Invertebrate Zoology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania (R. L. Davidson).

CNCI: Canadian National Collection, Biosystematics Research Institute, Agriculture and Agri-Food Canada, Ottawa, Canada (Y. Bousquet).

CUIC: Department of Entomology, Cornell University, Ithaca, New York (J. K. Liebherr).

EMEC: Essig Museum of Entomology, Berkeley, University of California, Berkeley, California (C. Barr).

INBC: Instituto Nacional de Biodiversidad (INBio), Costa Rica, Santo Domingo de Heredia.

IZWP: Instytut Zoologii, Polska Akademia Nauk, Warszawa, Poland (T. Huflajt).

KWWC: Kipling Will Collection, Berkeley, California.

MSNM: Museo di Storia Naturale di Milano, Milan, Italy (M. Pavesi, C. Leonardi).

MCZC: Department of Entomology, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (P. Perkins).

MHNP: Entomologie, Museum National d'Histoire Naturelle, Paris, France (T. Deuve).

MIZA: Museo del Instituto de Zoología Agrícola Francisco Fernández Yépez, Maracay, Venezuela (L. Joly, J. Clavio).

MNHB: Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin, Germany.

NMW: Zweite Zoologische Abteilung, Naturhistorisches Museum Wien, Wien, Austria (H. Schonmann, E. Kirschenhofer).

OSUC: Department of Entomology, Ohio State University, Columbus, Ohio (N. Johnson).

QCAZ: Catholic Zoology Museum, Pontificia Universidad Católica del Ecuador, Quito, Ecuador (G. Onore).

RSCI: Riccardo Sciaky Collection, Milan, Italy.

SEMC: Snow Entomological Division, The Natural History Museum of the University of Kansas, Lawrence, Kansas (R. Brooks, J. S. Ashe).

STOC: H. Stockwell Collection.

UASM: Strickland Museum, Dept. of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada (D. Shpeley, G. E. Ball).

UATU: Department of Entomology, University of Arizona, Tucson, Arizona (C. A. Olson, D. R. Maddison).

UMMZ: University of Michigan, Museum of Zoology, Ann Arbor, Michigan (M. O'Brien).

UVGC: Universidad del Valle de Guatemala, Guatemala City (J. Schuster).

USNM: Department of Entomology, United States National Museum of Natural History, Smithsonian Institution (T. L. Erwin, D. Furth)

Taxonomic Methods

Species Recognition.—Species were recognized by a set of defining characteristics that permit grouping like individuals from other such individuals with a different set of characteristics. This is essentially the species definition of Nixon and Wheeler (1990).

When multiple specimens were available, variation in characteristics for the species could be assessed and the limits of the defining characters understood. However, when only a single, notably different specimen is available it was necessary to decide if the difference was of specific value. For species based on one or very few specimens, I relied on characters that seemed to be beyond individual variation observed in species known from larger samples. In general these unique specimens were not dissected, so external characteristics that were found to be correlated with genitalic differences in better represented species were relied on. In a few cases a specimen was included within my interpretation of a species, though not in the type series, because it exhibited slight differences that may ultimately prove to define it as a member of a distinct species. I felt it was best not to multiply names in these marginal cases until more material is collected, permitting a robust test of stability of species definitions based on observed character differences.

Species of these genera, like nearly all of life, do not have any single characteristic or complex of characteristics that we can examine to inform us with certainty on their reproductive isolation, or any other possible mode of speciation. Entities named here may be explained, after they are recognized, as real biological and evolutionary individuals. But regardless whether the process thought to underlie species generation is correct or not, species recognition remains the same as it has for all of recorded history, based on empirical observation of characteristics augmented by knowledge of reproduction and development in the rare cases where those data are known. Of course, hypotheses may be adjusted, if necessary, in light of observations of reproductive isolation or interbreeding.

Ranking Criteria and Classification.—No general standard exists for recognizing supraspecific groups in pterostichine ground beetles. The repeated failure to support a monophyletic Pterostichini (*auctorum*) demonstrates that this taxon is a grade (Will, 2000). My use of the term *pterostichine grade* emphasizes the lack of monophyly among the presently included taxa.

The Holarctic pterostichine grade fauna, primarily *Pterostichus* Bonelli, 1810,

is superficially rather uniform in appearance and some recent authors have separated supraspecific groups by very small character differences. The application of similar criteria to the South American and Australian taxa has resulted in what I feel is an extreme emphasis on differences with less regard for grouping similarities. This has led to the recognition of too many supraspecific taxa. With this in mind I have attempted to minimize the number of formal names (genera and subgenera) proposed here, but have named clades (species-groups) that, based on the characters, seem to represent biologically interesting groups and groups of similar form. These names are provided for biologists who may need to discuss the ecology, behavior, etc., of a monophyletic group. When the higher elements of the pterostichine grade are established, some clades (genus-groups) may come to have a formal position in the Linnaean hierarchy.

It is neither practical nor desirable to have a name affixed to every branching point of the cladogram. The classification here is completely consistent with the phylogenetic hypothesis but is not identical to it. These two constructs, cladogram and classification, have slightly different but interconnected purposes. The former provides a complete summary of characters and relationships, and is the basis for discussion of hypotheses of common descent. The latter is the primary means of information retrieval for the taxa, and so should be a useful mnemonic device. In order to fulfill this function, the classification necessarily ignores some of the details of the cladogram and focuses on the aspects deemed likely to be biologically important.

I use the term *sedis mutabilis* as proposed by Wiley (1979; 1981) for the polytomous relationship of basal Abaridius species.

Phylogeny Reconstruction.—The matrix was constructed with the computer program WinClada (Nixon, 1999) and submitted to NONA (Goloboff, 1994) for analysis. NONA's default settings were used for a heuristic search for most parsimonious trees (see NONA documentation). The search was done by submitting the matrix via WinClada using number of replications = 100 (Mult*100), starting trees per replication = 15 (hold/15), random seed = Time (rs0) and the search strategy was multiple TBR+TBR (mult*100; Max*). Aspects of cladistic methods and subsequent interpretation of the pattern as a phylogenetic hypothesis employed here are discussed in my analysis of the genus *Lophoglossus* LeConte, 1852 (Will, 1999).

Preparation and Imaging Techniques.—External structures were examined using a dissecting stereo-microscope at magnification of 100× or less. Some smaller structures and microsculpture of legs, mouthparts, and elytra were examined and photographed using a Hitachi 4500 scanning electron microscope. Disarticulated cuticular structures, including all external parts of the body and various internal systems, were cleared in 10% KOH and mounted on glycerine slides, then examined using a phase-contrast compound microscope.

Methods generally used for preparation of male genitalia follow Allen (1972). However, the small size of most species did not allow for the successful eversion of the endophallus using Allen's methods. Two alternatives were tried with some success for each. First fluid pressure was applied to the foramen using the Phalloblaster machine (vesica everter, Matthews, 1998) for *Neotalus portai* (Straneo). The small size of *Abaris* specimens precluded the use of this machine as the needle diameter exceeds the diameter of the median lobe. Instead of direct fluid pressure, a rapid change in osmotic pressure was used to evert the endophallus in some species. The median lobe was softened in KOH and then dehydrated in 95% EtOH. In order to

increase pressure pushing out the endophallus, a small drop of water soluble glue was placed on the foramen to prevent equalization through the foramen. When the dehydrated median lobe was placed in distilled water, pressure from the flow of water into the lobe via the gonopore forced out the endophallus.

Preparation of female reproductive tracts and genitalia followed procedures outlined by Liebherr and Will (1998).

Initially, drawings were made as pencil line-drawings using an ocular grid or camera lucida. These line drawings were digitized using a flatbed scanner, "inked" and shaded on a personal computer using the Corel Photo-Paint™ version 7.467.

Some cases digital images of whole or slide-mounted portions of specimens were captured using a video microscope and a Snappy Video grabber version 3.0 connected to a personal computer. These images were enhanced in Corel Photo-Paint™ version 7.467 and either printed from a desktop printer or black and white print film.

Locality Information.—Locality information is provided for each species and is divided between type and non-type information. Data from type specimens that are verbatim from the labels are enclosed in double quotation marks with the description of the kind of label and a note if handwritten. Notes not on the specimen labels and the description of the labels are added for clarity and this information placed between square brackets ([. . .]). Unless otherwise noted, labels are white, rectangular with black ink. In as much detail as could be clearly confirmed locality data for other material examined is listed for each species by country in descending order from largest political unit to smallest site information, including latitude and longitude. Altitude and seasonal information are summarized in the section "Notes on Life History" and are listed under each species if any additional data were available beyond that found on the type specimens.

Maps show the location of collections for each of the species either from specimen data labels or from published records. A symbol on the map primarily represents a single collecting site. Multiple sites are represented by a single symbol in cases where collecting sites are very close and multiple symbols on the map would be impossible to discern or be confusing. If label data were unclear or the locality not definitively identifiable, the data are listed but not plotted on the map. In cases where this was the only record for a country a symbol was placed on the map with a "?" to identify it as a questionable record.

Terms

Measurements.—*Overall length* was measured using an ocular reticle and generally was the entire distance from the base of the labrum to the tip of the left elytron. In specimens where it was not possible to measure this way accurately because of the head position, length was standardized using the sum of lengths: 1. base of labrum to the cervical collar, 2. apex to base of pronotum along the midline, 3. base of scutellum to apex of left elytron.

The *ratio of elytral interval widths* is the width of interval 3 divided by the width of interval 2. Measurements were taken by placing an ocular reticle across the intervals at the level of the dorsal setigerous puncture.

Ocular ratio is a measurement of the relative size of the eyes or "bug eyedness" of the beetles. This ratio is the width over the widest point of the eyes divided by the width between the eyes at the level of the anterior supraorbital setae.

Body Parts.—Terms for adult external structures and segmentation follow

Lawrence and Britton (1994). One exception is the use of sterna II–VII for normally exposed ventral abdominal segments rather than sternites II–VII as used by Lawrence and Britton. This follows the definition of sternum as a single ventral division per segment, as is found in adult beetles, and sternites as subdivisions of a sternum as is found in many larvae (Snodgrass, 1935; Torre-Bueno, 1937).

Terms for the female reproductive tract and external genital structures follow Liebherr and Will (1998). Nomenclature of endophallic structures follows Noonan (1991).

The median lobe of the aedeagus is discussed using the following: basal bulb, generally expanded region of the foramen from the base to the parameres; blade, remaining section from the basal bulb to the tip; apex, apical portion of blade from the level of the ostium to the tip; and tip, portion of the apex of the median lobe beyond the ostium. Terms used for colors follow Torre-Bueno (1937).

The term scutellar stria has been used to refer to the short striae on the elytra near the scutellum even though they may not be homologous structures across all groups. The term has been used in reference to the parascutellar striae, which are directly adjacent to the scutellum and continuous with the basal marginal border of the elytra when the border is evident and striae are sulciform. Additionally, the term has been used for the short basal section of stria 1 when that stria is interrupted, even though this section is not adjacent to the scutellum. In order to be consistent with my hypotheses of primary homology I abandon the term scutellar stria but retain the use of *parascutellar stria* as restricted above. In all abariform taxa elytral stria 1 is continuous with the parascutellar stria. Stria 1 may end at its junction with the parascutellar stria or have a short, disconnected basal section arising from near the basal setigerous puncture. When stria 1 is interrupted and the disconnected basal section is present, it is referred to as the *basal section of stria 1*.

Discussion of Clades and Taxa.—*Cladistic diagnoses* are summaries of synapomorphic characteristics of a monophyletic group of taxa based on the cladogram present herein. The purpose of this section is to allow for quick assessment of group membership. The character states of a clade that apply to all included taxa, are not discussed in subordinate clades as they are plesiomorphic and are not useful for assessing group membership at that level.

Recognitory diagnoses correspond to the more traditional diagnosis found in most taxonomic works. The characteristics provided under this heading are intended to permit accurate recognition of specimens. This includes any general attributes and comparative aspects, without regard to phylogenetic implications of the characteristic.

TAXONOMIC AND CLADISTIC ACCOUNTS

Systematic Entomology

Order Coleoptera

Family Carabidae

Subfamily Harpalinae

Tribe Pterostichini (Auctorum)

KEY TO ADULT *NEOTALUS* NEW GENUS AND *ABARIS* DEJEAN SPECIES

1. Metacoxal anterior sulcus incomplete, ended medially on coxa, broadly arcuate in most species, not approaching anterior margin (Fig. 3A); basal section of stria 1 present or absent 2

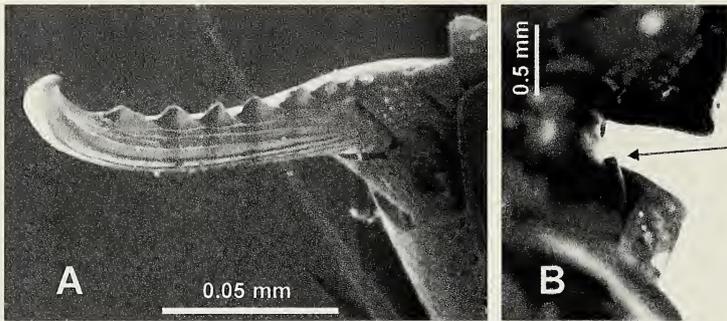


Fig. 2.—Structures of abariform species. A. Scanning electron micrograph, pro tarsal claw of *Abaris aenea* Dejean showing pectination. B. Digitized video-capture image, ventral view, pro and mesothoracic area, *Neotalus portai* (Straneo), mesepimeral tubercle indicated by arrow.

- 1'. Metacoxal anterior sulcus complete, ended at or near apex, straight, not broadly arcuate, approaching anterior coxal margin, (Fig. 3B); basal section of stria 1 absent. *Abaris tachypoides*-group 21
- 2 (1). Basal section of stria 1 absent 3
- 2'. Basal section of stria 1 present 8
- 3 (2). Sterna V–VII without sulci (Fig. 4C); tarsal claws pectinate (Fig. 2A) 4
- 3'. Sterna V–VII with sulci (Fig. 4A); tarsal claws smooth *Neotalus portai* (Straneo)
- 4 (3). Pronotum widest just before middle, lateral margin reflexed in basal third or not; most species shinier with faint or obsolete microsculpture; if microsculpture obvious, then pronotum in basal third laterally distinctly reflexed (Fig. 24D–E) 5
- 4'. Pronotum widest slightly behind middle, lateral margin not reflexed in basal third (Fig. 25D); dull species, microlines forming reticulate microsculpture obvious. Argentina [12] *Abaris basisstriata* Chaudoir (in part)
- 5 (4). Microsculpture faint but visible on head and pronotum 6
- 5'. Microsculpture obsolete on head and pronotum [4] *Abaris aenea* Dejean
- 6 (5). Elytral interval 3 much broader than 2; width ratio 3/2 > 1.4 7
- 6'. Elytral interval 3 only slightly wider than 2; width ratio 3/2 < 1.4 [5] *Abaris erwini* new species
- 7 (6). Pronotum punctate basally and laterally, base laterally sinuate with median base distinctly extended posterad of hind angles (Fig. 24H) South America [7] *Abaris notiophiloides* Bates
- 7'. Pronotum impunctate laterally, base in some with a few shallow punctulae, base not

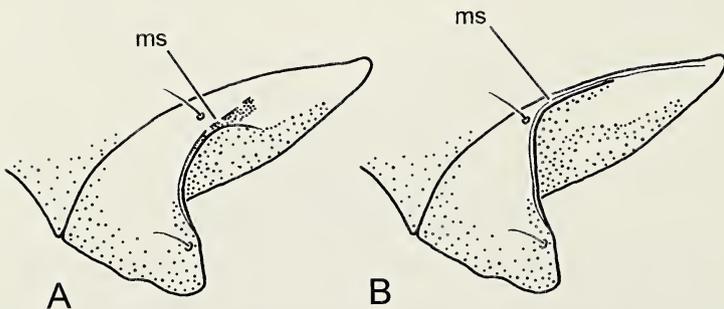


Fig. 3.—Line drawing illustrating diagrammatically abariform left metacoxae. A. With incomplete/arcuate metacoxal anterior sulcus (ms). B. With straight/appressed metacoxal anterior sulcus (ms).

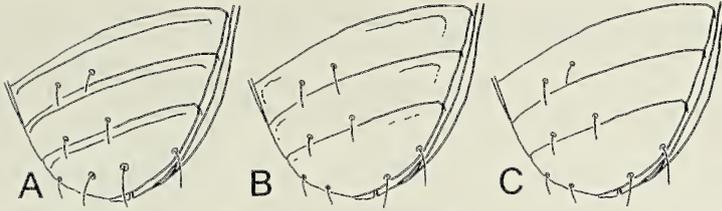


Fig. 4.—Line drawing illustrating diagrammatically abariform abdominal sterna. A. With complete transverse sulci. B. Incomplete/laterally present sulci. C. Sulci absent.

	sinuate; hind angles only slightly anterior to median base (Fig. 24G) Central America/ Mexico	[6] <i>Abaris aquilonaria</i> new species
8 (2').	Sterna V–VII with lateral sulci, medially complete or interrupted (Fig. 4A–B); sulci shallowly to deeply impressed, best developed on sternum VI (variable species handled in both halves of couplet)	9
8'.	Sterna V–VII without a trace of lateral or medial sulci (Fig. 4C)	19
9 (8).	Sulci on sterna V–VII complete (Fig. 4A)	10
9'.	Sulci on sterna V–VII broadly interrupted medially and slightly developed laterally (Fig. 4B)	12
10 (9).	Pronotum constricted at base, widest in anterior half; both basal foveae distinct	11
10'.	Pronotum widest at base; outer basal foveae absent (Fig. 25E)	[13] <i>Abaris metallica</i> new species
11 (10).	Dorsum of head and pronotum metallic green, elytra cupreous; lateral pronotal margins sinuate to base, hind angles clearly denticulate (Fig. 25F)	[14] <i>Abaris bicolor</i> new species
11'.	Entire dorsum cupreous; lateral pronotal margins convexly arcuate to base, hind angles minutely denticulate (Fig. 25G)	[15] <i>Abaris nobilis</i> new species
12 (9').	Disc of pronotum shiny, without obvious microsculpture	13
12'.	Disc of pronotum dull, with obvious mesh microsculpture either reticulate or somewhat transversely elongate	18
13 (12).	Pronotal lateral margin sinuate anterior of hind angles, reflexed in basal third (Fig. 24A–B); narrowly convex immediately lateral of basal fovea	14
13'.	Pronotal margin laterally arcuate and straight or subsinuate anterior of hind angles, not reflexed laterally; convex from basal fovea to lateral margin. (Fig. 25B–C)	17
14 (13).	Pronotum with outer basal foveae present, punctate or rugose along base and/or punctulate in foveae (Fig. 24A–B)	16
14'.	Pronotum with outer foveae absent, impunctate (Fig. 24C)	15
15 (14).	Median lobe tip asymmetrical in dorsal view, left edge emarginate (Fig. 21E)	<i>Abaris striolata</i> Bates (in part).
15'.	Median lobe tip nearly symmetrical in dorsal view, left edge convex (Fig. 21G)	[3] <i>Abaris robustula</i> Tschitschérine
16 (14).	Pronotal base distinctly rugose medially and around basal foveae; aedeagus median lobe tip very broad in dorsal view (Fig. 21A–C)	[1] <i>Abaris napoensis</i> new species
16'.	Pronotal base impunctate or faintly punctured medially and around basal foveae; aedeagus median lobe tip acuminate in dorsal view (Fig. 21D–E)	[2] <i>Abaris striolata</i> Bates (in part)
17 (13').	Pronotal base impunctate (Fig. 25C); endophallus of aedeagus without spine patch visible at bend of median lobe (Fig. 23D); spermathecal duct tightly twisted	[11] <i>Abaris mina</i> new species
17'.	Pronotal base punctate (Fig. 25B); endophallus of aedeagus with spine patch visible at bend of median lobe (Fig. 23A); spermathecal duct broad, not twisted (Fig. 19E)	[10] <i>Abaris picipes</i> Bates

- 18 (12'). Pronotal base with coarse punctulae in basal foveae (Fig. 25A); dorsum black; obvious reticulate microsculpture on pronotum, transversely elongate mesh on elytra, elytra shiny. Mexico [9] *Abaris bigenera* Bates
- 18'. Pronotal base without coarse punctulae (Fig. 24I); dorsum aeneous; reticulate microsculpture obvious throughout, dull species. South America [8] *Abaris impunctata* new species
- 19 (8'). Pronotal lateral margins not reflexed, arcuate, straight just anterior to slightly obtuse hind angles (Fig. 25B-D) 20
- 19'. Pronotal lateral margins distinctly reflexed basally and subsinuate to right angled hind angles (Fig. 24B) [2] *Abaris striolata* Bates (in part)
- 20 (19). Reticulate microsculpture obvious on head and pronotum; dorsal surface duller [12] *Abaris basistriata* Chaudoir
- 20'. Microsculpture obsolete on head and pronotum; dorsal surface very shiny [10] *Abaris picipes* Bates
- 21 (1'). Sterna V-VII with lateral sulci, medially complete or interrupted (Fig. 4A-B) 22
- 21'. Sterna V-VII without sulci (Fig. 4C) 25
- 22 (21). Pronotal base without punctulae; if punctulae present then outer basal foveae clearly round (Fig. 26A) [17] *Abaris franiai* new species
- 22'. Pronotal base with coarse punctulae; outer basal foveae elongate 23
- 23 (22'). Apex of pronotum wider, tip of front angles distant from occiput and slightly produced (Fig. 25H, 26B) 24
- 23'. Apex of pronotum narrow, tightly rounded and appressed to occiput, front angles not produced (Fig. 9) [19] *Abaris tachypoides* Bates
- 24 (23). Pronotum medially punctate between inner foveae (Fig. 25H); mental tooth broadly flattened at apex [16] *Abaris nitida* new species
- 24'. Pronotum medially impunctate between inner foveae (Fig. 26B); mental tooth rounded at apex [18] *Abaris inflata* new species
- 25 (21'). Pronotum relatively small, lateral margins sinuate and narrowly constricted basally (Fig. 26D-E); width of pronotum at base less than width across eyes, or if approximately equal then legs bicolored 25
- 25'. Pronotum relatively larger, lateral margins sinuate or not; width of base greater than or equal to width across eyes, legs not distinctly bicolored 26
- 26 (25). Coxae, trochanters and base of femora darkly infuscated, contrasted with flavous apices of femora, tibiae and tarsi; dorsum black; pronotal base punctulate; front angles of pronotum slightly produced (Fig. 26D) [21] *Abaris nigra* new species
- 26'. Legs concolorous, flavous; dorsum bronzed; pronotal base smooth, only foveae impressed; front angles of pronotum round and tightly appressed to occiput (Fig. 26E) [22] *Abaris inaequaloides* new species
- 27 (25'). Pronotal base with irregular, coarse punctulae at least in area of basal foveae; if punctulae restricted to fovea then head dull from reticulate microsculpture 28
- 27'. Pronotal base without punctulae or with only a few shallow punctulae in basal foveae; if punctulae present then head quite shiny, micro-lines scarcely visible 29
- 28 (27). Mental tooth form simple, sagittiform [25] *Abaris wardi* new species
- 28'. Mental tooth apex blunt and slightly emarginate [23] *Abaris opaca* new species
- 29 (27'). Elytral intervals convex, more prominently so in apical third; eastern and southern Mexico, Central or South America [24] *Abaris splendidula* (LeConte)
- 29'. Elytral intervals flat throughout their length; northwestern Mexico, Baja California, Arizona, southern California [26] *Abaris aequinoctialis* Chaudoir
- 30 (29). Dorsum uniformly shinier, though not brilliantly so, microsculpture of pronotal disc transverse, somewhat irregular mesh, transverse mesh on elytra. Central America, Mexico [26] *Abaris aequinoctialis* Chaudoir
- 30'. Pronotal disc very dull from reticulate microsculpture; elytral microsculpture reticulate, shinier than pronotal disc. South America 31
- 31 (30'). Pronotal base not bordered laterally (Fig. 26C) [20] *Abaris convexa* new species
- 31'. Pronotal base with distinct lateral border (Fig. 27C) [27] *Abaris retiaria* new species

Classification and Checklist of Abariform Genera, Subgenera and Species

(*Pseudabarys* (*Neotalus* + *Abaris*))

Neotalus Will, new genus (one species)

Neotalus portai (Straneo)

Abaris Dejean (27 species)

Abaris sensu stricto

[*A. striolata*-group]

1. *A. napoensis* Will, new species
2. *A. striolata* Bates

[*A. aenea*-group]

3. *A. robustula* Tschitschérine
4. *A. aenea* Dejean
5. *A. erwini* Will, new species
6. *A. aquilonaria* Will, new species
7. *A. notiophiloides* Bates

[*A. picipes*-group]

8. *A. impunctata* Will, new species
9. *A. bigenera* Bates
10. *A. picipes* Bates
11. *A. mina* Will, new species
12. *A. basistriata* Chaudoir
13. *A. metallica* Will, new species

Abaridius Chaudoir

[*sedis mutabilis*]

14. *A. bicolor* Will, new species
15. *A. nobilis* Will, new species

[*A. tachypoides*-group]

16. *A. nitida* Will, new species
17. *A. franiai* Will, new species
18. *A. inflata* Will, new species
19. *A. tachypoides* Bates
20. *A. convexa* Will, new species
21. *A. nigra* Will, new species
22. *A. inaequaloides* Will, new species
23. *A. opaca* Will, new species
24. *A. splendidula* (LeConte)
25. *A. wardi* Will, new species
26. *A. aequinoctialis* Chaudoir
27. *A. retiaris* Will, new species

Accounts of Clades

Abariform Clade (*Pseudabarys* (*Neotalus* + *Abaris*))

Cladistic Diagnosis.—All members of the abariform clade share the following non-homoplasious synapomorphies (Fig. 31: characters 2, 8, 12, 26): eyes large, ocular ratio greater than 1.60; humeral umbilicate puncture 2 displaced medially from 1 and 3; ventral setae of tarsomere 5 of unequal length and paired; dorsal bursal glands present (Fig. 5A–B).

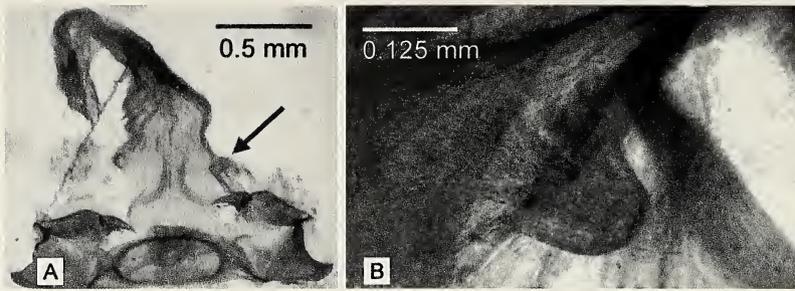


Fig. 5.—*Abaris aenea* Dejean digitized video-capture images of female reproductive tract, showing paired dorsal glands. A. Ventral view of bursa laid flat, arrow indicates gland. B. Single gland enlarged.

Clade (*Neotalus* + *Abaris*)

Cladistic Diagnosis.—All members of this clade share the following synapomorphies (Fig. 31: characters 1, 25): maxillary palpomere 3 much smaller than palpomere 4 (Fig. 28B), diverticulum of the spermatheca appended gland absent.

Neotalus, new genus

Type Species.—*Bothynoproctus portai* Straneo; here designated.

Etymology of Generic Name.—Noun in apposition, masculine. *Neotalus* is a genus-group name formed from the Greek neos (νεος)—new and Talos (Ταλος)—the name of the bronze giant faced by the Argonauts in Crete. The single New World species placed in this genus is larger than species in the genus *Abaris*, has a distinctive metallic luster and lacks the pectinate claws found in *Abaris* species.

Nomenclatural and Taxonomic Notes.—Straneo (1941) described *Bothynoproctus portai* placing it with *B. mattoensis* Tschitschérine, 1900, the type species for the genus. No doubt as a result of World War II, Stefano Straneo did not have the benefit of seeing the type of *B. mattoensis*, and therefore he misplaced his new species. The characteristic deep punctures of the submentum and sternum VII in *B. mattoensis* are lacking in *N. portai*. The former is not closely related to the abariform genera and is more closely related to *Dyschromus* Chaudoir and *Tichonilla* Strand, 1942 (Will, 2000), whereas the latter has several significant synapomorphies in common with *Abaris* species.

Based on these characteristics and my analysis of a broader set of characters (Will, 2000), Straneo's species is removed from *Bothynoproctus* and a new genus, *Neotalus*, is proposed to hold this species. Therefore, *Neotalus portai* (Straneo) is the type species for this monotypic genus.

Cladistic Diagnosis.—As this is a monotypic genus, its synapomorphic characters cannot be specified. If a second species is found that groups with *N. portai* it will likely share some of the apomorphic characteristics described for the species below.

Recognitory Diagnosis of Adults.—See species below and characters in the key.

Description of Adults.—None required because the genus is monotypic. Its characters are as in the type species described below.

Distribution.—See species account below and figure 10.



Fig. 6.—Dorsal habitus of *Neotalus portai* (Straneo).

Species Account

Neotalus portai (Straneo, 1941), **new combination**

Fig. 2B, 6, 10

Bothynoproctus portai Straneo, 1941:28.

Type Material.—HOLOTYPE. Female. Labeled: "Forêt Vierge, au bord de Riv. Paraguay, S Antonio" [handwritten]/"Holotypus portai" [red label]/"portai Stran." [handwritten, red ink], [MSNM]. ALLOTYPE. Male, labeled: "S. Antonio" [handwritten], "Allotypus" [red label]/[dissected genitalia and mouthparts glued to card] [MSNM]. PARATYPES. 2 Males, same data as Allotype, both labeled with "M.C.Z. Paratype 28422", MCZC.

Type Locality.—Paraguay, S Antonio, Staz. Entomol. Fabre., from original description.

Range.—Bolivia, Brazil, Paraguay (Fig. 10)

Recognitory Diagnosis of Adults.—Recognized from all other Carabidae by the combination of form of mouthparts—labial palpi short and broad, lacinia large with a thick, curved apical digitus, maxillary palpi broadly fusiform—and mesepisterna with large tubercle (Fig. 2B) and a corresponding protuberance of pronotal base, tarsal claws smooth, and female reproductive tract with paired bursal glands (Fig. 5A–B).

Description.—In addition to characteristics of the *Neotalus* + *Abaris* clade, large sized, 7.0–8.5 mm. Elytra aeneous or cupreous to vinous, head and pronotum darker, shiny. Ventral surface black, tarsi and palpi paler brunneous.

Head. Large, very broad, frontal impressions deep, divergent. Fronto-clypeal suture impressed, clypeus emarginate, membrane at base of labrum exposed. Eyes very large and prominent, hemispherical, ocular ratio 1.62–1.72. Submentum separated from mentum by distinct suture. Mentum very broad, with epilobes slightly produced beyond broad, apically emarginate medial tooth. Ligula with glossal sclerite broad and convexly rounded at apex with two large setae. Paraglossae very long and free with cristate microspicules, especially laterally and near apex. Labial palpi short and broad, palpomere 2 with two large medial setae and 2–3 small apical setae, palpomere 3 with small scattered setae. Maxillae with lacinia large and with a thick, curved apical digitus plus a medial field of large spines with scattered finer setae. Cardo distinctly developed, stipes with two large setae, one apical one basal. Palpifer simple, maxillary palpi fusiform but broad; palpomere 1 broad with a few small setae at apex, palpomere 3 very short relative to palpomere 4 and with several small setae at its apex, palpomere 4 expanded at tip with scattered small setae, 2–3 lateral setae larger. Galea with two small terminal setae. Mandibles with retinaculum discrete, premolar and molar teeth small.

Thorax. Ventral thoracic segments impunctate and moderately shiny, microsculpture faint mesh. Pronotum broad, lateral margins straight before hind angles, apical margin straight, front angles very slightly produced, basal margin straight, inner basal foveae present, broadly impressed, outer basal foveae shallow round depressions. Prosternal process apically margined. Metepisternum quadrate. Flight wings small scales. Elytra broad, depressed, oblong-ovate, humeri angulate, equal to width of pronotal base, striae deep, smooth (Fig. 6); stria 1 continuous with parascutellar stria, basal section of stria 1 absent, elytral intervals slightly convex; each elytron with a single setigerous dorsal puncture in apical half of third interval; second and third intervals of approximately equal width. Legs of moderate length; metacoxal anterior sulcus divergent, and arcuately ended medially in coxa, coxae each with two large setae; pro and meso-trochanters each with a single large seta, metatrochanter apically rounded without setae; femora slender, setation as follows: profemora—anterior face, 1 apical, 1 medial; dorsal face, 1 apical and 2 subapical; posterior face, 1 apical, 1 medial and 1 basal; mesofemora—anterior face, 1 apical, 1 medial and 1 basal; dorsal face with row of 4 setae, 2–4 apical; posterior face, 0–2 setae and occasional scattered setae laterally; metafemora—anterior face, 1 apical, 1 medial; dorsal face with row of 2–4 setae; posterior face glabrous. Tibiae slender; protibia with a row of 3–4 fine setae on medial face and a row of 3–5 coarser setae laterally, two clip setae, anterior brush of fine setae ends at enlarged medial seta; meso- and metatibiae with four rows of prominent setae, medial row very fine, others much stouter. Male protarsomeres expanded, first to third with articulo-setae ventrally (Stork, 1980). Four basal protarsomeres of female and four basal meso- and metatarsomeres in both sexes with two, more or less distinctly defined rows of ventral setae and numerous scattered setae, most scattered setae smaller than the row setae. Fifth tarsomere with two pairs of fine ventral setae, apical nearly twice length of subapical. Tarsal claws smooth.

Abdomen. Sterna moderately shiny, microsculpture obscure. Transverse sulcus of sterna V–VII present and entire. Male genitalia simple, endophallus minutely spinose and scrotiform. Median lobe of aedeagus straight, smooth. Female reproductive tract with spermatheca not discrete from duct, duct broad. Gonocoxite-1 with 3 small ensiform setae near apex, gonocoxite-2 arcuate and laterally excavated, apex round, 1 dorsal and 1 lateral large ensiform seta, 2 nematiform setae in elongate furrow. Paired bursal glands dorsally present.

Additional character information is provided in original description.

Notes on Life History.—The only information beyond data given for the types is on a specimen from Sará, Bolivia, collected at 450 m in November.

Material Examined.—Twelve specimens, including the type series, were examined. Nontype material from: **BOLIVIA**. La Paz: Sud. Yungas. Ocbaya [MSNM]. **Sar:** [CMNH, MNHB].

BRAZIL. Chapada [CMNH].

PARAGUAY. Central: [MHNP].

UNKNOWN: [MSNM].

Genus *Abaris* Dejean, 1831

Abaris Dejean, 1831:780. TYPE SPECIES (by monotypy): *Abaris aenea* Dejean, 1831:781. Dejean and Boisduval, 1832:211. Laporte, 1840:118. Chaudoir, 1852:76–77. Chenu, 1851:161. Lacordaire, 1854:347. Bates, 1871:218–220. Bates, 1882:85. Csiki, 1930:576. Straneo, 1939:38. Blackwelder, 1944:35. Reichardt, 1977:409. Straneo, 1977:111,115. Straneo, 1979:350,352. Bousquet, 1984:384–389. Bousquet and Laroche, 1993:165. Bousquet and Lieberr, 1994:435–441. Lorenz, 1998:243. Bousquet, 1999:48–51. Ball and Bousquet, 2001:85.

Abarys Agassiz, 1846:1 (unjustified emendation). Gemminger and Harold, 1868:366. Chaudoir, 1873:96. Tschitschrine, 1898:83.

Abaridius Chaudoir, 1873:97. Reichardt, 1977:409. Erwin, 1991:40. **New Synonymy**: Type species (original designation): *Abaris tachypoides* Bates, 1871:220.

Etymology.—Dejean constructed the generic name from the Greek using α , absence of, and $\beta\alpha\rho\nu\sigma$, heavy, in reference to the lightly constructed form and fleetness of foot for the included species. Dejean transcribed $\beta\alpha\rho\nu\sigma$ with $\nu = i$. Most Greek lexicons transcribe $\nu = y$, which led to the unjustified emendation of *Abaris* by Agassiz (1846) to *Abarys*. Indeed, a strict transcription of *Abaris* back to the Greek would mean “not boat shaped,” whereas *abarys* would translate to “not heavy” as described by Dejean. Nonetheless, the ICZN (1999, Art. 33.2.3) does not allow emendation of a name based on changes in character transcription.

Abarys ($\alpha\beta\alpha\rho\nu\sigma$) is a masculine word in Greek, but *Abaris* as used by Dejean is a feminine form. He did this in conjunction with the single species he named *aenea*, which is clearly feminine. Therefore, various specific epithets that have been changed to, or originally formed in the masculine must be made to agree in gender with *Abaris* as a feminine Latinized noun.

Synonymy.—Bates (1871) described five *Abaris* species. These plus *A. aequinoctialis* described by Chaudoir (1852) increased the total number of *Abaris* species to seven. Bates does not mention the presence of pectinate tarsal claws in his discussion of the characteristics of the genus, but does note the transverse sulci on the sterna of some species. Chaudoir (1873) subsequently newly defined two genera, *Abaridius* and *Pseudabarys* that included two of Bates’ species, *A. tachypoides* and *A. robustus*, respectively. The three genera were diagnosed as follows: *Abaris* species with pectinate claws and smooth sterna, *Abaridius* species with both pectinate claws and ventral sulci, and *Pseudabarys* with smooth claws and a sulcate venter. My study of these characteristics and additional characters shows that *Abaris* and *Abaridius* are congeneric. *Abaris* is distinct from *Pseudabarys*, but the latter is in need of revision and its monophyly has not been tested.

Cladistic Diagnosis.—*Abaris* is considered a monophyletic group within the larger abariform clade and is defined by the synapomorphic presence of pectinate claws (Fig. 2, Fig. 31: character 11).

Recognitory Diagnosis.—Recognized from all other Carabidae by the combination of pectinate claws, distinctly developed internal and external elytral plica (sensu Lieberr, 1986:90–91) and paired bursal glands in the female reproductive tract (Fig. 5).

Description of Adults.—In addition to characteristics of the *Neotalus* + *Abaris* clade, small to medium sized ground beetles, 4.8–8.9 mm. Nearly all individuals with an aeneous or virescent luster, sometimes brilliantly so (only *A. nigra* and some individuals of *A. bigenera* black without metallic luster). Nearly all individuals shiny or very shiny. Body ventrally piceous, rufous or ferruginous, legs and mouthparts paler than venter in most, some individuals variously infuscated.

Head. Head large, relatively broad. Frontal impressions present, deep in most species, shallowest in members of the *A. picipes*-group. Eyes very large and prominent, hemispherical, ocular ratio 1.63–

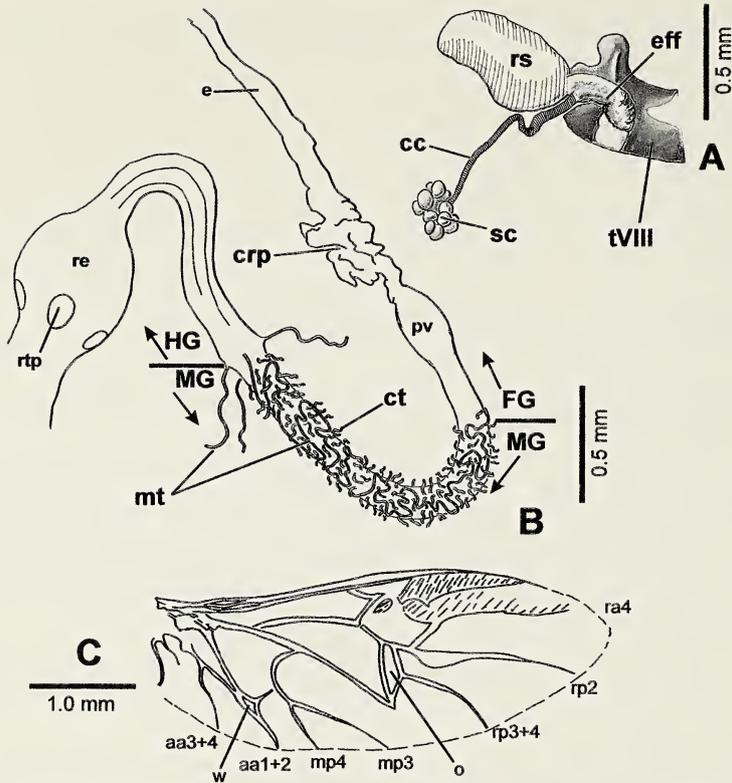


Fig. 7.—Structures of *Abaris splendidula* (LeConte). A. Pygidial gland system, ventral view of right gland. B. Extracted gut. C. Right hind wing, dorsal view. Legend: aa1+2, anterior anal vein 1+2; aa3+4, anterior anal vein 3+4; cc, collecting canal; crp, crop; ct, crypt; e, esophagus; eff, efferent duct; FG, foregut; HG, hindgut; MG, midgut; mt, Malpighian tubules; mp3, posterior medial vein 3; mp4, posterior medial vein 4; o, oblong cell; pv, proventriculus; ra4, anterior radial vein 4; re, rectum; rp2, posterior radial vein 2; rp3+4, posterior radial vein 3+4; rs, gland reservoir; rtp, rectal pad; sc, secretory cells; tVIII, tergite VIII.

1.91, most greater than 1.70, eyes least developed in *A. nobilis*. Submentum separated from mentum by well-marked suture. Mentum broad, with epilobes produced anterad medial tooth. Mentum tooth may be entire or emarginate at the apex, broad or slightly acuminate in form but not sharply pointed. Ligula with glossal sclerite broad at apex, with 2 large apical setae. Paraglossae long and free with cristate microspicules, especially near apex and medially. Labial palpi fusiform, palpomere 2 with 2 large medial setae and 2–3 small apical setae, palpomere 3 with small scattered setae. Maxillae with lacinia large and with thick, curved apical digitus and medial field of large spines. Cardo distinctly developed, stipes with 2 large setae, 1 apical 1 basal. Palpifer simple, maxillary palpi fusiform. Palpomere 1 broad with few small setae at apex, palpomere 3 very short relative to palpomere 4 and with several small setae at its apex, palpomere 4 with scattered small setae, 2 lateral setae larger in most individuals. Galea with 2 small terminal setae. Mandibles with retinaculum discrete, premolar and molar teeth small.

Thorax. Ventral thoracic segments impunctate except for a few punctures on mesepisternum in some individuals, shiny, microsculpture obsolete or faint, irregular mesh, or slightly transverse. Pronotum variously formed, lateral margins sinuate or subsinuate in most species, apical margin straight or front angles slightly produced, basal margin straight or bi-sinuate, inner basal foveae present, sharply impressed in most species, outer basal foveae quite variable among species and somewhat variable among individuals. Prosternal process apically margined. Metepisternum longer than wide. Flight wings full (Fig. 7C) in all individuals investigated. Elytra oblong-ovate, free at suture, broad across humerus and

humeri angulate in most species, slightly wider than pronotum; striae deep, smooth; stria 1 continuous with parascutellar stria; intervals convex to flat; third interval broader than other intervals in some species, notably in species of the *A. aenea*-group; each elytron with a single setigerous dorsal puncture in third interval behind middle, in contact with second stria in most individual. Legs slender and of moderate length. Metacoxal anterior sulcus appressed along anterior margin (Fig. 3B), or divergent, and arcuate/sinuate ended medially in coxa (Fig. 3A), coxae with two setae. Pro- and mesotrochanters with a single large seta, metatrochanter apically rounded or slightly pointed, without setae. Femora slender, setation various between species and individuals but in most individuals as follows: profemora—anterior face, 1 apical, 1 medial; dorsal face, 1 apical, 1 subapical; posterior face, 1 apical, 1 medial and 1 basal, presence of basal seta quite variable; mesofemora—anterior face, 1 apical, 1 basal and 2 medial; dorsal face with row of 8–16 setae, 2–4 setae apical; posterior face, 0–2 setae; meta-femora—anterior face, 1 apical, 1 medial; dorsal face with row of 3–4 setae; posterior face glabrous. Tibiae slender; protibia with row of 3–4 fine setae on medial face and row of 3–5 stouter setae laterally, 2 clip setae and anterior brush of fine setae ended at enlarged medial seta; meso- and metatibiae with four rows of prominent setae, medial row with very fine, others rows with much stouter seta. Male protarsomeres expanded, 1–3 with articulo-setae ventrally (Stork, 1980). Female protarsomeres 1–4 as well as meso- and metatarsomeres 1–4 in both sexes with two more or less well-defined rows of ventral setae and numerous, scattered setae that are mostly smaller than row setae; fifth tarsomere with two pairs of fine ventral setae, apical nearly twice length of subapical. Tarsal claws pectinate, with 4–6 small denticles on each claw (Fig. 2A).

Abdomen. Sterna in most species shiny, microsculpture in all species obscure medially, more prominent laterally. Transverse sulcus of sterna V–VI present and entire or medially absent, or completely absent. Male genitalia (Fig. 21–23) either simple, median lobe relatively straight, endophallus minutely spinose and scrotiform, or variously modified with median lobe slightly curved and endophallus with fields of large spines and sacculi. Median lobe smooth in most species, strigose in some species of the *A. picipes*-group. Female gonocoxite-1 with 0–4 small ensiform setae near apex, gonocoxite-2 arcuate and laterally excavated, apex round, 1 dorsal and 1 lateral large ensiform seta, 2 nematiform setae in elongate apical furrow (e.g., Fig. 19A). The gut of a single specimen of *A. splendidula* was dissected (Fig. 7B). Crop (crp) pouched ventrally; proventriculus (pv) with 4 compact, fibrous pads; mid-gut (MG) covered by short similarly shaped crypts (ct) and 4 Malpighian tubules (mt) intertwined along its length; hind-gut (HG) with 5 oval rectal pads (rtp). Pygidial gland reservoir (rs) simple, oval (Fig. 7A), efferent duct (eff) broad, subequal in length to reservoir. Collecting canal (cc) short, ramified 10–12 times, each ended with secretory cell (sc). Collecting canal 1 mm long approximately 2× length of efferent duct, efferent duct joined by canal just above midpoint.

Defensive chemical compounds. Methacrylic and tiglic acids, undecane, dodecane and tridecane produced by pygidial glands (Will et al., 2000, 2001).

Species Accounts

Subgenus *Abaris sensu stricto*

Cladistic Diagnosis.—All members of this clade share the synapomorphic laterally sulcate basal bulb of the aedeagal median lobe (Fig. 21B, Fig. 31: character 19).

A. striolata-group

Cladistic Diagnosis.—Individuals of this group have the tip of the aedeagus very thin, blade-like in the lateral view (Fig. 21A–B,D, Fig. 31: character 22) and the appended gland of the spermatheca (sg) elongate (Fig. 19B, Fig. 31: character 30).

(1) *Abaris napoensis*, new species Fig. 11, 18A, 19A–B, 21A–C, 24A

Type Material.—HOLOTYPE. Male, labeled: “Ecuador, Napo: Onkone Gare Camp, 00°39'10"S, 76°26'00"W, 220 m, terra firma forest, flowerfall-leaf litter; at night; 5&8.X.1995; 07-95. T.L. Erwin Ecuador Expedition 1995, G.E. Ball & D. Shepeley”, USNM. ALLOTYPE. Female, same data as holotype, USNM. PARATYPES. 2 females, same data as holotype, UASM, CMNH. 7 males, same data as holotype, UASM(4), CMNH(1), QCAZ(1), KWWC(1).

Type Locality.—As given for holotype.

Range.—Ecuador (Fig. 11).

Recognitory Diagnosis.—The prominent baso-lateral punctation of the pronotum (Fig. 24A) and form of the tip of the aedeagal median lobe (Fig. 21A–C) are distinctive. Photograph of dorsal view figure 18A.

Description.—Medium sized, overall length 6.5–6.8 mm. Very shiny, aeneous head and pronotum darker than virescent elytra. Ventral body surface, legs, mouthparts and antennae ferrugineo-testaceous; legs and abdominal sterna slightly paler than other areas.

Head. Ocular ratio 1.80–1.84. Head very shiny, reticulate microsculpture scarcely visible, frontal impressions deep, short, slightly convergent, not clearly delimited medially, clypeus shallowly depressed apically and laterally. Mentum tooth form simple, broad.

Thorax. Pronotum (Fig. 24A) sinuate laterally; basolateral region reflexed in basal third of pronotum but slightly convex near hind angles; front angles scarcely produced; apex not narrowly constricted; hind angles denticulate; lateral bead broad in basal third, then sharply narrowed to hind angles; basolateral margin not bordered; microsculpture on disc very faint, transverse mesh. Elytra with transverse microsculpture; basal section of stria 1 present; intervals 2–3 equal width, intervals flat; humeral tooth produced anterad interval 8. Mesepisternal angle produced as small rounded tubercle. Metacoxal sulcus arcuate, ended medially in coxa (in some specimens sulcus very short and so not arcuate, but still divergent from apical margin).

Abdomen. Sterna V–VI with lateral sulci. Basal bulb of male median lobe laterally sulcate (Fig. 21A–C), endophallus folding pattern visible in cleared lobe; blade smooth, sinuate; tip thin, reflexed, with broad asymmetrically expanded area. Female reproductive tract (Fig. 19B) seminal canal broad with few loose twists, receptaculum not discrete from canal, expanded base of seminal canal very large and continuous with bursa, appended gland elongate; gonocoxite-1 with 3 apicolateral ensiform setae.

Etymology.—Specific epithet is Latinized adjective based the type region.

(2)*Abaris striolata* Bates, 1871

Fig. 16, 21D–E, 24B

Abaris striolata Bates, 1871:220.

Type Material.—LECTOTYPE (here designated). Male, labeled: “Ega” [handwritten]; “*Abaris striolata* type, Bates” [handwritten]; “Ex Musaeo H.W. Bates, 1892”, MHNP.

Type Locality.—Brazil, Tefé [Ega]. From original description.

Range.—Brazil, Peru (Fig. 16).

Recognitory Diagnosis.—Individuals small, with the pronotal base smooth in most individuals, outer basal foveae shallow, and baso-lateral region reflexed. Best separated from other species by the characteristic pronotum (Fig. 24B) and character combinations in the key.

Description.—Small sized, overall length 5.3–6.2 mm. Elytra cupreous, head and pronotum black with slight metallic reflection. Ventral body surface, mandibles and labrum piceous; legs, palpi and antennae ferruginous to brunneous.

Head. Ocular ratio 1.71–1.90. Mentum tooth emarginate at apex. Microsculpture of head obsolete; frontal impressions short, deep, parallel.

Thorax. Pronotal basolateral region convex, apex broad, front angles not produced, hind angles denticulate, lateral bead narrow, basolateral margin not bordered (Fig. 24B); microsculpture on disc transverse. Microsculpture of elytra transverse, basal section of stria 1 present, elytral humeral tooth anterad interval 8; intervals flat on disc, more convex laterally, intervals 2–3 of equal width. Metacoxal sulcus arcuate, ended medially in coxa. Mesepisternal angle produced as small sharp tubercle.

Abdomen. Abdominal sulci present laterally on sterna V–VI. Basal bulb of male median lobe laterally sulcate; endophallus folding pattern visible; tip thin in lateral profile, asymmetrical in dorsal/ventral views (Fig. 21D–E). Female tract with seminal canal broad, straight; receptaculum not discrete from canal; spermatheca without basal bulb, expanded base of seminal canal large and continuous with bursa; appended gland elongate; gonocoxite-1 with 2 apicolateral ensiform setae.

Notes on Life History.—Adults have been collected in July and September—

November at elevations of 290–840 m. A single specimen was collected at mercury vapor light and one at a “Fig fall.” Other notes include collections in subtropical moist forest, leaf litter in a dry stream or simply “on ground.”

Material Examined.—In addition to type, 12 specimens. **PERU. Cusco:** Quincemil [MCZC]. **Junín:** San Beni Valley 8 km E Satipo [SEMC]. **Madre de Dios:** Río Tambopata Reserve, 30 km (air) SW of Puerto Maldonado [USNM]; Río Tambopata Reserve, 30 km (air) SW of Puerto Maldonado 12°50'S, 69°20'W [BMNH, DHK]. Tambopata Reserve, 30 km (Air) SW of Puerto Maldonado, main trail -tf, 12°50'S, 69°20'W [USNM].

A. aenea-group

Cladistic Diagnosis.—All members of this clade have the lateral area in the basal third of the pronotum reflexed and flat laterad the outer basal foveae (Fig. 31: character 13). A similar condition is known in species of *Prosopogmus* and other Carabidae. These other occurrences of this condition are considered analogous.

(3)*Abaris robustula* Tschitschérine, 1898 Fig. 15, 21F–G, 24C

Abaris robustulus Tschitschérine, 1898:83.

Type Material.—HOLOTYPE. Female, labeled: “Mih'om” [questionable interpretation of handwriting], “*Abarys robustulus* m. typ. Tschitscherin det” [handwritten name on printed determination label], “Coll. Mus. Vindob, TYPUS” [red paper], NMW.

Type Locality.—Brazil, as given in original description.

Range.—Bolivia, Brazil, Peru (Fig. 15).

Recognitory Diagnosis.—Pronotum distinctive with outer basal foveae absent and a nearly flat, reflexed area along the margin (Fig. 24C). Very similar in general facies to *A. striolata* but male median lobe is straighter and thicker at the tip (compare Fig. 21D–E to Fig. 21F–G).

Description.—Small sized, overall length 6.4–6.9 mm. Black with aeneous luster, less pronounced on head and pronotum. Ventral body surface, mandibles and labrum piceous; legs, palpi and antennae paler brunneous.

Head. Ocular ratio 1.62–1.88. Mentum tooth shallowly emarginate at apex. Microsculpture of head faint, nearly effaced on disc, reticulate, micropunctulae present in some individuals (visible at 25×). Frontal impressions short, shallow, not clearly delimited medially.

Thorax. Pronotal (Fig. 24C) basolateral region reflexed, apex broad, front angles produced, hind angles denticulate, lateral bead narrow, margin sinuate to base, basolateral margin not bordered, outer basal foveae absent, inner punctiform; microsculpture on disc transverse, faint and shiny. Microsculpture of elytra transverse; basal section of stria 1 present, intervals 2–3 of equal width, intervals flat to slightly convex; elytral humeral tooth anterad interval 8. Metacoxal sulcus arcuate.

Abdomen. Shallowly sulcate laterally on sterna V–VI. Basal bulb of male median lobe laterally sulcate, median lobe with subapical expansion visible in dorsal view (Fig. 21F–G); endophallus folding pattern visible. Female reproductive tract with seminal canal narrow with many tight twists, receptaculum distinct, spermatheca without basal bulb, appended gland spherical; gonocoxite-1 with 2–3 apicolateral ensiform setae.

Notes on Life History.—Collected in September, October and November at elevations of 400–750 m. The Pakitza specimen was collected in the leaf litter in a dry, stony stream and the Bolivia specimen was taken at mercury vapor light.

Material Examined.—In addition to type, 4 specimens. **BRAZIL.** unknown [NMW].

PERU. Madre de Dios: Pakitza, Zone-3, 12°07'S, 70°58'W; In leaf litter of stony dry stream, Trail Castanal [USMN]. **Cuzco:** Quincemil, Peña.[MCZC].

BOLIVIA. Santa Cruz: Ichilo Province, Buena Vista [CMNH].

(4)*Abaris aenea* Dejean, 1831
Fig. 5, 8, 14, 18C, 21H–I, 24D–E

Abaris aenea Dejean, 1831:781.

Type Material.—LECTOTYPE, (here designated). Male, labeled: “♂” [drawn on green paper]; “aenea. mihi, Carthagenæ” [handwritten on green paper]; “ex Museo, Chaudoir” [red ink], MHNP.

Abaris darlingtoni Straneo, 1939:38. [New Synonymy].

Type Material.—HOLOTYPE. Male, labeled: “Barro Colorado, Canal Zone, May 17 1929, Darlington; 23393, MCZC. Type, darlingtoni” [red paper]; “Holotype” [red paper]; “Abaris darlingtoni, Holotypus n.sp., det. ing. Straneo; ADP. 03439; ♀ winged”; MCZC. ALLOTYPE. Female labeled: “Barro Colorado, V.18.26, C.Z. Van Tyne” [handwritten]; Allotype [red paper], “77” [red], “Darlingtoni Straneo”, MSNM.

Type Locality.—Cartagena, Bolivar, Colombia.

Range.—Colombia, Ecuador, Panama, Peru, Venezuela (Fig.14).

Recognitory Diagnosis.—Small and very shiny. Similar to *A. erwini* but distinguished by the obsolete microsculpture of the head and pronotum. Habitus figure 18C.

Description.—Small sized, overall length 5.0–6.0 mm. Bronze or virescent, head and often pronotum darker and greener than elytra. Ventral body surface brunneous, legs and mouthparts paler rufous or ferrugino-testaceous.

Head. Ocular ratio 1.71–1.83. Clypeus medially tumescent, apically and laterally depressed and finely strigate or rugose in region near hind setigerous puncture, frontal impressions parallel. Microsculpture absent except as faint mesh on depressed portion of clypeus; scattered micropunctulae on dorsum. Mentum tooth slightly emarginate at apex.

Thorax. Pronotum (Fig. 24D–E) flat and reflexed in basolateral region, apex broad, front angles slightly produced, margins subsinuate to base and broadly reflexed in basal half; lateral bead of uniform width throughout, irregularly punctulate-rugose in basal quarter. Some specimens with faint rugosities and punctulae along lateral margin (Fig. 24E) (This is constant and more developed in specimens from Ecuador, only slightly punctate in specimens from Peru and mixed in specimens from Panama. In all specimens pronotum is smoother than in *A. notiophiloides*, though approaching the condition in that species in Ecuadorian populations). Hind angles slightly denticulate. Elytral microsculpture transverse; basal section of stria 1 absent, intervals slightly convex, interval 3 width 1.2–1.57× interval 2 (see synonymy below). Metepisternal angle produced as small round tubercle. Metacoxal anterior sulcus arcuate, ended medially in coxa.

Abdomen. Sterna without sulci. Basal bulb of male median lobe laterally sulcate, endophallus structure visible in repose as a darker medial area in cleared lobe (Attempts to evert endophallus only succeeded to expose it half way. From this, it appears to be scrotiform, uniformly covered with spines, without sacculi.) Female tract with seminal canal long and narrow, with numerous tight twists, receptaculum distinct, appended gland spherical; gonocoxite-1 with 1–2 apicolateral ensiform setae.

Chemical data. Defensive chemicals secreted from the pygidial glands are methacrylic and tiglic acids, undecane, dodecane and tridecane (Will et al., 2000, 2001).

Notes on Life History.—Adults have been collected in all months of the year except April and September, most commonly at 150–200 m elevation. Specimens have been collected mostly at night and in thin, relatively dry leaf litter. Several Ecuadorian specimens were collected in primary tropical forest on a well-drained ridge in red clay soil by raking leaf litter and scraping the humus and root layer beneath ferns at night. Although rotten *Ficus* fruits were found nearby—and in association with the fruit a species of *Pseudabarys* Chaudoir and several species of Harpalini—*A. aenea* was not found to be associated with the fruit. Specimens have been collected in leaf litter and at flower falls both during the day and night at several sites. A few specimens have been taken at ultraviolet or white lights.

Synonymy.—Straneo (1939) described *A. darlingtoni* from Barro Colorado Is., Panama. Given the small amount of material at his disposal, Straneo determined

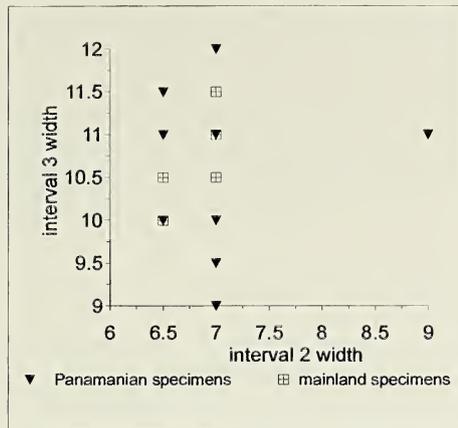


Fig. 8.—Graph of width ratio of elytral intervals for specimens of *Abaris aenea* Dejean. Average ratio of interval 3 (Y axis)/2(X axis). Units on axes in ticks of ocular reticle. Standard deviation and number of individuals measured: “darlingtoni” Panamanian form, 1.57 ± 0.04 , $n = 12$; Columbia, 1.45 ± 0.31 , $n = 6$; Venezuela, 1.47 ± 0.27 , $n = 3$; Ecuador, 1.50 ± 0.13 , $n = 4$.

that specimens with a relatively wider third elytral interval, as compared to *A. aenea*, combined with a lack of lateral pronotal punctures, as in *A. notiophiloides*, belonged to a distinct species. Based on the larger amount material I have at hand, it is clear that interval width variation is not a sufficient character for species recognition in this complex.

Individuals were measured for the ratio of interval 3/interval 2 from all collecting sites, representing both South American *A. aenea* and the Panamanian “*darlingtoni*” form (Fig. 8). No discrete difference can be seen when all data are compared. Individuals from the island population are very similar to each other, but are within the variation seen in the Venezuelan, Ecuadorian and Colombian populations. Similarly, all other characteristics show no difference among populations of *A. aenea* that are not subsumed by variation between individuals. Likewise, the Panamanian “*darlingtoni*” form is not distinguishable from South American specimens of *A. aenea*.

Material Examined.—133 specimens. **COLOMBIA**: [IZWP]; Cartagena [BMNH, MHNP]; Río Frío, Magdalena [MCZC].

ECUADOR. Napo: Onkone Gare Camp, $0^{\circ}39'10''S$, $76^{\circ}26'0''W$ [UASM]; Limoncocha [UASM]; Yasuni Scientific Station, $00^{\circ}40'36''S$, $76^{\circ}24'02''W$ [KWWC, CUIC].

PANAMA. Canal Zone: Barro Colorado Island [CMNH, MCZC], $9^{\circ}9'15''N$, $79^{\circ}15'0''W$, [USNM]; Chepo, Altos de Maje [STOC].

PERU. Madre de Dios: Río Tambopata Reserve, 30 km (air) SW Pto., Maldonado, $12^{\circ}50'S$, $06^{\circ}20'W$ [BMNH]; Río, Tambopata Reserve, 30 km, (air) SW of Puerto Maldonado, $12^{\circ}50'S$, $69^{\circ}20'W$ [DHK].

VENEZUELA. [MHNP]; San Esteban [MHNP].

(5)*Abaris erwini*, new species

Fig. 11, 18B, 21J–M, 24F

Type Material.—HOLOTYPE. Male, labeled: “Peru: MADRE DE DIOS, Pakitza, Zone 02, 9&12 Feb90 T L Erwin, $70^{\circ}58'W$ $12^{\circ}07'S$; Under leaves and, fallen fruit, Tr. Aguajal 107; BIOLAT,COLE, 000007170”, USNM. ALLOTYPE. Female with same data except last label, “BIOLAT,COLE, 000007153”, USNM. PARATYPES. 5 males with the same data as the Holotype except the following labels; BIOLAT,COLE, 000007156; BIOLAT,COLE, 000007152; BIOLAT,COLE, 000007154; BIOL-

AT,COLE. 000007155; BIOLAT,COLE, 000002472, USNM, and 5 females with the same data as the holotype except the following labels; BIOLAT,COLE, 000007157; BIOLAT,COLE, 000007169; BIOLAT,COLE, 000007164; BIOLAT,COLE, 000007156; BIOLAT,COLE, 000007154, USNM. Female, Chambireyacu, pres Yurimaguas, (Huallaga-Pérou), M. de Mathan, Juin-Août 1885, MHNP. Female, Peru, Madre de Dios, Río Tambopata Res., 30 km (air) sw Pto., Maldonado, 12°50'S 069°20'W; B.M.1983.455, N.E. Stork, 3.x.-15.xi.1983, on ground, BMNH. Male, Peru: Tambopata Prov., Madre de Dios Dplo.15 km NE Puerto; Maldonado, Reserva, Cuzco Amazónica, 12°33'S, 69°03'W, 200 m, Plot #Z1E9; 17 June 1989, J.S Ashe, R.A.Leschen #136, ex. Flight intercept trap, SEMC. Male, Peru, Junín San Ramón de Pangoa 40 km SE Satipo, Schuh, R.T.& J.C., 7 June 1972, Soils-litter layer in primary forest, AMNH.

Type Locality.—As given for holotype.

Range.—Peru, Bolivia (Fig. 11).

Recognitory Diagnosis.—Small and shiny, somewhat variable species, separated from *A. aenea* by the more evident microsculpture on the head and generally less punctate pronotum. Separated from other similar species by characters in the key. Photograph of dorsal view figure 18B.

Description.—Small sized, overall length 5.3–5.9 mm. Shiny, aeneous, head and pronotum darker, virescent. Ventral body surface, labrum and mandibles dark brunneous; legs either brunneous or slightly paler than venter of body; tibiae, tarsi palpi and distal antennomeres paler.

Head. Ocular Ratio 1.73–1.78. Frontal impressions short, parallel, shallow, sharply delimited externally. Mentum tooth slightly emarginate at apex. Microsculpture of head very faint, reticulate.

Thorax. Pronotal basolateral region slightly convex though obscured in some individuals by punctures; apex broad, front angles little produced, margins subsinuate; hind angles not denticulate, lateral bead uniform thickness throughout or narrowed in apical quarter, basolateral margin not bordered; microsculpture transverse, very faint, shiny. Elytral microsculpture transverse; basal section of stria 1 absent, intervals flat, interval 3 width 1.1–1.4× interval 2, mesepisternal angle produced as low flat tubercle; elytral humeral tooth anterad interval 8. Metacoxal sulcus arcuate, ended medially in coxa.

Abdomen. Sterna without sulci. Male aedeagus (Fig. 21J–M) with basal bulb of median lobe laterally sulcate (Fig. 21J, bs); endophallus folding pattern visible in cleared lobe (I attempted to evert the endophallus of several specimens but the internal sac only everted half way. A basal right sacculus covered in medium length spines was apparent on everted portion); median lobe blade smooth. Female tract with seminal canal thin with many tight twists, receptaculum distinct, appended gland spherical; gonocoxite-1 with 3 apicolateral ensiform setae.

Variation.—In regard to pronotal form, this species is rather variable and may prove to be a complex of species rather than one polymorphic species.

Notes on Life History.—Adults have been collected in January, February, June, July and September–November at elevations of 200–750 m. Specimens were collected in leaf litter and in areas with fallen rotten fruits, such as *Ficus* fruits.

Material Examined.—29 specimens examined, including types. **BOLIVIA**. Chapare [MSNM].

PERU. **Huallaga**: Yurimaguas, Chamireyacu [MHNP]. **Junín**: San Ramón de Pangoa 40 km SE Satipo [AMNH]. **Madre de Dios**: Pakitza, 12°7'0"S, 70°0'0"W [USNM]; Pakitza, Río Manu, BIOLAT Sta. 11°56'47"S, 71°17'0"W [USNM]; Pakitza, Zone 04, 12°7'0"S, 70°0'0"W [USNM]; Río Tambopata Reserve, 30 km (air) SW of Puerto Maldonado, 12°50'0"S, 69°20'0"W [CASC]; Río Tambopata Reserve, Explorer's Inn 12°50'0"S, 69°17'0"W [USNM].

Etymology.—Eponym based on the surname of the collector and carabidologist Terry L. Erwin.

(6)*Abaris aquilonaria*, new species

Fig. 12A, 20A, 21N–O, 24G

Type Material.—HOLOTYPE. Female, labeled: "Mexico, Chiapas, 3200'. 11.6 mi. N Ocozocuautila, vi.10–13.1966; George E. Ball, D.R.Whitehead collectors", USNM. ALLOTYPE. Male, labeled: "Coyame, Lake Catemaco, Veracruz, Mexico, 10–18.VII.63-Black lts. D.R.Whitehead", USNM. PARATYPES. Female, label data same as holotype, UASM. Female, labeled: "Mexico, Chiapas 11.6 mi.N Ocozocuautila, 3200', May 25 & June 20 '72, A.Meyer, G.E.& K.E. Ball, Collectors", UASM. Male, same label data as allotype, KWWC. Male, genitalia dissected, labeled: "Mexico, Chiapas,

Parque Laguna Belgica 19 km N.Ocozocoautla, 2 June 1991, 970 m, J.S.Ashe Coll#46, ex; flight intercept trap", SEMC.

Type Locality.—As given for holotype.

Range.—Costa Rica, Honduras, Mexico (Fig. 12A).

Recognitory Diagnosis.—Similar to *A. aenea* but the presence of visible microsculpture on the pronotum and the lack of punctation along the base immediately distinguishes *A. aquilonaria*.

Description.—Small sized, overall length 5.4–6.1 mm. Shiny, aeneous, with head and pronotum slightly darker. Ventral body surface dark brunneous; legs, antennae and mouthparts paler brunneous to ferrugino-testaceous.

Head. Ocular ratio 1.74–1.85. Mentum tooth slightly emarginate at apex, microsculpture of head faint, reticulate. Frontal impressions short, deep, not clearly delimited medially. Clypeus smooth or with a few shallow lines.

Thorax. Pronotum (Fig. 24G) with obvious, slightly transverse mesh microsculpture; region laterad of basal foveae flat and reflexed, apex broad, front angles not produced, hind angles denticulate, lateral beads uniform or slightly narrower at hind angles, lateral margins sinuate to base. Metacoxal sulcus arcuate, ended medially in coxa. Basal section of elytral stria 1 absent; intervals slightly convex. Elytra with interval 3 width 1.5–2.1× interval 2, humeral tooth anterad interval 8; microsculpture transverse.

Abdomen. Sterna without sulci. Basal bulb of male median lobe laterally sulcate, blade smooth (Fig. 21N). Female reproductive tract (Fig. 20A) with seminal canal long, narrow with a few (4–5) tight twists, receptaculum distinct, appended gland (sg) spherical; gonocoxite-1 with 2 apicolateral ensiform setae.

Notes on Life History.—Adults collected in May–July at elevations of 700–970 m. Collections have been made using flight intercept traps and ultraviolet lights.

Material Examined.—6 specimens in addition to types. **COSTA RICA. Guanacaste:** Guanacaste Conservation Area, Martínez Biological Station [CASC]. This specimen was not included in the type series as it differs in color (bright green) and the pronotum has longer straight sections in front of the hind angles. However, no other differences could be found in the external characteristics or the median lobe of the aedeagus. Additional material of *A. aquilonaria* will either show population level variation that includes this form, or the necessity of describing a new species.

HONDURAS. San Juan Pueblo [USNM]. This specimen is all black, much duller, and the pronotum is somewhat flatter without the sharp denticles of the hind angles of the pronotum found in the typical *A. aquilonaria*. Unfortunately, genitalia of this male specimen are lost. In general form it is quite similar to typical specimens but, like the Costa Rican form, may represent another species. Again, additional material is needed. [USNM].

MEXICO. Chiapas: 11.6 mi. N Ocozocoautla. **Veracruz:** Coyame, Lake Catemaco [UASM, teneral and damaged specimens not included in type series]

Etymology.—Latin adjective *aquilonaris* (northern). This refers to the fact that this species ranges farther north than any other *A. aenea*-group species.

(7)*Abaris notiophiloides* Bates, 1871

Fig. 11, 19C, 21P–Q, 24H

Abaris notiophiloides Bates, 1871:220. *Abarys notiophiloides* (Chaudoir, 1873:98).

Type Material.—LECTOTYPE (here designated). Female: Labeled: "Ega" [Handwritten]; "Ex. Museo H.W.Bates, 1882", "Abaris notiophiloides Bates type" [Handwritten]; "Lectotype Abaris notiophiloides Bates, K.W.Will 1997" [red paper label], MHNP.

Type Locality.—Brazil, Tefé [Ega], from original description.

Range.—Brazil (Fig. 11).

Recognitory Diagnosis.—Immediately recognizable by the greatly widened elytral interval 3 in combination with the punctate pronotal margins.

Description.—Small sized, overall length 4.8–5.1 mm. Brunneous with a cupreous luster, head and

pronotum in most individuals, some with only head, slightly darker. Ventral body surface somewhat paler; legs, palpi and antennae paler.

Head. Ocular ratio 1.79–1.86. Mentum tooth shallowly emarginate at apex. Microsculpture of head reticulate, frontal impressions short, divergent, not clearly delimited medially.

Thorax. Pronotal (Fig. 24H) basolateral region flat and reflexed, apex broad, front angles not produced, punctate along margin anterior to outer foveae; margins sinuate, hind angles denticulate, lateral bead narrow and of uniform thickness, basolateral margin not bordered; microsculpture transverse on disc, more irregular at base and near foveae. Elytra with basal section of stria 1 absent, intervals moderately convex, flatter dorsally, interval 3 width 2× width of interval 2, elytral humeral tooth anterad interval 8; microsculpture transverse, faint. Mesepisternal angle produced as small flat tubercle. Metacoxal sulcus arcuate, ended medially in coxa.

Abdomen. Sterna without sulci. Basal bulb of male median lobe laterally sulcate, endophallus folding pattern visible, blade smooth (Fig. 21 P–Q). Female reproductive tract (Fig. 19C) with seminal canal short, broad, straight, receptaculum not discrete from seminal canal, without basal bulb, fibrous region at base of spermatheca, appended gland spherical, gonocoxite-1 with 2 apicolateral ensiform setae.

Notes on Life History.—Found together with *Pseudabarys robustus* (Bates) (Bates, 1871:220).

Material Examined.—Including types, 12 specimens examined. **BRAZIL.** Chapada [MSNM]; Ega [MHNP]; Itaituba, Amazonas (Hahnel) [MHNP]; Santarém [CMNH]; Unknown; [MHNP].

A. picipes-group

Cladistic Diagnosis.—Members of this clade have either faint or obsolete transverse microsculpture on the pronotal disc and the region near the basal foveae (Fig. 31: characters 16, 17). This clade includes some of the most widespread and variable species in the genus. Although the general form and internal structures of the male genitalia are similar among all species in the clade, it is not possible to define any non-homoplasious synapomorphies of the male genitalia that characterize the clade at the level of the species-group. Within the group, strigose ventral surface of the median lobe (character 21) found in *A. mina*, *A. picipes*, and *A. basistriata* is a synapomorphy for those species. The median lobe of *A. metallica* is not known, but is predicted to be strigose as well (Fig. 31).

(8)*Abaris impunctata*, new species

Fig. 15, 21R–S, 24I

Type Material.—HOLOTYPE. Male, labeled: “Brazil, Santa Catarina, Nova Teutonia, 27°11'0"S, 52°23'0"W, 300–500 m, FPlaumann”, MCZC.

Type Locality.—As given for holotype.

Range.—Brazil (Fig. 15).

Recognitory Diagnosis.—Recognizable, dark species with dull surface from reticulate and somewhat granulate microsculpture and impunctate pronotal base (Fig. 24I).

Description.—Medium sized, overall length 7.0 mm. Black with a slight aeneous luster. Ventral body surface, legs and mouthparts brunneo-piceous.

Head. Ocular ratio 1.67. Mentum tooth form simple. Microsculpture of head reticulate; frontal impressions short, punctiform.

Thorax. Pronotal basolateral region convex, apex broad, front angles very slightly produced, hind angles minutely denticulate; lateral bead of uniform width through most of its length narrowed just before hind angles; basolateral margin not bordered (Fig. 24I); microsculpture reticulate and surface dull. Microsculpture of elytra obvious, reticulate; basal section of stria 1 present, intervals flat, intervals 2–3 equal width, mesepisternal angle produced as small flat tubercle; humeral tooth anterad interval 8. Metacoxal sulcus arcuate, ended medially in coxa.

Abdomen. Sterna V–VI shallowly sulcate laterally, deeper on VI where it is oblique to base of

sternum. Male median lobe (Fig. 21R–S) basal bulb laterally sulcate, endophallus folding pattern visible in cleared median lobe, blade smooth, tip symmetrical. Female genitalia and reproductive tract not studied.

Etymology.—Specific epithet is a Latin adjective referring to the lack of obvious punctures along the base of the pronotum.

(9)*Abaris bigenera* Bates, 1882

Fig. 12B, 19D, 22A–D, 25A

Abaris bigenera Bates, 1882:86. Larval description by Bousquet and Liebherr (1994).

Type Material.—LECTOTYPE, (here designated). Male, labeled: “Oaxaca, Mexico. Hoege”, BMNH.

Type Locality.—Mexico, Oaxaca, from original description.

Range.—Guatemala, Honduras, Mexico (Fig. 12B).

Recognitory Diagnosis.—One of the most common Mexican species. Easily separated from the other common Mexican species, *A. aequinoctialis*, by the larger size and more somber color. Relatively large and dark species, frontal impressions effaced, rather variable but recognizable using characters in the key.

Description.—Variable in size but most relatively large sized, overall length 6.4–7.9 mm. Dark, moderately shiny, metallic luster faint, cupreous in most individuals, but striking blue or green in a few individuals; head and pronotum concolorous with elytra in most, darker in some individuals. Ventral body surface brunneous; legs, mouthparts and antennae slightly paler but infuscated in some individuals, especially mandibles, antennae and femora.

Head. Ocular ratio 1.68–1.80. Mentum tooth shallowly emarginate at apex. Microsculpture of head reticulate; frontal impressions short, shallow and convergent or effaced.

Thorax. Pronotal margins smoothly arcuate or subsinuate to hind angles that are either minutely denticulate or not; apex wide, front angles slightly produced, lateral bead narrow and uniform throughout its length, basal margin not bordered, basolateral region slightly convex; microsculpture reticulate, surface dull. Basal section of elytral stria 1 present, intervals flat, intervals 2–3 of equal width, elytral humeral tooth anterad interval 8; microsculpture transverse; surface moderately shiny. Metacoxal sulcus arcuate, ended medially in coxa. Mesepisternal angle very small, produced as low round tubercle.

Abdomen. Abdominal sulci present laterally on sterna V–VI. Median lobe basal bulb laterally sulcate, endophallus (Fig. 22C–D) with ventral field (vs) of large spines and left and right basal-lateral sacculi (lls, rls), right sacculus recurved, partially spine covered with its position corresponding to spined ridge in *A. basistriata*; median lobe (Fig. 22A) ventrally smooth, lobe tip asymmetrically produced to right (Fig. 22B). Female reproductive tract (Fig. 19D) with seminal canal narrow with many tight twists, receptaculum distinct, appended gland (sg) spherical, gonocoxite-1 with 2, 3 or 4 apicolateral ensiform setae.

Notes on Life History.—Adult specimens have been collected in April–September at elevations of 200–1680 m. When habitat was noted, most specimens were collected in the leaf litter of relatively dry oak-pine forest, e.g., “oak-pine zone, *Alnus* near stream in litter.” Specimens were also collected in oak forest, wet oak-pine forest and montane tropical forest. Other habitat associations include coffee finca, crustose fungi and crustose fungi on logs or under logs and gilled mushrooms. In addition to collecting from leaf litter, pan traps were reported as a collection method for some specimens.

Material Examined.—Including type, 223 specimens. **GUATEMALA**. Baja Verapaz, 7.6 km W Chilacó [SEMC]; Baja Verapaz, 1.6 km S Pantin 15°16'0"N, 90°14'0"W [USNM]; Baja Verapaz, 8 km S Purulhá [UASM]; El Quiché, 7.3 m S Chichicastenango 14°54'0"N, 91°7'0"W [USNM]; S Geronimo [MHNP]; Sacatepequez Florencia [UVGC]; El Progreso 21 km NE San Agustíne Acaguastlán [UASM]; Zacapa Dept., San Lorenzo [CNC]; Sierra de las Minas [CNC].

HONDURAS. Los Piños, 14°32'0"N, 87°53'0"W [UASM]; Ocotepeque 12.7 km E & 10.6 km S Ocotepeque lower slopes El Pital, 14°25'0"N, 89°4'0"W [SEMC]. **Morazán**: Francisco 21.3 km N Tegucigalpa, la Tigra, 12°14'0"N, 86°6'0"W [SEMC].

MEXICO. Chiapas: 6 km SE Tolimen [UASM]; 18.7 km W Rizo de Oro, Chiapas/Oaxaca border [UASM]; 3.1 mi. N Pueblo Nuevo [UASM]; 3.1 mi. N Pueblo Nuevo, Rte195 [UASM]; 8.6 mi. E San Cristobal, rte 190 [UASM]; El Rincón [CNC]; Lagos de Monte Bello National Park [UASM]; Municipio de Ocosingo 2nd ridge NE of Las Margaritas above La Soledad [CASC]. **Guerrero:** 12.1 mi. W Chilpancingo [UASM]; 13.9 mi. W Chilpancingo [UASM]; 143.1 km NE Atoyac de Alvarez [UASM]; 2 km SW Yerba Santa 39 km S Filo de Caballo [CMNH]; 52.9 km NE Atoyac de Alvarez [UASM]; 78.5 km N junction Rt200 on rt134 to Ciudad Altamirano [UASM]; B. Vista de Cuellar, "El Pochote" [UASM]; Omiltemi [MHNP, UASM]. **Jalisco:** 10.8 mi. S Talpa de Allende [UASM]; 12.4 mi. S Tecalitan [UASM]; 21.4 mi. S Tecalitan [UASM]; 42.4 km NW Cuatla [UASM]; 5.5 mi. NW Cuatla [UASM]; 7 km S Tequila rd to Microondas [UASM]; 8.8 km NW Cuatla [UASM]; 9.6 km S Tequila on rd to Microondas [UASM]; El Ricon 30.5 mi. NW Los Volcanes [UASM]; Mexico, 2.7 km NE Temascaltepec, rte130 [UASM]. **Michoacan:** 97.7 km W Apatzingán on road to Dos Aguas [UASM]. **Oaxaca:** 11.4 mi. E Sta. Catarina Juquila [CNC, UASM]; 12.8 mi. E Sta. Catarina Juquila [UASM]; 14.3 km E Ixtlán de Juárez [UASM]; 14.9 km N Sola de Vega [UASM]; 14 km E Mitla (road to Zacatepec) [CUIC]; 15.7 km E Rte190 road to Ojo de Agua [UASM]; 20 mi. S Juchatengo, rt131 [UASM]; 2 km W Capulalpam [UASM]; 4.9 mi. E Sta. Catarina Juquila [UASM], 6.6 mi. E Sta. Catarina Juquila [UASM], 7.3 mi. E Sta. Catarina Juquila [UASM], 11.4 mi. E Sta. Catarina Juquila [UASM], 12.8 mi. E Sta. Catarina Juquila [UASM]; Hoega [MHNP]; NW Sta. María Nizavaguiti 16°41'0"N, 95°50'0"W [UASM]; Hwy135, 23.6 km N Jct190 at Huitzo [CUIC]; Hwy175, 18.3 km S Guelatao (7.5 km N El Punto) [CNC, CUIC]; Rte131, 21.8 mi. N Juchatengo [UASM]; Queretaro, 17.8 mi. E Landa de Matamoros [UASM]; 6.4 mi. E Pinal de Amoles [UASM]. **San Luis Potosí:** 24.7 mi. S Landa de Matamoros [UASM]; 4.3–17.9 mi. E Ciudad del Maíz rte80 [UASM]. **Sinaloa:** 60.9 km E Concordia rte 40. **Veracruz:** 16.4 km S Orizaba on road to Tlaquilpan [UASM]; 2.3 km S Jalapa on rd to Coatepec [UASM].

(10)*Abaris picipes* Bates, 1871

Fig. 13, 18D, 19E, 23A–C, 25B

Abaris picipes Bates, 1871:220.

Type Material.—LECTOTYPE (here designated). Female, labeled: "Tapajos" [handwritten]; "Abaris picipes type, Bates" [handwritten]; "Ex Musaeo H.W. Bates, 1892" [printed], MHNP.

Type Locality.—Brazil, Tapajos, from original description.

Range.—Argentina, Bolivia, Brazil, Paraguay (Fig. 13).

Recognitory Diagnosis.—Very similar in general form to *A. mina* (see description of that species) but can be separated from that species by the punctate pronotal base. Photograph of dorsum figure 18D.

Description.—Small to medium sized, overall length 5.5–6.4 mm. Shiny, black with cupreous luster; less metallic on head and pronotum, head and pronotum slightly darker in most individuals. Ventral body surface brunneous to piceous; legs, mouthparts and antennae concolorous or slightly paler than ventral body surface.

Head. Ocular ratio 1.67–1.74. Mentum tooth shallowly emarginate at apex. Microsculpture of head obsolete, dorsal micropunctulae present; frontal impressions very short, shallow almost effaced.

Thorax. Pronotal (Fig. 25B) basolateral region convex, punctate in region of basal foveae (single female from Bolivia lacks punctures), apex broad, front angles produced, hind angles with or without a small denticle, lateral bead narrow and of uniform thickness, basolateral margin in some specimens with a fine engraved line in form of border at margin beneath lateral foveae; microsculpture of pronotum obsolete; very shiny. Microsculpture of elytra transverse, faint; basal section of stria 1 present, intervals flat, intervals 2–3 of equal width, humeral tooth anterad interval 8. Mesepisternal angle produced as small tubercle. Metacoxal sulcus arcuate.

Abdomen. Abdominal sulci absent in most individuals, but in some present laterally as faintly impressed, irregular lines. Median lobe (Fig. 23A–C), aedeagal basal bulb laterally sulcate, endophallus folding pattern (fp) visible as a large dark region in cleared lobe, spine patch visible in bend of median lobe; blade strigate (Fig. 23A), tip (Fig. 23B) asymmetrically produced to right. Female reproductive tract (Fig. 19E) with seminal canal broad, simple; receptaculum distinct, slightly enlarged relative to canal; appended gland (sg) spherical; gonocoxite-1 with 0–2 apicolateral ensiform setae.

Notes on Life History.—Adults have been collected in January, February, June,

October–December at elevations of 450–1000 m. Habitat associations include forested areas, in leaf litter and in a litter filled ravine.

Material Examined.—In addition to type, 65 specimens. **ARGENTINA.** Mendoza [MSNM]; Tartagal Salta, Dio San Martín [MSNM]; Tucumán [MHNP]; Jujuy Calilegua National Park, Aguas Negras [CNC]; Jujuy Calilegua National Park, Estaca El Cero [CMNC].

BOLIVIA. Santa Cruz: Alto de Chaves Ascención [MHNP]; Andrés Ibanez Potrerillo de Guenda, Terebinto 17°40'20"S, 63°27'0"W [CMNH]; Prov. Andrés Ibanez, Vallecito [CMNH]; Sará [CMNH, MSNM]; Villa Montes [UASM].

BRAZIL. Chapada [CMNH,MSNM]; Mtt. Grosso, Corumbá [MCZC]; Santarém [CMNH]; Tapajos [MHNP]; Bahia Bon "jiue-garbe" [illegible handwriting] [MHNP]; Bahia, Encruzilhada [MHNP]; Distrito Federal, 20 km E Brasilia [CNC], Goias, Cuyaba [MHNP]; Río Verde [MHNP]; Jatahy [MHNP]; Minas Gerais, Aquas Vermelhas [CMNH]; São Paulo, Teodoro Sampaio [CMNH].

PARAGUAY. [MNHB]; Dralze [MCZC]; Puerto Bertoni [MCZC]; Sa. Trinidad [MNHB]; Villarrica [MSNM,MCZC]; vic. Horqueta [MSNM, MCZC]; Boquerón Medina-cue [MCZC]; Paraguari, Parc. Nac. Ybycuí [USNM].

UNKNOWN: Molinasque [MCZC]; Salta Urundel [MHNP].

(11)*Abaris mina*, new species

Fig. 16, 23D–F, 25C

Type Material.—HOLOTYPE. Female, labeled: "Brazil, Chapada, Acc. No 2966", CMNH. ALLOTYPE. Male, same label data as holotype, CMNH. PARATYPES. Female, same data as holotype and "Oct", CMNH. Female, same data as holotype and "Aug", CMNH. Male, same data as holotype and "Sept", USNM. Male, labeled: "Brazil, Goyaz, Jatahy, Museum Paris, Ex. Coll. M. Maindron, Coll. G. Babault 1930", MHNP. Male, labeled: "Goyaz, Río Verde, Museum Paris, Ex. Coll. M. Maindron, Coll. G. Babault 1930", MHNP. 2 Females, labeled: "Brésil, Jatahy, Prov. De Goyaz, Donchier march 1903, Museum Paris, Ex. Coll. M. Maindron, Coll. G. Babault 1930", MHNP. Female, labeled: "Brazil, 20 km E. Brasilia, DF, III-4-1970,1000 m, JM& BA Campbell", CNC. Female, labeled: "Paraguay, Stapua Cantera" [handwritten], MNHP. Female, labeled: "Paraguay", MSNM. Female, labeled: "vic. Horqueta, Paraguay", MCZC. Female, labeled: "Villarrica, Paraguay, VI-1932, Zool. Mus. Berlin", MNHB. Female, labeled: "Paraguay, leg. Piebrig, Zool. Mus. Berlin", MNHB. Female, labeled: "Bolivia, Santa Cruz, Ichilo Province, Buena Vista, 400 m, R.Ward, mercury vapor light", CMNH.

Type Locality.—Brazil, Chapada.

Range.—Brazil, Bolivia, Paraguay (Fig. 16).

Recognitory Diagnosis.—Very similar in form to *A. picipes* but distinguished from that species by the smooth pronotal base.

Description.—Medium sized, overall length 6.0–6.7 mm. Shiny, black, aeneous, or virescent in some individuals. Ventral body surface, legs, mouthparts and antennae brunneous.

Head. Ocular ratio 1.67–1.74. Mentum tooth shallowly emarginate at apex. Microsculpture of head obsolete, surface shiny; frontal impressions shallow or effaced.

Thorax. Pronotal (Fig. 25C) basolateral region convex, apex broad, front angles produced, lateral margins arcuate almost to hind angles or slightly anterad base; hind angles with or without small denticle, lateral bead narrow, of uniform thickness throughout; basolateral margin without border in most, few specimens with finely engraved line in form of border along base posterad foveae; microsculpture obsolete on disc, very shiny. Microsculpture of elytra transverse; basal section of stria 1 present, elytral humeral tooth anterad interval 8. Mesepisternal angle produced as a very small round tubercle. Metacoxal sulcus arcuate.

Abdomen. Abdominal sulci present as very shallow irregular lateral lines on sterna V–VI, best developed on V. Median lobe (Fig. 23D–F) basal bulb laterally sulcate, endophallus folding (fp) pattern visible as large dark area in cleared median lobe, blade (Fig. 23D) strigate ventrally, tip (Fig. 23E) symmetrically produced. Female tract with seminal canal narrow with many tight twists, receptaculum distinct, appended gland spherical; gonocoxites-1 with 2–3 apicolateral ensiform setae.

Notes on Life History.—Adults have been collected in March, June, and August–November. Only one specimen was labeled with elevation data, a collection at 1000 m.

Material Examined.—Including types, 22 specimens. **ARGENTINA**. Unknown [MCZC].

BRAZIL. Goias, Jatahy [MHNP].

UNKNOWN: [MNHB].

Etymology.—Specific epithet is a Latin adjective that refers to the smoothness of the pronotum of this species.

(12)*Abaris basistriata* Chaudoir, 1873

Fig. 14, 18E, 22E–I, 25D

Abarys basistriatus Chaudoir, 1873:98.

Type Material.—LECTOTYPE, (here designated). Female, labeled: “ex Museo, Chaudoir” [red ink], “Brézil, Schlb-jun” [? Handwritten, not legible], “Lectotype, *Abarys basistriatus* Chd., K.W.Will 1997” [Red label], MHNP.

Type Locality.—Nova Friburgo, Brazil, from original description.

Range.—Argentina, Bolivia, Brazil, Colombia, Paraguay, Peru, Venezuela (Fig. 14).

Recognitory Diagnosis.—Similar to *A. mina* and *A. picipes* in general form but recognizable by the reticulate microsculpture on the dorsum. Photograph of dorsum figure 18E.

Description.—Medium to small sized, overall length 5.4–6.6 mm. Black with aeneous luster, only moderately shiny. Ventral body surface, legs, mouthparts and antennae brunneous.

Head. Ocular ratio 1.74–1.86. Mentum tooth emarginate at apex. Microsculpture of head reticulate; frontal impressions shallow, not clearly delimited medially.

Thorax. Pronotal (Fig. 25D) basolateral region slightly convex, apex broad, front angles produced, hind angles not denticulate; basolateral bead narrow, uniform thickness; basolateral margin not bordered, margins subsinuate or straight to base; microsculpture reticulate, surface dull. Basal section of elytral stria 1 present, (a single specimen from Río Salado, Argentina lacks the basal section of stria 1, except for a slight trace on the right elytron); mesepisternal angles produced as small sharp tubercles, elytral humeral tooth anterad interval 8; microsculpture reticulate, intervals flat, intervals 2–3 of equal width, striae fine. Metacoxal sulcus arcuate ended medially in coxa.

Abdomen. Sterna without sulci. Basal bulb of male median lobe laterally sulcate, endophallus (Fig. 22H–I) with apico-ventral field (als) of large spines extended dorsally near base, prominent ventro-medial spined row (sr), a long right lateral scale (ls) that is apically free, and a short dorso-basal scale (dbs) that is spine tipped and held appressed to tip of median lobe when endophallus is everted, median lobe ventrally strigate (Fig. 22E), lobe tip asymmetrical, produced to right. Female reproductive tract with seminal canal long, thin and with many tight twists, receptaculum distinct, appended gland spherical; gonocoxite-1 with 2–3 apicolateral ensiform setae.

Notes on Life History.—Adults have been collected in all months of the year at elevations of 100–3600 m. The two specimens from Huánuco, Peru, labeled 2500–3600 m are from a much higher elevation than known for any other *Abaris* species. It is likely that these represent a chance collection or are mislabeled specimens, as all other records for *A. basistriata* are for elevations of 1550 m or less. The only additional information is from a specimen collected using a flight intercept trap in subtropical humid forest, one marked as collected “under stones” and ten specimens collected at Mercury vapor or ultra-violet lights.

Material Examined.—In addition to type 166 specimens examined. **ARGENTINA**. Eldorado Misiones [AMNH]; Gargas [MHNP]; LaPampa (Pico) [MCZC]; Río Salado [MSNM, MHNP]; Cata-marca, S of La Viña, 28°3'0"S, 65°35'0"W [AMNH]; Salta, La Caldera, El Ucuma, 1550 m [CMNC]; San Martín, Tatagal Salt. [MSNM].

BOLIVIA. Santa Cruz: Alto de Chaves Ascención [MSNM]; Ichilo, Bueno Vista [CMNH]; Andrés Ibáñez Potrerillo de Guenda, Terebinto, 17°40'20"S, 63°27'0"W [CMNH]; Sará [CMNH, MNHB].

BRAZIL. [IZWP, MCZC]; Chapada [CMNH]; Guapi [USNM]; São Paulo Curitiba [MNHB]; Santarém [AMNH, CMNH]; Bahia, Encruzilhada [MHNP]; Distrito Federal, Estacao Florestal Cabeça do

Veado [CNC]; Goiás, Cuyaba [MHNP]; Ríó Verde [MHNP]; Jatahy [MHNP, MNHB]; Mato Grosso do Sul, R. Caraguata [MCZC]; Minas Gerais Aquas Vermelhas [MSNM]; Belo Horizonte [MHNP]; Lambary [USNM]; Parana, Bocaiuvu [UASM]; Caviuna [AMNH]; nr. Pato Branco [UASM]; Ríó Grande do Sul, S.Rosa [MCZC]; Sta. Catarina, Nova Teutonia, [CASC, MCZC, USNM]; Nova Teutonia 27°11'0"S, 52°23'0"W [MSNM, MCZC, MHNP, UASM, USNM]; Nova Teutonia, Sa Catharina [MCZC]; nr Chapaco [UASM]; São Paulo, Campos do Jordao [CMNH].

COLOMBIA. NW Sierra N de Sta. María [MCZC].

PARAGUAY. 40 km E Villarrica [MSNM]; vic. Horqueta [MCZC]; Amabay Cerro Cora [USNM]; Central San Lorenzo [MHNM, CMNH].

PERU. Chanchamayo [MSNM]; Ríó Pampas (Hyw 7) [CASC]; Huanuco [MCZC]; Piedras Grandes [SEMCI].

VENEZUELA. [MHNP]; Caracas [MHNP, MNHB]; Aragua, El Limon [MIZA]; Bolivar, Guri Ríó Caroni [MIZA].

UNKNOWN: [MHNP], [?]Araras-Sp. [USNM]; [?]Delbrando Leme-Sp.[USNM]; [?]Lagoa santa [IZWP]; [?]Ríó Jan. [MHNP]; [?]Tlupinangu [MHNP].

(13)*Abaris metallica*, new species

Fig. 13, 25E

Type Material.—HOLOTYPE. Female, labeled: "Venezuela, Bolivar, Kavanayen, Aug 8 1970; R.E.Dietz IV, 1000 m.", USNM. ALLOTYPE. Male, labeled: "Caracas" [handwritten on green paper other writing is not legible], MNHB.

Type Locality.—As given for holotype.

Range.—Venezuela (Fig. 13).

Recognitory Diagnosis.—Distinctly amariform and so set apart from all other *Abaris* species. Shiny virescent green with a proportionally large head and pronotum that is broadest at the base.

Description.—Medium sized, overall length 5.8–6.3 mm. brilliant green luster. Ventral body surface, mouthparts, antennae and legs ferruginous to ferrugino-testaceous.

Head. Relatively large, ocular ratio 1.71–1.72. Mentum tooth emarginate at apex. Microsculpture of head reticulate; frontal impressions shallow and broad, clypeus anterior margin slightly emarginate.

Thorax. Pronotal (Fig. 25E) front angles produced, hind angles obtuse, not denticulate, lateral bead very narrow and uniform throughout, basolateral margin not bordered although obscure impression along margin suggests border; microsculpture distinct, reticulate, shiny. Elytra broad, humeral angles prominent, microsculpture on disc reticulate and surface shiny, basal section of stria 1 present, intervals flat dorsally, 2–4 very wide; striae 3–5 almost effaced dorsally; elytral humeral tooth anterad interval 8. Mesepisternal angle produced as prominent, sharp tubercle. Metacoxal sulcus arcuate, ended medially in coxa.

Abdomen. Abdominal sulci complete, finely engraved, very shallow medially. Male genitalia and female genitalia and reproductive tract not studied.

Etymology.—Specific epithet is a Latinized adjective referring to the metallic luster of this species.

Subgenus *Abaridius* Chaudoir, 1873:97

Type Species.—*Abaris tachypoides* Bates.

Cladistic Diagnosis.—Support for this clade comes from two homoplasious characters; form of the pronotal bead (character 15) and the microsculpture in and near the lateral foveae (character 17). A wide bead that sharply narrows before the hind angles is characteristic of the basal grade species and a more uniform bead is characteristic of species in the clade including *A. tachypoides* and the remaining species (Fig. 32: character 15). The wider/narrowing lateral bead is also known from *A. napoensis* but is hypothesized as a convergent occurrence. The second character, microsculpture in and near the lateral foveae, is highly homoplasious in regard to the selected phylogenetic hypothesis for the genus. The basal species of *Abaridius* have a generally shiny surface, and very faint and



Fig. 9.—Dorsal habitus, *Abaris tachypoides* Bates.

transverse microsculpture in this region, whereas most derived members have reticulate and more or less obvious microsculpture.

Two species, *A. bicolor* and *A. nobilis*, included in the subgenus *Abaridius* lack the more convincing synapomorphies of the *A. tachypoides*-group (see below) and are considered *sedis mutabilis* within the subgenus. Both are large and brilliantly metallic, but otherwise not particularly similar to each other. The form of the pronotum is quite different between the two, with *A. bicolor* (Fig. 25F) more similar to *A. inflata* (Fig. 26B) or *A. nitida* (Fig. 25H), whereas *A. nobilis* has a pronotum that is unique in the genus. Neither male nor female genitalia have been studied for either species as each is represented by only a single

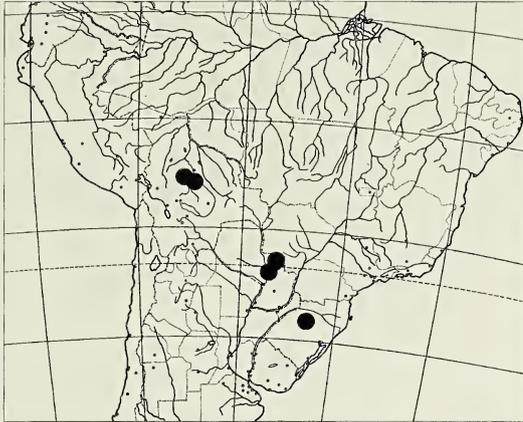


Fig. 10.—Locations of collecting sites for *Neotalus portai* (Straneo) specimens in South America.

specimen. Characteristics of these systems may resolve the relationships of these taxa.

(14) *Abaris bicolor*, new species

Fig. 15, 25F

Type Material.—HOLOTYPE. Male, labeled: “Ecuador, Napo, Onkone Gare Camp, 00°39'10"S, 76°26'00"W, 220 m; terra firma forest, flowerfall, litter, at night; T.L. Erwin, G.E. Ball & D. Shpeley; 5&8.X.1995; 07-95, T.L. Erwin Ecuador Expedition 1995”, USNM.

Type Locality.—As given for holotype.

Range.—Ecuador (Fig. 15).

Recognitory Diagnosis.—Distinguished by its large size, smooth pronotum and subdepressed form.

Description.—Large sized, overall length 8.5 mm. Very shiny with brilliant metallic luster, head and pronotum dark virescent, elytra cupreous. Ventral body surface dark brunneous; legs, mouthparts and antennae slightly paler.

Head. Ocular ratio 1.63. Mentum tooth emarginate at apex. Microsculpture of head faint, reticulate; frontal impressions sharp, parallel.

Thorax. Pronotum (Fig. 25F) sinuate to base, basolateral region convex, apex broad, front angles not produced, hind angles denticulate; pronotal basolateral bead broad, sharply narrowed near base; margins paler than disc; basolateral margin not bordered; pronotal microsculpture mesh pattern transverse, very faint, shiny. Basal section of elytral stria 1 present; mesepisternal angle slightly produced as small rounded tubercle; elytral humeral tooth anterad interval 8; microsculpture faint, transverse; intervals slightly convex, intervals 2–3 of equal width. Metacoxal sulcus arcuate, ended medially in coxa.

Abdomen. Abdominal sulci complete, deeply and finely engraved. Male genitalia and female genitalia and reproductive tract not studied.

Etymology.—Specific epithet is a Latin adjective referring to the color contrast between the elytra and forebody.

(15) *Abaris nobilis*, new species

Fig. 15, 25G

Type Material.—HOLOTYPE. Female, labeled: “Brazil, Pará: 5 km E Belém, Soil-litter layer in primary “terra firma” forest. June 6:1973, R.T.Schuh”, AMNH.

Type Locality.—As given for holotype.

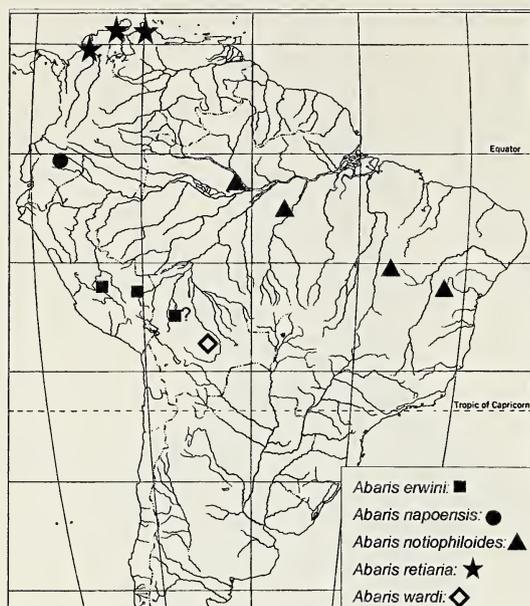


Fig. 11.—Locations of collecting sites for *Abaris* species specimens in South America.

Range.—Brazil (Fig. 15).

Recognitory Diagnosis.—Distinctive species. Largest member of the genus, bright coppery color and arcuate pronotal margins readily distinguishes this species from all others.

Description.—Large size, overall length 8.9 mm. Cupreous throughout; ventral body surface, labrum and mandibles piceous; legs antennae and palpi brunneous.

Head. Eyes relatively small, ocular ratio 1.65. Frontal impressions deep, short, divergent. Mentum tooth deeply emarginate at apex. Microsculpture of head very faint, reticulate.

Thorax. Pronotal (Fig. 25G) basolateral region convex, apex broad, front angles slightly produced, hind angles denticulate, lateral bead broad narrowed to base, basolateral margin not bordered; pronotal microsculpture transverse, very faint, surface shiny. Microsculpture of elytra transverse; basal section of stria 1 present, intervals convex, intervals 2–3 of equal width; humeral tooth anterad interval 8. Mesepisternal angle produced as rounded tubercle. Metacoxal sulcus arcuate.

Abdomen. Sterna V–VI with complete transverse sulci. Male genitalia and female genitalia and reproductive track not studied.

Etymology.—The specific epithet is the Latin adjective *nobilis* (noble) referring to the large size and brilliant copper color of holotype, making it a noble looking animal.

A. tachypoides-group

Cladistic Diagnosis.—All members of this clade share a derived form of the metacoxal sulcus. The metacoxal sulcus is straight and appressed to the apical coxal margin (Fig. 3B, Fig. 32: character 6). The basal grade species, *A. nitida*, *A. frantiai* and *A. inflata*, are relatively large and somewhat or quite convex in form. They are similar to *A. bicolor* but have the distinctive straight metacoxal sulcus, not the arcuate condition of *A. bicolor*. The male and female reproductive structures have not been studied for these species. All three species have complete transverse sternal sulci, as does the more apically placed *A. tachypoides*. However,

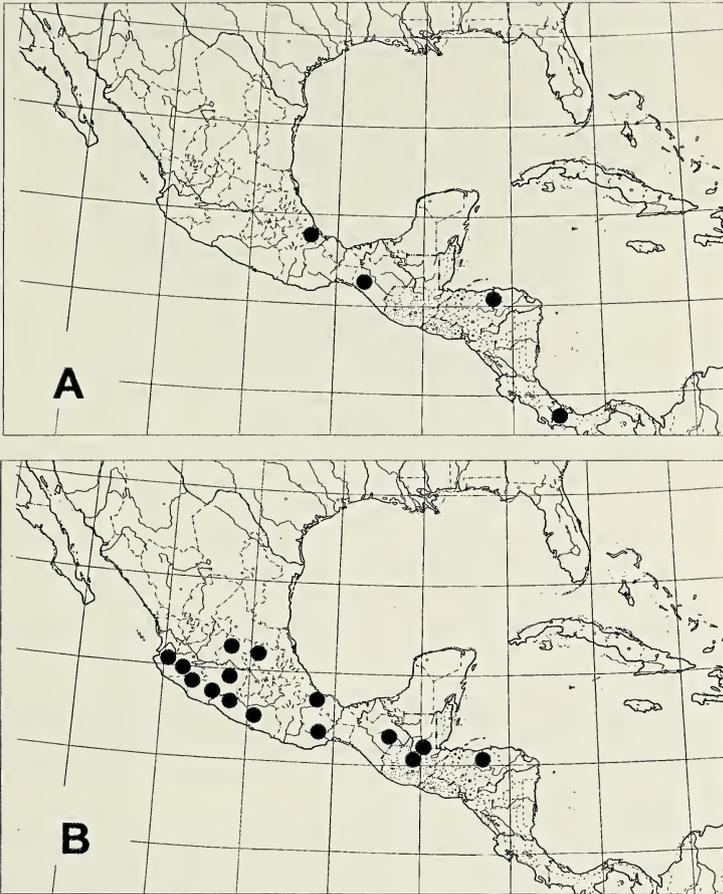


Fig. 12.—Locations of collecting sites in Central America for *Abaris* species specimens. A. *A. aquilonaria* n.sp. B. *A. bigenera* Bates.

A. tachypoides is much smaller, and has a very different general form than any of these species.

The mid-grade species, *A. tachypoides*, *A. convexa*, *A. nigra* and *A. inaequaloides*, are small, have rather narrow pronota with constricted apices. In general, their form somewhat resembles ants or lachnophorine ground beetles.

(16)*Abaris nitida*, new species

Fig. 13, 25H

Type Material.—HOLOTYPE. Male, labeled: "Ecuador, Napo, Limoncocha, 100 m, H. Frania, Apr 13–24:1979, Swamp Forest, leaf litter", USNM. ALLOTYPE. Female, labeled: "Ecuador, Napo, Yasuni Scientific Station, 0°40'36"S, 76°24'2"W, 210 m, K.Will, 24:IV:1998", CUIC.

Type Locality.—As given for holotype.

Range.—Ecuador (Fig. 13).

Recognitory Diagnosis.—Distinguished from other member of the group by convex form, deep basal foveae and general form of the pronotum (Fig. 25H).

Description.—Medium sized, overall length 6.7–7.1 mm. Shiny bright aeneous elytra; head and

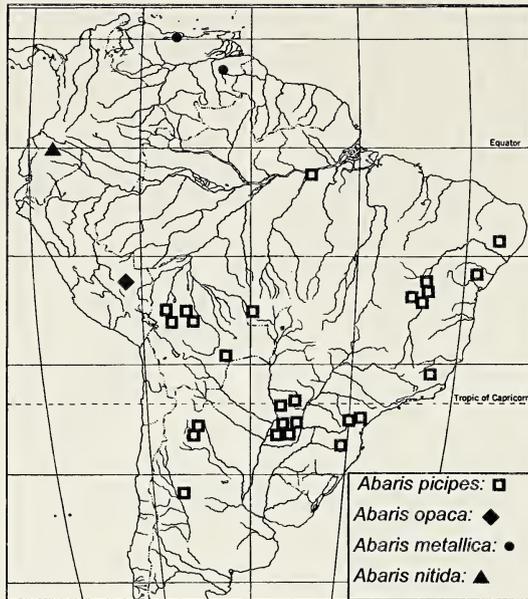


Fig. 13.—Locations of collecting sites for *Abaris* species specimens in South America.

pronotum darker, slightly virescent. Ventral body surface brunneous; mouthparts, antennae and legs paler, ferrugino-testaceous; femora either concolorous with ventral body surface or paler.

Head. Relatively large, ocular ratio 1.67–1.72. Mentum tooth flat and broad at apex, form simple. Head smooth throughout, microsculpture obsolete. Frontal impressions moderately deep, slightly divergent, not delimited medially.

Thorax. Pronotum (Fig. 25H) microsculpture faint, transverse; form very convex, narrow at apex, front angles scarcely produced, lateral bead thick, widened in basal third and narrowed just before denticulate hind angles. Basal section of elytral stria 1 absent; humeral tooth anterad interval 8; microsculpture transverse mesh. Mesepisternal tubercle large. Metacoxal sulcus linear, appressed.

Abdomen. Abdominal sulci complete. Male genitalia and female genitalia and reproductive tract unstudied.

Notes on Life History.—Collected in April at 100–210 m elevation. The Limoncocha specimen was collected in a swamp forest from leaf litter and the Yasuni specimen was collected while using a headlamp and searching leaf litter along a trail in terra firme forest.

Etymology.—The specific epithet is a Latin adjective referring to the shiny appearance of these beetles.

(17)*Abaris franiai*, new species

Fig. 16, 26A

Type Material.—HOLOTYPE. Male, labeled: “Bolivia, Cochabamba, Villa Tunari, For. leaf litter, 430 m, May 9:1979, H. Frania”, USNM.

Type Locality.—As given for holotype.

Range.—Bolivia (Fig. 16).

Recognitory Diagnosis.—Relatively large and robust form with a relatively broad head. Similar to *A. inflata* and *A. nitida* and must be separated from these by the characters given in the key, e.g., the impunctate pronotal base and sulcate sterna.

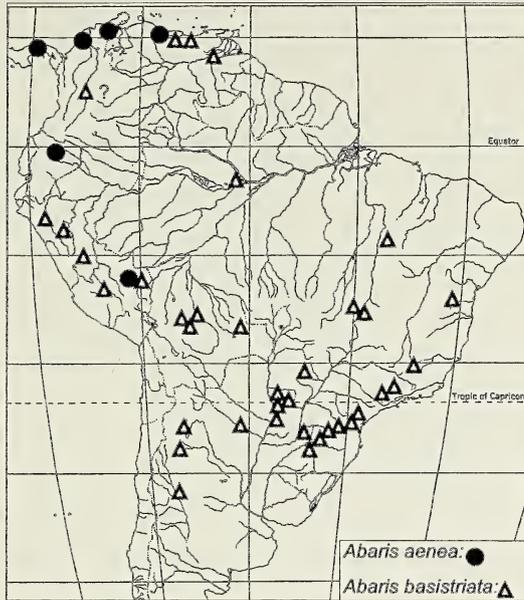


Fig. 14.—Locations of collecting sites for *Abaris* species specimens in South America.

Description.—Large sized, overall length 7.9 mm. Aeneous, head and pronotum virescent. Ventral body surface, labrum and mandibles brunnescens; legs, palpi and antennae paler.

Head. Ocular ratio 1.89. Mentum tooth form simple. Microsculpture of head faint, reticulate; frontal impressions short, sharply divergent; clypeus with setigerous punctures surrounded laterally by depressions.

Thorax. Pronotal (Fig. 26A) basolateral region slightly convex, apex broad, front angles slightly produced, hind angles with small denticle, lateral bead broad and narrowed to base, basolateral margin not bordered; microsculpture transverse, faint mesh, surface shiny. Microsculpture of elytra transverse; basal section of stria 1 absent, intervals convex, intervals 2–3 of equal width; elytral humeral tooth anterad interval 7. Mesepisternal angle produced as small sharp tubercle. Metacoxal sulcus linear, appressed.

Abdomen. Sternal sulci complete. Male genitalia and female genitalia and reproductive tract unstudied.

Etymology.—Specific epithet is an eponym based on the surname of the collector H. Frania.

(18) *Abaris inflata*, new species

Fig. 16, 26B

Type Material.—HOLOTYPE. Male, labeled: "Bolivia, Cochabamba, Chapare Alto Pol. mar, XI: 1960" [handwritten], MSNM [Straneo Collection].

Type Locality.—As given for holotype.

Range.—Bolivia (Fig. 16).

Recognitory Diagnosis.—Relatively large species, very convex with the pronotum broad.

Description.—Large sized, overall length 7.5 mm. Moderately shiny; elytra with aeneous luster, head and pronotum slightly darker. Ventral body surface, coxae and trochanters brunnescens; remaining leg segments, mouthparts and antennae paler.

Head. Relatively broad, ocular ratio 1.78. Mentum tooth form simple, apex broadly rounded. Microsculpture of head obsolete, frontal impressions short, not delimited medially. Clypeus tumescent near frontal suture and depressed near apex.

Thorax. Pronotum (Fig. 26B) convex, front angles scarcely produced, hind angles about right,

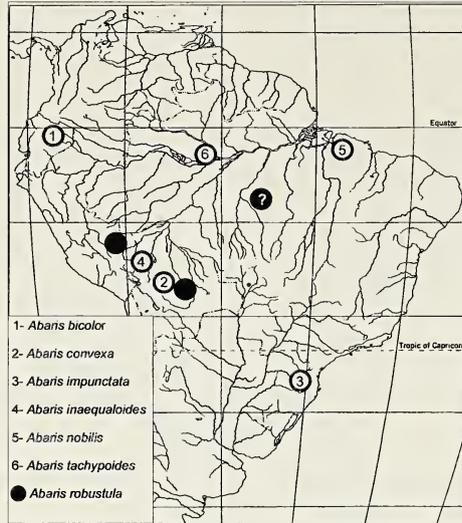


Fig. 15.—Locations of collecting sites for *Abaris* species specimens in South America.

denticulate, lateral bead broad in basal third and sharply narrowed to hind angles, without basolateral border; microsculpture faint and transverse. Elytra basal section of stria 1 absent; mesepisternal angle prominently produced as sharp tubercle, elytral humeral tooth anterad interval 7; microsculpture transverse mesh, intervals 2–3 of equal width. Metacoxal sulcus linear, appressed.

Abdomen. Male genitalia and female genitalia and reproductive tract unstudied.

Etymology.—The Specific epithet is a feminized Latin adjectival of *inflatus* (to blow into) referring to the generally tumescent or robust form of the body.

(19)*Abaris tachypoides* Bates, 1871, revised combination

Fig. 9, 15, 21T–U

Abaris tachypoides Bates, 1871:220.

Type Material.—LECTOTYPE (here designated). Male, labeled: “Ega” [handwritten]; “*Abaris tachypoides* type, Bates” [handwritten]; “Ex Musaeo H.W. Bates, 1892”; “Lectotype, *Abaris tachypoides* Bates, K.W. Will”, MHNP.

Type Locality.—Brazil, Tefé [Ega], from original description.

Range.—Brazil (Fig. 15).

Recognitory Diagnosis.—The relatively large head and narrow pronotum are distinctive (Fig. 9). Similar to *A. inaequaloides*, but distinguished from that species by the straight striae, equal width of elytral intervals and darker, more cupreous body color.

Description.—Small sized, overall length 5.7–6.4 mm. Cupreous, head and pronotum black with slight metallic luster. Ventral body surface, mandibles and labrum brunneous to piceous; legs, palpi and antennae paler ferrugino-testaceous.

Head. Head relatively large, ocular ratio 1.84–1.91. Mentum tooth form simple. Microsculpture of head obscure, reticulate; frontal impressions long, deep, parallel.

Thorax. Pronotal basolateral region convex, apex narrowly constricted, front angles not produced, appressed to occiput, hind angles not denticulate, lateral bead narrow, basolateral margin not bordered; microsculpture on disc reticulate. Elytral microsculpture transverse; basal section of stria 1 absent, intervals convex, intervals 2–3 of equal width; elytral humeral tooth anterad interval 7. Mesepisternal angle produced as small, flat tubercle. Metacoxal sulcus linear, appressed.

Abdomen. Sternal sulci complete, very finely engraved. Basal bulb of male median lobe unmodified

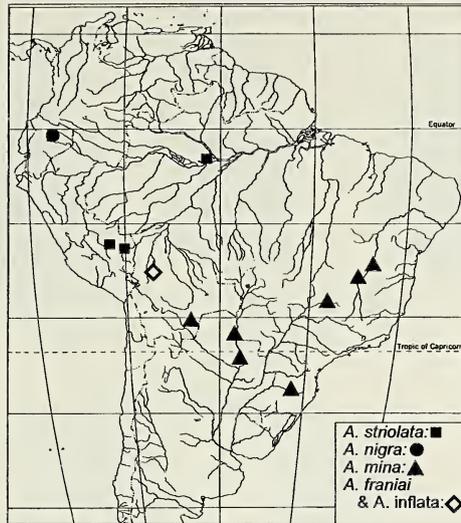


Fig. 16.—Locations of collecting sites for *Abaris* species specimens in South America.

(Fig. 21T–U), endophallus folding pattern not visible, blade smooth (Fig. 21T). Female genitalia and reproductive tract not studied.

Material Examined.—Five specimens examined. **BRAZIL**. Ega [MHNH]; Amazonus [BMNH].
UNKNOWN: [BMNH].

(20) *Abaris convexa*, new species

Fig. 15, 23G–H, 26C

Type Material.—**HOLOTYPE**. Male, labeled: “Bolivia, Cochabamba, Villa Tunari, 430 m, H.Frania, inundation for., 9–10:V:1979, rotting flood debris”, USNM.

Type Locality.—As given for holotype.

Range.—Bolivia (Fig. 15).

Recognitory Diagnosis.—A small species dorsal surface somewhat dull, more convex in form and with relatively larger eyes than other species of similar size.

Description.—Small sized, overall length 5.4 mm.

Head.—Ocular ratio 1.90. Mentum tooth form simple. Microsculpture of head reticulate; frontal impressions moderately deep, parallel.

Thorax. Pronotal (Fig. 26C) basolateral region convex, apex narrow; front angles not appressed to occiput, not produced; lateral margins subsinuate, hind angles not denticulate, lateral bead uniformly thick, basolateral margin not bordered; microsculpture obvious, reticulate mesh, surface dull. Microsculpture of elytra distinct, transverse; basal section of stria 1 absent, mesepisternal angle produced as small flat tubercle, elytral humeral tooth anterad interval 7. Metacoxal sulcus linear, appressed.

Abdomen. Sterna without sulci. Median lobe (Fig. 23G–H) basal bulb unmodified, endophallus folding pattern not visible; lobe tip (Fig. 23H) bluntly rounded, symmetrical. Female genitalia and reproductive tract unstudied.

Etymology.—Specific epithet is a Latin adjective referring to the convex form of this species.

(21) *Abaris nigra*, new species

Fig. 16, 20B, 23I–J, 26D

Type Material.—**HOLOTYPE**. Female, labeled: “Ecuador, Napo Prov., Tena, Misahualli Hotel Jungle Lodge. 30:I:1999. Italo Tapia”, CUIC. **ALLOTYPE**. Male, same data as holotype, CUIC. **PARATYPES**: Female, same data as holotype, UASM; Male same data as holotype, QCAZ; Female, labeled: “Ecuador, Napo, Anaconda Lodge, Napo River, D. Brzoska, 14:II:1991”, SEMC.

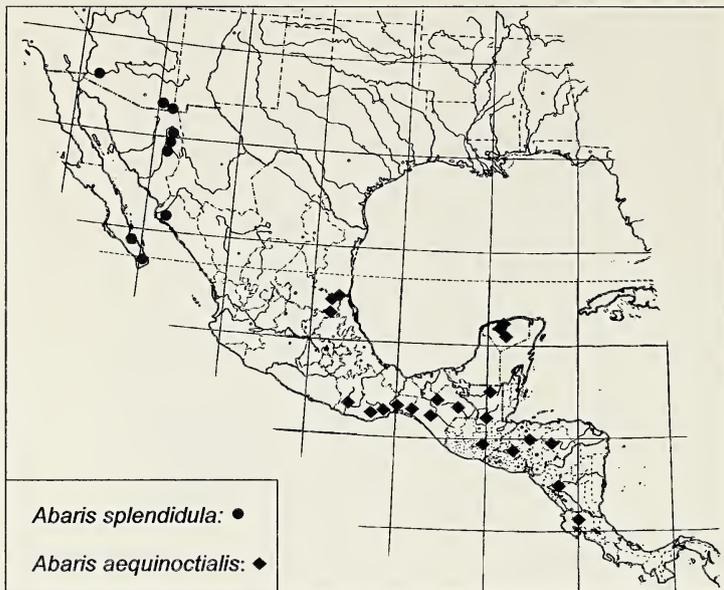


Fig. 17.—Locations of collecting sites for *Abaris* species specimens in southern North America and Central America.

Type Locality.—As given for holotype.

Range.—Ecuador (Fig. 16).

Recognitory Diagnosis.—The dark bronze-black color, bicolored legs, and rounded humeral angles set this species apart from all others. Somewhat similar to *A. inaequaloides*, but front angles not tight to occiput as in that species.

Description.—Small sized slightly built, overall length 6.0–6.2 mm. Black with bronze luster. Ventral body surface black; legs, except femora, mouthparts and antennae brunneous with darker infuscation; femora flavotestaceous, distinctly contrasted with ventral surface, only darker near base.

Head. Ocular ratio 1.74–1.80. Mentum tooth form simple. Microsculpture of head reticulate; frontal impressions deep, divergent, not clearly delimited medially.

Thorax. Pronotal (Fig. 26D) basolateral region convex, apex narrow, front angles not produced, lateral margins sinuate, hind angles not denticulate, lateral bead narrow and uniformly thick, basolateral margin not bordered; microsculpture on disc reticulate, distinct mesh, surface dull. Elytral microsculpture transverse; basal section of stria 1 absent; intervals slightly convex, flatter on disc; intervals 2–3 of equal width, both widened medially; stria 3 sinuate in basal quarter; elytral humeral tooth anterad interval 7. Mesepisternal angle produced as very small, sharp tubercle. Metacoxal sulcus linear, appressed.

Abdomen. Sterna without sulci. Median lobe (Fig. 23I–J) basal bulb unmodified, endophallus folding pattern visible in cleared lobe, blade (Fig. 23I) smooth. Female reproductive tract with broad, straight seminal canal, receptaculum large, distinct, spermatheca with a large basal expansion, appended gland spherical; gonocoxite-1 with 2 apicolateral ensiform setae.

Notes on Life History.—Specimens have been collected in January and February. The Misahualli site was sampled in April, May and October as well, and no *A. nigra* were found during these months. The habitat in the area of the type locality is terra firme forest that is mostly secondary growth mixed with small plots of primary forest.

Material Examined.—Six specimens examined. In addition to the type material, a single male with the same data as the holotype was preserved in 100% EtOH, KWWC.

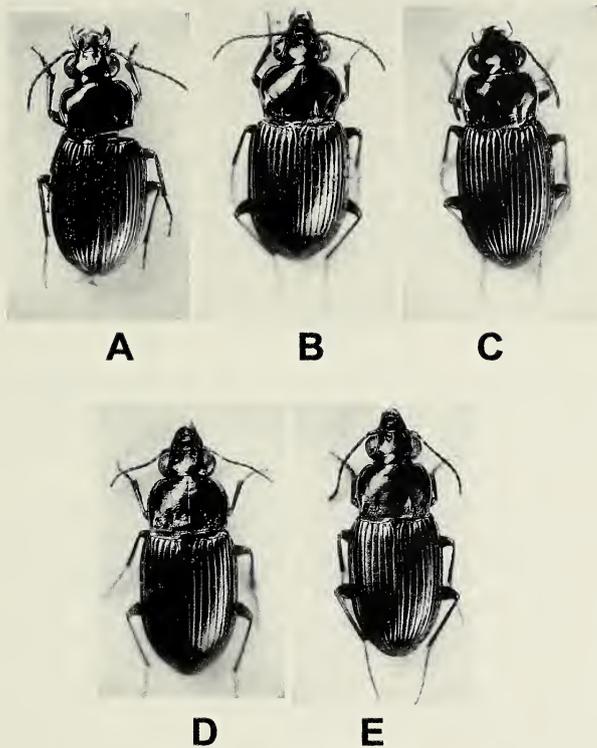


Fig. 18.—Photographs of dorsal view of *Abaris* species. A. *A. napoensis* n.sp. B. *A. erwini* n.sp. C. *A. aenea* Dejean. D. *A. picipes* Bates. E. *A. basistriata* Chaudoir.

Etymology.—Specific epithet is a Latin adjective referring to black body color in this species.

(22)*Abaris inaequaloides*, new species

Fig. 15, 26E

Type Material.—HOLOTYPE. Female, labeled: “Bolivia, Beni, Cercado, 1 km N Ballivian, Río Ibare, 14°47’S, 64°59’W, 124 m, 3 Apr 1994, R.Ward”, CMNH.

Type Locality.—As given for holotype.

Range.—Bolivia (Fig. 15).

Recognitory Diagnosis.—Very distinctive species, at once recognized by the reticulate microsculpture, dull dorsal surface, bronze color and narrow pronotum relative to the large head.

Description.—Medium sized, overall length 6.3 mm. Head and pronotum dull, elytra moderately shiny, bronze luster throughout. Ventral body surface, coxae and trochanters brunneous; remaining leg segments, mouthparts and antennae paler, flavotestaceous.

Head. Relatively large, ocular ratio 1.85. Mentum tooth form simple. Microsculpture of head pronounced, reticulate; surface finely strigate laterad frontal impressions. Frontal impressions short, parallel and moderately deep.

Thorax. Pronotum (Fig. 26E) relatively narrow, basolateral region convex, front angles rounded, not at all produced, hind angles obtuse, not denticulate, lateral bead narrow uniformly thick, laterobasal margin not bordered; microsculpture reticulate mesh; surface dull. Elytra shiny, microsculpture reticulate mesh; basal section of stria 1 absent, interval 3 width 1.7× interval 2, dorsal punctures foveate,

striae 4–5 slightly sinuate in basal third; humeral tooth anterad interval 7. Mesepisternal angle slightly produced, broad and rounded. Metacoxal sulcus linear, appressed.

Abdomen. Sterna without sulci. Male genitalia and female genitalia and reproductive tract unstudied.

Etymology.—Specific epithet is Latinized adjective referring to this species' general similarity to species of the *B. inaequale*-group of the genus *Bembidion* Latreille, 1802.

(23)*Abaris opaca*, new species

Fig. 13, 26F

Type Material.—HOLOTYPE. Female, labeled: "Peru, Madre de Dios, Tambopata Res. Zone, Explorer's Inn, 12°50'S, 69°17'W, Fig fall, at night, Río La Torre to Sunset Point trail, 1 Nov 1982, 290 m, T.L.Erwin and L.Sims", USNM.

Type Locality.—As given for holotype.

Range.—Peru (Fig. 13).

Recognitory Diagnosis.—Black species with reticulate microsculpture on dorsum. Very similar to *A. wardi* but with the mentum tooth form broad and slightly emarginate at the apex. Pronotal apex narrow but angles not appressed to occiput as in *A. inaequaloides*.

Description.—Medium sized, overall length 6.5 mm. Black with aeneous luster, less pronounced on head and pronotum. Ventral body surface piceous; legs, mouthparts and antennae brunneous.

Head. Ocular ratio 1.89. Mentum tooth form broad, and emarginate at apex. Microsculpture on head reticulate mesh; frontal impressions shallow, sharp, slightly divergent, not clearly delimited medially.

Thorax. Pronotal basolateral region convex, apex narrow; hind angles very slightly obtuse to right angled, not denticulate; lateral bead uniformly thick, basolateral margin not bordered; obvious microsculpture on disc, reticulate; surface dull. Microsculpture of elytra reticulate; basal section of stria 1 absent, intervals slightly convex, interval 3 width 1.4× interval 2, humeral tooth anterad interval 8. Mesepisternal angle barely produced, not tuberculate. Metacoxal sulcus linear, appressed.

Abdomen. Sterna without sulci. Male genitalia and female genitalia and reproductive tract unstudied.

Etymology.—Specific epithet is a Latin adjective referring to the dull of the dorsal surface.

(24)*Abaris splendidula* (LeConte, 1863)

Fig. 1, 7A–C, 17, 23K–L, 27B

Pterostichus splendidulus LeConte, 1863:10. *Abaris splendidula*: redescription (Bousquet 1984:384).

Type Material.—HOLOTYPE. Female, labeled: [round label with yellow = western states]; "979"; "Type 5648"; "Pterostichus splendidulus Lec."; "J.LeConte collection; *Abaris splendidula* (LeC.) Det. 1982, Y.Bousquet", MCZC. Redefined by Bousquet (1984).

Type Locality.—Fort Yuma, California, from original description.

Range.—Mexico, southwestern USA (Fig. 17).

Recognitory Diagnosis.—Moderately shiny with a convex form and flat elytral intervals. No other *Abaris* species is known from the region inhabited by *A. splendidula*.

Description.—Small sized, overall length 5.4–6.5 mm. Black with a cupreous or virescent luster. Ventral body surface, mandibles and labrum rufopiceous; legs, palpi and antennae ferruginous.

Head. Ocular ratio 1.75–1.86. Mentum tooth form simple. Microsculpture of head reticulate; frontal impressions deep, sharply delimited laterally, obscurely so medially.

Thorax. Pronotal (Fig. 27B) basolateral region convex, apex broad, front angles not produced, margins subsinuate, hind angles not denticulate, lateral bead narrow and uniformly thick, basolateral margin bordered; microsculpture transverse. Microsculpture of elytra reticulate, obvious; basal section of stria 1 absent, intervals flat, intervals 2–3 of equal width, humeral tooth anterad interval 8. Mesepisternal angle produced as a very small round tubercle. Metacoxal sulcus linear, appressed. Hind wing as in figure 7C.

Abdomen. Sterna without sulci. Pygidial gland system as in figure 7A. Alimentary tract as in figure 7B. Basal bulb of male median lobe (Fig. 23K–L) unmodified, endophallus folding pattern not visible; blade smooth (Fig. 23K). Female reproductive tract seminal canal narrow with few tight twists along

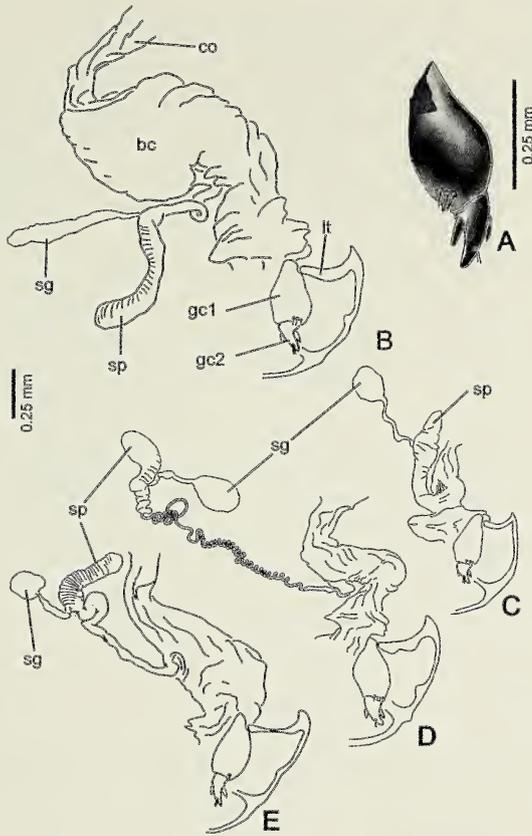


Fig. 19.—*Abaris* species female reproductive tract and genitalic features of *A. napoensis* n. sp. A. Ventral view of right gonocoxite. B. Ventral view of reproductive tract and genitalia, right gonocoxite removed. Same for C. *A. notiophiloides* Bates. D. *A. bigenera* Bates. E. *A. picipes* Bates. Scale for B, C, D and E at left. Legend: bc, bursa copulatrix; co, common oviduct; gc1, basal gonocoxite; gc2, apical gonocoxite; it, laterotergite IX; sg, appended gland of spermatheca; sp, spermatheca.

length, receptaculum distinct, appended gland spherical; gonocoxite-1 with 1 apicolateral ensiform seta.

Notes on Life History.—Bousquet (1984) cited comments by G. E. Ball on the situation in which *A. splendidula* was collected in Mexico. Specimens were collected “in thin leaf litter, on damp sandy-clay spots in open woodland dominated by acacias and on the flood plain of a riparian forest.” Two specimens I collected in Arizona, USA in November were found by raking *Salix* leaf litter on sandy soil along the Santa Cruz River. I collected many additional specimens in various sites in Arizona in July and August in similar situations along washes with or without water present. Individuals were generally 1–3 meters back from the main erosion channel in semi-shaded areas with ample leaf litter. Some activity was observed in late afternoon but most beetles were found at night while searching with a headlamp. Two specimens collected at light in Tucson were found at large fluorescent lights at the edge of the city on evenings when it rained either before or just after collecting the beetles. This suggests some relationship between timing of dispersal activity and rain patterns. Adults have been collected in January, July,

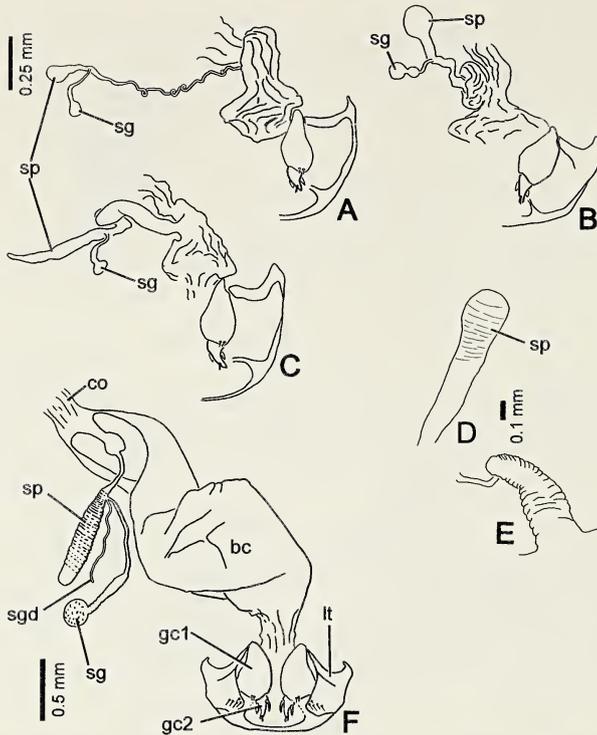


Fig. 20.—Abariform species female reproductive tract and genitalia features of A. *Abaris aquilonaria* n.sp., ventral view of reproductive tract and genitalia, right gonocoxite removed. Same for B. *A. nigra* n.sp. C. *A. aequinoctialis* Chaudoir. D–E. *A. retiaria* n.sp. F. *Pseudabarys* undescribed sp. Ecuador, both gonocoxites shown. Scale for A, B, and C at upper left. Legend: bc, bursa copulatrix; co, common oviduct; gc1, basal gonocoxite; gc2, apical gonocoxite; lt, laterotergite IX; sg, appended gland of spermatheca; sgd, spermathecal gland duct diverticulum; sp, spermatheca.

August and November at elevations from sea level to 1100 m. Data labels include collections in several similar forest types; dry tropical scrub, gallery, riparian, riparian tropical scrub forests. Specimens have been taken in leaf litter and rarely at lights ($n = 3$).

The male and female collected in Arizona in November were dissected and reproductive organs examined. Neither specimen was in breeding condition, i.e., ovaries were not enlarged and male accessory glands were not turgid. Beetles collected from July to August were kept alive and actively mated producing eggs.

Material Examined.—More than 100 specimens examined. **MEXICO. Baja California Sur Notri:** 18 km S Loreto [UASM]. **Sonora:** 17 km sw Moctezuma rte 21[UASM]; 19.3 km n Imuris Rte 15 [UASM]; 55 km sw Moctezuma rte 21 [UASM]; Fuerte, 18 km n Los Mochis on rte15 [UASM]; Sta. Ana [EMEC].

UNITED STATES. Arizona. Cochise Co.: St. David [UASM]; rt 80 at San Pedro River[KWWC]. **Pima Co.:** 31 km NW Tucson [CMNH]; Arivaca [UASM]; Florida Cyn.Sta Rita Range Res.[UATU]; Green Valley [AMNH]; Waterman Mtns. [UATU]; Baboquivari Mnts, Brown Canyon [KWWC]; Arivaca Wash, Arivaca [KWWC]; Tucson at lights [KWWC]. **Sta. Cruz Co.:** [USNM]; Patagonia [USNM]; Tumacacori at Sta. Cruz River, 31°33'46"N, 111°2'43"W [KWWC].

(25)*Abaris wardi*, new species
Fig. 11, 23M–N, 27A

Type Material.—HOLOTYPE. Male, labeled: “Bolivia, Santa Cruz, Ichilo Province, Buena Vista, 400 m R.Ward, 3:X:1994, MV light”, CMNH. ALLOTYPE. Female, labeled: “Bolivia, Cochabamba Puerto Villarroel”, UASM. PARATYPES. Female, labeled: “Brazil, Cuyaba, Mtt. Grosso”, MCZC; Male, labeled: “Bolivia, Sta Helena, W.M.Mann, X, Mulford BioEpl 1921–22”, USNM. Male, labeled: “Cetto Verde (S.Ama) Bechyne, 16:V:1969”, MSNM. Female, labeled: “Bolivia, Santa Cruz, Province Andres Ibanez Vallecito, 4–5 Oct 1994, R.D.Ward”, CMNH.

Type Locality.—As given for holotype.

Range.—Bolivia, Brazil (Fig. 11).

Recognitory Diagnosis.—Medium to small size with obvious, reticulate microsculpture. Very similar to *A. opaca* but separable from that species by the simple form of the mentum tooth. Pronotal apex narrow but front angles not appressed to occiput as in *A. inaequaloides*.

Description.—Medium to small sized, overall length 5.8–7.0 mm. Black with bronze or cupreous luster. Ventral body surface piceous; legs, mouthparts and antennae paler brunneous or rufous.

Head. Ocular ratio 1.74–1.82. Mentum tooth form simple. Microsculpture of head reticulate; frontal impressions long, divergent or sinuate, not clearly delimited medially.

Thorax. Pronotal (Fig. 27A) basolateral region convex, apex narrow, front angles not produced, hind angles not denticulate, lateral bead narrow, basolateral margin not bordered; microsculpture obvious on disc, reticulate; surface dull. Microsculpture of elytra reticulate; basal section of stria 1 absent, intervals convex to almost flat, interval 3 width equal to or up to 1.4× interval 2, elytral humeral tooth anterad interval 8. Mesepisternal angle rounded, not produced. Metacoxal sulcus linear, appressed.

Abdomen. Sterna without sulci. Basal bulb of male median lobe (Fig. 23M–N) unmodified, endophallus folding pattern not visible, lobe smooth, apical blade uniform, straight, thin. Female tract with seminal canal broad, straight, receptaculum not distinct from canal, spermatheca without basal bulb, appended gland spherical; gonocoxites-1 with 3 apicolateral ensiform setae.

Etymology.—Specific epithet is an eponym based on the surname of the collector Robert D. Ward.

(26)*Abaris aequinoctialis* Chaudoir, 1852
Fig. 17, 20C, 23O–P, 26G–H

Abaris aequinoctialis Chaudoir, 1852:76. *Abarys aequinoctialis*: Chaudoir, 1873:98.

Type Material.—LECTOTYPE, (here designated). Female, labeled: “ex Museo Chaudoir” [red ink]; “Lectotype” [Handwritten on circular label with purple edge]; “Lectotype, *Abaris aequinoctialis* Chd., Det. G.E.Ball '72”, MHNP.

Type Locality.—Temax, Yucatan, Mexico, from original description.

Range.—Mexico, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua (Fig. 17).

Recognitory Diagnosis.—Most common species from southern Mexico and Central America. Similar in form to *A. splendidula* but separable by the transverse microsculpture of the elytra. The known range of *A. aequinoctialis* is not overlapping and south of *A. splendidula* (Fig. 17).

Description.—Small sized, overall length 5.1–6.5 mm. Dorsal surface shiny, virescent or cupreous throughout, or bicolored with head and pronotum darker green and elytra dark cupreous. Ventral body surface rufous; legs and mouthparts paler rufous or ferrugino-testaceous; coxae and femora concolorous with ventral body surface; tibiae and tarsi paler in some individuals, nearly flavescent.

Head. Ocular ratio 1.74–1.88. Mentum tooth form simple. Microsculpture of head faint, reticulate. Clypeus smooth, fronto-clypeal suture evident, frontal impressions short and not clearly delimited medially.

Thorax. Pronotum convex, margins sinuate anterad base and convex laterad basolateral foveae, hind angles slightly obtuse, not denticulate, lateral bead narrow, uniformly thick; microsculpture on disc transverse (microsculpture faint and surface shiny in most specimens from Guatemala and Yucatan,

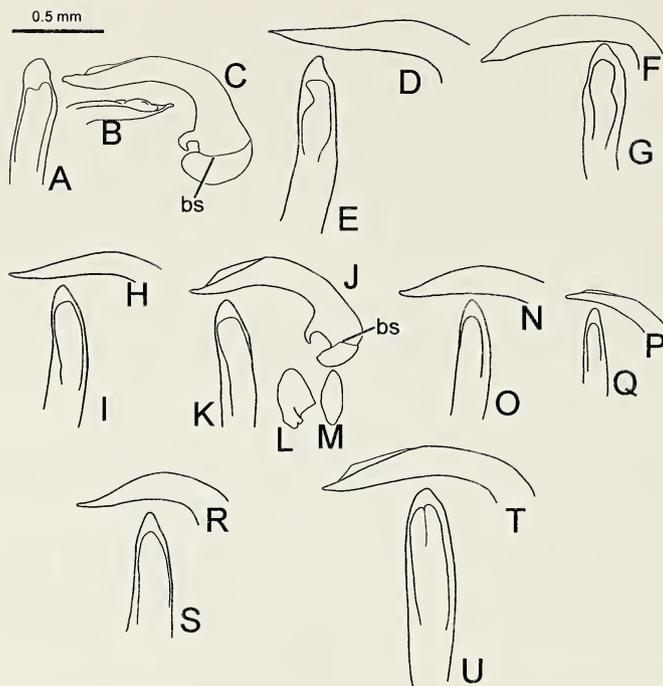


Fig. 21.—Features of male genitalia of *Abaris* species. A, E, G, I, K, O, Q, S, U, dorsal view blade of median lobe; D, F, H, N, P, R, T, right lateral view of blade; C, J, right lateral view of median lobe; B, left lateral view of blade; L, left paramere; M, right paramere. A–C. *A. napoensis* n.sp. D–E. *A. striolata* n.sp. F–G. *A. robustula* Tschitschérine. H–I. *A. aenea* Dejean. J–M. *A. erwini* n.sp. N–O. *A. aquilonaria* n.sp. P–Q. *A. notiophiloides* Bates. R–S. *A. impunctata* n.sp. T–U. *A. tachypoides* Bates. Legend: bs, basal bulb sulcus.

Mexico, obvious mesh in most specimens from other areas). Base of pronotum with or without lateral border (best developed in Yucatan, Mexico specimens). Basal section of elytral stria 1 absent; position of humeral tooth variable either anterad interval 7, stria 7, or barely attaining interval 8; microsculpture transverse; intervals 2–3 subequal.

Abdomen. Sterna without sulci. Blade of median lobe (fig. 230–P) thin, smooth; tip (Fig. 23P) bluntly rounded, endophallus folding pattern not visible, basal bulb unmodified laterally. Female reproductive tract with seminal canal straight, broad, receptaculum not distinct; appended gland spherical; gonocoxite-1 with 2–3 apicolateral ensiform setae.

Notes on Life History.—Specimens have been collected in all months. Habitat data includes leaf litter of rainforest, coffee finca and palm forest. Specimens were collected at sea level to 1400 m elevation. One record was associated with rotting fruit. Nine specimens were taken at “lights” or Ultraviolet light.

Material Examined.—239 specimens. **COSTA RICA.** unknown [USNM]; Guanacaste Prov.; 3 km N Cañas Hac. La Pacifica [UASM]; 5 km N Cañas [UASM]; Las Cañas [UASM]; Santa Rosa National Park Administr. & Research Center, 150 m [CASC]; 30 km norte de Liberia, Finca Jenny [INBC]; 3 km N de Nacaome, P.N.Barra Honda [INBC]; 8 km S de Caujiniquil, Est. Muriélago [INBC]; Barra Honda, A.C.Tempisque, Los Mesoes [INBC]; Est. Cacao, Lado suroeste del Vol. Cacao [INBC]; Est. Las Pailas, P.N.Rincon de la Vieja [INBC]; Est.Lomas Barbudal, A.C.T. [INBC]; Est.Maritza, Lado oeste del Volcan Orosi [INBC]; Est.Palo Verde, P.N.Palo Verde [INBC]; Est.Sta Rosa, P.N.Guanacaste [INBC]; Ojochal, P.N.Sta. Rosa [INBC]; P.N. Barra Honda [INBC]; Parcelona.Asemtamiento Juan Santamaria [INBC]; Playa Naranjo, P.N.Sta. Rosa [INBC]; Ref.Nac.Fauna Silvestre R.L.Rodríguez [INBC].

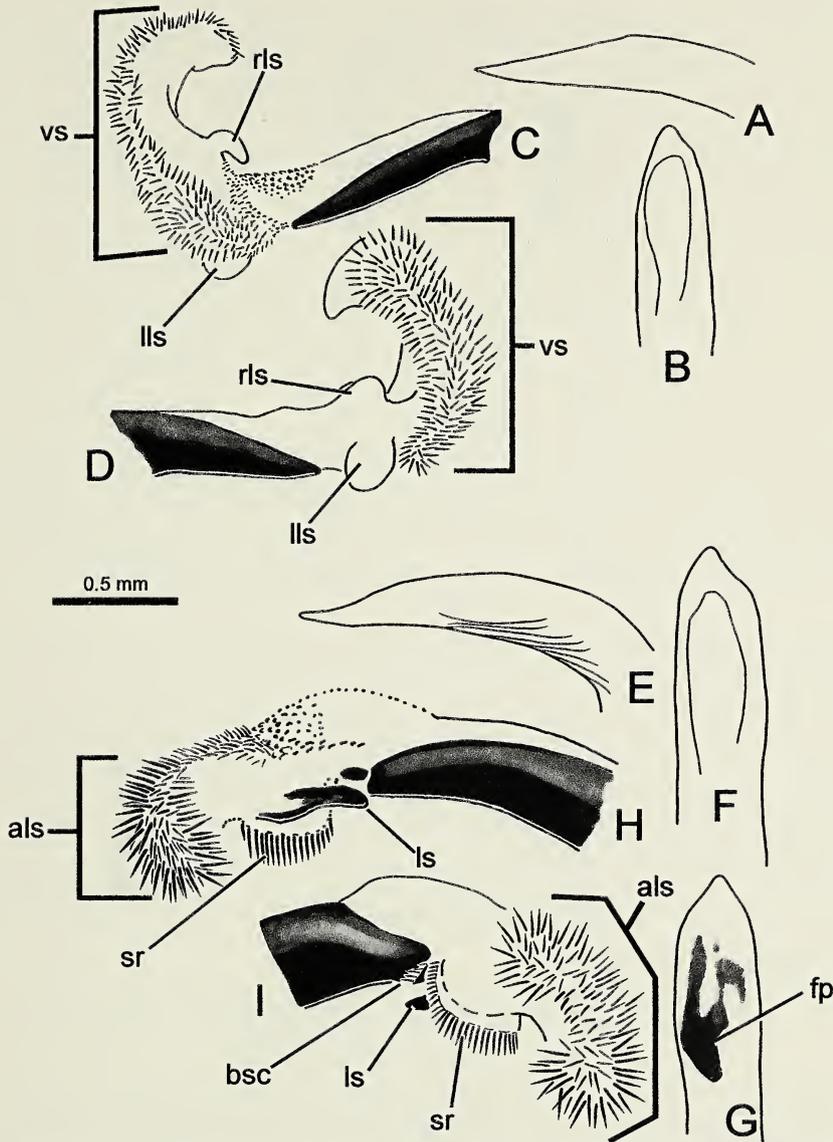


Fig. 22.—Features of male genitalia of *Abaris* species. B, F, dorsal view blade of median lobe; A, E, right lateral view of blade; G, ventral view of blade; C, H, right lateral view tip of median lobe and everted endophallus; D, I, left lateral view tip of median lobe and everted endophallus. A–D, *A. bigenera* Bates. E–I, *A. basistriata* Chaudoir. Legend: als, anterior spine field; bsc, basal scale; fp, folding pattern of endophallus; lls, left lateral sacculus; ls, lateral scale; rls, right lateral sacculus; sr, spine row; vs, ventral spine field.

EL SALVADOR. Isalco [USNM]; Sta. Anna, 6 km W Hwy.CA1, above Lago de Coatepeque, [USNM].

GUATEMALA. 250 km N San Felipe [BPBM]; Tikal [BPBM, RSCI]; Tikal Rainforest, [UASM]; Zapote [MCZC, MHNP]; El Progreso, 6 km E San Cristobal, Acasaguastlan [USNM]; Peten, Tikal [USNM, UASM].

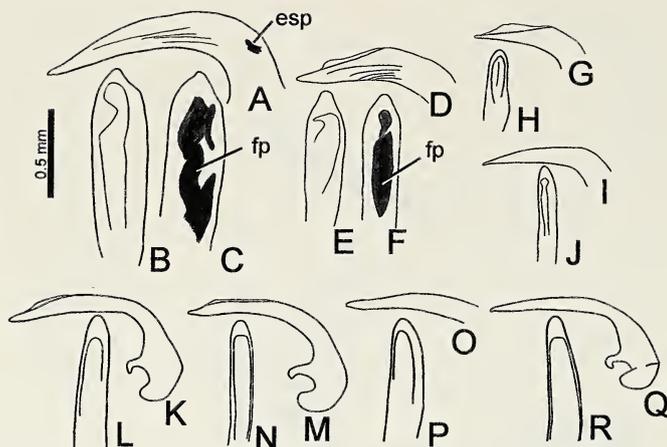


Fig. 23.—Features of *Abaris* species male genitalia. B, E, H, J, L, N, P, R, dorsal view blade of median lobe; A, D, G, I, O, right lateral view of blade; C, F, ventral view of blade; K, M, Q, right lateral view of median lobe. A–C. *A. picipes* Bates. D–F. *A. mina* n.sp. G–H. *A. convexa* n.sp. I–J. *A. nigra* n.sp. K–L. *A. splendidula* (LeConte). M–N. *A. wardi* n.sp. O–P. *A. aequinoctialis* Chaudoir. Q–R. *A. retiaria* n.sp. Legend: esp, endophallus spine patch; fp, endophallus folding pattern.

HONDURAS. [MHNP]; Honduras, Copán, Ruinas de Copán [UMMZ]; Morazán, Esc. Agr. Pan. Zamorano [UMMZ]; Francisco, Zamorano, 47°0'N–80°0'W [SEMC].

MEXICO. unknown [MHNP]← Paz, V.San Yicente Finca, J.Bechyne [MHNP]; 18 mi. N San Andre V [MHNP]. **Chiapas:** 32.5 mi. E Comitán, Rte190 [UASM]; 4.9 mi. N Frontera Comalapa, 727 m; 7.7 mi. N Frontera Comalapa [UASM]; 5.3 mi. S Union Juárez; Cinco Cerros; Cinco Cerros, km30 on Hwy190 [UASM]; El Aguacero, 16 km W Ocozocuatla [UASM]; Trinitaria [UASM]; Puente Macuilapa nr. Los Amates [CASC]. **Hidalgo:** 7 mi. NE Jacala [OSUC]. **Oaxaca:** 5.0 mi. E Tapanatepec, rte190 [UASM]; 7.6 mi. W Zanatepec, rte190 [UASM]; Río Miltepec 18.4 mi. W Zanatepec, rte190 [UASM]; Hy200 km194 E Puerto Angel [AMNH]. **San Luis Potosí:** 1.8 mi. N El Naranjo [UASM]; El Salto de Agura [CNC]; El Salto de Agura, 7 mi. N El Naranjo [UASM]. **Tamulipas:** 1.4 mi. SE Chamal [UASM]. **Yucatán:** 12 km N Piste [UASM]; 2 km E Chichen Itza [UASM]; Chuminopolis [AMNH]; Tehuantepec [AMNH]; Temax [MHNP]; Zopilote, 1.5 mi. E nr.Pan Am. Hwy. [UASM].

NICARAGUA. Chontales [MHNP].

(27) *Abaris retiaria*, new species

Fig. 11, 20D–E, 23Q–R, 27C

Type Material.—HOLOTYPE. Male, labeled: “Venezuela, Falcon, Paraguana Pen S Jose Cueva Piedra Honda, 100 m, S.Peck, 3:III:1971”, USNM. ALLOTYPE. Female, labeled: “Colombia, Magdalena, Río Frio, P.J.Darlington, 1:XI:1928”, MCZC. PARATYPES. Female, label data same as allotype, MSNM. Male, label data same as allotype, MCZC. 3 females, label data same as allotype except date Sept, XI and VIII respectively, MCZC. Female, labeled: “Venezuela, Buena Vista Paraguana, Falcon, Bordon, 2:I:1971”, BORD. Male, labeled: “Venezuela, Maracaibo”, USNM.

Type Locality.—As given for holotype.

Range.—Colombia, Venezuela (Fig. 11).

Recognitory Diagnosis.—Easily recognized from all other species by the obvious reticulate mesh microsculpture, square form and bordered base of the pronotum.

Description.—Small sized, overall length 5.1–5.8 mm. Brunneous with a cupreous or virescent luster. Ventral body surface, legs and mouthparts paler.

Head. Ocular ratio 1.64–1.75. Mentum tooth form simple. Microsculpture obvious on head, reticulate; frontal impressions sharp, divergent, clypeus finely strigate.

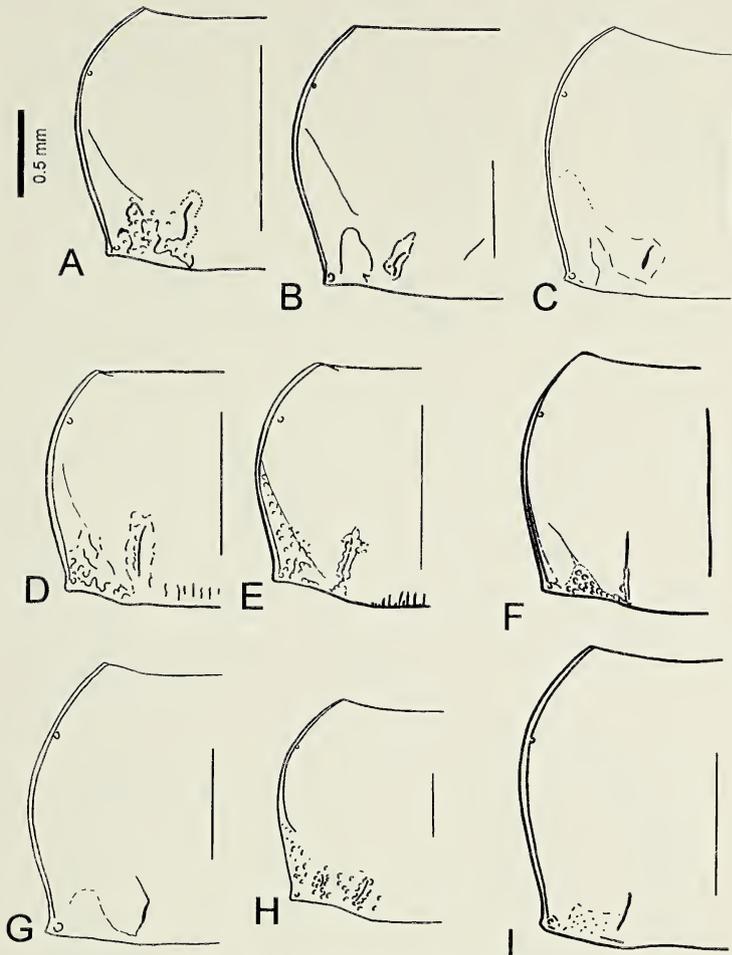


Fig. 24.—Pronota of *Abaris* species. A. *A. napoensis* n.sp. B. *A. striolata*. C. *A. robustula* Tschitschérine. D. *A. aenea* Dejean, smooth form. E. Same, punctate form. F. *A. erwini* n.sp. G. *A. aquilonaria* n.sp. H. *A. notiophiloides* Bates. I. *A. impunctata* n.sp.

Thorax. Pronotal (Fig. 27C) basolateral region slightly convex, apex broad, front angles produced, lateral margins straight, hind angles obtuse, not denticulate; pronotal lateral bead uniformly thick, continuous laterally on base; microsculpture obvious, reticulate, dull. Elytral microsculpture reticulate; basal section of stria 1 absent, intervals little convex, intervals 2–3 of equal width, elytral humeral tooth anterad interval 8. Metacoxal sulcus linear, appressed to apical margin of coxae. Mesepisternal angles produced as low tubercle.

Abdomen. Sterna without sulci. Basal bulb of male median lobe (Fig. 23Q) unmodified, endophallus folding pattern not visible; median lobe straight, smooth; tip (Fig. 23R) evenly rounded. Female tract with seminal canal broad, straight, receptaculum not discrete, spermatheca with basal bulb, appended gland unknown (Fig. 20D–E); gonocoxite-1 with 2 apicolateral ensiform setae. (Because all female specimens were collected into very strong EtOH by P.J. Darlington, female tracts could not be removed without damage. Therefore, this description is based on the fragments of the attempted dissections and may require subsequent revision.)

Etymology.—Specific epithet is a feminized noun in apposition based on the Latin *Retiarius* (type of Roman gladiator bearing a net to entangle his adversary). This calls attention to the net-like reticulate mesh of microsculpture on the pronotum.

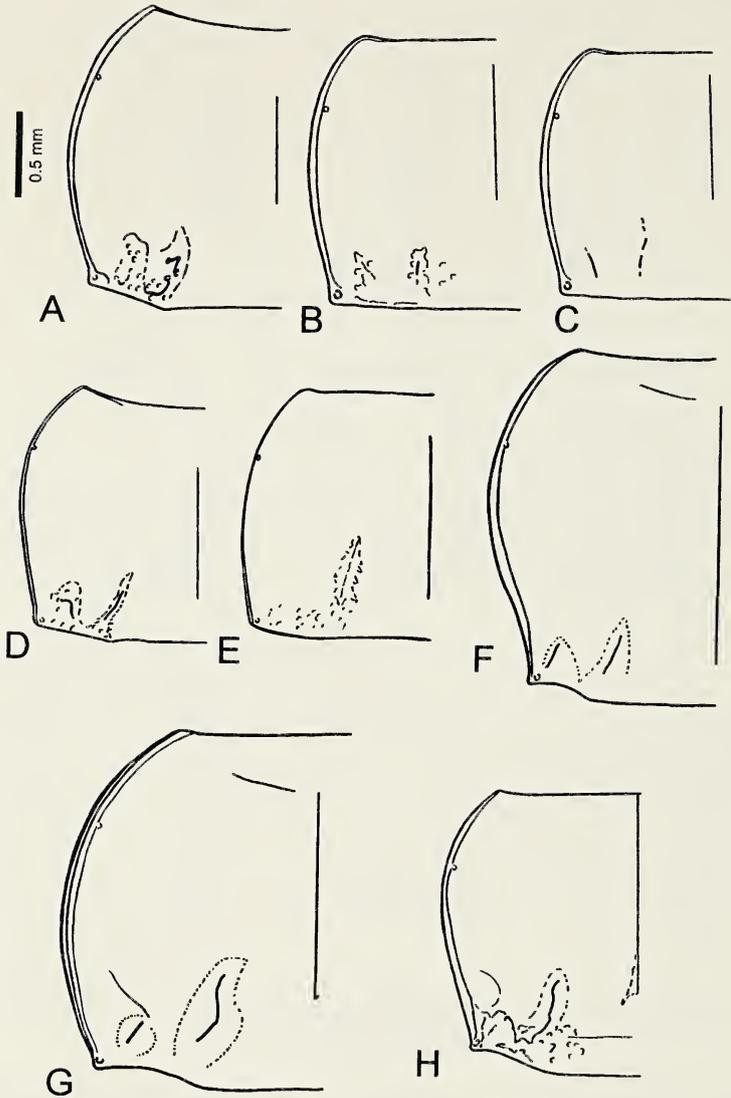


Fig. 25.—Pronota of *Abaris* species. A. *A. bigenera* Bates. B. *A. picipes* Bates. C. *A. mina* n.sp. D. *A. basistriata* Chaudoir. E. *A. metallica* n.sp. F. *A. bicolor* n.sp. G. *A. nobilis* n.sp. H. *A. nitida* n.sp.

CLADISTIC ANALYSIS

Outgroup Selection

Three genera, *Orthomus*, *Prosopogmus*, and *Pseudabarys*, were used as outgroups in this analysis. They were selected from among 115 genera examined as the basis of the analysis of pterostichine taxa (Will, 2000). All three outgroups plus *Neotalus* and *Abaris* comprise a taxon characterized by a “gooseneck” shaped bursa of the female reproductive tract (e.g., Fig. 19B, 20F). *Orthomus*, *Pseudabarys* and *Abaris* share a reduced or absent coronal suture in the larvae (Bousquet and Liebherr, 1994; Will, 2000). *Prosopogmus* adults are very similar

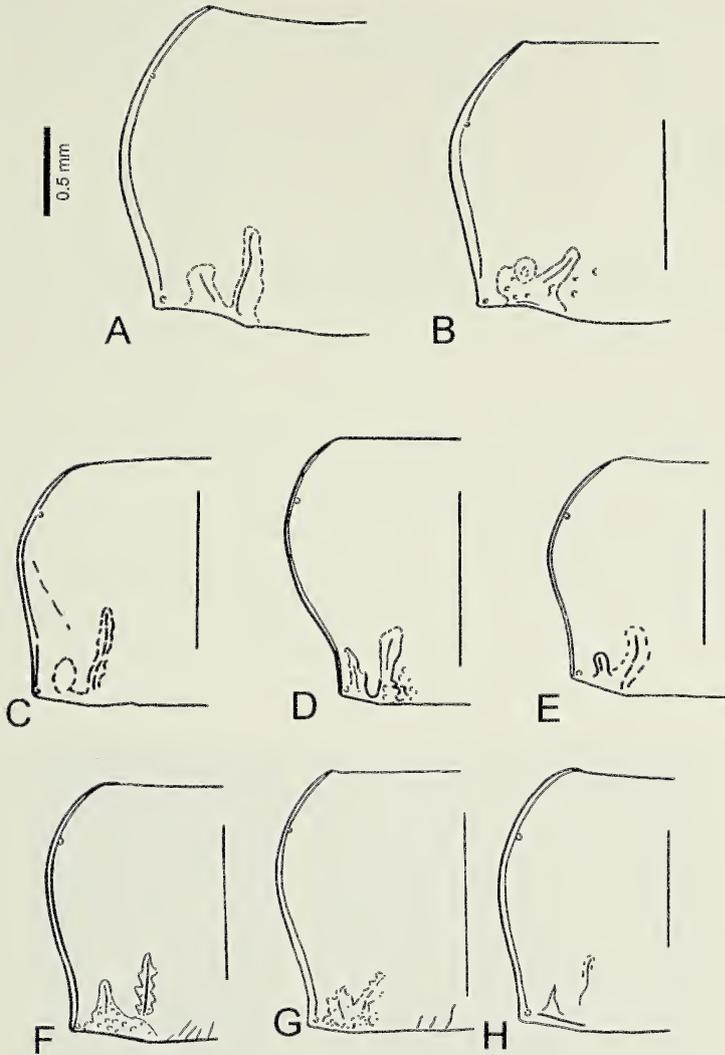


Fig. 26.—Pronota of *Abaris* species. A. *A. frania* n.sp. B. *A. inflata* n.sp. C. *A. convexa* n.sp. D. *A. nigra* n.sp. E. *A. inaequaloides* n.sp. F. *A. opaca* n.sp. G. *A. aequinoctialis* Chaudoir, punctate form, Chiapas, Mexico. H. Same, smooth and basally bordered form, Guatemala.

in general form to some *Abaris* species and *Pseudabarys* shares the paired dorsal bursal glands with *Neotalus* and *Abaris*. Although some of the relationships hypothesized in my higher level analysis (Will, 2000) are not found in the consensus of all most parsimonious cladograms, the set of relationships (*Orthomus* (*Protopogmus* (*Pseudabarys* (*Neotalus* + *Abaris*)))) is supported under every resolution in the full character analysis. Therefore, rooting between *Orthomus* and the remaining taxa is clearly justified.

Character List

1. Maxillary palpomere 3: greater than half length of palpomere 4 (Fig. 28A) (0); less than half length of palpomere 4 (Fig. 28B) (1).

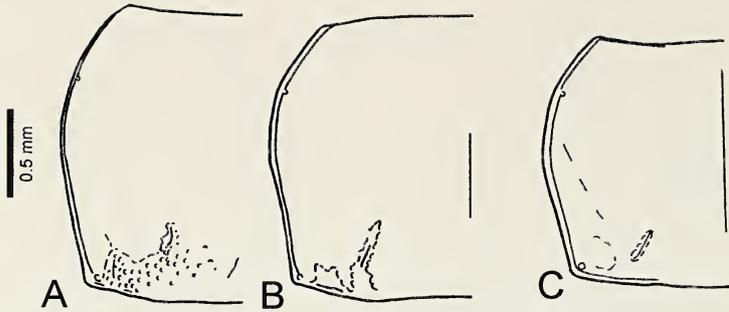


Fig. 27.—Pronota of *Abaris* species. A. *A. wardi* n.sp. B. *A. splendidula* (LeConte). C. *A. retiaria* n.sp.

2. Ocular ratio, measured as width across eyes/width between eyes at level of anterior supraorbital setae (Fig. 29). Less than 1.55 (0); Greater than 1.60 (1). Measurements of ocular ratio were taken to determine if a discrete gap existed between clusters of measurements. Species with similarly developed eyes could then be coded as having the same character state. Measurements of three individuals per species were taken if specimens were available. This ratio was plotted and a gap between 1.55 and 1.60 was found and used to establish states. Figure 29 shows a plot of the measurements and indicates the gap between states.

3. Mentum tooth apex emarginate (0); simple, not emarginate (1).

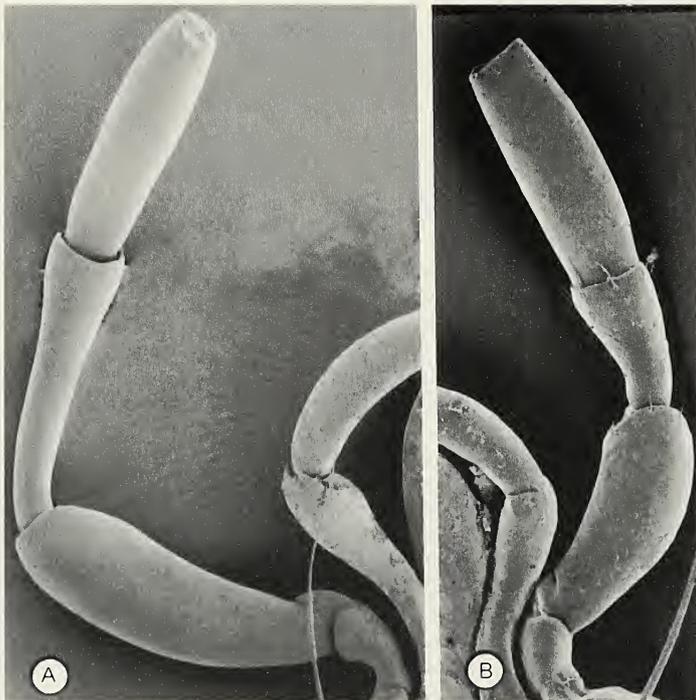


Fig. 28.—Scanning electron micrograph, ventral view. A. Right maxillary palpi *Lophoglossus scrutator* (LeConte) Pterostichini. B. Left maxillary palpi *Abaris aenea* Dejean.

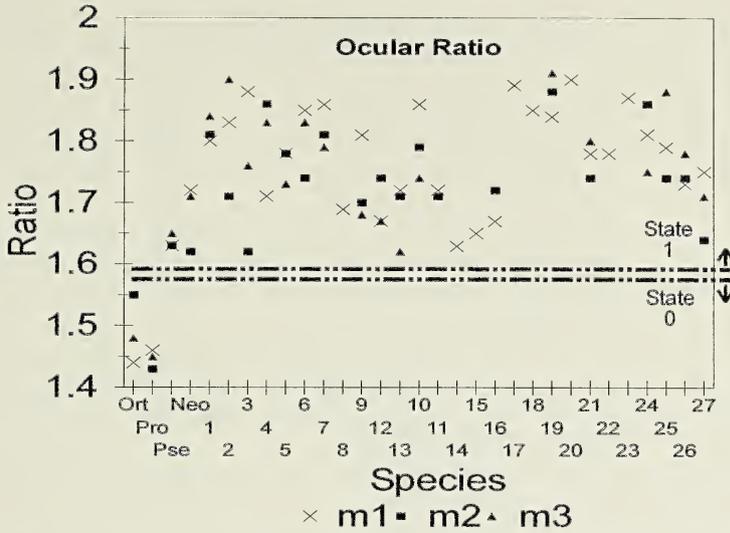


Fig. 29.—Graph of ocular ratio measurements showing separation of states for the character. Up to three measurements were taken for each species. Legend: m1, m2, m3, measurements; Ort, *Orthomus*; Pro, *Prosopogmus*; Pse, *Pseudabarys*; Neo, *Neotalus*; Numbers 1–27 correspond to *Abaris* species numbers in the text.

4. Reticulate microsculpture on vertex of head. Very faint but visible in clean specimens (0); obsolete (1).

5. Micropunctulae present on vertex of head (0); absent (1). These punctures are small (visible at 25× or greater) and irregularly scattered.

6. Metacoxal sulcus arcuate and divergent from apical margin, ended medially in coxae or, if short, divergent from margin (Fig. 3A) (0); sulcus linear, complete or not, appressed to margin; if incomplete then not divergent from margin (Fig. 3B) (1).

7. Basal section of stria 1 present (0); absent (1).

8. Elytral setigerous lateral umbilicate puncture 2 in line with puncture 1 and 3(0); 2 distant from margin, separated from margin by a distinct convexity and mesad of 1 and 3 (1).

9. Elytral humeral tooth anterad and in line with interval 8, elytra across humeri broad and humeral angles sharp (0); tooth anterad interval 7, elytra with rounder and narrower humeral angles (1). Only the position of the tooth was scored. The general shape is not considered discrete.

10. Microsculpture on elytra reticulate and isodiametric (0); transversely elongate mesh (1).

11. Tarsal claws smooth (0); pectinate (Fig. 2A) (1).

12. Ventral setae of fifth tarsomere subequal in length (0); unequal in length, apical pair much longer (ca 2×) than subapical pair (1).

13. Pronotal basolateral region outside outer basal foveae convex (0); basolateral region flat and reflexed (1).

14. Pronotum front margin broad, front angles produced or not, separate from occiput (0); pronotum narrow, appressed to occiput, front angles not protruding (1).

15. Pronotal lateral bead narrow and of uniform width throughout, if narrowing

at all then narrowed just before hind angles (0); bead narrower in apical third, then broadened near middle and again narrowed near base, basal taper starts well before hind angles (1).

16. Pronotal disc microsculpture obsolete (0); transverse and faint, surface shiny (1); transverse and well developed, microlines clearly visible and surface slightly duller (2); reticulate and isodiametric mesh regular or somewhat irregular, surface dull (3) [nonadditive].

17. Microlines in and near basal fovea of pronotum obsolete (0); transverse and faint, surface shiny (1); transverse and well developed, microlines clearly visible and slightly duller (2); reticulate and isodiametric or somewhat irregular, surface dull (3) [nonadditive].

18. Transverse sulci on sterna V–VI complete across sternum (0); laterally present and medially absent (1); completely absent (2). This character was considered additive to set adjacency of states. State 1, interrupted medially, is equally similar to completely absent and entire.

19. Median lobe basal bulb unmodified, small and smoothly rounded (0); basal bulb enlarged and laterally sulcate (1).

20. Endophallus folding pattern and/or spine fields not visible in cleared lobe (0); endophallus folding and pattern and/or spine fields visible as darker regions in lobe (1). Only in a few specimens was the endophallus successfully everted. However, it is presumed that development of larger spines, lobes and scales, that can be seen through the median lobe, is a character that may group taxa. It is likely to be less informative than the multiple characters that potentially exist in the various structures of an everted endophallus, e.g., *A. basistriata* (Fig. 22E–I).

21. Blade of median lobe smooth ventrally (0); ventrally strigate (1).

22. Tip of median lobe tapered gradually to apex, not noticeably thin in lateral view (0); tip very thin in lateral view (1).

23. Apex of median lobe approximately symmetrically narrowed in dorsal view (0); apex distinctly asymmetrically produced to right (Fig. 22D) (1).

24. Blade of median lobe smoothly curved and uniformly tapered in lateral view, slightly curved in dorsal view (Fig. 21M–R) (0); blade uniformly thin from bend to tip in lateral view and straight and narrow in dorsal view (Fig. 23Q–R) (1).

25. Diverticulum of appended gland present (Fig. 20F) (0); diverticulum absent (Fig. 19B) (1).

26. Paired bursal glands absent (0); present (Fig. 5) (1).

27. Seminal canal straight and simple or few (<3) loose twists, duct relatively broad (Fig. 19E) (0); duct narrow with a few (4–5) tight twists along its length (Fig. 20A) (1); duct narrow with many tight twists along its length (Fig. 19D) (2). This character was set as additive to establish adjacency of similar states.

28. Receptaculum of spermatheca discrete from duct as an expanded, annulated in most species, reservoir (Fig. 19D) (0); receptaculum not distinct from duct (Fig. 20C) (1).

29. Spermatheca without basal bulb (0); base of spermathecal duct expanded as a bulb (Fig. 20B) (1).

30. Appended spermathecal gland spherical (0); elongate (1).

Results of Cladistic Analysis

Of the 100 search replications (mult*100), 40 found trees of length 88 steps. Of these 34 were unique arrangements. Swapping on these trees (max*) found

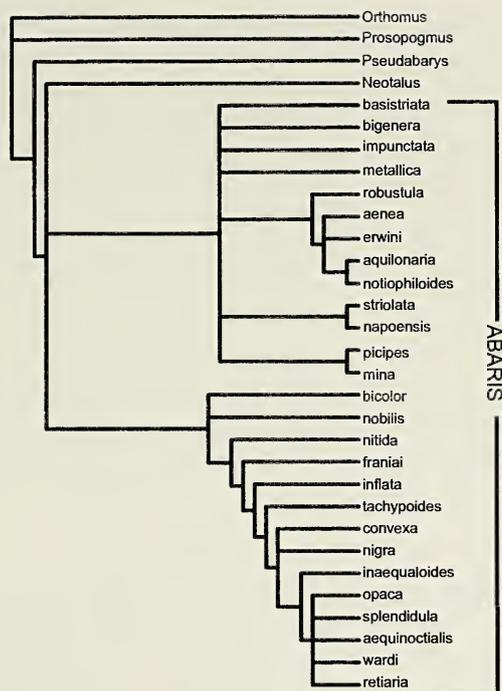


Fig. 30.—Consensus cladogram of the 36 MPTs of 88 steps.

two additional trees. A total of 36 most parsimonious cladograms was found (RI = 71, CI = 40, length 88 steps). These scores show that a reasonable level of grouping information is present and homoplasy is within the expected range (de Queiroz and Wimberger, 1993; Sanderson and Donoghue, 1989) for this matrix of taxa and characters.

The consensus cladogram (Fig. 30) is largely resolved, with monophyly for all clades named in the classification supported except the generic separation of *Neotalus* and *Abaris* and grouping of the members of the *A. picipes*-group.

In some resolutions *Neotalus* is placed as sister to *Abaridius*. This placement is not preferred as it is supported only by the lack of obvious structure of the endophallus of the median lobe and would require accepting the hypothesis that pectinate claws gained in the common ancestor of *Abaris* were lost in *Neotalus portai*. The endophallic structure is not known for most of the *Abaridius* species, absent in five species and is present in *A. nigra*. In other groups of Carabidae, and particularly in pterostichine clade taxa, the endophallus has been best used for differentiating between species and is assumed a less suitable system for generic distinction in abariform taxa.

A number of resolutions have the clade of *A. mina* + *A. picipes* placed as sister to the *A. striolata*-group. This placement is not preferred as the grouping is based only on the microsculpture of the head and requires parallel gains of a very similarly shaped and strigate median lobe in both *A. mina* + *A. picipes* and *A. basistriata*. Grouping *A. mina*, *A. picipes*, and *A. basistriata* minimizes homoplasy in the characteristic form of the median lobe. This preferred arrangement also minimizes the hypothesized number of origins of the long, narrow and tightly

twisted spermathecal canal. It does require a hypothesis that this peculiar form of spermatheca reversed to a simpler, straight form in *A. picipes*.

Little support exists for any particular arrangement of *Abaridius* species and thus relationships among them are largely unresolved in the consensus.

The selected cladogram (Fig. 31, 32) shows only clades supported by unambiguous character state changes. These groups are supported under both accelerated and delayed transformation optimizations. This arrangement is one of three that are consistent with my preferred placement of *Neotalus* and the clade of *A. mina* + *A. picipes*. These three differ only in the arrangement of the species within the *A. tachypoides*-group.

Interpretation of the Pattern

Based on the selected arrangement, it is possible to discuss the pattern in terms of evolutionary process. This involves extrapolation from the observed and summarized data to the likely conditions of the hypothetical ancestors and the character state transformation.

Character Evolution

Of the 30 characters included in the analysis based on my initial hypothesis of homology (Patterson, 1982; de Pinna, 1991), 12 are perfectly congruent ($ci = 1.0$) and can be considered to have passed the test of secondary homology (de Pinna, 1991) (Fig. 31, 32: characters 1, 2, 6, 8, 11, 12, 19, 21, 22, 25, 26, 30). Other characters show some homoplasy but still provide grouping information for some taxa as reversals or convergent origins of states, e.g., the loss of the basal section of stria 1 (Fig. 31: character 7) and the flat-reflexed baso-lateral margin of the pronotum (Fig. 31: character 13). States of only two characters (Fig. 31, 32: characters 14, 29) were shown to be entirely parallel occurrences of conditions not otherwise distinguishable.

The female reproductive tract has several interesting characters that define both generic and species level relationships. The paired dorsal glands of the bursa (Fig. 5) in species of the abariform genera are similar to those found in cicindelines (Deuve, 1993) and some platynines (Liebherr and Zimmerman, 1998), but are unique among all pterostichine taxa. The absence of the diverticulum is a return to the plesiomorphic condition for the pterostichines (Will, 2000), but is clearly a synapomorphic loss for *Neotalus* + *Abaris*. The form of the spermatheca is at once synapomorphic at some levels, e.g., for *A. aenea*-group + *A. picipes*-group clade, and convergent in pairs of different states. Pairing occurs in the *A. striolata*-group [state 0] and (*A. aenea*-group + *A. picipes*-group) [2, although reversed in some]; *A. mina* [0] and *A. picipes* [2]; *A. aquilonaria* [1] and *A. notiophiloides* [0]; and *A. splendidula* [1] and the terminal polytomy including *A. aequinoctialis* [0]. Since some of the species pairs are entirely sympatric, these strikingly different forms of the spermatheca may be indicative of differences in oviposition and/or mating behavior. The ovipositors, however, are almost identical in all species. Most of the variation in form of the bursa and spermatheca is found in species of *Abaris* s.str., e.g., *A. striolata*-group and *A. notiophiloides*. These taxa also have the greatest modifications of the male genitalia.

The male genitalia are quite simple in most species and with a trend toward a very simple, straight median lobe and unmodified endophallus in species of the subgenus *Abaridius*. Paralleling the modifications in the female reproductive tract,

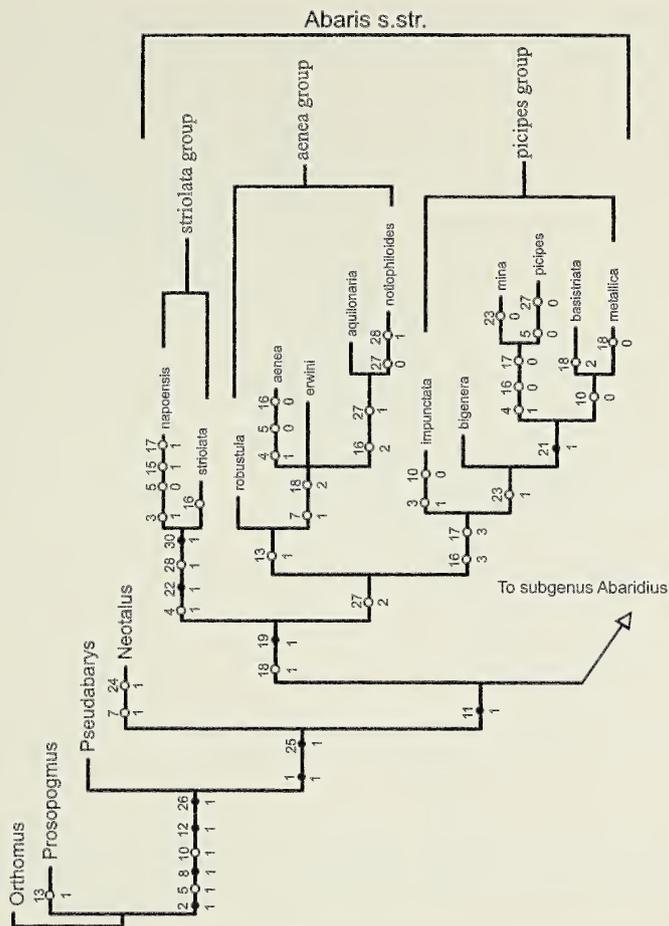


Fig. 31.—Portion of selected cladogram showing outgroup genera, *Neotalus* and *Abaris* (s.str.) species. Unambiguous character state changes are mapped on the cladogram, black discs—non homoplasious change, white—homoplasious change. Numbers above branches are character numbers, below are character state.

species of *Abaris* s.str. have smaller parameres, a relatively larger basal bulb of the median lobe, variously modified median lobe tip, and a spinose and lobed endophallus in some species.

Microsculpturing shows no clear transformation series and is highly homoplasious. From the cladogram one can only generalize that transverse (either faint, obvious or irregular) is in most clades plesiomorphic, and all the other states are frequently derived from it.

Biogeographical Overview

Plant and animal distributions in tropical America have been the data source for many studies on ecological and historical biogeography (see Whitmore and Prance, 1987). Carabid beetles are well represented in these studies (Shpeley and Ball, 1993; Noonan, 1985 and included references). The distribution of *Abaris*

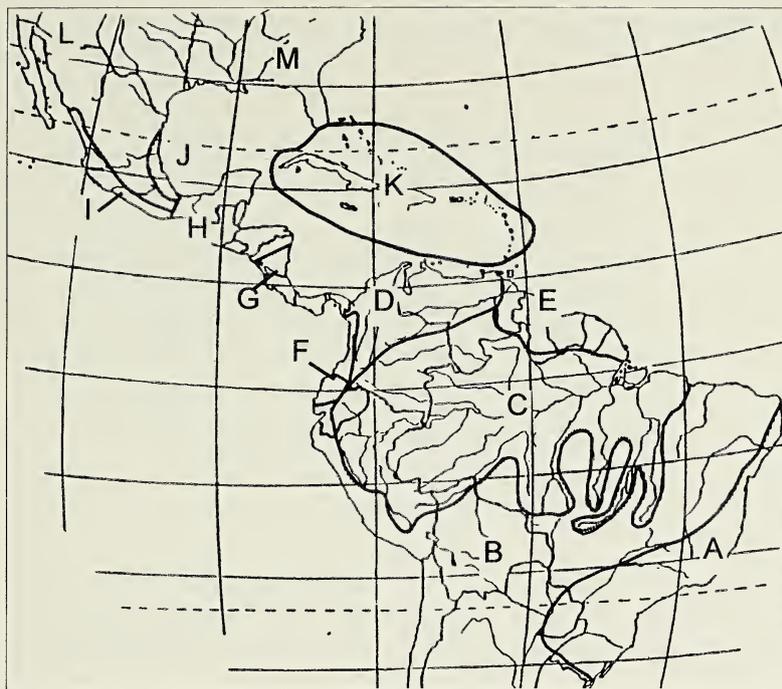


Fig. 33.—Zoogeographic zones in southern North America, the West Indies, Central and South America for *Abaris* and *Coptodera* species. From Shpeley and Ball (1993). See text for explanation of zones.

sumably fly; however, the more arboreal habits and the relatively more numerous records of flight for *Coptodera* species suggest its members fly more frequently.

Descriptive Aspects of Distributions

Refer to distribution maps of species for the following discussion (Fig. 10–17) and to table 1 and figure 33 for zones. Because of the paucity of material and limited number of collecting sites, the analysis of the biogeographical patterns for species of *Neotalus* and *Abaris* must assume the material in hand represents the ranges of species, and therefore the areas assigned to them in the analysis. Several species that have been sampled more adequately have large ranges, and in many cases are sympatric with one or more other species. The collection of more material, especially from the vast and under-collected areas in Brazil, may corroborate or call for revision of hypotheses presented here.

Most *Abaris* species (13 spp.) live entirely or in part in tropical lowland forests corresponding to zone C or the drier forests south of the Amazon Basin, zone B (11 spp.). Only four species, all members of the *A. picipes*-group, have ranges that extend southward beyond the tropics. *Abaris splendidula* is the only species that ranges north of the tropics. The range of *N. portai* also extends south of the tropics.

Members of the *A. aenea*-group and *A. picipes*-group show a marked divergence in habitat breadth. The *A. aenea*-group species are relatively stenotopic and found in moist tropical lowland forest from Bolivia to southern Mexico at ele-

Table 1.—Zoogeographic zones from Shpeley and Ball (1993) used as areas for biogeographical analysis for *Abaris* and *Coptodera* species.

Zone	Area
A	Southern Atlantic South America. Atlantic forest
B	cis-Andean South America south of Amazon Basin from eastern slope of Andes west of zone A
C	Amazon Basin
D	cis-Andean South America north of the Amazon Basin and west of zone E
E	cis-Andean South America north of the Amazon Basin including northern Brazil and the Guianas
F	Chocó refugium in trans-Andean Colombia and Ecuador
G	Lower Central America north to southern Nicaragua
H	Nuclear Central America from Nicaragua to the Isthmus of Tehuantepec in southern Mexico
I	Mexico north of the Isthmus of Tehuantepec, Pacific versant
J	Mexico north of the Isthmus of Tehuantepec, Gulf versant
K	West Indies
L	Southwest United States and northern Mexico
M	Eastern United States

vations of 100–970 m, with most specimens collected from between 200–400 m. In contrast, members of the *A. picipes*-group are centered in drier forests south of the Amazon Basin (zone B), are generally more widespread, and apparently eurytopic. The widespread *A. picipes*-group species have been collected at elevations of 100–1680 m (or as high as 3600 m, see discussion under *A. basistriata* above). In the *A. aenea*-group, *A. aenea* ranges into lower Central America and *A. aquilonaria* is found through nuclear Central America and into southern Mexico at elevations of 200–970 m. Similarly *A. bigenera* and *A. (Abaridius) aequinocialis* are found through nuclear Central America and into southern Mexico. The former, like other *A. picipes*-group species, has been collected at a variety of elevations (200–1680 m) and in several habitat types. Conversely the latter, like the *A. aenea*-group species, has been found only at elevations less than 850 m. Most *Abaridius* species are known from zones B and C; only *A. aequinocialis* and *A. splendidula* occur outside of South America. *Abaris splendidula* lives in drier and cooler habitats and, like the species of the *A. picipes*-group, can be found across a wide range of elevations (0–1100 m).

Biogeographic Analysis

Biogeography is a synthetic field that draws a constellation of data from other disciplines such as systematics, geology and ecology. Historical biogeography (Rosen, 1978:160) specifically attempts to reconstruct the origin of taxa and biotas based on the pattern of relationships found through the systematic study of taxa and the resulting implied genealogy. If each terminal taxon lived exclusively in one area then, the area relationships and historical pattern could be read by replacement of the taxa with their areas on the cladogram. However, distributional patterns are complicated by widespread taxa and redundant areas, i.e., sympatric species distributions (Page, 1990; Nelson, 1984).

Several methods have been proposed to reduce complex taxon-area cladograms to a fundamental area cladogram (Nelson and Platnick, 1981) in which areas occur only once. Component analyses include various conversion rules that make assumptions regarding missing areas, widespread taxa and redundant distributions

(Page, 1990). The methods include Assumption 0 (= Brooks parsimony analysis (BPA), Wiley, 1987); Assumptions 1, 2 (Nelson and Platnick, 1981), and three-area statements (TAS) (Nelson, 1991).

Assumption 0 (BPA) has been criticized as restrictive in its treatment of widespread taxa (Page, 1990:124). Assumptions 1–2 are increasingly more realistic but because of memory handling limitations of the only available computer program, Component 1.5 (Page, 1989), the large number of hypotheses that can result from complex data under these assumptions makes analyses under these assumptions impossible to complete. TAS and three-taxon analysis (3TA) methods and implications have come under extensive criticism (Farris and Kluge, 1998).

An alternative parsimony criterion to the component based analyses is reconciled tree analysis or tree mapping (Page, 1990, 1994; Nelson and Platnick, 1981) (referred by some authors as a component analysis, e.g., Morrone and Carpenter, 1994:101). Although no criteria have been presented that allow for determining a single best method for biogeographical analysis (Morrone and Carpenter, 1994: 111), reconciled tree analysis as implemented in Component 2.0 is interpretable and practical means for analyzing biogeographical data and is used herein.

Reconciled tree analysis finds the best fitting pattern(s) of area relationships for the observed taxon-area cladogram by inserting terms (leaves or components (Page, 1993)) into a user-tree until the observed pattern is reconciled with the presumed area relationships. Three measures of fit for the reconciled tree that have been proposed are (Page, 1994), 1. duplications, 2. leaves added, and 3. number of losses.

“Real” duplication events manifest as redundant nodes (Page, 1994:65) and are explained as primitive sympatry or secondary dispersal events subsequently followed by vicariance (Liebherr and Zimmerman, 1998:157). Minimizing duplications results in a set of trees that generally includes trees produced by minimizing “leaves added”, and so is equal to or larger than that set. The number of leaves added is often reported as items of error (IOE), to measure fit between two trees (Nelson and Platnick, 1981). IOE is readily calculated by doubling the number of leaves added to the observed tree. The measure is easily derived but biological interpretation of this measure is unclear (Page, 1994).

In regard to the reconciled tree, losses are supposed ancestral species that did not disperse into an area or became extinct before a vicariance event resulted in two areas. Thus, absence of potential descendant taxa is accounted for by a single event in the ancestor rather than an event for each leaf and component. This is most clearly thought of in a strictly cospeciation situation when a parasite is lost from a host through extinction. Counting leaves or using IOE may overestimate the number of such events (Page, 1988) by preferring the addition of leaves to reduce duplications. When a heuristic search is conducted for best fitting user-trees for a set of areas where dispersal is deemed likely, minimization of duplications and leaves is appropriate. Such is the case in the Hawaiian Islands (Liebherr and Zimmerman, 1998). In such a system, no preference for ancient versus recent extinction events is defensible.

Focusing on duplications and leaves can increase the number of losses. In a hypothetical example shown in figure 34, the single duplication of the user-tree in 34B requires 3 losses and 10 IOE (5 leaves added) to account for the observed occurrence of area II and its sister-area relationship with area III. Conversely figure 34A has the same number of leaves added (5 leaves = 10 IOE) as 34B, but the paraphyletic relationship of II+III requires one less loss than in 34B. In

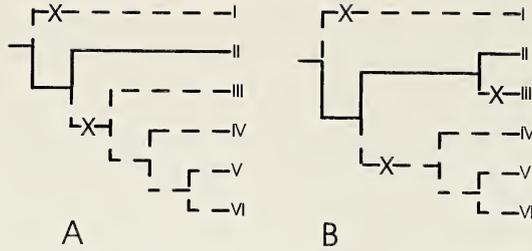


Fig. 34.—Hypothetical components from two reconciled trees for areas I–VI. Both represent a single duplication of the respective user-tree requiring 5 added leaves (dashed lines). Area II represents the occurrence of the area in the observed tree. Losses are mark with an “X.” A. 2 losses. B. 3 losses.

the user-tree 34A, only 2 events (primitive losses or failure of the ancestor to disperse) are required.

In a system where vicariance and not dispersal is held to be the primary type of event, minimizing losses is a more reasonable parsimony criterion. By this method, more tree duplications are acceptable if they result in fewer losses (extinction events) during the history of diversification. This is reasonable for the large continental areas occupied by *Abaris* and *Coptodera* species. Using this criterion does not preclude dispersal as an explanation for parts of the resulting pattern that include duplications. However, these may be best explained as primitive sympatry and subsequent vicariance.

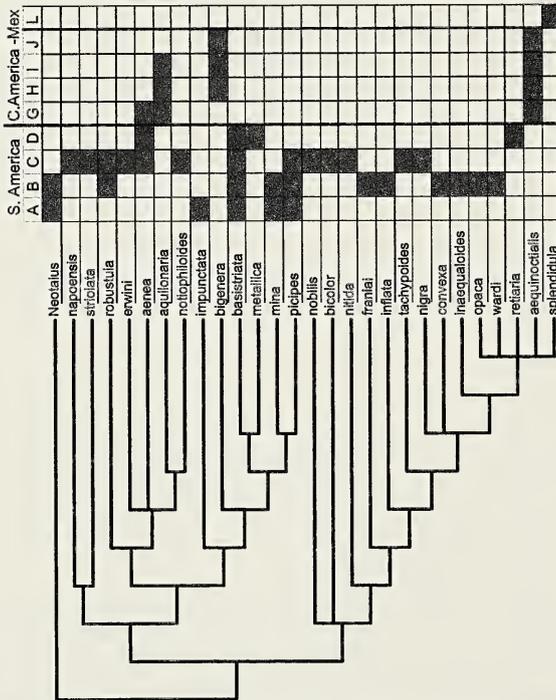


Fig. 35.—Taxon-area cladogram for *Neotalus* and *Abaris* species. See text and figure 33 for explanation of zones.

By looking at the areas relative to their relationships on the preferred cladogram (taxon-area cladogram Fig. 35), it is likely that the present distribution is the result of 4–5 separate dispersal/speciation events into or in Central America. Three pieces of evidence suggest that these dispersals are relatively recent, probably occurring no earlier than the early Pliocene when the Central American land bridge was formed (Stehli and Webb, 1985): 1. few *Abaris* species are present in Central America; 2. no species are found in the West Indies; and 3. all are apparently fully winged. This contrasts with other groups whose ancestors are presumed to have undergone earlier emigration from South America. These groups have greater numbers of Central American and Mexican species (e.g., *Coptodera* (Shpeley and Ball, 1993), *Pseudabarys* (Will, unpubl.)); species in the West Indies (e.g., *Coptodera*, *Dyschromus* (Erwin, 1979)); and/or species with brachypterous flight wings in some Central American species (e.g., *Dyschromus*, *Pseudabarys*).

When no preferred geological hypothesis is available, a heuristic search for a best fitting set of area relationships, a fundamental area cladogram, can be conducted using Component 2.0 (Page, 1993, 1994). Options used in heuristic search and reconciled tree analyses of *Coptodera* and *Neotalus* + *Abaris* included the following: 1. absence was treated as missing data, 2. widespread associates were mapped, 3. branch swapping used was nearest-neighbor interchange, 4. optimality criterion used was minimize losses.

Since the preferred cladogram contains unresolved nodes, Component necessarily resolves them arbitrarily before running the analysis. Allowing these arbitrarily resolved cladograms could permit the use of resolutions that are suboptimal in length. Therefore, a fully resolved cladogram (Fig. 36A) was constructed that was of length 88 steps and contained nearest geographic neighbors. The phylogenetic hypothesis for *Coptodera* also contained unresolved nodes (Shpeley and Ball, 1993, their figure 36). These polytomies were resolved following the species pairs found in the cladistic analysis of Liebherr (presented in appendix B of Shpeley and Ball, 1993; their figure 41A–B). Taxa and area cladograms were submitted to Component and a heuristic search conducted as described above. For the *Neotalus* + *Abaris* species, 196 rearrangements produced 14 area cladograms that equally minimized losses (47 losses, 24 duplications, 164 leaves added), and for *Coptodera* species, 66 rearrangements produced 3 area cladograms that equally minimized losses (99 losses, 36 duplications, 380 leaves added) (Fig. 37A–C). The two sets of area relationships were compared by using Component's quartet dissimilarity measure. Two of the 14 *Neotalus* + *Abaris* species cladograms were found to be more similar to the three *Coptodera* species cladograms than the others (Fig. 37B–C). These two cladograms were used to develop the general historical relationships of the areas and the hypotheses for the process leading to the current distribution of *Abaris*. The strict consensus was also found for each set of data (Fig. 36D, 37D).

Based on the consensus cladograms for the areas, *Neotalus* + *Abaris* diversified in South America first with vicariance of the Atlantic forest (zone A), followed by isolation of the Amazon Basin (zone C), and finally separation of the *cis*-Andean region (zone B). The latter may have remained in contact with zone D by way of habitats along the lower-mid elevation corridor west of the Amazon Basin. This hypothesized corridor would have species distributions like those seen today from Bolivia, Peru, Ecuador, and Colombia, e.g., *A. erwini* and *A. aenea* (Fig. 11, 14). Plausibly, the common ancestor of *Neotalus* + *Abaris* originated in southern South America and species were restricted there until the Pliocene. This

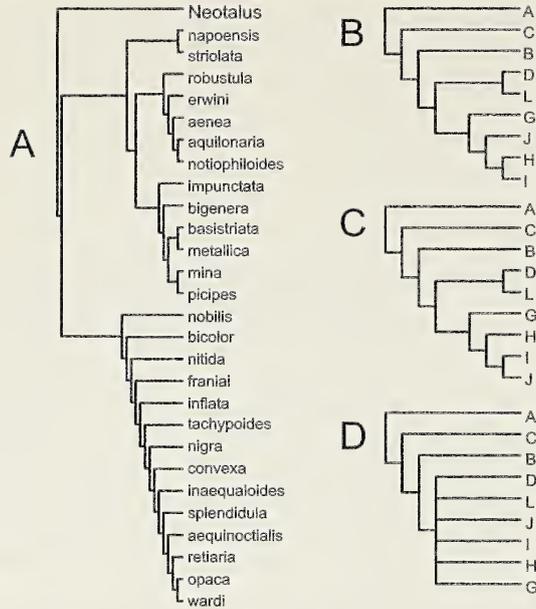


Fig. 36.—Cladograms for *Neotalus* + *Abaris* species and resulting relationships from biogeographical analyses. A. Fully resolved cladogram submitted to Component. B, C. Two of the 14 resulting fundamental area cladograms that were most compatible with the fundamental area cladogram derived from the *Coptodera* analysis. D. Consensus of the 14 fundamental area cladograms.

pattern and timing is similar to the hypothesis presented for ground beetles of the subgenus *Anisotarsus* Chaudoir, 1837 (*Notiobia* Perty, 1830) by Noonan (1981). However, *Abaris* would probably have been found in the subtropical and tropical habitats, as it is today, and not in the warm temperate habitats favorable to *Anisotarsus*.

The consensus cladogram (Fig. 36D) is not resolved for any of the Central American zones. This is a result of having only a few, primarily widespread species in these areas. If the two cladograms that are maximally similar to the results based on *Coptodera* are considered (Fig. 36B–C), the Central American and southern Mexican zones have separated sequentially from south to north. Unlike the results from the analysis of the *Coptodera* data, zones D, northern *cis*-Andean and zone L, northern Mexico + southwestern United States, are shown to have separated from the Central American zones. This suggests additional taxa may remain to be sampled in Central America that would provide evidence for area relationships similar to those resulting from the analysis of *Coptodera* species data.

By comparison, the pattern resulting from analysis of the *Coptodera* species shows a general pattern involving an early divergence of the northern and southern regions and then parallel differentiation proceeding within both sets of areas (Fig. 37A–D). Again, this is consistent with a group reaching proto-Middle America and North America earlier and more frequently than observed for *Abaris*. Such an early divergence (late Cretaceous or early tertiary) and frequent dispersals (10 events south to north) was proposed for *Coptodera* species by Shpeley and Ball (1993:162, 167).

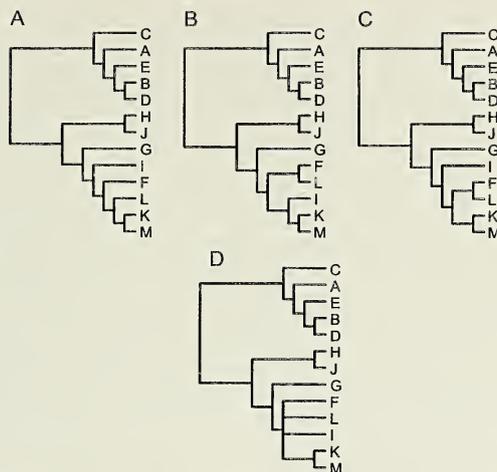


Fig. 37.—Resulting cladograms from the biogeographical analysis of *Coptodera* species. A, B, C. Three possible area relationships produced. D. Consensus cladogram of the three cladograms above.

It is surprising, given the apparent dispersal abilities of *Abaris* species (full flight wings and broad distributions of some species) that none have been found west of the Andes in the Chocó region (zone F) or on any island in the Carribean (zone K). Other carabid groups found in tropical lowland habitats, such as platynines, have established and diversified on all the Antilles (Liebherr, 1997). *Platynus* Bonelli, 1810 is species rich in the islands, *Glyptolenus* Bates, 1878 somewhat less diverse (Liebherr, 1997) and *Abaris* and *Pseudabarys* are completely absent, even from the island of Trinidad. Since *Abaris* is apparently no less vagile than these platynine taxa (some abariform taxa have been collected at lights and are known to fly). The difference may be related to biotic factors (likely for the islands of the West Indies) or inadequate collecting (probable for western South America).

Relative to apparently older elements (e.g., *Dyschromus*), the hypothesis that *Abaris* species simply did not reach northern South America until relatively recently may be sufficient explanation for their absence from the West Indies.

CONCLUSIONS

The monophyletic *Neotalus* + *Abaris* is revised. After necessary nomenclatural changes and the description of 17 newly recognized species (nearly tripling the species number of *Abaris*), the species of *Neotalus* and *Abaris* are now available to students of carabids and tropical biology. It is hoped that the ability to identify species will lead to more extensive study of their habits and perhaps studies that lead to a functional explanation for structures such as the paired bursal glands and pectinate claws.

The remaining abariform genus *Pseudabarys* stands, like *Abaris* stood, with few named species and many recognizable unnamed forms. Once these species are treated to the level of *Abaris*, a broader synthesis will be possible and hopefully another level of understanding reached in Neotropical pterostichine ground beetles.

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APPENDIX 1

Characters 1–30

	5	10	15	20	25	30	
Orthomus	00010	00000	00000	030	00	00000	00000
Prosopogmus	00000	00000	00100	220	01	00000	00000
Pseudabarys	01001	00101	01000	120	01	00000	10000
Neotalus	11001	01101	01000	220	00	00011	10000
aenea	11010	01101	11100	022	11	00001	12000
aequinoctialis	11101	111*1	11000	222	00	00011	10100
aquilonaria	11001	01101	11100	222	11	00001	11000
basistriata	11001	00100	11000	332	11	10101	12000
bicolor	11001	00101	11001	110	??	?????	?????
bigenera	11001	00101	11000	331	11	00101	12000
convexa	11101	11111	11000	332	00	0000?	?????
erwini	11001	01101	11100	122	11	00001	12000
franiai	11101	11111	11001	110	??	?????	?????
impunctata	11101	00100	11000	331	11	0000?	?????
inaequaloides	11101	11110	11010	312	??	?????	?????
inflata	11111	11111	11001	130	??	?????	?????
metallica	11001	00100	11000	330	??	?????	?????
mina	11011	00101	11000	001	11	10001	12000
napoensis	11110	00101	11001	111	11	01001	10101
nigra	11101	11111	11000	332	01	00001	10010
nitida	11111	11101	11001	110	??	?????	?????
nobilis	11001	00101	11001	110	??	?????	?????
notiophiloides	11001	01101	11100	222	11	00001	10100
opaca	11001	11100	11000	332	??	?????	?????
picipes	11010	00101	11000	00(1,2)	11	10101	10000
retiaria	11101	11100	11000	332	00	00011	10?1?
robustula	1100*	00101	11100	121	11	00001	12000
splendidula	11101	11100	11000	232	00	00001	11000
striolata	11011	00101	11000	221	11	01001	10101
tachypoides	11101	11111	11010	330	00	0000?	?????

wardi 11101 11100 11000 332 00 00011 10100

State unknown = ?, Polymorphic = *.

APPENDIX 2

The Nexus File Submitted to Component 2.0 for Neotalus + Abaris

#NEXUS

BEGIN TAXA;

 DIMENSIONS NTAX=9;

 TAXLABELS

 A

 B

 C

 D

 G

 H

 I

 J

 L

 ;

ENDBLOCK;

BEGIN DISTRIBUTION;

 TITLE='BLOCK 1';

 NTAX=28;

 RANGE

 nap : 3,

 str : 3,

 rob : 2 3,

 erw : 3,

 aen : 3 4 5,

 aqu : 5 6 8,

 not : 3,

 imp : 1,

 big : 6 7 8,

 bas : 1 2 3 4,

 met : 4,

 min : 1 2,

 pic : 1 2 3,

 nob : 3,

 bic : 3,

 nit : 3,

 fra : 2,

 inf : 2,

 tac : 3,

 nig : 3,

 con : 2,

 ine : 2,

 spl : 9,

 aeq : 5 6 7 8,

```

ret      : 4,
opa      : 2,
war      : 2,
Neo      : 1 2
;
TREE T1=(28,(((1,2),(3,(4,(5,(6,7))))),(8,(9,((10,11),(12,13)))))),(14,(15,
(16,(17,(18,(19,(20,(21,(22,(23,(24,(25,(26,27))))))))))))));
ENDBLOCK;
BEGIN TREES;

[!>Heuristic search settings:
> Trees fitted to block BLOCK 1
> Absence is treated as missing data
> Widespread associates mapped
> Nearest neighbor interchange (NNI) branch swapping performed
> Total number of rearrangments tried = 196
> Criterion minimised = number of losses
> Trees found = 14
> Minimal value = 45
]

TRANSLATE
1 A,
2 B,
3 C,
4 D,
5 G,
6 H,
7 I,
8 J,
9 L
;
TREE T1=(1,(3,(2,(4,(5,(9,(8,(6,7)))))))));
TREE T2=(1,(3,(2,(4,(5,(9,(7,(6,8)))))))));
TREE T3=(1,(3,(2,(4,(5,((6,8),(7,9)))))));
TREE T4=(1,(3,(2,(4,(5,(9,(6,(7,8)))))))));
TREE T5=(1,(3,(2,(4,((5,9),(8,(6,7)))))));
TREE T6=(1,(3,(2,(4,(9,(5,(8,(6,7)))))))));
TREE T7=(1,(3,(2,(4,((5,9),(7,(6,8)))))));
TREE T8=(1,(3,(2,(4,(9,(5,(7,(6,8)))))))));
TREE T9=(1,(3,(2,(4,((5,(6,8)),(7,9)))))));
TREE T10=(1,(3,(2,(4,((5,9),(6,(7,8)))))));
TREE T11=(1,(3,(2,(4,(9,(5,(6,(7,8)))))))));
TREE T12=(1,(3,(2,((4,9),(5,(8,(6,7)))))));
TREE T13=(1,(3,(2,((4,9),(5,(7,(6,8)))))));
TREE T14=(1,(3,(2,((4,9),(5,(6,(7,8)))))));
ENDBLOCK;

```

The Nexus File Submitted to Component 2.0 for Coptodera

```

#NEXUS
BEGIN TAXA;

```

DIMENSIONS NTAX=13;
TAXLABELS

A
B
C
D
E
F
G
H
I
J
K
L
M

;

ENDBLOCK;

BEGIN DISTRIBUTION;

TITLE='BLOCK 1';

NTAX=43;

RANGE

sal	: 8 10,
ver	: 3,
nisig	: 3,
lin	: 7 8 9 10,
sch	: 3 4 7 8,
rel	: 3,
elon	: 7 8 10,
nvir	: 8 10,
sah	: 1 2 3,
meg	: 3,
ruf	: 1 5,
cham	: 6 7,
chal	: 3,
pic	: 1 2 3 4 5 7 8 10 11 13,
fov	: 10,
poe	: 7,
aen	: 3 5,
aer	: 13,
vir	: 9,
pak	: 3,
way	: 3,
acu	: 1 3 4 5 6 7 8 10,
apic	: 6,
sto	: 7,
fest	: 3 7 8 9 10 11 13,
drom	: 1 2 3 5,
nit	: 1 2 3 5 6 7 8 9 10 12,
brun	: 8 10 12,

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erw      : 3,
ema      : 1 2 3 5,
nig      : 3 5,
teut     : 1,
braz     : 1,
aur      : 8 10,
dep      : 1 2 4,
cup      : 1 2 7 8 10,
sig      : 1,
squ      : 1,
tran     : 1 2 3 4 7 8 9 10,
ful      : 1,
bif      : 1,
xan      : 8 9,
tri      : 1 3;

```

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TREE T1=((1,((7,((5,10),(12,23))),42,(19,34))),((2,35),(((26,(3,(40,(31,(4,
24))))),39,(37,38))),((9,((16,(6,20)),25,(15,(8,(11,32)))))),((17,
(13,(22,30)),((33,36),(41,43))),14,((21,(18,29)),(27,28))))));

```

ENDBLOCK;

BEGIN TREES;

[!>Heuristic search settings:

- > Trees fitted to block BLOCK 1
- > Absence is treated as missing data
- > Widespread associates mapped
- > Nearest neighbor interchange (NNI) branch swapping performed
- > Total number of rearrangments tried = 66
- > Criterion minimised = number of losses
- > Trees found = 3
- > Minimal value = 99

]

TRANSLATE

```

1 A,
2 B,
3 C,
4 D,
5 E,
6 F,
7 G,
8 H,
9 I,
10 J,
11 K,
12 L,
13 M

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;

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TREE T1=((3,(1,(5,(2,4))),((7,(9,(6,(12,(11,13)))))),(8,10)));

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TREE T2=((3,(1,(5,(2,4))),((7,((6,12),(9,(11,13))))),8,10)));

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TREE T3=((3,(1,(5,(2,4))),((7,(9,((6,12),(11,13))))),8,10)));

```

ENDBLOCK;

FROM THE ARCHIVES AND COLLECTIONS

W. J. HOLLAND'S ROLES IN THE 1902 MEETINGS OF THE AMERICAN ASSOCIATION FOR THE ADVANCEMENT OF SCIENCE AND THE AMERICAN ANTHROPOLOGICAL ASSOCIATION

DAVID R. WATTERS¹

THE PITTSBURGH VENUE

One hundred years ago, Pittsburgh was the host city for the 51st Annual Meeting of the American Association for the Advancement of Science (AAAS), from June 28 to July 3, during which the American Anthropological Association (AAA) held its founding meeting on June 30. The meetings actually convened in the Oakland district of the city, although each organization consistently listed Pittsburgh as the venue for its meeting (Howard, 1902; MacDougal, 1902*a*; McGee, 1902*c*; Smith, 1902). In 1890 the city's name had begun to be spelled Pittsburg, the "h" having been dropped following a decision by the U.S. Geographic Names Board (rescinded in 1911), but in practice both spellings were still commonly used in 1902 (e.g., MacDougal, 1902*a*; McGee, 1902*c*).

William Jacob Holland (Fig. 1) deserves credit both for attracting the AAAS meeting to Pittsburgh and selecting Oakland as the venue for its activities. Documents in the Holland Archives at Carnegie Museum of Natural History provide information on his efforts to promote the city as the convention site, the assistance he enlisted to bring this meeting to fruition, and the obstacles he overcame to do so. His achievement is even more impressive when one realizes that Holland had become the Director of Carnegie Museum only four years before the AAAS meeting, had served concurrently as the Chancellor of the Western University of Pennsylvania (now the University of Pittsburgh) for three of those years, until 1901, and was simultaneously involved in intensive efforts to reorganize the museum, acquire collections, institute fieldwork, and plan the museum's expansion in the enlarged Carnegie Institute facility that opened in 1907 (Watters, 2002).

Holland achieved his goal of bringing the AAAS meeting to Pittsburgh because of his prior involvement with AAAS, his personal contacts with important persons in the city, his long-term involvement with the Oakland district, his own organizational skills, the support given by the Museum Committee, and the assistance provided by local corporations, scientific associations, and Pittsburgh's social elite. His ability to orchestrate the overall organization of the 51st AAAS annual meeting derived from his position as Chairman of the local Executive Committee, one of nine local planning committees established to ensure the success of the venture (Table 1).

The purpose of this paper is to present the results of research about the venue of the founding meeting of the American Anthropological Association within the context of the AAAS meeting and the activities of its Section H (Anthropology).

¹ Curator, Section of Anthropology



Fig. 1—William Jacob Holland, Director Emeritus of Carnegie Museum, c. 1930. (Holland Archives, Carnegie Museum of Natural History).

That Pittsburgh was the location for the founding of AAA ties directly to W. J. Holland's desire to have the city host the 51st Annual Meeting of the AAAS. The research project makes use of unpublished documents in the Holland Archives and published data available in the Proceedings of the AAAS 51st Annual Meeting (Howard, 1902) and assorted articles.

PROCURING AND PLANNING THE AAAS MEETING

Holland wanted to host the AAAS 50th Annual Meeting in 1901, but he had to settle for the next year. He first broached this idea to the members of the Museum Committee in June 1900, a mere month after informing them that he would accept the Carnegie Museum directorship on a fulltime basis and would tender his resignation as Chancellor of the Western University of Pennsylvania, as soon as a suitable replacement could be found (which happened in 1901). Holland's rationale for proposing Pittsburgh is preserved:

Table 1.—*Local committees and supporting organizations for the 1902 AAAS Meeting.*

LOCAL COMMITTEES AND CHAIRS FOR THE PITTSBURGH MEETING
Honorary President—George Westinghouse, Jr.
Executive Committee—W. J. Holland
Finance Committee—John B. Jackson
Committee for the Reception and Entertainment of Visiting Ladies—Miss Julia Morgan Harding
Reception and Entertainment Committee—W. N. Frew
Committee on Accommodations, Hotels, etc.—R. D. McGonnigle
Committee on Room, Halls, and Equipment—C. R. Cunningham
Committee on Excursions—Charles F. Scott
Committee on Transportation—Samuel Moody
Committee on Press and Printing—Rev. P. A. McDermott
SUPPORTING ORGANIZATIONS FOR THE PITTSBURGH MEETING
The Trustees of the Carnegie Institute
The Chamber of Commerce of the City of Pittsburgh
The Trustees and Faculty of the Western University of Pennsylvania
The Faculty of the Pittsburgh College of the Holy Ghost
The Engineers' Society of Western Pennsylvania
The Academy of Science & Art of Pittsburgh
The Western Pennsylvania Botanical Society
The Twentieth Century Club
The Pittsburgh Chapter of the Daughters of the American Revolution
The Dolly Madison Chapter of the Sons and Daughters of the War of 1812
The University Club and several other organizations had "announced their intention"

Sources: Howard, L. O. (ed.), 1902, *Proceedings of the 51st AAAS Meeting* (pp. 8–9); *Monthly Report of the Director [for February] to the Museum Committee*, March 3, 1902, pp. 4–5.

INVITATION TO AMERICAN ASSOCIATION FOR THE ADVANCEMENT OF SCIENCE

The Director stated that the American Association for the Advancement of Science, which is now about fifty years old, had never held a meeting in Pittsburgh, for the reason, he believed, that no formal invitation had ever been pressed upon the body. He thought that Pittsburgh would be a most interesting place for the next meeting of the Association, and he recommended that an invitation to meet at the Carnegie Institute next year be extended, and that a committee of three be appointed for that purpose. Whereupon the following resolution was adopted:

Resolved: That a committee of three, consisting of Dr. W. J. Holland, Chairman, C. C. Mellor and John A. Brashear be appointed with instructions to extend an invitation to the American Association for the Advancement of Science to hold its next annual meeting in the year 1901 in the city of Pittsburgh.

Resolved, further, That this committee be instructed to secure, in the extending of this invitation, the assistance and cooperation of the municipal authorities, the trustees of the Carnegie Institute, and the various institutions of learning and learned societies of the cities of Pittsburgh and Allegheny.

Resolved, further, That for this purpose the committee be given full

power to act. (Carnegie Museum, Minutes of the Museum Committee [for July 16, 1900], vol. II, January 3, 1898 to April 1, 1905).

Mellor was the Chairman and Brashear a member of the Museum Committee, so their willingness to appoint themselves to the AAAS invitation committee ensured the close cooperation desired by Holland, as its Chair. Their involvement likewise enabled and facilitated his contact with important local persons who would play key roles in planning an AAAS meeting. Samuel H. Church, the only member of the Museum Committee who did not serve on the invitation committee, became involved with the AAAS meeting in other ways. Pittsburgh and Allegheny (now Pittsburgh's North Side) then were separate cities.

Brashear and Holland had close ties to AAAS. Brashear, a Life Member, joined AAAS in 1884 at its 33rd meeting, became a Fellow in 1885, belonged to three scientific Sections, and in 1900 served as Vice-President of Section D (Mechanical Science and Engineering) at the New York meeting (Howard, 1902:7, 20, 53). Holland joined in 1888 at the 37th meeting, became a Fellow in 1896, and belonged to Section F (Zoology) (Howard, 1902:92). Mellor had been a member of AAAS since 1889 at the 38th meeting, but he did not join a specific scientific Section (Howard, 1902:114). Church became a member at the Pittsburgh meeting, joining two Sections (Howard, 1902:60).

The Minutes of the Museum Committee contain nothing more about the hoped for 1901 AAAS meeting (it went to Denver), and there are only two entries concerning the 1902 meeting. That Pittsburgh had been selected is evident in the Minutes from November 30, 1901, which contain a resolution on the need for a special meeting "... to discuss matters relating to the coming meeting of the American Association for the Advancement of Science." The February 3, 1902 Minutes direct Holland to look into organizing a "... committee for the entertainment of the American Association for the Advancement of Science. ..."

There is another set of documents that provides better background on Holland's efforts to organize the 1902 AAAS meeting. These efforts are outlined in his Monthly Reports of the Director to the Museum Committee, with the reports of April 30 and November 30, 1901, and February 1, March 3, April 30, May 31, and June 30, 1902, pertaining to the AAAS meeting. The April 30, 1901 Monthly Report mentions his effort to "... increase the [AAAS] membership in Pittsburgh ... in view of the fact that that distinguished body is to hold its meeting in 1902 in this city ..." which confirms that Pittsburgh by then had been selected as the location. The November 30 Monthly Report references a letter received from Dr. Charles S. Minot, AAAS President, asking that "... makers of scientific apparatus ..." be invited to exhibit at the meeting, and the report also includes an appeal by Holland to the Museum Committee stating that the preliminary arrangements "... should be taken up by us at once and with energy."

Holland's comments in the Monthly Report for February 1, 1902 are especially interesting in terms of identifying the range of activities involved in preparing for the meeting, for which "... not another moment ought to be allowed to elapse." He says the department of paleontology's entire force was "... busily engaged in extracting material from the matrix and in preparing the same for exhibition in view of the meeting." He had received valuable information from Denver, the site of the preceding AAAS meeting, and mentions a "... gentleman who might perhaps be secured to act as a press agent." He had secured use of the Bellefield Presbyterian Church and the Oakland Methodist Episcopal Church buildings, ob-

tained options on the Music Hall and small lecture room of Carnegie Institute, and notified the proprietor of the Hotel Schenley that his hotel would be the headquarters. Holland had to “. . . take these steps promptly . . .” to forestall use of the buildings by the State Teachers Association of Pennsylvania, which planned to meet in Pittsburgh at the same time as the AAAS.

The March 3 Monthly Report lists ten local groups which already had appointed arrangement committees for the AAAS meeting (Table 1). One might well have empathy for Holland who was to “. . . convene these committees to meet in the Lecture Room of the institution on Friday next at three o'clock.” However, events were “. . . progressing favorably . . .” by the time he wrote his April 30 Monthly Report, to the extent that he had turned his attention to raising “. . . a considerable sum of money . . .” with the expectation that “. . . a generous response will be rendered by our fellow-citizens to the appeal that is about to be made to them for financial assistance.”

The Museum Committee was informed in Holland's May 31 Monthly Report only that “. . . we have been exceedingly busy.” On June 30 he reported “. . . arrangements are well nigh satisfactorily completed” (one would hope so since the AAAS opening general session was held that morning), and he announced that almost “nine thousand dollars has been contributed by the citizens towards the entertainment of the Association. . . .” It is of more than passing interest that there was no Monthly Report for July, and in his August 30 report Holland says “After an absence of between three and four weeks I returned to the Museum on August the 11th.” Even the indomitable Holland deserved a respite.

OAKLAND FACILITIES AND AAAS ACTIVITIES

The facilities Holland reserved initially, the Bellefield Presbyterian Church, the Oakland Methodist Episcopal Church, and Carnegie Institute, had insufficient space for the numerous meetings planned by AAAS and its Affiliated Societies. He expanded the available venues by securing the use of the First United Presbyterian Church, the Bellefield School House, and the Botanical Lecture Hall of Phipps Conservatory, the latter located in nearby Schenley Park (Anonymous, 1902:802). All facilities were within five minutes' walk of the Hotel Schenley, AAAS headquarters (Fig. 2). Carnegie Institute's Music Hall was the venue for general sessions of AAAS, whereas individual Sections and Affiliated Societies held their sessions in the other buildings.

Carnegie Institute, of which Carnegie Museum was one component, was built on the edge of Schenley Park in 1895, one of the first cultural institutions constructed in the developing Oakland district. Holland had close ties to this area long before he assumed the directorship of Carnegie Museum. He had lived in Oakland ever since becoming the pastor of the Bellefield Presbyterian Church, where he served for seventeen years (1874–1891), before becoming Chancellor of the Western University of Pennsylvania, and his home, the former manse adjacent to that church, was but a brief walk from Carnegie Museum. Use of meeting rooms in the Oakland churches by the AAAS was due, in large part, to Holland being a member of the Bellefield Presbyterian Church and to his personal ties to the pastors and trustees of the other churches.

The scientific sessions were the principal reason for attending the AAAS annual meeting. However, members also could avail themselves of excursions from Oakland to many of the manufacturing establishments in the region, which appear to

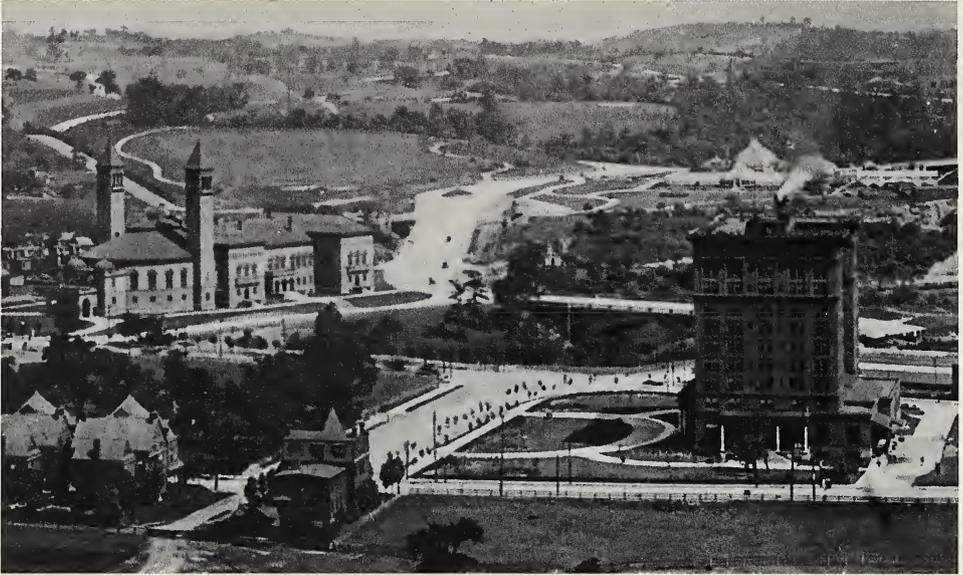


Fig. 2—The Oakland district of Pittsburgh, c. 1905. Carnegie Institute is the building on the left (with the two towers later removed during the 1907 expansion), Hotel Schenley is in the right foreground, and Phipps Conservatory is the domed structure (beyond the hotel) in Schenley Park in the background. (Holland Archives, Carnegie Museum of Natural History).

be the reason the 51st annual meeting was especially well attended by persons representing physics, chemistry, and mechanics and engineering (MacDougal, 1902a:41). The excursions and social activities are documented in Pittsburgh newspapers (e.g., *The Pittsburg Press*, July 1 edition, p. 11) but are mentioned only in passing in the 51st AAAS Proceedings. These extracurricular activities were well received:

The arrangements for the excursions and for the general entertainment of the members were on a larger scale than anything attempted at recent meetings of the Association, the local committee having collected and at its disposal a fund of \$9,000.00 for this purpose. (MacDougal, 1902a:4).

A general schedule for daily activities was outlined in *Science* about five weeks before the meeting:

It is expected that the Council will meet daily at 9 a.m., and that the usual brief general session will assemble at 10:00 a.m., the meetings of the scientific sections following, with a brief interruption for lunches, until 4 o'clock p.m. (Anonymous, 1902:802).

THE AMERICAN ASSOCIATION FOR THE ADVANCEMENT OF SCIENCE

The American Association for the Advancement of Science, at the time it met in Pittsburgh, included ten scientific Sections (A–I and K) and numerous Affiliated Societies (Table 2). A President headed AAAS; Vice-Presidents chaired the Sections. The AAAS Council was comprised of the Past Presidents, Vice-Presidents from the two previous meetings (in New York and Denver), Officers of the Pitts-

Table 2.—*Scientific Sections and Affiliated Societies of AAAS.*

SCIENTIFIC SECTIONS AT THE PITTSBURGH MEETING
Section A. Mathematics and Astronomy
Section B. Physics
Section C. Chemistry
Section D. Mechanical Science and Engineering
Section E. Geology and Geography
Section F. Zoology
Section G. Botany
Section H. Anthropology
Section I. Social and Economic Science
Section J. [None listed]
Section K. Physiology and Experimental Medicine
AFFILIATED SOCIETIES AT THE PITTSBURGH MEETING
American Anthropological Association (affiliated in Pittsburgh)
American Chemical Society
American Folk-Lore Society
American Microscopical Society
American Psychological Association
American Physical Society
American Society of Naturalists
Association of Economic Entomologists
Botanical Society of America
Geological Society of America
National Geographic Society (affiliated in Pittsburgh)
Society for the Promotion of Agricultural Science
Society for the Promotion of Engineering Education

Sources: Howard, L. O. (ed.), 1902, Proceedings of the 51st AAAS Meeting (pp. 3–4, 7); Anonymous, 1902, *Science*, 15:803; and MacDougal, D. T., 1902a, *Science*, 16:43.

burgh Meeting (the incoming Vice-Presidents and Secretaries of the Sections), Members from the Association at Large, and Members from the Affiliated Societies (Howard, 1902:7).

The AAAS met as a body in general sessions, of which the first was held in the Music Hall at 10:00 a.m., Monday, June 30, when retiring President Charles S. Minot relinquished the position to President-Elect Asaph Hall. W. J. Holland, Chair of the local Executive Committee then welcomed members on behalf of Pittsburgh and Allegheny, followed by remarks by Samuel H. Church, Secretary of Carnegie Institute, and George H. Anderson. Their speeches are included in the Proceedings of the 51st Annual Meeting (MacDougal, 1902b:551–558). The Music Hall was the location of three other general sessions, for speeches presented by Leonard P. Kinnicutt, Minot, and Robert T. Hill in the evenings of June 30 and July 1 and 3, respectively (MacDougal, 1902a:44). *The Pittsburgh Gazette* (July 2 edition) reported that more than 1,000 persons attended Minot's speech. According to a report in *The Pittsburg Press* (July 2 edition), the entire Museum Committee—W. J. Holland, C. C. Mellor, S. H. Church, and J. A. Brashear—stood in the receiving line at Minot's reception.

MacDougal (1902a:41–42), AAAS General Secretary, reported 431 members in attendance and 320 papers and addresses read before scientific Sections and Affiliated Societies, with special lectures and evening sessions raising total presentations to nearly 350. MacDougal (1902a:47) lists by name the 73 members

elected AAAS fellows at the Pittsburgh meeting (oddly, MacDougal, 1902*b*:569, says eighty, but provides no names). Smith (1902:201–202) identified nine new fellows as being “. . . interested in anthropology . . .”: Livingston Farrand, William C. Mills, Charles L. Owen, A. E. Jenks, A. H. Thompson, J. D. McGuire, Frank W. Blackmar, William Wallace Tooker, and William Henry Goodyear.

George Westinghouse, Jr., the Honorary President of the Pittsburgh Meeting (Table 1), was elected an Honorary Fellow, only the ninth person so honored by AAAS (Howard, 1902:40–41; MacDougal, 1902:47). Holland emphasized that Westinghouse was deserving of this great honor because of his “. . . knowledge of physics and of mechanics as sciences . . .” (1902:502), not merely for having been the Honorary President. Holland was honored by colleagues in Section F (Zoology), who elected him to the AAAS Council as their Member at Large (Howard, 1902:7, 426). The AAAS selected Washington, D.C., as the venue for its winter meeting six months later, from December 29, 1902, to January 3, 1903.

AAAS SECTION H—ANTHROPOLOGY

Anthropology as a discipline was first represented in AAAS in 1875 at the 24th meeting, when the Subsection of Anthropology was organized under then Section B, the Section of Natural History. Anthropology was assigned to Section H in 1882, at the 31st meeting when AAAS reorganized into nine sections (Howard, 1902:18, 21). Frederick Ward Putnam was the key individual promoting this discipline within AAAS, and he did so during a quarter-century-tenure (1873–1897) as its Permanent Secretary (Kohlstedt, 1999:39–49). Section H had existed for twenty years at the time of the Pittsburgh meeting.

The activities of Section H at the 51st AAAS Annual Meeting are well reported by Harlan I. Smith (1902), the Section’s Secretary. The officers, standing committees, and resolutions (Table 3) are extracted from Smith’s report, augmented by additional sources. J. Walter Fewkes, the retiring Vice-President, was succeeded by Steward Culin; Smith replaced George Grant MacCurdy, the retiring Secretary. When and where the transition occurred are documented:

Section H was organized, in the audience room of the Bellefield [Presbyterian] Church, on Monday morning, June 30, immediately after the adjournment of the general session, and, with two later mentioned exceptions, held all of its sessions in the same place. (Smith, 1902: 201).

The general session to which Smith refers was the first session, convened at 10:00 a.m. in the Carnegie Institute Music Hall, when Asaph succeeded Minot as AAAS President and where Holland, Church, and Anderson welcomed the members. Therefore, Section H’s organizing meeting would have occurred in the late morning, probably around 11:00 a.m. on June 30.

The retiring Vice-President traditionally gave a keynote address to the scientific section he had chaired. J. Walter Fewkes spoke on “Prehistoric Porto Rico” to Section H on Monday afternoon, June 30, at the Oakland Methodist Episcopal Church, referred to by Smith (1902:202) as the Oakland church. *The Pittsburgh Gazette* (July 1 edition) confirms that Fewkes had given his address the day before at the Oakland Methodist Episcopal Church. Fewkes’ (1902*a*, 1902*b*) address was published in *Science* and the 51st Proceedings.

The next two days, July 1 and 2, were devoted to Section H scientific sessions. The Bellefield Presbyterian Church (Fig. 3) was the main venue for anthropology papers, based on Smith’s statement that Section H had “. . . held all of its sessions

Table 3.—AAAS Section H (*Anthropology*) at Pittsburgh.

OFFICERS OF SECTION H

Vice-President: J. Walter Fewkes, 1901 (retiring); Stewart Culin, 1902 (incoming); George A. Dorsey, 1903 (elected)
 Secretary: George Grant MacCurdy, 1901 (retiring); Harlan I. Smith, 1902 (incoming); Roland H. Dixon, 1903 (elected)
 Member of Council: W J McGee (incoming)
 Sectional Committee: Culin and Smith; *ex-officio*, Fewkes and MacCurdy; at large, Franz Boas, G. A. Dorsey, and W. H. Holmes
 Member of the General Committee: Walter Hough

STANDING COMMITTEES OF SECTION H

Committee on Anthropometric Measurements: J. McK. Cattell, W. W. Newell, W J McGee, and Franz Boas
 Committee on the Teaching of Anthropology in America: W J McGee (Chairman), G. G. MacCurdy, Frank Russell, Franz Boas, and W. H. Holmes
 Committee on the Protection and Preservation of Objects of Archaeological Interest: Chairman (open due to the death of Thomas Wilson), F. W. Putnam, N. H. Winchell, G. K. Gilbert, A. W. Butler, and G. A. Dorsey

RESOLUTIONS

On the American International Archaeological Commission: Stewart Culin, Chairman; Harlan I. Smith, Secretary
 On the death of Dr. Thomas Wilson: Warren K. Moorehead, Stewart Culin, Harlan I. Smith, and J. Walter Fewkes
 On the American Anthropological Association: Franz Boas

Sources: Howard, L. O. (ed.), 1902, *Proceedings of the 51st AAAS Meeting* (pp. 5–14); MacDougal, D. T., 1902a, *Science*, 16:45–46; Smith, H. I., 1902, *Science*, 16:201–202; McGee, W J, 1902c, *American Anthropologist*, 4:467–471.



Fig. 3—The Bellefield Presbyterian Church, c. 1900. (Courtesy of the Carnegie Library of Pittsburgh, Pennsylvania Department).

in the same place" (1902:210), with only two exceptions. The first was Fewkes' speech on June 30 at the Oakland Methodist Episcopal Church. The second exception was a brief change of venue from the Bellefield Presbyterian Church to the Bellefield School, during the Tuesday, July 1 afternoon session, for two papers requiring facilities for lantern-slides (Table 4).

A total of 30 papers on anthropological topics were presented at the scientific sessions on July 1 and 2 (MacDougal, 1902*a*:42). The order of presentation and the venues in Table 4 are derived from Smith's (1902:202–212) report, which also abstracts salient points from most papers and mentions persons discussing certain papers. Four papers were read by title only. The Section H sessions on July 2 were held jointly with the American Folk-Lore Society in the morning and the American Anthropological Association in the afternoon. Howard (1902:513–516) lists the same 30 titles, but his ordering differs somewhat from Smith's (cf. McGee, 1902*c*:471–481 for other comments on the papers). Smith (1902:210) and McGee (1902*c*:477) acknowledge the role played by W. J. Holland in arranging for Carnegie Museum's loan of a sculpture, exhibited in conjunction with Marshall H. Saville's lecture on "A Rare Form of Sculpture from Eastern Mexico" on July 2 (Table 4). This sculpture probably was one of the casts of Mexican sculptures recently donated by Andrew Carnegie (Watters, 2002).

THE AMERICAN ANTHROPOLOGICAL ASSOCIATION

The founding meeting of the American Anthropological Association was held in the Oakland district of Pittsburgh at 2:00 p.m. on Monday, June 30, 1902, the same day as the opening general session of the 51st Annual Meeting of the American Association for the Advancement of Science. The AAA founding meeting's time, day, and date and the reason it happened in Pittsburgh are known. What has been uncertain for a century is the meeting's venue; that is, the building in which the AAA founding meeting convened—either the Bellefield Church or the Oakland Church.

Two pre-founding meeting reports by McGee announced the day, date, hour, and place; his post-meeting report corroborated the day, date, and hour but differed in place. McGee (1902*a*:353; 1902*b*:1035) beforehand said the venue would be "... the audience room of Bellefield Church ..." but afterwards stated the "... meeting was held in Oakland Church ..." (McGee, 1902*c*:464). He omitted the denominations of the churches in all three reports.

Smith (1902:201) confirmed that the AAA founding meeting had occurred but did not specify its date or location. Smith wrote this report in his capacity as Secretary of Section H, and it therefore logically focuses on Section H activities. Nevertheless, the report is a valuable document with respect to the AAA, because it clarified one confusing point and provided a lead that was key to determining the venue. Smith (1902:201) places the Section H organizing meeting, at which its new officers were installed (Table 3), at the Bellefield Church in the morning of June 30, and this meeting most likely began around 11:00 a.m., since it followed the AAAS opening general session at 10:00 a.m. Smith's record allows us to discount the notion that the Section H meeting and the AAA founding meeting were held jointly. Even though they happened on the same day and involved many of the same anthropologists, Section H's organizing meeting was in the morning and AAA's founding meeting in the afternoon.

Smith (1902:202) names the "... Oakland church ..." as the location of Vice-

Table 4.—*Anthropological papers presented in Pittsburgh.*

RETIRING VICE-PRESIDENT'S SPEECH TO SECTION H

Monday afternoon, June 30 (at Oakland Methodist Episcopal Church)
 Fewkes, J. Walter, "Prehistoric Porto Rico"

SECTION H SCIENTIFIC SESSIONS

Tuesday, July 1, morning session (at the Bellefield Presbyterian Church)
 Mills, William C., "The Human Effigy Pipe, taken from the Adena Mound, Ross Co., Ohio"
 Moorehead, Warren K., "Gravel Kame Burials in Ohio"
 Mills, William C., "Microscopical Sections of Flint from Flint Ridge, Licking Co., Ohio"
 Hitchcock, C. H., "The Hernandes Shell-heap, Ormond, Florida"
 Moorehead, Warren K., "The Late Dr. Thomas Wilson"
 Dorsey, George A., "An Osage Mourning—War Ceremony"

Tuesday, July 1, afternoon session (at the Bellefield Presbyterian Church)
 Wright, G. Frederick, "Anthropological Museums in Central Asia"
 Wright, G. Frederick, "Climatic Changes in Central Asia traced to their Probable Causes, and discussed with Reference to their Bearing upon the Early Migrations of Mankind"
 McGee, W J, "Mortuary Ceremonies of the Cocopa Indians"

Tuesday, July 1, afternoon session (at the Bellefield School where the session adjourned to avail itself of lantern facilities for the next two papers)
 MacCurdy, George Grant, "A Collection of Crania from Gazelle Peninsula, New Pomerania"
 Mills, William C., "Burials of Adena Mound"

Wednesday, July 2, morning session (at the Bellefield Presbyterian Church; joint meeting with American Folk-Lore Society)
 Houghton, Frederick, "Cooperation Between the Anthropological Museum and the Public School"
 Smith, Lee H., "Uses of Archaeological museums in Education in the Public Schools" (read by title only)
 Hough, Walter, "Explorations of 1901 in Arizona"
 Pepper, George H., "The Throwing-stick of Prehistoric People of the Southwest"

Wednesday, July 2, afternoon session (at the Bellefield Presbyterian Church; joint meeting with American Anthropological Association)
 Fewkes, J. Walter, "A War Festival of the Hopi Indians"
 Saville, Marshall H., "A Rare Form of Sculpture from Eastern Mexico"
 Surface, H. A., "The Possible Origin of the Folk-Lore about Various Animals" (read by title only)
 McGee, W J, "The Place of Anthropology among the Sciences"
 Culin, Stewart, "Anthropological Museums and Museum Economy"
 Holmes, William H. "Classification and Arrangement of the Collections of an Anthropological Museum"
 Smith, Harlan I., "Methods of Collecting Anthropological Material"
 Hough, Walter, "The Preservation of Museum Specimens"
 Fowler, J. A., "The Australian Native" (read by title only)
 Boas, F., "The Growth of Children" (read by title only)
 Moseley, E. L., "Charcoal Covered by Stalagmite in Put-in-Bay"
 Moseley, E. L., "The Sandusky Engraved Slates"
 Smith, Harlan I., "Exhibition of a Modern Clay Tablet from Michigan"
 Leon, Nicolas, "Square Occipital in the Cranium of a Modern Othomi Mestizo"
 Wardle, Harriett Newell, "Evanescent Congenital Pigmentation in the Sacro-Lumbar Region"

Sources: Smith, H. I., 1902, *Science*, 16:202–212; Howard, L. O., 1902, Proceedings of the 51st AAAS Meeting (pp. 513–516); McGee, W J, 1902c, *American Anthropologist*, 4:471–481. [Note: the order of papers, including those read by title only, and the venues are derived from Smith; Howard's list verified the titles but his ordering differed; McGee aggregates papers by related topics, not chronologically; Howard lists journals in which some of the papers were published.]

President Fewkes' address to Section H on Monday afternoon, June 30. He was the only writer to locate Fewkes' speech to a specific building. Moreover, Smith emphasizes the point that the speech at the Oakland church was one of two exceptions to the normal meeting place, the Bellefield Church, for Section H

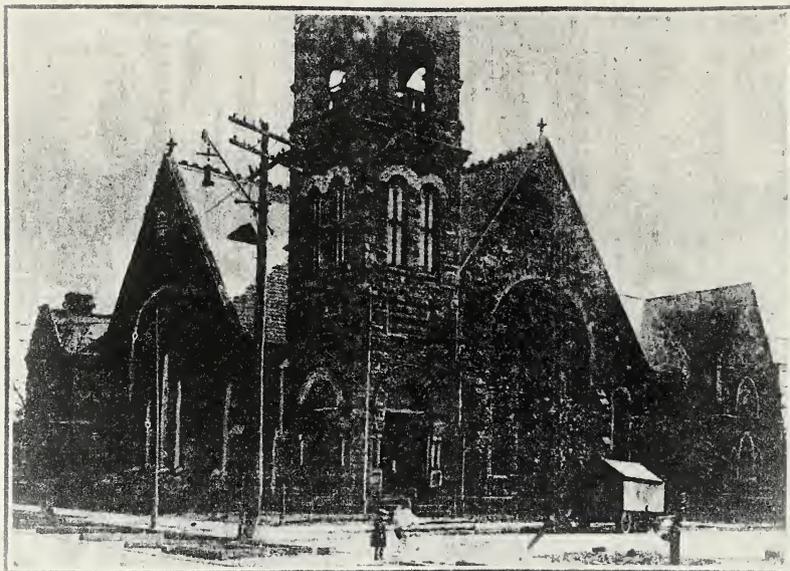


Fig. 4—The Oakland Methodist Episcopal Church one year after it hosted the founding meeting of the American Anthropological Association (from the *Chronicle Telegraph*, October 16, 1903 edition). (Courtesy of the Carnegie Library of Pittsburgh, Pennsylvania Department).

scientific sessions (the other exception was the two lantern-slide talks given on July 1 at Bellefield School). However, Smith does not mention the time when Fewkes gave his address. Smith omitted the denominations of the churches, as had McGee.

A third source, the authorship of which has been attributed to McGee or George A. Dorsey (Stocking, 1960:1 and fn. 2), contains the most detailed account of the events surrounding the founding meeting in Pittsburgh (Anonymous, 1903:184–186). It reiterates the “Oakland Church” as the location for the 2:00 p.m. meeting and adds that Culin, the newly installed Vice-President of Section H, served as the founding meeting’s Chair and Dorsey as its Secretary. This source also lists the thirteen participants: Franz Boas, Stewart Culin, George A. Dorsey, J. Walter Fewkes, J. N. B. Hewitt, William H. Holmes, Walter Hough, George Grant MacCurdy, W J McGee, Joseph D. McGuire, F. W. Putnam, Marshall H. Saville, and Harlan I. Smith.

The evidence better supports the conclusion that the founding meeting of the American Anthropological Association convened in the Oakland Methodist Episcopal Church (Fig. 4) at 2:00 p.m. on Monday, June 30, 1902 (Watters and Fowler, 2002). Three statements support this view. McGee (1902c:464), the newly elected AAA president, named the Oakland Church as the venue, in contradiction to his pre-meeting announcements listing the Bellefield Church. The anonymous author (1903:184) lists the Oakland Church and places Fewkes at the founding meeting before he gave his speech. Smith (1902:202) locates the Section H anthropologists in the Oakland church (a venue exceptional to the norm) on that Monday afternoon to hear Fewkes deliver his address. The sequence of events that afternoon was the AAA founding meeting at 2:00 p.m. followed by Fewkes’ speech sometime later, with both events taking place in the Oakland Methodist Episcopal

Table 5.—*American Anthropological Association (founding meeting) at Pittsburgh.*

 OFFICERS OF AAA

President: W J McGee
 Vice-President (four years): F. W. Putnam
 Vice-President (three years): Franz Boas
 Vice-President (two years): W. H. Holmes
 Vice-President (one year): J. W. Powell
 Secretary: George A. Dorsey
 Treasurer: Roland B. Dixon
 Editor: F. W. Hodge

COUNCIL OF AAA

Frank Baker, Charles P. Bowditch, A. F. Chamberlain, Steward Culin, Livingston Farrand, J. Walter Fewkes, Alice B. Fletcher, J. N. B. Hewitt, Walter Hough, Aleš Hrdlička, A. L. Kroeber, George Grant MacCurdy, O. T. Mason, Washington Matthews, J. D. McGuire, James Mooney, W. W. Newell, Frank Russell, M. H. Saville, Harlan I. Smith, Frederick Starr, John R. Swanton, Cyrus Thomas, and E. S. Wood

EXECUTIVE COMMITTEE

Boas, Culin, Dorsey, Fewkes, Hodge, Holmes, MacCurdy, McGee, and Putnam

STANDING COMMITTEES

Program: Putnam, Boas, Holmes, Powell, Dorsey, Fewkes, and Russell
 Publication: Hodge, Baker, Boas, Chamberlain, Culin, Dorsey, Fletcher, Holmes, Powell, and Putnam
 Finance: not then appointed

AAA REPRESENTATIVES TO COUNCIL OF AAAS

W. H. Holmes and Franz Boas

Sources: Anonymous, 1903, *American Anthropologist*, 5:184–185; McGee, 1902c, *American Anthropologist*, 4:465–466.

Church. This scenario means that anthropologists attending the AAAS annual meeting assembled in two different churches on June 30: (1) in the late morning at the Bellefield Presbyterian Church for the AAAS Section H organizing meeting, and (2) in the afternoon at the Oakland Methodist Episcopal Church for the AAA founding meeting and to hear Fewkes' address.

The officers of AAA and the members of its Council, Executive Committee, and Standing Committees were elected and installed at the founding meeting in Pittsburgh (Table 5). *The Pittsburgh Gazette* (July 1 edition) was the only newspaper reporting the officers elected the day before. There was much overlap between AAA and Section H, both in officers and members (Tables 3 and 5). W J McGee served as AAA President and as the Section H Associate at Large Member of the AAAS Council. Section H President Stewart Culin and Secretary Harlan I. Smith were members of AAA Council and Culin was on its Executive Committee. Franz Boas and William H. Holmes, two of the Vice-Presidents for AAA, served on the Sectional Committee of Section H and as the AAA (Affiliated Society) Representatives to the AAAS Council. There are three examples of specific activities corroborating this close relationship. Franz Boas proposed and Section H adopted the following resolution:

Resolved, That it is the sense of this meeting that it is desirable to bring about the closest possible correlation between the work of Section H of the American Association for the Advancement of Science and the American Anthropological Association. (Smith, 1902:202).

Second, AAAS officially admitted the American Anthropological Association as an Affiliated Society while the Pittsburgh meeting was still in progress (MacDougal, 1902a:43). Third, the scientific session in the afternoon of July 2, only two days after the founding meeting, was a joint meeting of Section H and AAA (Smith, 1902:209).

The AAA founding meeting was the culmination of a lengthy process to create a national anthropological organization, the need for which had been discussed for years (Stocking, 1960; Darnell, 1998:245–254). At a conference in Chicago, held six months before the Pittsburgh meeting, representatives of AAAS Section H, the Anthropological Society of Washington, and the American Ethnological Society met to discuss various issues pertaining to a national organization (Anonymous, 1903; McGee, 1902a, 1902b). Three months after the Chicago meeting, in March 1902, the American Anthropologic[al] Association was incorporated in Washington, D. C. (Anonymous, 1903:181), thereby providing the legal status necessary for the election of officers at the AAA founding meeting in Pittsburgh three months later.

The AAA founding meeting was, in one sense, a *pro forma* meeting, because extensive correspondence and discussion had settled many items on the agenda ahead of time (Stocking, 1960). Details about AAA continued to be worked out at other meetings held at the Hotel Schenley (Anonymous, 1903:184, 186). The relationship of Section H to AAA was a point of discussion on July 1, even before the scientific sessions started at the Bellefield Presbyterian Church (Smith, 1902:202). Thus, the Oakland Methodist Episcopal Church was the building where the AAA founding meeting formally convened, but there certainly were other buildings in Oakland where other meetings were held, before and after the founding meeting, that became instrumental in determining the future directions of the American Anthropological Association (Watters and Fowler, 2002).

The single most contentious issue in the founding of AAA was whether the organization should adopt an exclusive or inclusive policy regarding membership. Boas (1902) and other anthropologists in favor of an exclusionary policy wanted to restrict membership to professional anthropologists, whereas McGee and many others were inclined toward including amateurs or non-professionally trained anthropologists in the membership of AAA. Although this issue nominally dealt merely with membership, in reality it was one aspect of a broader debate centering on the professionalization of the discipline (Stocking, 1960; Darnell, 1998:249–251). McGee and others involved with the March 1902 incorporation of AAA proposed a list of 60 anthropologists to be invited to the founding meeting in Pittsburgh. Boas and his supporters whittled that number down to 40 persons who were canvassed for their views before the Pittsburgh meeting. If the anonymous author (1903:184) is accurate in listing the persons who attended, there were only 13 anthropologists who actually participated in the AAA founding meeting in the Oakland Methodist Episcopal Church.

Not only did the “inclusive” membership policy carry the day, but the period of time in which an individual could be classed as a “founder” of AAA was also extended:

... one of the most important actions taken at Pittsburg was that providing that other anthropologists who so desire may, during the remaining months of the year [1902], become affiliated with the Association and classed as founders. (McGee, 1902c:466).

Anonymous (1903:191–192) confirms that many persons took advantage of the chance to become AAA founders. The list of Life Members (5) and Members (160) covers two pages; of these 165 individuals, 142 (86%) have asterisks beside their names indicating they were “founders of the Association.” Ironically, for reasons that make no sense apart from asterisks having been omitted, inadvertently or otherwise, five of the 13 participants attending the founding meeting in Pittsburgh are not indicated as founders. Franz Boas, J. Walter Fewkes, J. N. B. Hewitt, and Harlan I. Smith have no asterisks, and Marshall H. Saville’s name is not on the list at all.

W. J. Holland and C. C. Mellor, two of the individuals listed as AAA founders, very likely would not have made the list had the exclusionary policy advocated by Boas been adopted in Pittsburgh.

W. J. HOLLAND, THE AAAS, AND THE AAA IN RETROSPECT

Holland rightfully was pleased with the success of the 51st Annual Meeting of AAAS and the roles played by Carnegie Institute and nine local committees in ensuring its success. He expressed these sentiments in his Editorial appearing in the *Annals of Carnegie Museum* later that year. He closed that article by stating:

One of the most gratifying features of the occasion was the universal recognition on the part of the assembled body of scientific men and women of the thoroughness and success of the work which is being done in that department of the Institute which stands for the advancement of science. A becoming modesty forbids us to quote the expressions which were publicly heard, but the appreciation of what has been done in the Museum in the few years of its life, by men who are most competent to express a just judgment, was most gratifying and encouraging. (Holland, 1902:503).

L. O. Howard, the AAAS Permanent Secretary, wrote an overall favorable review of the meeting (though he incorrectly referred to it as the “fifty-second annual meeting”):

In many respects it has been one of the most successful meetings which the Association ever held. The attendance, while not very large, has been composed of members of the active working class, many of them being Fellows, and the meeting may be safely characterized as a working meeting. The registration has shown four hundred and thirty-five members in attendance. . . . It must be remembered as usual that the number registered, namely, 435, includes only the active members and associates of the Association, and that as a matter of fact there are always a few members in attendance who are so characteristically forgetful of all things except scientific matters that they entirely fail to register. . . . [E]ven affiliated societies of a national scope have met with us and have swelled the gathering of scientific men in Pittsburgh during the past week to approximately 750 individuals. The meeting has, therefore, been a scientific congress of great importance. (Howard, 1902:572).

MacDougal (1902a:41) reported a registration of 431 persons while Howard (1902:572) stated 435, so one can surmise that four of the forgetful scientists

must have remembered eventually to register. Howard's comment about the "not very large" attendance is odd, because the same Proceedings volume (Howard, 1902:16) discloses the number of members in attendance at Pittsburgh surpassed the figures for the two prior meetings in New York (434) and Denver (311).

However, not everything went smoothly: "... it must be added, somewhat ungraciously perhaps, that the agreement with the headquarters hotel [Schenley] was so loosely made that exorbitant rates were demanded ..." (MacDougal, 1902*a*:42).

The industrial sector of the economy of Pittsburgh and Allegheny assuredly was a major factor in drawing members of some of the AAAS scientific Sections and Affiliated Societies to the 51st Annual Meeting. Holland, working with Brash-ear and Mellor, the nine local committees, and the supporting organizations was able to draw heavily on the managers of these industries to facilitate the scientific excursions and support the social activities (Table 1). Holland, Church, and Anderson consistently associated science with industry in their speeches (in MacDougal, 1902*b*:551-558). The connection was not lost on AAAS President Asaph Hall, who responded:

It is fortunate for us to meet in the city of Pittsburg, famous for its wonderful production of iron and steel, materials which lie at the foundation of modern civilization. We are glad to see the homes of men who are the munificent benefactors of our libraries and of our scientific institutions. We shall be interested in visiting the great shops where you convert the products of a generous nature into articles for our daily use. (quoted in MacDougal, 1902*b*:558-559).

One of Holland's earliest concerns, expressed in his April 30, 1901 Monthly Report of the Director to the Museum Committee, was to increase the membership of AAAS in Pittsburgh. The AAAS rolls list 12 members from Allegheny and 66 from Pittsburgh (Howard, 1902:240, 246-248), not including other members in a number of nearby towns. Whether the number of local members increased overall as a result of Holland's efforts is uncertain, but his own effort assuredly paid off in terms of persons he employed at Carnegie Museum. Five Carnegie Museum employees, John Bell Hatcher, John A. Shafer, Herbert H. Smith, Douglas Stewart, and Frederick S. Webster are listed as AAAS members (Howard, 1902:247-248), and most appear to have joined for the Pittsburgh meeting. Joining AAAS proved beneficial for Hatcher, Shafer, and Webster because Holland, six months later, sent them to the next AAAS meeting, in Washington, D.C. (Monthly Report of the Director to the Museum Committee, December 31, 1902).

Holland apparently did not present a scientific paper at the Pittsburgh AAAS meeting, as none is listed for him in the papers read before Section F (Zoology). John Bell Hatcher presented the only paper attributed to Carnegie Museum, "Structure of the Pelvic Girdle in the Sauropoda" in Section F (Howard, 1902:459). However, other papers by Carnegie Museum personnel could have been given in meetings of the various Affiliated Societies, since those papers are not always listed in the AAAS Proceedings.

Holland monetarily assisted Carnegie Museum in one instance as a direct result of the AAAS meeting:

After paying all the expenses of the meeting there remains a balance of approximately two thousand dollars [of the \$9,000 raised], which the

donors have unanimously consented to allow to be applied to the acquisition of Egyptian collections for the Carnegie Museum. (Holland, 1902:501).

This money went to the Pittsburgh Chapter of the Egypt Exploration Fund, formally chartered at Carnegie Museum in 1901 largely through Holland's efforts and through which Carnegie Museum obtained substantial Egyptian collections (Watters, 2002; Watters and Patch, 1985).

Holland did not attend the American Anthropological Association's founding meeting, even though he later was classed as a founder. In fact, the only evidence of Holland being involved, even indirectly, with anthropologists in Pittsburgh was the loan he arranged of the Mexican sculpture for Saville's lecture in the joint Section H and AAA scientific session. Nevertheless, Holland can be said to have provided the Oakland Methodist Episcopal Church venue for the AAA founding meeting, since he arranged for the church buildings used for meetings by the Affiliated Societies and scientific Sections. Had the founding meeting taken place, as originally scheduled, in the Bellefield Presbyterian Church, where he formerly had been pastor, the irony would have been delicious.

Holland must be credited with being the person primarily responsible for bringing the 51st Annual Meeting of the American Association for the Advancement of Science to the Oakland district of Pittsburgh. It was the first AAAS meeting held in the city. Pittsburgh twice more hosted AAAS annual meetings (Kohlstedt, Sokal, and Lewenstein, 1999:179), in December 1917, while Holland was still Director of Carnegie Museum, and December 1934, two years after he died. It has not hosted one since.

ACKNOWLEDGMENTS

Throughout Holland's tenure as Director, the institution was known as Carnegie Museum, being changed to Carnegie Museum of Natural History only in 1973. I discovered Holland's involvement with the AAAS 51st Annual Meeting while conducting research into the life of Carl V. Hartman (first anthropology curator at Carnegie Museum) under a grant awarded by the Adrienne and Milton Porter Charitable Foundation. Purely by chance, Don D. Fowler of the University of Nevada, Reno, a professor of mine when I received my M. A. degree there, contacted me in the late summer of 2001 regarding the AAA founding meeting in Pittsburgh in 1902. Don was researching the event for a paper he delivered at the American Anthropological Association annual meeting that fall. It is no small irony that Don and I each received our Ph.D. at the University of Pittsburgh. We decided to join forces and contribute a short report (Watters and Fowler, 2002) to *Anthropology News* (then running a series of reports on the AAA centenary), with Don focusing on historical contexts, while I explored the church venue issues. I opted to write the present article to document the data obtainable from unpublished materials reposing in the Holland Archives (a largely untapped resource pertinent to intriguing scientific and historical issues). I am grateful to CMNH Research Associate Hazel Johnson for researching newspaper reports concerning Holland and the 1902 meetings; CMNH Librarian Bernadette Callery for access to archival and library resources vital to this study; Gil Pietrzak of the Carnegie Library of Pittsburgh for images of the churches; and Don D. Fowler, who many years ago showed me that an undergraduate degree in history could be transformed into a master's degree in anthropology, with interesting results.

A NOTE ON SOURCES

There are three instances where very similar articles were published by the same author in different sources. McGee's (1902*a* and 1902*b*) short articles, both of which announced the upcoming AAA founding meeting, are essentially identical apart from the final paragraph in 1902*a*, listing the prospective founders, that is omitted in 1902*b*. W J McGee's idiosyncrasy of not using periods after his initials has been respected in this publication. MacDougal's 1902*a* report is an abbreviated version of the 1902*b* report in the 51st Proceedings; the latter contains materials omitted from the former, the

speeches of Holland, Church, and Anderson being an example. J. Walter Fewkes' (1902*a*, 1902*b*) Vice-Presidential address is published identically in two sources. I have retained his use of "Porto Rico," but note that it represented the U.S. Government's attempt to anglicize spelling of Spanish words in that newly occupied territory. Authorship of the Anonymous (1903) article, an important resource about the AAA founding meeting, has been attributed to McGee and to Dorsey (see Stocking, 1960:1 and fn. 2, for discussion). I have opted to retain it as anonymously authored. Howard is listed as editor of the 51st AAAS Proceedings (1902), and I have attributed all information therein to him, unless specified otherwise (e.g., MacDougal, 1902*b*; Fewkes, 1902*b*). Pittsburgh newspapers provided coverage of the AAAS meeting, and they contain the only information about certain excursions and most social events. The July 1 and 2 editions of *The Pittsburg Press* and *The Pittsburgh Gazette* are recommended especially (note the newspapers' inconsistent spelling of the city).

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- 4) Chapter in an edited volume:

RAUSCH, R. L. 1963. A review of the distribution of Holarctic mammals. Pp. 29–43, in *Pacific Basin Biogeography* (J. L. Gressitt, ed.). Bishop Museum Press, Honolulu, Hawaii.

- 5) Unpublished dissertation:

SMITH, J. P. 1976. Review of Eocene Mammals. Unpublished Ph.D. Dissert., University of California, Berkeley, California.

- 6) Book:

WHITE, M. J. D. 1961. *The Chromosomes*. Methuen and Co., Ltd., London, United Kingdom.

- 7) Journal articles with usual volume and issue number:

ANDERSON, W. I. 1969. Lower Mississippian condonts from northern Iowa. *Journal of Paleontology*, 43:916–928.

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A LATE MIOCENE–EARLY PLIOCENE POPULATION OF *TRACHEMYS*
(TESTUDINES: EMYDIDAE) FROM EAST TENNESSEEPAUL W. PARMALEE¹

Research Associate, Section of Vertebrate Paleontology

WALTER E. KLIPPEL²PETER A. MEYLAN³J. ALAN HOLMAN⁴

ABSTRACT

A Late Miocene–Early Pliocene (cf. Hemphillian) deposit of plant and vertebrate remains was exposed during preliminary highway construction in Spring 2000 near the city of Gray, Washington County, upper East Tennessee. In addition to as yet unidentified fish, frog, salamander, crocodylian, and rodent species, two taxa of snakes (cf. *Sistrurus* sp., cf. *Regina* sp.), rhinoceros (*Teleoceras* sp.), tapir (*Tapirus*, cf. *T. polkensis*), sloth (cf. *Megalonyx* sp.), gomphothere (Gomphotheriidae), peccary (cf. *Catagonus* sp.), shrew (Soricidae), mustelid (Mustelidae), bear (cf. *Ursus* sp.), and turkey (*Meleagris* sp.) are represented. Remains of at least eight aquatic turtles of the genus *Trachemys* were also recovered, whereas others were lost due to construction and fossil collectors. The pronounced rugosity of the costal bones, deeply serrated anterior and especially posterior peripherals, and deeply incised pygal of the carapace, and a pronounced and deeply serrated anterior margin of the plastron suggest a relationship close to *Trachemys inflata*, an Early Pliocene turtle previously known only from Florida. The numerous individuals represented at the Gray Site indicate a well-established population and may reflect, along with crocodylians and certain terrestrial mammals, a warm environment at some period(s) during the Late Miocene–Early Pliocene.

KEY WORDS: Gray Site, Tennessee, Miocene, Pliocene, *Trachemys*, Carapace, Plastron

INTRODUCTION

In May 2000, Tennessee Department of Transportation (TDOT) construction crews widening State Highway 75 near the city of Gray, Washington County, Tennessee unearthed layers of soft gray clay and an approximately two-meter thick black, ancient lake/swamp deposit rich in plant macrofossils and articulated (for the most part) skeletons of extinct animals. During the summer highway construction was discontinued, and Highway 75 was redesigned to bypass the fossil bed. A chain-link fence was erected around the site, and straw and grass seed were blown over the exposed surfaces to provide protection against erosion. Subsequent core drillings indicated that part of the site (lacustrine deposits) is in excess of 30 meters in depth and covers an area of up to 1.6 hectares. The total area of the site is estimated to be approximately 3.0 hectares, of which 1.4 hectares were exposed during construction.

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Vertebrates identified thus far include a small fish (Osteichthyes), salamander (Caudata), frogs (Ranidae), crocodylians (Alligatoridae), snakes (cf. *Sistrurus* sp., cf. *Regina* sp.), turtles (*Trachemys* sp.), turkey (*Meleagris* sp.), tapir (*Tapirus*, cf. *T. polkensis*), rhinoceros (*Teleoceras* sp.), gomphothere (Gomphotheriidae), sloth (*Megalonyx* sp. or *Pliometanastes* sp.), peccary (cf. *Catagonus* sp.), bear (cf. *Ursus* sp.), shrew (Soricidae), small mouse (Rodentia), and a mustelid (Mustelidae). The occurrence of *Tapirus*, cf. *T. polkensis*, *Teleoceras* sp., a small *Megalonyx* sp. or *Pliometanastes* sp., and cf. *Catagonus* sp. strongly suggests that the mammals from the fossil bed belong to the Hemphillian Land Mammal Age and date to the Late Miocene–Early Pliocene (≥ 4.5 million years ago). Plant remains are extremely abundant, including tree trunks, limbs, seeds, and leaf impressions and occur throughout the various layers of sediment. To date, remains of hickory nuts (*Carya* sp.), acorns (*Quercus* sp.), grape seeds (*Vitis* sp.), and hazel nuts (*Corylus* sp.) have been identified, but a detailed study of the macroflora and pollen has not yet been undertaken. Thus far, preliminary geological investigations have included core samples, stratigraphic profiles, and paleomagnetic dating, but these have yielded inconclusive evidence as to the exact age and formation of the site. The site, believed to be a large water-filled sinkhole or natural basin, provided habitat for a diverse aquatic fauna. Although aquatic mollusks were apparently common during the interval, they were poorly preserved, and most appear as white stains in the lacustrine sediments. A species of pea clam (Spheriidae) and gastropod (Planorbidae: *Helisoma* sp.?) were also identified.

MATERIALS AND METHODS

Throughout late spring and early summer of 2000, students and faculty from the University of Tennessee, Knoxville, periodically collected fossils exposed by earth-moving equipment. Specimens were prepared and catalogued at the University's Zooarchaeology Laboratory and the Frank H. McClung Museum. With few exceptions, all vertebrate specimens recovered at the Gray Site were salvaged after being unearthed during highway construction and/or after the bone-bearing matrix was removed and deposited on fields adjacent to the site. Consequently, few elements survived intact; this was especially true of the turtles. The balance of work at the site in 2000–2001 consisted primarily of salvaging specimens exposed on the surface. Plans for future excavations are being formulated that will be carried out by researchers from the University of Tennessee, Knoxville, and East Tennessee State University, Johnson City, Tennessee.

Well-preserved elements of the plastron and carapace of several individuals were recovered, although in most cases shells were fragmented or disarticulated as a result of the unavoidable method of removal. None of the skeletons of individual turtles encountered were complete. Depending upon the type of matrix in which they were preserved, some shells could easily be removed, cleaned (brushing with water, soaking in calgon), and repaired, whereas others were cemented to a conglomerate of sand and pebbles, usually to the inside of the carapace. Except for sections of a lower jaw found with one individual and fewer than a dozen fragmented limb bones, the majority of appendicular skeletal elements appear either to have been lost during removal of the deposit by earth-moving equipment or were disassociated from the shell prior to burial.

The most complete sections of plastron and carapace recovered at the Gray Site, representing several individuals, were compared with the modern skeletons

of the genera *Chrysemys*, *Trachemys*, and *Graptemys* housed in the collections of the Zooarchaeology Section, Department of Anthropology, University of Tennessee, Knoxville and the Michigan State University Museum, East Lansing. On the basis of descriptions and illustrations of fossil turtles of Hemphillian Age in North America by Hay (1908) and Weaver and Robertson (1967), and comparison with those of other repositories, the aquatic turtles from the Gray Site can be assigned to the genus *Trachemys* within the Family Emydidae, as possibly a representative of the *Trachemys scripta* complex or a closely related species within the genus.

DESCRIPTION AND DISCUSSION

The characters used most frequently to distinguish among the closely related living species of sliders and cooters of the genera *Pseudemys* and *Trachemys* are external. They include general carapace shape and the colors and patterns of the shell, head, neck and limbs. Because very few skulls of this group have been described, the systematics of fossil cooters and sliders is based almost entirely on variation in the shell, including differences in bone and scute arrangement, size and overlap of certain scutes, surface texture, bone thickness, and within *Trachemys*, degree of carapacial inflation (e.g., Hay, 1908). Within the larger group, members of the genus *Trachemys* are easily recognized. They are the only forms with doubly serrate carapacial margins (Seidel and Jackson, 1990). In fossil and living *Trachemys* (except some neotropical forms), there is a notch in the carapacial margin at the sulcus between each pair of marginal scutes and a notch between each pair of peripheral bones. Together, these features produce a doubly-serrate posterior carapace margin. Although recognition of the genus is not problematic, because of the subjective nature of the characters used, and because the types of several species are fragmentary pieces of shell, the validity of several fossil *Trachemys* species have been questioned. Weaver and Robertson (1967) re-evaluated the nine species of *Trachemys* listed by Hay (1908) and synonymized six with *Chrysemys* (= *Trachemys*) *scripta petrolei*, a mid-Pleistocene subspecies. Moreover, they identified one as *Terrapene*, another as *Deirochelys*, and a third as closer to *Chrysemys picta* than to *T. scripta*.

Weaver and Robertson (1967:58) described two new fossil species of *Chrysemys* (= *Trachemys*) from Florida, *T. inflata* from the Pliocene, and *T. platymarginata* from the Pleistocene. They concluded that *T. inflata* was a member of the *T. scripta* complex "... the basis of the highly sculptured scute areas of the nuchal bone, the associated double toothed peripheral bones, epiplastra having an extensive gular scute overlap and nuchal bone with extensive nuchal scute underlap, and neural bones whose architecture suggests the presence of a well defined median keel on the carapace." In addition, they indicated that *Trachemys inflata* differed from the fossil *T. scripta petrolei* and living *T. s. scripta*, *T. s. troosti*, and *T. s. elegans* by the shape, depth, and width of the anterior nuchal notch and the smooth medial half of the marginal scute area of the nuchal bone.

There is some doubt that *Trachemys inflata* is a valid species, as well as uncertainty as to its evolutionary position in the *T. scripta* complex. Weaver and Rose (1967:70) commented that "*Chrysemys* [*Trachemys*] *inflata* is unquestionably a member of the evolutionary line leading to North American *C. scripta*..." This view was also repeated by Auffenberg (1972). Weaver and Robertson (1967:65), on the other hand, expressed the view that "The extent of the nuchal and peripheral bone notching and the massive, rugose grooves and ridges

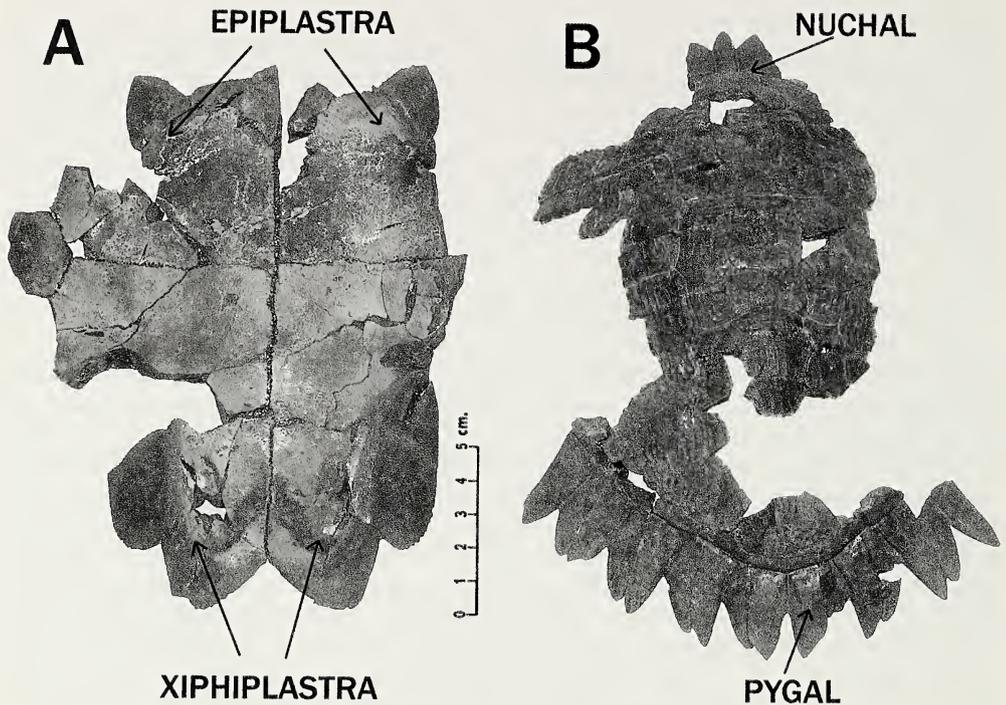


Fig. 1—Plastron TDOT 13.01A and carapace TDOT 13.02B sections (same individual) of *Trachemys*, cf. *T. inflata* from the Gray Site, Tennessee. Note the characteristic deeply serrated posterior peripheral bones of the carapace. Catalog Nos.: A. TDOT 13.01. B. TDOT 13.02.

of *C. inflata* suggest that it was a specialized or aberrant species characterized by an extreme development of *Trachemys* features and not representative of the main evolutionary sequence leading to recent *C. scripta*.”

Specimens from the Gray Site tend to exhibit characters of *Trachemys scripta*, and particularly those of *T. inflata*. The general shape, sculpture, and deep notching of the nuchal bone, the exaggerated rugosity of the costals, and especially the deeply notched, sharp-angled posterior peripheral bones (Fig. 1B) are suggestive of *T. inflata*. As in most extant subspecies of *Trachemys scripta*, and the few known specimens of *T. inflata*, neural bones of the Gray Site specimens are smooth and lack any evidence of a median keel on the carapace. Although incomplete, plastra (Fig. 2) from the Gray Site compare closely with those of taxa belonging to the *T. scripta* complex except for the deeper, narrower anal notch, and the anterior margin of the epiplastra, which exhibits a more pronounced and deeper serrated edge than is found in living *Trachemys*.

Representative plastra and carapace sections of *Trachemys* from the Gray Site were compared with the type and other material of *T. inflata*, a large series of *T. platymarginata*, and undescribed specimens of the *T. scripta* group from the Moss Acres Racetrack Site (Hulbert, 2001), all from Florida fossil sites and housed in the Florida Museum of Natural History, Gainesville. In the holotype of *T. inflata* the bone under each scute area on the nuchal is greatly inflated, as are the adjacent peripherals. In the Gray Site specimens the scute areas are thick but not noticeably

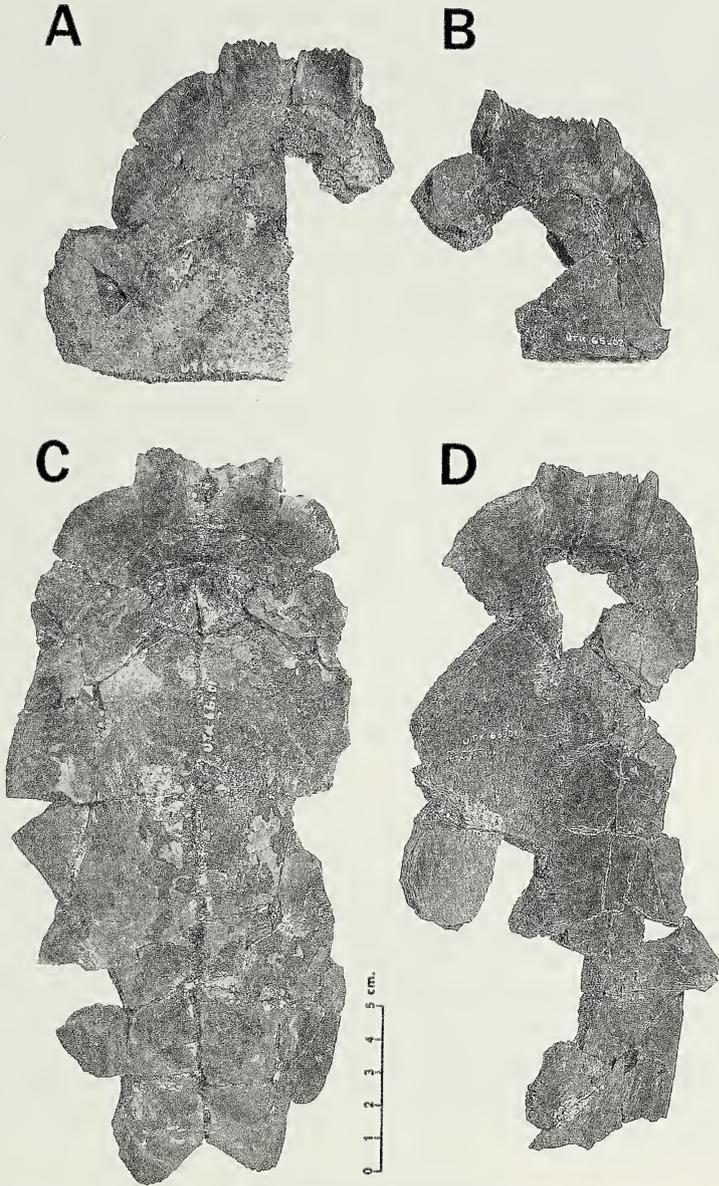


Fig. 2—A–D. Selected examples of plastra of *Trachemys*, cf. *T. inflata* from the Gray Site, Tennessee, exhibiting a pronounced and deeply serrated anterior margin. Catalog Nos.: A. UTK 65.02. B. UTK 64.02. C. UTK 63.01. D. UTK 66.01.

inflated. However, it seems possible that this character, involving the degree of inflation, may vary with size and/or age.

Of the eight individuals of *Trachemys* represented in the Gray Site emydid material recovered so far, only one carapace (Fig. 1B) and one plastron (Fig. 2C) of different individuals could be restored to permit a total length measurement.

Both measured 210 mm and compare well in size to the Moss Acres Racetrack Site *T. scripta* specimens, but are much smaller than those of *T. inflata* and *T. platymarginata* (Late Pliocene). In addition, *Trachemys* from the Gray Site differs from *T. platymarginata* in having a much more rugose carapace, especially anteriorly, and in the anterior margin being deeply serrate.

As already noted, the carapace of the Gray Site *Trachemys* is extremely serrate, especially the posterior peripheral bones, and the serrations are deeper than those observed in *T. platymarginata*, *T. inflata*, and the undescribed specimens of *T. scripta* from the Moss Acres Racetrack Site. On the other hand, the plastron of the Gray Site specimens are comparable to the Moss Acres Racetrack Site *T. scripta* in having projecting epiplastra with a finely serrate anterior margin. However, the pygal of the Gray Site specimens is more like *T. inflata* in being deeply incised.

Taking into account the variability of certain characters used to distinguish among the species of *Trachemys* from the Late Miocene–Early Pliocene, we refer the Gray Site specimens to *Trachemys*, cf. *T. inflata*. The presence of this species of aquatic turtle, as well as the crocodylians, tapirs, rhinoceros and peccaries, suggests that the climate during which the Gray Site (sinkhole?) sediments accumulated was warm. Farlow et al. (2001) described a diverse fauna of Hemphillian Age (in part) from the Pipe Creek Sinkhole Site in north-central Indiana as also indicating a warm environment with possibly an adjacent dry, open grassland or savannah habitat. In the case of the Gray Site, however, the vertebrate taxa identified thus far in association with the macroflora constitute a unique assemblage that will permit reconstruction of a Late Miocene–Early Pliocene biota unequalled in most other regions of eastern North America.

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REDESCRIPTION OF *EOPELOBATES GRANDIS*, A LATE EOCENE ANURAN FROM THE CHADRON FORMATION OF SOUTH DAKOTA

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ABSTRACT

Eopelobates grandis, an anuran from the Upper Eocene Chadron Formation (Ahern Member) of South Dakota, is redescribed and its generic assignment confirmed. The pterygoid, which was originally identified as the suprascapula, and parahyoid bones are described for the first time for this taxon, and the presence of a quadratojugal is verified. *Eopelobates grandis* can be distinguished from other *Eopelobates* species by its highly tuberculated dermal sculpture, broad frontoparietal, and rounded otic ramus of the squamosal. A preliminary analysis of interspecific relationships indicates that *E. grandis* is more closely related to the European *E. anthracinus* and *E. bayeri* than to *E. hinschei* and *E. wagneri*, also from Europe. The Late Cretaceous record of *Eopelobates* from the Lance Formation of Wyoming and the Hell Creek Formation of Montana is placed in doubt. Based on the current fossil record, *Eopelobates* was thus restricted to the Tertiary of North America and Europe. Dispersal of *Eopelobates* probably occurred during the Late Paleocene/Early Eocene when a North Atlantic land-bridge connected North America and Europe.

KEY WORDS: Amphibia, Anura, Pelobatidae, *Eopelobates*, Late Eocene, South Dakota

INTRODUCTION

The pelobatid anuran *Eopelobates* was thought to have a Holarctic distribution spanning the Cretaceous to the Miocene, based on descriptions of ten species from North America, Europe, and Asia (Duellman and Trueb, 1986). However, the relatively recent restudy of some of these species has suggested that the diversity, geographic distribution, and geologic time span of this genus may not be as great as was once indicated. Two species from the Upper Cretaceous of Mongolia and Uzbekistan that represented the only described and named Cretaceous and Asian record of *Eopelobates* have been reassigned to a different genus and family (Špinar and Tatarinov, 1986; Roček and Nessov, 1993). In a review of Anura, Sanchíz (1998) considered the European record of *Eopelobates*, which is restricted to the Tertiary, to be the only valid one for the genus, because the generic identification of North American *Eopelobates* species had been questioned by Roček (1981). Without giving them new generic names, Sanchíz (1998) tentatively assigned the North American species of *Eopelobates* to Megophryinae following Zweifel (1956) and Estes (1970), who noticed similarities between North American *Eopelobates* and megophryids. The most recent overview of the genus is provided by Roček and Rage (2000) in a review of Tertiary anurans. This paper presents the second part of a study that I have undertaken in an attempt to clarify the taxonomic status of North American *Eopelobates*.

Two species of *Eopelobates* have been described from North America: *E. grandis* and *E. guthriei*. Roček (1981) cast doubt on their placement in *Eopelobates*, because their frontoparietals were figured and/or described as being paired by Estes (1970:fig. 13, 14) in contrast to *Eopelobates* and *Pelobates*, which have a

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frontoparietal derived from three ossifications. Roček further suggested that *E. grandis* and *E. guthriei* are more closely related to the North American pelobatid *Scaphiopus* which, like most anurans, has paired frontoparietals. Presumed lack of a quadratojugal was given as evidence supporting their relationship with *Scaphiopus* (Roček, 1981).

A recent reexamination (Henrici, 2000) of the oldest described North American *Eopelobates*, *E. guthriei* from the Lower Eocene Wind River Formation of Wyoming, reidentified it as cf. *Scaphiopus guthriei*. The generic reassignment was based on the following derived characters: 1) presence of an elongate postchoanal ramus of the vomer that articulates with the pars palatina of the maxilla; 2) lack of hyossification of cranial bones; and 3) presence of a long, low, arcuate ventral flange of the pterygoid. Definite placement of this species in *Scaphiopus* was not made because the postcranial skeleton remains largely unknown, and thus it could not be determined if cf. *S. guthriei* possesses documented derived postcranial features (Henrici, 1994; Maglia, 1998) shared by *Scaphiopus* and the closely related *Spea*.

The taxonomic status of the other described North American *Eopelobates* species, *E. grandis*, is the focus of this study. Zweifel (1956) named this species on the basis of a single, articulated, and well-preserved specimen (YPM-PU 16441) from the Ahern Member of the Chadron Formation of South Dakota. At the time of Zweifel's (1956) description, the Chadron Formation was regarded as Early Oligocene, but now it is placed in the Late Eocene based on recalibration of the geologic time scale (Berggren et al., 1995). A brief redescription of this specimen was provided by Estes (1970).

Two other occurrences of *Eopelobates* in North America have been reported. Some isolated bones recovered from the Lance Formation of Wyoming were questionably referred to Pelobatidae by Estes (1964). Part of this material, as well as some new specimens (isolated bones) from the Hell Creek Formation, Montana, was questionably identified as either *Eopelobates* or a related pelobatid (Estes et al., 1969; Estes, 1970). Estes and Sanchíz (1982) later identified these specimens as *Eopelobates* sp. Because Sanchíz (1998) did not consider the North American record of *Eopelobates* to be valid, he questioned the assignment of these specimens to this genus. Roček (2000), however, did not dispute the generic assignment of the Lance and Hell Creek anurans in his review of Mesozoic anurans.

In a publication on the Middle Eocene Green River fauna and flora, Grande (1984:fig. III.1a) published a photograph of a nearly complete anuran skeleton that he identified as possibly a new species of *Eopelobates*. An additional specimen of this taxon is housed in the collections of the Staatliches Museum für Naturkunde, Karlsruhe, Germany (Wuttke, personal communication). Roček and Rage (2000) provide a brief description of the specimen figured by Grande (1984), and they suggested that it is close to *Eopelobates* and *Pelobates*. As this specimen lacks the burrowing specializations found in the skeleton of *Pelobates*, its affinities most likely lie with *Eopelobates*, and it will thus be referred to here as the "Green River *Eopelobates*."

ABBREVIATIONS

Institutional Acronyms.—CM, Carnegie Museum of Natural History, Pittsburgh; FMNH, Field Museum of Natural History, Chicago; GM, Geiseltalmuseum, Halle; SMF, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt;

YPM-PU, Yale Peabody Museum, Yale University, New Haven (formerly housed at Princeton University).

SYSTEMATIC PALEONTOLOGY

Class Amphibia Linnaeus, 1758

Order Anura Rafinesque, 1815

Family Pelobatidae Bonaparte, 1850

Genus *Eopelobates* Parker, 1929

Revised diagnosis (modified from Sanchíz, 1998).—*Eopelobates* differs from other pelobatids by the following unique characters: 1) nasal triangular with relatively straight anterolateral margin and long, slender lateral process; and 2) combined length of tibiofibula and femur subequal to or greater than the snout-vent length. *Eopelobates* further differs from other pelobatids by the following unique combination of characters: 1) dermal sculpture present and generally consists of pits and grooves, although tubercles are present in one species; 2) frontoparietal comprised of three ossifications; 3) sphenethmoid anteriorly wide and blunt; 4) ilial shaft strongly arched and bears crest in midshaft region; 5) tibiofibula length equal to or greater than length of femur; and 6) bony spade absent.

Eopelobates grandis Zweifel 1956

Holotype.—YPM-PU 16441; mostly complete skeleton.

Horizon and Type Locality.—Late Eocene; Ahern Member of the Chadron Formation. Divide between West Fork and Main Fork of Indian Creek, one half mile south of forks. SE1/4, S34, T.3S, R.12E, Pennington County, South Dakota.

Revised diagnosis.—*Eopelobates grandis* differs from other members of the genus by the following unique characters: dermal sculpture highly tuberculated; frontoparietal broad, in which the width is about 84% of the length; and otic process of squamosal rounded.

Description and Comparisons

The skeleton of the holotype (Fig. 1–4) and only known specimen (YPM-PU 16441) is fairly complete, but lacks the snout, most of the left maxillary arch, the left forelimb, right manus, and portions of both hind feet. Extensive dorsoventral compression has caused considerable overall flattening of the specimen and many of the individual bones, resulting in disarticulation of some of the bones which, for the most part, have remained closely associated. Additionally, numerous cracks and breaks are present in the bones. The skeleton is a large example of *Eopelobates*, having an estimated snout-vent length (snout-vent length measured here as anterior tip of skull to distal end of ischium) of 82 mm.

Since Zweifel's description of *E. grandis* and sometime before this study the specimen underwent a considerable amount of preparation that resulted in exposure of some new features as well as damage to others. Minor preparation has been undertaken for this study to better expose a few aspects of the skeleton, mainly the left nasal, right quadratojugal, and right vomer.

Skull.—The frontoparietals, nasals, maxillae, and squamosals are heavily sculpted (Fig. 3). Although matrix obscures the pattern of sculpturing somewhat, it can be discerned that the sculpture is extremely reticulated and tubercular. It most closely resembles that occurring in a large *Scaphiopus holbrooki* specimen



Fig. 1—Skeleton of *Eopelobates grandis* (holotype, YPM-PU 16441) in dorsal aspect. Scale bar = 1 cm.

(CM 18719, snout-vent length = 73mm). In smaller *S. holbrooki* (CM 374400, snout-vent length = 57mm; CM 118968, snout-vent length = 52mm) the tubercles are more widely spaced and the reticulations are not as well defined. The dermal sculpture differs somewhat dramatically from that of other *Eopelobates*, which have pits that in places form a reticulated pattern, and grooves but no tubercles.

The frontoparietal is broadest at roughly two-thirds the length from the anterior end; its breadth being roughly 84% of the length of the bone. The fontanelle is not exposed. An important character of the frontoparietal is whether it is paired, as in most anurans, or comprised of three ossifications, as in *Eopelobates* and *Pelobates* (Roček, 1981; Henrici, 1994). Although Zweifel (1956) did not state that the frontoparietal of *E. grandis* is paired, Estes (1970:fig. 13A) illustrated it as paired. A median suture is visible (Fig. 3) in a broad, deep groove that extends

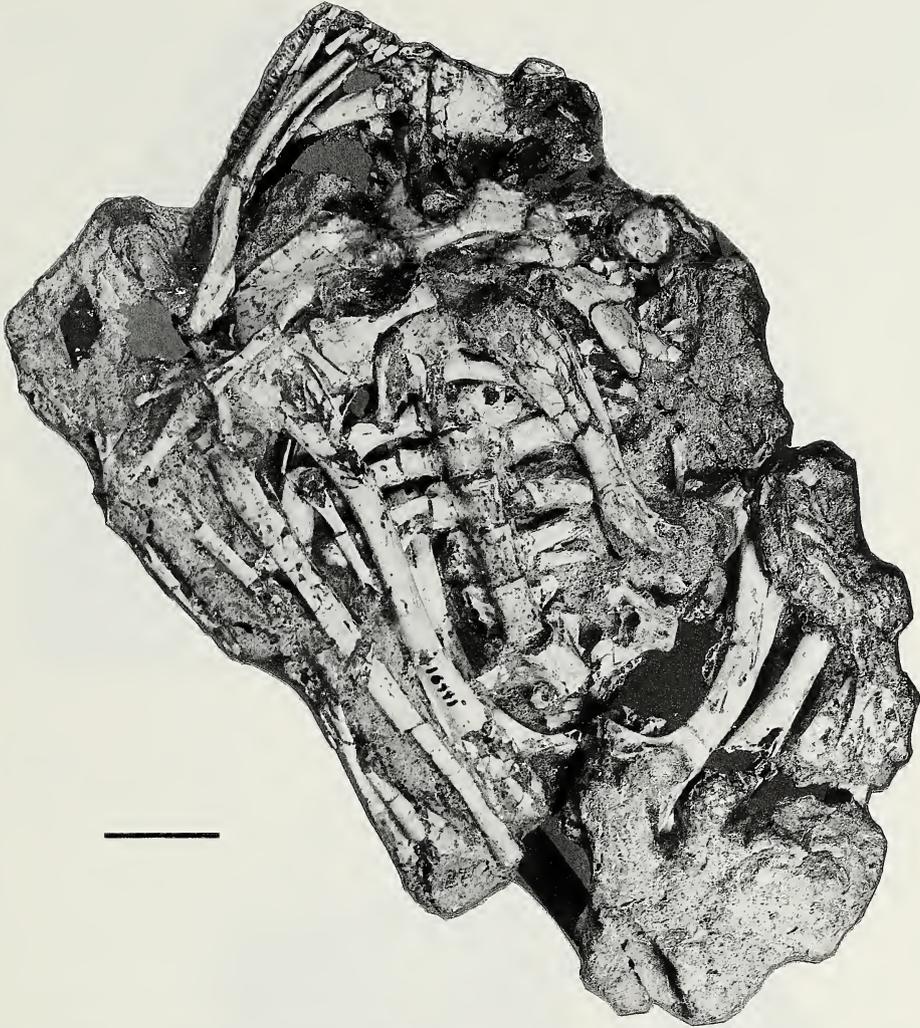


Fig. 2—Skeleton of *Epelobates grandis* (holotype, YPM-PU 16441) in ventral aspect. Scale bar = 1 cm.

two-thirds of the length from the anterior end. The groove appears to be the result of preparation to make the median suture more visible. Posteriorly, the groove narrows and then disappears near the widest point of the frontoparietal. The highly sculpted surface and matrix, which cannot be removed without damaging the specimen, make it impossible to trace the suture farther posteriorly. The posterior margin of the frontoparietal forms a very small, posteriorly-projecting median apex (Fig. 4) that lacks sculpturing and, more importantly, does not bear a median suture. This is in contrast to *Scaphiopus*, where in some specimens the median suture is obscured by dermal sculpture except for the smooth bone of the median apex where the suture is highly visible. The lack of a median suture on the smooth bone of the median apex in YPM-PU 16441 provides evidence that a postero-median ossification is present because it prevents the median suture from reaching

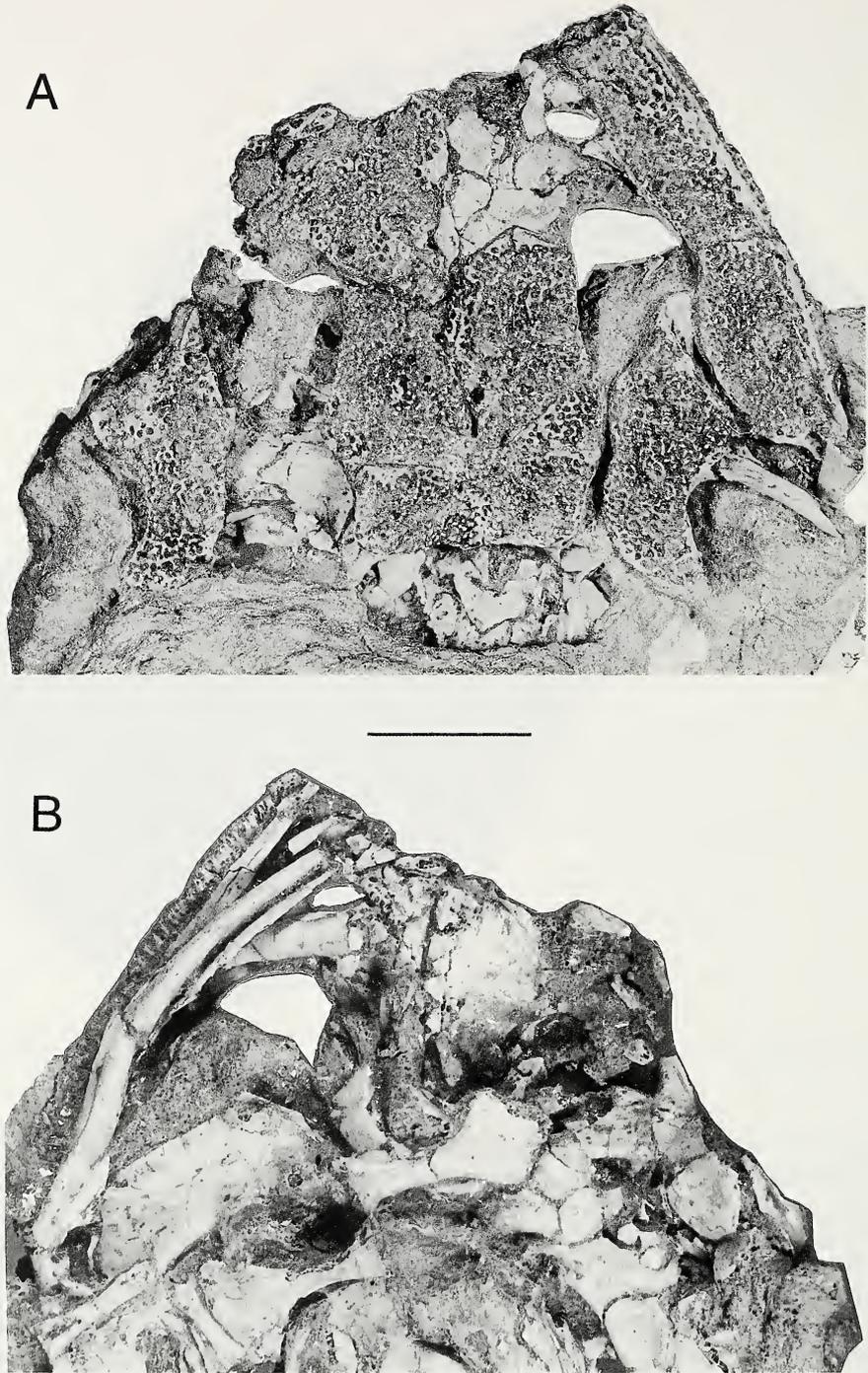


Fig. 3—*Eopelobates grandis* (holotype, YPM-PU 16441). Photograph of skull. A. Dorsal aspect. B. Ventral aspect. Scale bar = 1 cm.

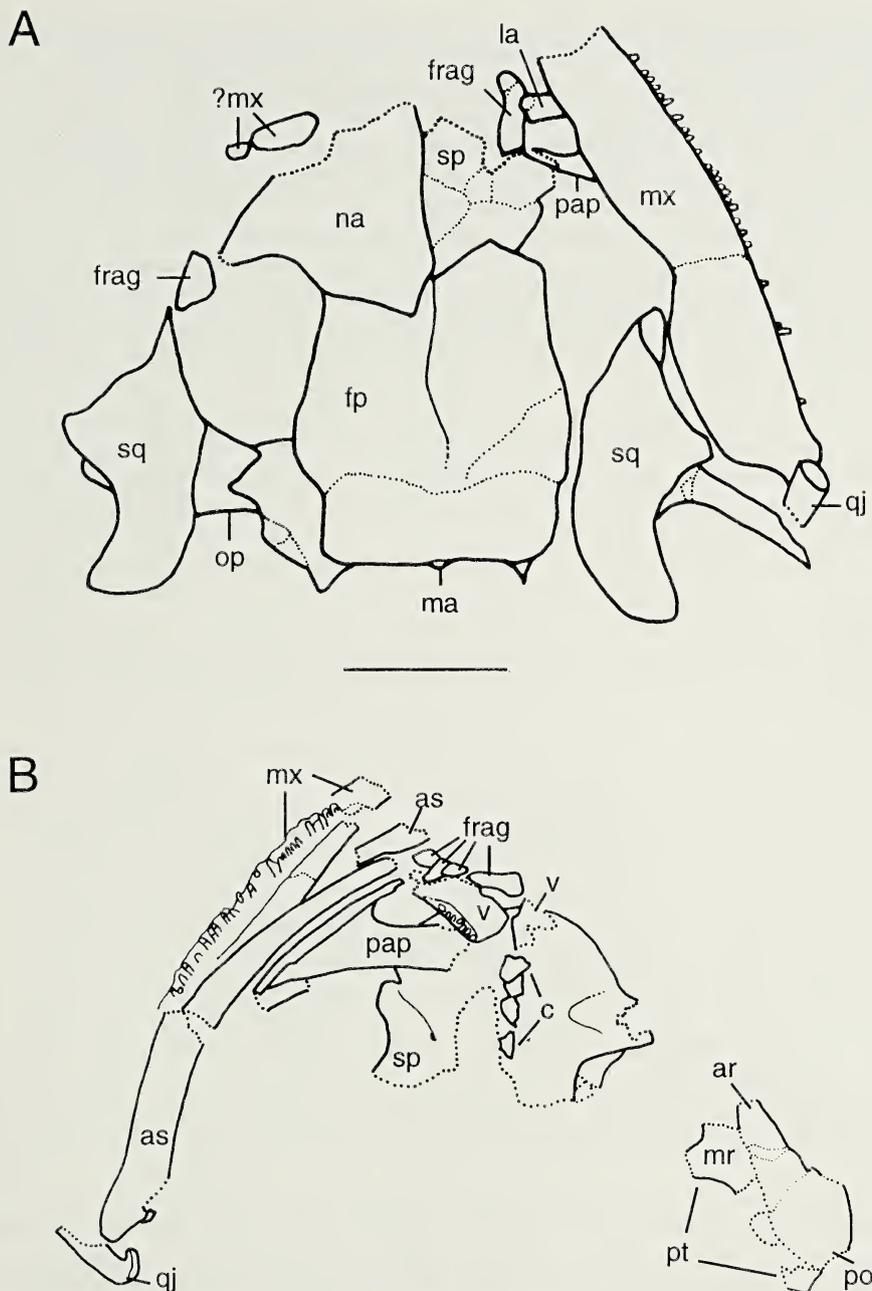


Fig. 4—*Eopelobates grandis* (holotype, YPM-PU 16441). Line drawing of skull. A. Dorsal aspect. B. Ventral aspect. Scale bar = 1 cm. Abbreviations: ar, anterior ramus of pterygoid; as, angulosplenial; c, cultriform process of parasphenoid; frag, unidentified bone fragment; fp, frontoparietal; ma, median apex of frontoparietal; la, lateral process of vomer; mr, medial ramus of pterygoid; mx, maxilla; na, nasal; op, otic plate of squamosal; pap, palatine process of maxilla; po, posterior process of pterygoid; pt, pterygoid; qj, quadratojugal; sp, sphenethmoid; sq, squamosal; v, vomer. Finely dotted lines indicate cracks in the bone, whereas coarsely dotted lines indicate incomplete bone margins.

the posterior end of the frontoparietal. Thus the frontoparietal of this specimen is assumed to be derived from three ossifications instead of being paired.

Both nasals are preserved, but the right has been removed, intact, since Zweifel's (1956) description. The nasal (Fig. 3, 4) has an overall triangular shape in which the anterolateral border is relatively straight, and the posterior border is concave where it forms the anterior orbital rim. The nasals are in contact medially except near their posterior ends where they diverge, allowing for dorsal exposure of the sphenethmoid. Because the anterolateral margin is straight, the nasal does not have distinct rostral, lateral, and parachoanalis processes, and the lateral process is thereby demarcated by its ventral flexure. Even though the relative length of the lateral process cannot be determined because the distal end is missing in both nasals, enough is preserved to indicate that the lateral process is long and slender.

The maxilla (Fig. 3, 4) bears teeth along the length of its pars dentalis, but all of the tooth tips are missing. Medially, a large, well-defined palatine process arises from the pars facialis and projects medially, as in other pelobatids. This process was incorrectly identified by Zweifel (1956) and Estes (1970) as the palatine. Posteriorly, the maxilla bears a well-developed posterior process for articulation with the quadratojugal. Zweifel (1956) was not able to identify a quadratojugal in this specimen, but Estes (1970:308) considered the bone identified by Zweifel (1956) as a columella to be the quadratojugal because it "... is excavated for a posterior projection of the maxilla as in *Megophrys*." Roček (1981) speculated that the bone in question is too robust to be a quadratojugal, based on the photograph of *E. grandis* in Zweifel (1956:fig. 1). Comparison of this bone to the quadratojugal of *Pelobates cultripes* (CM 55769) reveals that they are essentially identical in morphology, which thereby confirms Estes's identification of it. The anterior end of the quadratojugal (Fig. 4A) is robust and bears on its lateral surface, as observed by Estes (1970), a wedge-shaped trough for reception of the posterior process of the maxilla. This trough is not visible in the illustrations of the specimen provided by Zweifel (1956:fig. 1, 2) or those presented here. Posteriorly (Fig. 4B), a broad, ovoid protuberance projects ventrally beyond the level of the shaft of the quadratojugal, and in lateral aspect is separated from the shaft by a channel. This protuberance occurs in *P. cultripes* as well, and in this species the ventral ramus of the squamosal covers the dorsal portion of the protuberance, and the quadrate articulates with the inner surface of the protuberance. The quadratojugal of *E. grandis* lacks sculpturing, as is the case in most pelobatids that possess one. Sculpturing does occur on the quadratojugal of *P. decheni* (Böhme et al., 1982), and I also have observed its occurrence in two *P. cultripes* specimens (CM 54755, 55769).

The squamosal (Fig. 3A, 4A) bears a long, deep, rounded otic ramus and a slightly longer, wedge-shaped zygomatic ramus. The unsculpted ventral ramus is subequal in length to the otic ramus. A dorsal process, that in most *Pelobates* articulates with the superior lateral process of the frontoparietal (Roček, 1981), is absent. Zweifel (1956) described a broad contact between the squamosal and frontoparietal, but Estes (1970) later correctly pointed out that this contact was the result of postmortem displacement of the squamosal.

Most of the palate is covered by shoulder girdle and vertebral elements (Fig. 3B, 4B). The right vomer (Fig. 4B) is preserved, and it has rotated about 45° clockwise from its normal orientation. It appears to bear the three typical vomerine processes, two of which bound the choana. The lateral process forms the anterior

border of the choana, and posteriorly the short, triangular postchoanal ramus, or process, forms the medial border of the choana. The palatine process of the maxilla borders the choana posteriorly. A prominent, transverse ridge on the vomer bears seven tooth positions, of which four hold teeth. Three of these teeth are sheared off near their bases and the other at its base. The transverse ridge abuts the medial edge of the vomer and, just lateral of the last vomerine tooth, abruptly thins to become confluent with the lateral process. The distal end of the lateral process appears to be missing. Possibly one of several overlying bone fragments could be the displaced distal end of this process. Anteriorly, the vomer extends as a sheet of bone that also thins laterally, resulting in the medial edge of the vomer being considerably thicker than the lateral edge. A small notch is located on the anterior border of the vomer near the midpoint of its length. The anterior process arises lateral to this notch, but bone fragments cover most of its surface. Only a small portion of the medial end of the left vomer (Fig. 4B) is preserved.

The right anterolateral corner of the sphenethmoid is now dorsally exposed (Fig. 3A, 4A) because the right nasal was removed. Although the tectum nasi is somewhat fragmented, it can be determined that it did at least partially roof the nasal capsules. The tectum nasi is preserved as a step-like series of fragments leading from the midline down to and ending at the ridge of what Estes (1970) termed the "turbinal fold" of the solum nasi. Posteriorly, the tectum nasi extends laterally as a sheet of bone to the distal end of the lateral process of the sphenethmoid. The portion of the solum nasi that is exposed includes the posterolateral slope of the turbinal fold and the valley that lies between it and the postnasal wall. The septum nasi is not visible, although it was figured by Estes (1970:fig. 4b). In ventral aspect the sphenethmoid (Fig. 3B, 4B) has a broad and rounded anterior process. Lateral processes extend only a short distance from the main body of the sphenethmoid and would have been underlain by the palatine process of the maxilla in life. A prominent suture scar on the left lateral process and main body of the sphenethmoid indicates that the palatine process of the maxilla would have extended across the lateral process to reach slightly onto the main body of the sphenethmoid. The right palatine process of the maxilla lies in line with the right lateral process, but it is ventrally displaced and thus does not contact the lateral process. The orbitonasal foramen is located on the posterior surface of the base of each lateral process. Posteriorly, the sphenethmoid seems to end near the midpoint of the length of the orbit, but overlying bone fragments and matrix makes this difficult to determine with certainty. A linear series of bone fragments, which probably are the remains of the cultriform process of the parasphenoid, extend along the exposed portion of the midline of the sphenethmoid. The remainder of the parasphenoid is not visible.

The bone identified by Zweifel (1956:fig. 4) as the suprascapula is here interpreted as the left pterygoid (Fig. 4B) for the following reasons: 1) the suprascapula is cartilaginous in extant pelobatids, and because it has never been reported as ossified in *Epelobates* (Špinar, 1972; Špinar and Roček, 1984) it is assumed to be cartilaginous in this taxon as well. 2) The shape of this bone does not resemble a suprascapula, which in pelobatids forms a thin sheet that is bordered anteriorly by the cleithrum. 3) Finally, it exhibits the typical triradiate pattern of an anuran pterygoid. Only the proximal portion of the anterior ramus of the pterygoid is preserved, so it cannot be determined if this process has the typical broad articulation with the maxilla. The medial ramus of the pterygoid is broken off from and displaced slightly ventral and anterior to the rest of the pterygoid,

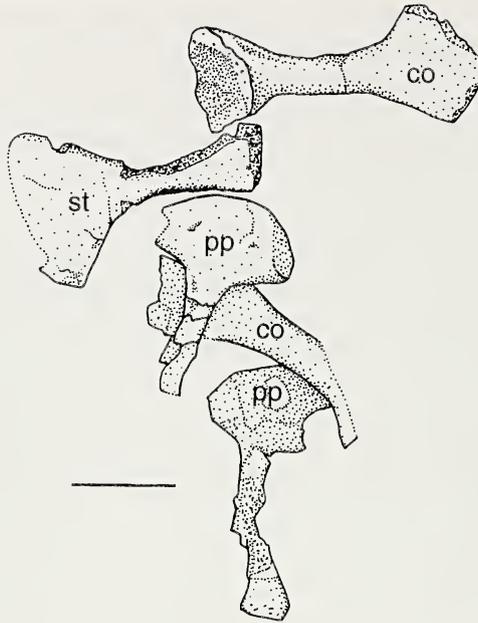


Fig. 5.—Posteromedial processes of parahyoid plate and some similarly-shaped bones of the shoulder girdle, as preserved in the holotype of *Eopelobates grandis* (YPM-PU 16441). Scale bar = 5 mm. Abbreviations: co, coracoid; pp, posteromedial process of hyolaryngeal apparatus; st, sternum.

and its proximal end disappears into some bone fragments and matrix. The posterior process of the pterygoid is nearly complete and short. A short, prominent ventral flange, similar in shape to that of *Pelobates*, is present.

Hyolaryngeal apparatus.—Both posteromedial processes of the hyoid plate are preserved (Fig. 5). These were illustrated in the line drawing of the skeleton in Zweifel (1956:fig. 4) but are not identified or described. The right posteromedial process rests along the ventral midline of the specimen at the level of the first and second presacrals, whereas the left is preserved on the ventral surface of the right transverse processes of presacrals II–IV. It is flat and very broadly expanded anteriorly with a slender shaft that expands slightly at its distal end. A parahyoid bone is not preserved and may have been absent, as in other pelobatids.

Postcranial skeleton.—Eight presacral vertebrae are present. The unfused presacral vertebrae I and II are dorsally exposed, whereas presacrals II–VIII are visible on the ventral side of the specimen (Fig. 1, 2). Neural arches, on the basis of presacrals I and II, are imbricate, elongate, and bear a strong, longitudinal neural spine. Transverse processes on presacrals II–IV are long, stout, and laterally oriented. Transverse processes on presacral V are not as long as the preceding ones and are oriented slightly anteriorly. Those on presacrals VI and VII are missing their distal ends, but their bases are present and oriented more strongly anteriorly than the transverse processes on presacral V. In presacral VIII only the right transverse process is preserved, and it is oriented strongly anteriorly. The presence of transverse cracks near the bases of transverse processes on presacrals II–IV makes it appear as though free ribs are present. However, a crack does not occur on the left transverse process of presacral IV, and in the other vertebrae the cracks occur in different positions on the transverse processes. This indicates that

they are just cracks and not the line of articulation between rib and transverse process. The vertebrae are procoelous as indicated by presacrals VI and VII, in which the posterior condyle is exposed, and by presacral VII and VIII, in which the anterior cotyle is visible. The outline of the anterior cotyle in presacral VIII forms an oval, in which the long axis is laterally oriented. The centrum is not pierced for passage of the notochord. The sacral vertebra has been separated from the specimen and the left diapophysis lost since Zweifel's (1956) description. The right sacral diapophysis is intact but only partly exposed in ventral aspect, being covered by vertebrae and the right ilium. Zweifel (1956) described the joint between the sacrum and urostyle as unfused and probably monocondylar. Although the sacral vertebra is now isolated from the skeleton, damage to its condylar region and also to the cotylar region of the urostyle makes it impossible to determine with certainty the condition of the joint. Measurements of the sacral diapophyses in Zweifel (1956) indicate that they are slightly wider (20.0 mm) than long (19.1 mm). The urostyle, which is incomplete distally, bears two short diapophyses, as observed by Zweifel (1956).

All of the shoulder girdle bones that are typically ossified in anurans are preserved, except for the cleithrum. Zweifel (1956) identified some bone fragments adjacent to the left scapula as the suprascapula, but, as previously mentioned, they have been interpreted here as the left pterygoid. The right scapula is long and bears a well-developed anterior lamina that makes the anterior border straight, as observed by Estes (1970). A narrow cleft separates the broad pars acromialis from the pars glenoidalis. The left clavicle is preserved in articulation with the scapula. Although the right coracoid covers most of the joint between the clavicle and scapula, it can be seen that the clavicle does not articulate with the anterior edge of the scapula, and thus the clavicle most likely abuts the medial edge of the scapula as in other pelobatids. The distal end of the clavicle is expanded slightly anteriorly. The right clavicle, which was removed intact since Zweifel's (1956) description, is strongly arched. The sternal end of the left coracoid is covered by the right posteromedial process of the hyoid apparatus, and the glenoid end is overlain by the left humerus. The better exposed right coracoid (Fig. 5), on which the following description is based, is preserved in articulation with the right scapula. The coracoid's contribution to the glenoid fossa forms a cup. A triangular prominence arises from the glenoid end, extends anteriorly, and probably contacted the clavicle in life. The preserved portion of the sternal end is flat and broadly expanded, more so anteriorly, being approximately three times the width of the narrowest part of the cylindrical shaft.

Zweifel (1956) mentioned the presence of an ossified sternum, although he did not identify it in his figure 4. The dorsoventrally thin sternum (Fig. 5) is preserved perpendicular to the long axis of the skeleton with its posterior end resting between the glenoid end of the right coracoid and the anterior margin of the left posteromedial process of the hyoid. The anterior half describes a fan with relatively straight sides. The shaft is narrowest near the midpoint of the sternum's length, from which point it gradually widens posteriorly. The posterior end is roughly a quarter of the width of the anterior end.

The forelimb is represented by the humerus, radioulna, and some scattered phalangeal elements (Fig. 1, 2). The left humerus is exposed in dorsomedial aspect, and only the ventral aspect of the proximal end of the right is exposed. The shaft is gently bowed ventrally. A moderately developed crista ventralis extends from the midpoint of the shaft to near the proximal end. Medial of the crista

ventralis is a shorter but well-developed crest. The distal ball, eroded in places, is round and positioned slightly medial to the long axis of the shaft. In both humeri the medial epicondyle is broken off. A medial crest is absent. The lateral epicondyle is broken off as well, although the lateral crest is present. Assuming that *Eopelobates*, like other pelobatids, had better-developed crests in males than in females, then this specimen represents a female. Determination of the size and shape of the fossa is hindered by crushing. Dorsally, the olecranon scar is situated with its apex lateral to the midline of the humerus, but the scar does not reach the lateral edge of the bone.

The right radioulna has been exposed in anterior aspect since Zweifel's (1956) description. Only the proximal-most end of the left radioulna is visible. The proximal end is broad, being subequal in width to the distal end. This, coupled with a short olecranon process, results in a broad and shallow cup for articulation with the humeral distal ball. The manus is represented by a few scattered phalanges.

Both ilia are partially exposed, the left being more visible (Fig. 1, 2). The shaft approximately equals the combined length of presacrals II–VII. The strongly arched shaft broadens dorsoventrally in the midshaft region where a thin crest arises from the dorsal surface. The crest is restricted to the midshaft region. Longitudinal ridges and narrow grooves for articulation with the sacral diapophyses are present on the dorsal surface of the proximal end of the shaft. Near the acetabular region the shaft is thin, and in cross-section would form a compressed oval that becomes less compressed towards the distal end of the shaft. Pelobatoids have a characteristic spiral groove that extends from the medial side of the shaft, across the dorsal surface, and opens into the preacetabular region. In the left ilium of *E. grandis*, the spiral groove appears to be absent, although small chips of bone are missing from the region in which the groove would occur, which could account for its apparent absence. This region in the right ilium is covered by the right femur. In *E. wagneri* the spiral groove exhibits varying degrees of development, from being barely visible to a deep groove, and this variation may have occurred in *E. grandis* as well. Dorsal and ventral acetabular expansions are of subequal length. Their junction with the shaft describes a slightly concave line for the dorsal acetabular expansion and a strongly concave line for the ventral acetabular expansion. The edges of the symmetrical and bell-shaped acetabular fossa are eroded. The dorsal protuberance consists of a small, low bump. A shallow depression that opens posteriorly lies just posterior to the dorsal protuberance.

Only the left ischium is exposed. It extends greatly posteriorly, and, as depicted by Zweifel (1956:fig. 7B), would have extended beyond the apex of the dorsal acetabular expansion. Zweifel (1956:6, fig. 7B) stated that "the pubis was probably ossified" and indicates its presence with dashed lines in his illustration of the pelvic girdle. Fragments of bone and bone impression adjacent to the ischium may represent the ossified pubis.

The right hind limb is more nearly complete and better preserved than the left, so the following description is based on the former. The femur has a sigmoid curve and is of subequal length with the slender tibiofibula. The tibiale is relatively long, has a slender shaft, and is missing its proximal end. Only the proximal half of the fibulare is preserved. Metatarsals and phalanges are scattered about the specimen, making determination of the phalangeal formula impossible. Distal tarsal bones are not exposed, and spades have not been identified. Zweifel (1956) theorized that spades were absent because the tibiale and fibulare are long and slender rather than short and stocky as in spade-bearing, burrowing anurans, a

theory with which I am in agreement. The combined length of the femur and tibiofibula (94.4 mm) is greater than the snout-vent length (82 mm).

GENERIC ASSIGNMENT OF *EOPELOBATES GRANDIS*

At the time that Zweifel (1956) described *E. grandis* the genus was poorly understood, being known by only a few, incomplete specimens. The genotype, *E. anthracinus*, then consisted of the dorsal impression of a skeleton housed in the Natural History Museum, London (Parker, 1929), and it was not until much later that the counterpart to this specimen was discovered by Dr. Špinar in the collections of the Geological Paleontological Institute of the Rheinische Friedrich-Wilhelms-Universität, Bonn (Špinar and Roček, 1984). The only other described species was *E. bayeri*, which was then represented by incomplete specimens (Špinar, 1952). Zweifel (1956) based his identification of YPM-PU 16441 as *Eopelobates* on its overall similarities to *E. anthracinus*, in particular the shape of the squamosal and sacral diapophyses, lack of a bony prehallux, limb proportions, and presence of a complete temporal arch. Concerning the latter most feature, Estes (1970) correctly determined that the apparently complete temporal arch was the result of postmortem deformation that caused the right squamosal to be preserved resting against the frontoparietal.

More recently, Roček (1981) questioned the generic assignment of *E. grandis* and suggested that it may be more closely related to the North American *Scaphiopus* and *Spea*, based on the number of bones comprising the frontoparietal. His justification was founded mostly on a drawing of the frontoparietal of *E. grandis* in Estes (1970:fig.13A) that depicted a median suture extending between the anterior and posterior margins of the element. This is in contrast to *Eopelobates* and *Pelobates*, which have three ossifications, rather than two, forming the frontoparietal. Roček (1981), in a detailed study of the ontogeny of *Pelobates fuscus*, documented the presence of a median ossification situated posteriorly adjacent to the paired frontoparietal ossifications. During the course of ontogeny the median ossification fuses with the paired frontoparietal ossifications, leaving no trace of sutures where it adjoins the paired frontoparietal ossifications. Furthermore, the presence of this median ossification prevents the median suture from reaching the posterior end of the frontoparietal complex, which is the only way that the presence of the median ossification can be inferred in adults. Roček (1981) demonstrated that this pattern occurs in *Eopelobates* as well, using a series of *E. bayeri* fossils representing several stages of premetamorphic tadpoles and adults. Roček (1981) further strengthened his theory of relationship of *E. grandis* by arguing that as in *Scaphiopus* and *Spea*, but unlike *Eopelobates*, the quadratojugal is absent. Estes (1970) had suggested that the bone identified by Zweifel (1956) as the stapes was actually the quadratojugal, but Roček (1981) argued that this bone is merely an unidentified fragment. He did caution that the holotype should be examined to verify the identity of this bone.

The most recent diagnosis for *Eopelobates* is given by Sanchíz (1998), who combined characters from Estes (1970) and Špinar and Roček (1984). It should be mentioned that Sanchíz (1998) did not include the North American species of *Eopelobates*, including *E. grandis*, in his diagnosis because their generic identification was then uncertain. The revised diagnosis given in the Systematic Paleontology section (above) was based on this diagnosis, in which several characters were omitted and a new one was added. Each of the diagnostic characters of

Sanchíz (1998) and its distribution among pelobatids as well as justification for omission of some of his characters from the revised diagnosis is discussed below.

- 1) Skull roof is concave to flat. This character was omitted from the diagnosis as it cannot be accurately assessed in *Eopelobates* because all of the known specimens are dorsoventrally flattened, some considerably so (Henrici, 2000).
- 2) Dermal sculpture is well developed, consisting of pits and grooves, but lacking tubercles. This is the one diagnostic character in which *E. grandis* differs from other *Eopelobates*. Although the sculpturing of *E. grandis* is well developed, having pits and grooves, it is also highly tuberculated. However, because the style of dermal sculpture can vary between species as well as within a species and ontogenetically, assignment of *E. grandis* to a new genus on the basis of this character is not justified. Dermal sculpture with tubercles also occurs in *Pelobates* and *Scaphiopus*; megophryines lack dermal sculpture. The dermal sculpture of *Macropelobates* is reticulated but is too damaged to determine if tubercles were present.
- 3) The frontoparietal is embryonically derived from three ossification centers. This character cannot be directly evaluated in *E. grandis* as the only specimen is a fully ossified adult. However, because the median suture is absent in the unsculpted median apex of the frontoparietal, a posteromedian element is assumed to be present in that it prevents the median suture from reaching the posterior end of the frontoparietal complex. A similar developmental pattern for the frontoparietal occurs in *Pelobates* as well. The other pelobatids have paired frontoparietals.
- 4) The frontoparietal complex is not in contact with the squamosal. As mentioned previously, Estes (1970) correctly pointed out that the frontoparietal and squamosal are not in contact. Some megophryines have contact between the frontoparietal and squamosal (Estes, 1970), via the inferior lateral process of the frontoparietal and the otic plate of the squamosal, and *Pelobates*, except for *P. fuscus*, has contact between the superior lateral process of the frontoparietal and the dorsal process of the squamosal (Roček, 1981). Other pelobatids lack contact between the squamosal and frontoparietal. Because most pelobatids lack contact between the squamosal and frontoparietal this character was removed from the diagnosis.
- 5) The sphenethmoid is anteriorly wide and blunt and dorsally roofs the nasal capsules. *Eopelobates grandis* complies with the former part of this character, but determination of the latter is problematic because of preservation. When Estes (1970) described this character he stated that it was only in *E. grandis* that the condition of the roof of the nasal capsule could be determined. Wuttke (1988) has since confirmed that in at least *E. wagneri* the sphenethmoid does roof the nasal capsule. In this region of the skull of *E. grandis* the bone is preserved as a series of descending step-like fragments, making it difficult to determine how much of the nasal capsule was actually roofed by the sphenethmoid. For this reason, only the shape of the anterior end of the sphenethmoid will be considered here. Megophryines are the only other pelobatid that have a wide, blunt anterior margin of the sphenethmoid.
- 6) The nasal is triangular with a relatively straight anterolateral margin and long and slender lateral process (Fig. 6). The nasal of *E. grandis* has an overall triangular shape and a straight anterolateral margin. Although the lateral process is not completely preserved in either nasal, enough is present to indicate that it was long and slender. *Eopelobates* is unique among pelobatids in having a triangular nasal. Megophryines also have a relatively straight anterolateral border of the nasal as well as a long, slender lateral process, but their nasal is reduced. The nasal of *Pelobates*, *Scaphiopus*, and *Spea* has a concave anterolateral border and the lateral process is short and blunt. The nasal

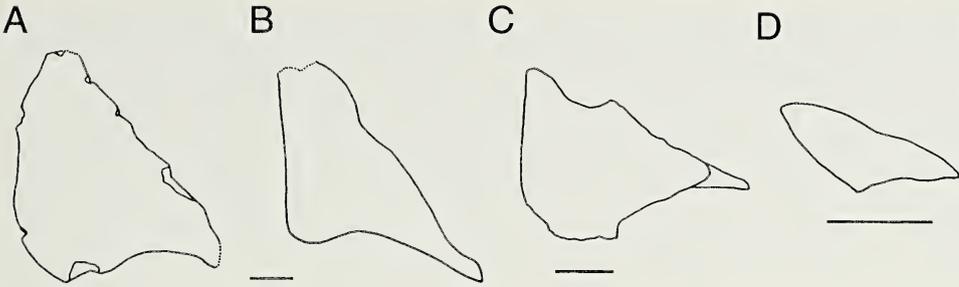


Fig. 6—Comparison of the right nasal in representative Pelobatoidea. A. *Eopelobates grandis* (holotype, YPM-PU 16441); B. *Eopelobates hinschei* (GM 6728); C. *Scaphiopus holbrooki* (image reversed, CM 32300); and D. *Scutigera mammatus* (FMNH 22286). Scale bar = 2 mm.

of the Oligocene *Macropelobates* is not known. 7) The sternum is ossified. *Eopelobates grandis* possesses a well-ossified sternum as do the megophryines and *Pelobates*. A sternum has not been identified in *Macropelobates* and is absent in *Scaphiopus* and *Spea*. As an ossified sternum is present in all but two pelobatids, its presence is not considered to be diagnostic of *Eopelobates* and was not included in the revised diagnosis. 8) Length of the tibiofibula is equal to or greater than that of the femur. In *E. grandis* the tibiofibula length (47.2 mm) equals that of the femur (47.2 mm). These bones are of subequal length in megophryines, and the femur is longer than the tibiofibula in other pelobatids. 9) The combined length of the femur and tibiofibula is subequal to or exceeds the snout-vent length. In *E. grandis* the combined length of the femur and tibiofibula (94.4 mm) is greater than the snout-vent length (82 mm). This is the second character in which *Eopelobates* is unique from other pelobatids. Using the same measure for comparison, megophryines, *Macropelobates*, *Pelobates*, and *Scaphiopus* have hind limbs that are considerably shorter than the snout-vent length. 10) A prehallux is not modified as a bony spade. A bony spade is not preserved in *E. grandis* and is assumed to be absent (see description section above for justification). Megophryines also lack a spade, whereas a spade is present in *Macropelobates*, *Pelobates*, *Scaphiopus*, and *Spea*. The following is a new character included in the revised diagnosis presented in this paper. The ilial shaft is strongly arched and bears a crest along the midregion of the shaft. The only other pelobatids that have a strongly arched shaft of the ilium are the megophryines examined for this study: *Megophrys*, *Leptobrachium*, and *Scutigera*. A crest occurs in varying degrees of development in *Megophrys* and *Leptobrachium*.

SPECIFIC ASSIGNMENT OF *EPELOBATES GRANDIS*

Two characters were identified by Zweifel (1956) to distinguish *E. grandis* from the other species of *Eopelobates* known at that time: large size and broad frontoparietal. Large size can no longer be regarded as a specific character for *E. grandis* because at least one specimen of *E. wagneri* (SMF 2576b) is of equivalent size. As for the breadth of the frontoparietal, in *E. grandis* it is roughly 84 percent of the length of the frontoparietal, whereas the range for the other species is 58 percent to 68 percent. Estes (1970) added to these characters the distinctive shape of the sphenethmoid and the rounded tympanic process (otic ramus in this paper) of the squamosal. Concerning the sphenethmoid shape, this character is problematic as Estes (1970) did not elaborate as to how the sphenethmoid of *E. grandis*

differs from other species. Because the sphenethmoid of *E. grandis* is not well exposed and the portion that can be seen is somewhat fragmentary, it will not be considered here. Sanchíz (1998) presents a lengthy specific diagnosis that is more descriptive in nature than diagnostic. His diagnosis includes characters discussed here as well as those that describe a condition that occurs either in other *Eopelobates* or other pelobatids. The remaining characters in his diagnosis are currently not useful as they are not preserved in some or all of the other species of *Eopelobates*. Characters that can be used to distinguish *E. grandis* from other *Eopelobates* include: highly tuberculated dermal sculpture; broad frontoparietal; and rounded otic ramus of the squamosal (Fig. 3, 4).

DISCUSSION

Eopelobates at one time was thought to have as many as ten species, ranging in age from the Cretaceous to the Miocene, and a Holarctic distribution. Its diversity has been greatly reduced with only three to five species currently recognized (Roček and Rage, 2000). The North American record now contains only one valid, described species, *E. grandis*. The number of European species is controversial, ranging from two to four, depending on whether the suggested synonymies of *E. bayeri* with *E. anthracinus* and *E. hinschei* with *E. wagneri* are accepted. Špinar and Roček (1984) proposed that *E. anthracinus*, from the Late Oligocene of Germany, and *E. bayeri*, from the Oligo-Miocene of central Europe, may be conspecific. Their reasoning was that the only difference between the two species was size, and as the then only known specimen of the smaller *E. anthracinus* represented an immature individual, it seemed likely that a fully grown *E. anthracinus* would be close in size to an adult *E. bayeri*. This theory was countered, however, when Roček (1995) described an adult specimen of *E. anthracinus* that was still considerably smaller in size than *E. bayeri*. Despite this evidence, Sanchíz (1998) continued to treat the two species as one. There are differences in the proportion of the squamosal, however, that support the theory they are distinct species: in *E. anthracinus* the zygomatic ramus is longer and narrower than the otic ramus, whereas in *E. bayeri* the otic and zygomatic rami are of similar size and shape. Roček and Rage (2000) suggested that *Eopelobates hinschei*, which occurs in the Middle Eocene of Germany (Estes, 1970) and possibly the Late Eocene of England (Milner et al., 1982; Milner, 1986), might be conspecific with the slightly younger Middle Eocene, German species, *E. wagneri* (Wuttke, 1988). Wuttke (1988), however, noted some differences between their frontoparietal, nasal, squamosal, and scapula. The brief description of *E. hinschei* provided by Sanchíz (1998) indicates that the differences noted by Wuttke (1988) in the frontoparietal and nasal are no longer valid. *Eopelobates hinschei* and *E. wagneri* do share some striking similarities. These include: a uniquely-shaped frontoparietal in which the posterior third is greatly constricted; nasals that are widely separated along the midline, which allows for considerable dorsal exposure of the well-ossified sphenethmoid; and slender zygomatic and otic rami of the squamosal. As pointed out by Sanchíz, (1998) *E. hinschei* lacks an adequate diagnosis and is in need of preparation using modern techniques before it can be fully evaluated.

With the reassignment of the Late Cretaceous, Asian species of *Eopelobates* (Špinar and Tatarinov, 1986; Roček and Nessov, 1993), *Eopelobates* now is definitely known only from the Tertiary of North America and Europe. The oldest,

definitive record of *Eopelobates* in North America is the Late Eocene *E. grandis*. If the identification of the Green River anuran as *Eopelobates* is correct (Grande, 1984), then the record extends back to the Middle Eocene, which roughly coincides with the oldest European record. Estes (1970; et al., 1969) had described some isolated bones from the Late Cretaceous Lance Formation of Wyoming and Hell Creek Formation of Montana as questionably *Eopelobates* and later (Estes and Sanchíz, 1982) confirmed this identification, observing that the squamosal most closely resembles that of *E. guthriei*. As *E. guthriei* has now been referred by Henrici (2000) to *Scaphiopus*, the identity of the Lance and Hell Creek anurans as *Eopelobates* is once more uncertain.

Preliminary study of *Eopelobates* suggests that two clades are present with one, possibly both, clades including species from Europe and North America. One clade consists of *E. anthracinus*, *E. bayeri*, and *E. grandis*, which share the characters of a well-ossified skull with deep otic and zygomatic rami of the squamosal. Using Pipoidae as an outgroup for determining character polarity indicates that a deep otic and zygomatic ramus is a derived character. *Eopelobates hinschei* and *E. wagneri* comprise the other clade. They have a less well-ossified skull in that the nasals do not meet along the midline, which allows for considerable dorsal exposure of the sphenethmoid, and the otic and zygomatic rami of the squamosal are slender. The "Green River *Eopelobates*" also possesses these features. Employing the same outgroup indicates that the former character is derived and the latter is primitive.

Estes (1970) had earlier observed that two lineages of *Eopelobates* were present, based on the length of the skull table, although his grouping of the species differs from that presented here. Using nasal-frontoparietal proportions he suggested that *E. hinschei* and *E. bayeri* comprised the long-skulled lineage, and that the more primitive short-skulled lineage consisted of *E. guthriei*, (now referred to *Scaphiopus* by Henrici, 2000), *E. grandis*, and *E. anthracinus*. A detailed phylogenetic analysis of interspecific relationships of *Eopelobates* cannot be undertaken at this time for the following reasons: 1) *E. wagneri* should be formally described and diagnosed as it currently appears only in dissertation form (Wuttke, 1988); 2) *E. hinschei* needs to be thoroughly redescribed and diagnosed, assuming that it is not synonymized with *E. wagneri*; and 3) An identification and thorough description of the "Green River *Eopelobates*" needs to be made.

Estes (1970) theorized that *Eopelobates* achieved a Holarctic distribution no later than the Late Paleocene or Early Eocene, observing that it was yet another example of similarity between North American and European faunas. The range of *Eopelobates* is now thought to be only North American and European, rather than Holarctic, but the timing of distribution suggested by Estes (1970) is reasonable. Recent studies (McKenna, 1983; Marincovich et al., 1990; Knox, 1998) indicate that a North Atlantic land-bridge passing through southern Greenland connected North America and Europe from the Late Paleocene into the Early Eocene (roughly the lower two-thirds of the reversed interval of Chron 24 of the magnetic polarity time scale). This bridge allowed for a broad interchange of terrestrial vertebrates between these continents (Marincovich et al., 1990). The high latitudes of the land-bridge would not have been inhospitable to frogs as the climate was considerably warmer in the North Atlantic realm than at present (Marincovich et al., 1990). As an example, the lower vertebrate fauna of the Lower Eocene, Eureka Sound Formation of Ellesmere Island includes a salamander, anguid and varanid lizards, a boid snake, several types of turtles including a

tortoise, and an alligator; of these taxa the varanid, tortoise, and alligator indicate an equable climate with winters that rarely experienced freezing temperatures (Estes and Hutchison, 1980). Thus it seems likely that *Eopelobates* could have taken part in the broad interchange of terrestrial vertebrates between North America and Europe.

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EXPEDITIONS, EXPOSITIONS, ASSOCIATIONS, AND MUSEUMS IN THE ANTHROPOLOGICAL CAREER OF C. V. HARTMAN

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ABSTRACT

Within a span of twenty years (1890–1910), Carl Vilhelm Hartman changed careers from botany to anthropology, achieved recognition as a professional colleague by peers on both sides of the Atlantic, pioneered systematic archaeological research in Costa Rica, and produced two widely acclaimed monographs about his fieldwork. Hartman's transition to anthropology ensued from four principal entities with which he became engaged—expeditions, expositions, associations, and museums, and through which he developed a broad network of contacts among European, Central American, and North American anthropologists and museologists. He effectively used these trans-Atlantic links to advance his anthropological career. Hartman, a Swede by birth, learned his field methods in the Old World but conducted research exclusively in the New World, where he incorporated high standards for archaeological fieldwork. His career, always firmly rooted in museum anthropology, included five years (1903–1908) as Carnegie Museum's first Curator of Ethnology and Archaeology. Hartman's term of employment at Carnegie Museum coincided with the onset of a gradual shift in the training of anthropologists, moving from the museum to the university setting, under the Boasian paradigm for professionalization of the discipline.

KEY WORDS: Costa Rica, museum anthropology, International Congress of Americanists, Carnegie Museum, Hjalmar Stolpe, W. J. Holland

INTRODUCTION

Carl Vilhelm Hartman, born August 19, 1862 in Örebro, Sweden, the son of a distinguished botanist initially pursued a career following in his father's footsteps. His university training was in botany, his initial work was in applied botany for the Swedish Academy of Agriculture, and he spent five years studying at major botanical gardens in Europe under a grant awarded by the Swedish Academy of Science (Brunius, 1984; Franzén, 1969).

In 1890, at the age of 28, Hartman joined an expedition that profoundly affected his life, stimulating a total change of career to the emerging discipline of anthropology. Within the span of a single decade, the 1890s, Hartman had established his professional credentials sufficiently to obtain employment as a museum anthropologist, a profession to which he would devote the remainder of his life.

How did it come to pass that a Swede, trained as a botanist, proficiently excavated Costa Rican archaeological sites and purchased collections of antiquities for a museum in the United States a century ago? This intriguing question, the impetus for this paper, implicitly acknowledges the inter-hemispheric links that characterize Hartman's career, from his training in the Old World and research in the New World, to his employment by museums on both sides of the Atlantic,

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Fig. 1.—C. V. Hartman (standing) and unidentified visitor at the Chinchilla site, Central Highlands, Costa Rica, in 1903. (Section of Anthropology glass-plate negative G998).

and to his collegial relations with anthropologists in Europe, Central America, and North America.

This paper's central thesis is that "internationalism," in the sense of inter-hemispheric linkages, was the driving force in the transformation of Hartman's career. We follow the theoretical orientation of Givens (1992:64): "The role of biography in explaining archaeology's past is to delineate and assess the place of the individual worker within the science." The purposes of this study are to document the four entities—expeditions, expositions, associations, and museums—in which this internationalism is manifested and, in turn, to analyze their relationships to Hartman's career transformation and his development as a professional anthropologist. The two decades (1890–1910) spanning Hartman's transition to and most active involvement with anthropology coincide with a period of significant developments in the discipline in the Americas and Europe.

In the Americas, Hartman is known as an archaeologist, most notably for his introduction of systematic field methods developed in Europe into Costa Rican archaeology (Fig. 1). The field methods he learned in Sweden have been discussed in depth by Rowe (1959) and commented upon briefly by Willey and Sabloff (1993:85). His pioneering research in Costa Rica was addressed by Fonseca Zamora (1984), Jones (1998), Ohlsson de Formoso (1991), and Skirboll (1984b);

his contributions were recognized by a symposium held in his honor at Carnegie Museum of Natural History (Skirboll and Creamer, 1984).

Hartman's anthropological research extended well beyond archaeology, a fact known in Sweden (Brunius 1984) but rarely acknowledged in the Americas (cf. Lutz, 2001). He wrote ethnographic (1895, 1897, 1901*b*, 1907*d*, 1907*e*) and ethnobotanical (1906, 1910*c*) articles and recorded but only sparsely published his linguistic and anthropometric data. Hartman's work as an anthropology curator and museum administrator likewise is also little appreciated in the Americas.

Carnegie Museum (it became Carnegie Museum of Natural History in 1973) employed Hartman as its first Curator of Ethnology and Archaeology in 1903, largely because of the anthropological experience he had gained in the previous decade (Richardson, 1980). His tenure coincided with the implementation of Director W. J. Holland's plan for a new Carnegie Museum, and he became a key player in fulfilling Holland's vision through various curatorial duties ranging from acquisition of collections, to installation of exhibits, to publication of scientific research. Viewed from one hundred years later, however, Hartman's primary legacy lies in the knowledge generated by his 1903 expedition to Costa Rica. The research resulted in his three publications (Hartman, 1907*a*, 1907*b*, 1910*a*) and subsequent studies based on collections he brought back, by Fonseca Zamora and Richardson (1978), Fonseca Zamora and Scaglione (1978), Heckenberger and Waters (1993), Skirboll (1981, 1984*a*), Swauger and Mayer-Oakes (1952), and Waters and Fonseca Zamora (2001*a*, 2001*b*).

MATERIALS AND METHODS

The present study makes liberal use of another of Hartman's legacies, the documents and photographs from his tenure at Carnegie Museum, which currently reside in the Hartman Archives at Carnegie Museum of Natural History, as well as Hartman-related documents contained in the Holland Archives of the same institution. These unpublished sources contain a wealth of biographical information about Hartman, insights into his views on the four entities stimulating his career change, and his perspectives on the colleagues and activities fostering his professional development in anthropology. The Holland Archives, especially his Reports of the Director to the Museum Committee and the Minutes of the Museum Committee's monthly meetings, document the interplay between Holland and Hartman during his five-year term of employment.

Published materials provide a second source of information. These include Hartman's articles and monographs and, where applicable, publications in which he is mentioned. The former category is particularly valuable for establishing Hartman's own perspectives on individuals who assisted his career (e.g., the prefaces to his two monographs). The latter category provides other persons' assessments of him, such as Carl Lumholtz's comments about Hartman's roles on the expedition to Mexico. These publications also provide the historical context for the four entities that facilitated his transition to anthropology, such as the proceedings of the various Sessions of the International Congress of Americanists he attended. Pittsburgh newspapers provide another source of published information.

We present initially the data from the four entities—expeditions, expositions, associations, and museums—that compose the structure or framework of C. V. Hartman's transition from botanist to anthropologist. In doing so, the chronological ordering of the events becomes of secondary significance. In the final section

of this paper, we restructure the primary events chronologically, discuss certain individuals who played key roles in Hartman's anthropological career, and place the twenty-year span (1890–1910) of his most active involvement with anthropology in historical context.

EXPEDITIONS

Hartman began his anthropological career during his first expedition to the New World and enhanced his standing as an anthropologist during two later ones. He was a crewmember on the first expedition but headed the second and third. The first expedition was the initial factor stimulating his transition to anthropology.

Lumholtz Expedition to Mexico

Hartman's career took a major turn in 1890 when he was selected as expedition botanist by Norwegian explorer and ethnographer Carl Lumholtz who, sponsored by the American Geographical Society of New York, led an expedition to the Sierra Madre mountains of northwestern Mexico. Lumholtz's expedition also was linked to the American Museum of Natural History, being allied loosely with its Hyde Expedition (Fowler, 2000:235). In all, Lumholtz spent five years in Mexico conducting field research on four expeditions between 1890 and 1898. Hartman served from September 1890 until summer 1892, and then rejoined Lumholtz for a few months in 1893.

Lumholtz (1902 I:vii–xix) provides information on the origin, support, staffing, and timing of the four Sierra Madre expeditions (cf. Lumholtz, 1891). He distinguishes between the first expedition (September 1890–April 1891) and the second (January 1892–August 1893) because in the intervening months he had returned to the United States to raise funds. Hartman stayed on in Mexico in charge of the expedition camp at San Diego and from his perspective the first expedition continued uninterrupted, from when he joined in September 1890 until he departed in the summer of 1892. He was the only member of the “scientific corps” carried over from the first to the second expedition, leaving in the midst of the second, seemingly the last of the “scientific corps” to depart. However, he resumed fieldwork with Lumholtz for several months in 1893 (Lumholtz, 1902 I:186, 444), and dated locality records for some of the plants he collected (Robinson and Fernald, 1895) verify that he had rejoined the second expedition in May. Lumholtz conducted fieldwork by himself for the remainder of the second expedition (summer 1892–August 1893), apart from the brief time he was rejoined by Hartman, and for all of the third (March 1894–March 1897). He was joined by physical anthropologist Aleš Hrdlička for the brief (four month) fourth expedition in 1898.

Lumholtz (1891:389; 1902 I:x, xii) identifies the members of his “scientific corps” from the first and second expeditions (Table 1). The first expedition's archaeologist, A. M. Stephen (Lumholtz just used initials and variably spelled the last name Stephens and Steven) is mentioned only three times in the 1902 book, in the first two chapters covering the expedition's early months; Stephen's assistant, R. Abbott, is mentioned only in the preface. It appears that Stephen and Abbott left the expedition early on, thus opening the way for Hartman to assume responsibility for archaeological projects. Hartman carried out archaeological excavations at mounds on the Piedras Verdes river (Lumholtz, 1902 I: xi, 93), at the time he headed the camp at San Diego while Lumholtz was away (April–winter 1891) between the first and second expeditions.

Table 1.—*The Scientific Corps of Lumholtz's first and second Sierra Madre expeditions.***First expedition** (September 1890–April 1891)

Physical geographer—Professor W. Libbey (of Princeton, NJ) and his unnamed laboratory man (possibly G. Haviland, as in Lumholtz, 1891:389)

Archaeologists—A. M. Stephen (also spelled Steven and Stevens by Lumholtz; almost certainly Alexander McGregor Stephen), assisted by R. Abbott

Botanists—C. V. Hartman and C. E. Lloyd (listed as F. Lloyd in Lumholtz, 1891:389)

Zoological collector—F. Robinette

Mineralogist—H. White

Second expedition (January 1892–August 1893)

Botanist—C. V. Hartman (only member of the scientific corps on both expeditions)

Civil engineer and photographer—C. H. Taylor

Mineralogist and zoological collector—A. E. Meade (also spelled Meeds)

Notes:

(1) Lumholtz (1891:389; 1902 I:x) twice lists members of the first expedition's scientific corps, but with some inconsistencies

(2) Second expedition members are from Lumholtz (1902 I:xii); none of the scientific corps members served for the entire second expedition

(3) Hartman served from September 1890 until the summer of 1892, and then rejoined Lumholtz for several months in 1893; he remained in Mexico in charge of the camp, succeeding H. White, between the first and second expeditions (April–winter 1891)

A. M. Stephen assuredly was Alexander McGregor Stephen, “. . . one of the more fascinating and least-known characters in the coterie of nineteenth-century Southwestern anthropologists” (Fowler, 2000:138). By 1890, when the Lumholtz expedition began, Stephen had a decade of experience helping organize expeditions for anthropologists from the Smithsonian Institution's Bureau of American Ethnology. Stephen had married a Navajo woman, lived at First Mesa, spoke Navajo and Hopi, and was friends with Thomas Varker Keam and John Gregory Bourke, two other persons involved with mounting expeditions (Fowler, 2000: 133–139; Parsons, 1936). The notion that this person was Alexander McGregor Stephen is supported further by Hartman: “The then archaeologist of the expedition, Mr. A. M. Stephen, who had spent some fifteen years studying tribes of the South-west . . .” (Hartman, 1897:120). Stephen's participation in the Lumholtz expedition and his link to Hartman, albeit brief, seem not to have been recognized previously. Stephen's archaeological assistant, R. Abbott, remains a complete mystery.

Hartman's exposure to and experience with anthropological fieldwork during the Lumholtz expedition dramatically changed his life. His botanical studies were important scientifically and resulted in some new species being identified (Robinson and Fernald, 1895), but his interests thereafter were directed more toward anthropology than botany. He confirmed the impact of this expedition in a 1903 letter to W. J. Holland, Director of Carnegie Museum, requesting employment as a curator:

When Dr. Carl Lumholtz (who is a Norwegian) organized his expedition for the exploration of Sierra Madre he engaged my services as a botanist. Soon however I became greatly interested in the archaeological and ethnological features and as Dr. Lumholtz needed a special assistant, I turned my attentions wholly to this line of investigation. (Hartman Archives, letter, February 20, 1903, C. V. Hartman to W. J. Holland).

As special assistant, Hartman gained experience in managing the expedition and Lumholtz apparently placed considerable trust in his abilities. Hartman had been kept on when the scientific corps was being reduced in number, assumed charge of the camp when Lumholtz returned to the United States, and he conducted excavations at various archaeological sites (Lumholtz, 1902 I:93, 186, 444). Hartman's name appears far more frequently in the index of this two-volume work than does any other member of the scientific corps.

The Lumholtz expedition resulted in Hartman's first anthropological paper, given at the 10th International Congress of Americanists in Stockholm in 1894, and his first anthropological publications (Hartman, 1895, 1897). He had published botanical papers before the Lumholtz expedition and a few later in his life, but ever after the expedition he published mostly on anthropological topics (Franzén, 1969). He combined his botanical and anthropological interests in his "tree calabash" publications, including an article in German in the Boas Anniversary Volume (Hartman, 1906), later translated into French (1910*c*), and two articles based on his Salvadoran research (1907*d*, 1907*e*).

Swedish Expedition to Central America

In May 1896, Hartman began a three-year expedition to Central America that was broad in anthropological scope, encompassing archaeological, ethnological, linguistic, and anthropometric research, and in geographic scale with fieldwork in Costa Rica, El Salvador, and Guatemala. He was the expedition's only full-time staff member, although he hired local workers as needed. He did not return to Sweden until the autumn of 1899.

The expedition, nominally sponsored by the Swedish Society for Anthropology and Geography, really was organized and funded by Åke Sjögren, a Swedish geologist and mining engineer who, while working in Costa Rica in the early 1890s, had become interested in the country's archaeology. Stolpe (1905) credits Sjögren with conceiving the idea and drawing up the overall plan for archaeological research implemented by Hartman. Sjögren's geological background led to his fascination with archaeology, which focused on jade artifacts found in Costa Rican sites and issues surrounding their origin (Wilson, 1902). In the years before he funded Hartman's expedition, Sjögren had visited the Smithsonian Institution and provided Costa Rican jade samples for microscopic and thin section analysis to curators at the United State National Museum (Wilson, 1898:458–459).

Hartman spent 17 months (May 1896–September 1897) excavating sites in Costa Rica's Atlantic plain, Central Highlands, and Pacific slope before moving on to El Salvador for ethnographic and linguistic studies of the Pipiles, and to Guatemala with the Xincas, through the spring of 1899 (Hartman, 1901*a*:1–2). He amassed a sizeable amount of Costa Rican antiquities that he presented to Åke Sjögren who, in turn, donated the collection to the Royal Ethnographical Museum in Stockholm (Stolpe, 1905).

He invoked this expedition when applying for the position at Carnegie Museum:

Returning to Sweden, I received a favorable offer to carry out explorations of my own in Central-America under the auspices of the Anthropol. Geogr. Society. This position I accepted and carried on explorations, which extended over a period of three years. (Hartman Archives, letter, February 20, 1903, C. V. Hartman to W. J. Holland).

The Central American expedition resulted in Hartman's first monograph on Costa Rican archaeology (1901*a*), published in English and summarized in Swedish (1902), and three ethnographic publications (1901*b*, 1907*d*, 1907*e*). Major figures in anthropology favorably reviewed his 1901 archaeological monograph in leading journals in Europe and North America (Gordon, 1906; MacCurdy, 1905; Peet, 1904; Seler, 1904). Such acclaim was an important step in his career advancement. His Swedish ethnographic article on El Salvador was translated recently into Spanish (Hartman, 2001).

Carnegie Museum Expedition to Costa Rica

Hartman reported for duty at Carnegie Museum on March 17, 1903 and departed Pittsburgh two weeks later on his second expedition to Costa Rica. In that brief period, Director Holland had obtained letters of introduction for Hartman from the Costa Rican embassy in Washington, written personal letters to influential individuals he knew in Costa Rica, arranged for wire transfer of monies, purchased necessary field equipment, and obtained a camera and photographic supplies for Hartman. Holland's two-page letter of instruction for the expedition directs Hartman to conduct archaeological research and "... incidentally if you are able to make collections of botanical, entomological and other specimens" (Holland Archives, letter, March 24, 1903, W. J. Holland to C. V. Hartman). Hartman returned to Pittsburgh in mid November, having spent about seven months excavating sites, purchasing collections, and conducting museum research. He also brought back zoological and botanical specimens.

Hartman concentrated his excavations in the Central Highlands (Fig. 2) and the Nicoya peninsula on the Pacific side, with only a brief excursion to the Atlantic plain. He studied and photographed artifacts in the National Museum of Costa Rica and expended a great deal of time, effort, and money in purchasing collections of antiquities from private collectors, an assignment given to him by Holland who clearly regarded that task as most important for Carnegie Museum (Watters, 2002*a*; Watters and Fonseca Zamora, 2001*b*). Hartman succeeded in that task. In the *Annual Report of the Director* it is stated: "All of the collections acquired by Mr. Hartman in Costa Rica, either by purchase or as the result of excavations, filling more than eighty large cases, have been brought to the Museum..." (Holland, 1904:27).

The Carnegie expedition resulted in Hartman's second monograph on Costa Rican archaeology (1907*a*), an *American Anthropologist* article on the alligator motif on pottery (1907*b*), and a comparative study of four grave forms (1910*a*). Leading anthropologists in Europe (Beuchat, 1909) and North America (Holmes, 1908) again favorably reviewed his monograph. Hartman had produced two important monographic works on his Costa Rican research in just six years.

EXPOSITIONS

Hartman's anthropological career coincided with a period during the late nineteenth and early twentieth centuries when international expositions ("world's fairs") were being staged at an accelerated rate in Europe (Greenhalgh, 1988) and the United States (Rydell, Findling, and Pelle, 2000). His personal involvement with such expositions was limited, but it nonetheless directly affected his career by expanding his knowledge of New World indigenous cultures and providing him with the opportunity to meet anthropologists from the Americas and Europe.



Fig. 2.—Hartman's 1903 excavations at the Chinchilla site on the slope of Irazú volcano. (Section of Anthropology glass-plate negative G979).

Hartman's enduring link to Costa Rican archaeology is tied to that country's national expositions and its subsequent involvement in international expositions.

Costa Rica's National Expositions and the Exposición Histórico-Americana

Activities sanctioned and sponsored by the Government of Costa Rica in the latter half of the 1880s were crucial for encouraging national and international interest in the country's archaeological patrimony. Kandler (1987) indicates Costa Rica's first National Exposition was held in 1885 and that others followed yearly, in preparation for the Universal Exposition at Paris in 1889, and subsequently the *Exposición Histórico-Americana* at Madrid in 1892, and the World's Columbian Exposition at Chicago in 1893. One of the reasons for incorporating artifacts in the national expositions was to develop and refine a systematic way of presenting Costa Rica's archaeological heritage to the international audiences (Garrón de Doryan, 1974:23, 26). The national expositions also promoted the creation of the Museo Nacional in 1887, an idea first proposed in 1862 (Peralta and Alfaro, 1893: xxix–xxx). Archaeology unquestionably was part of the nationalistic agenda of the times (Corrales Ulloa, 1999:6; Lines, 1934:5; Viales Hurtado, 1997:102–103).

Costa Rica disseminated information about the country and exhibited a variety of its products at these events, but

... it was the archeological collection that aroused the greatest interest on the part of the international public. For many, it was the first time to be able to view these artefacts and they were admired for their ex-

ceptional beauty and the mystery which surrounded them. (Kandler, 1987:24).

Hough (1893:273–274), clearly impressed with the Costa Rican antiquities he observed in Madrid, reported the exhibits occupied two halls and 40 cases, displayed pottery, stone carvings, gold objects, jade carvings, and ornamented metates, among other artifacts, and were augmented by paintings of the excavations, maps, and photographs.

Anastasio Alfaro, head of the National Museum, was largely responsible for the success of Costa Rica's involvement at the international expositions, following up on his efforts with the national expositions. His crucial role in the international effort is clear: "By government decree, Don Anastasio was appointed to organize how the country should be represented at these events" (Kandler, 1987:24). Alfaro's excavations in 1891 at the Guayabo de Turrialba site secured artifacts for these expositions, and that fieldwork earned him a silver medal award at Madrid, while the National Museum received a gold medal (Garrón de Doryan, 1974:34; Stone, 1956:12). He authored the exhibition catalog (Peralta and Alfaro, 1893) with Costa Rican historian Manuel M. de Peralta. Alfaro is characterized as one of Costa Rica's two pioneering professional archaeologists (Hartman is the other) by Fonseca Zamora (1984). The Madrid Exposition included Costa Rican ethnographic materials, obtained from the Talamanca Indians by Swedish naturalist Carl Bovallius in 1882 (Brunius, 1992:68).

World's Columbian Exposition

Alfaro accompanied the Costa Rican collection from Madrid to Chicago in 1893 and reinstalled it in the Anthropological Building at the World's Columbian Exposition, following the guidelines provided by Frederic Ward Putnam, head of its Department of Ethnology (Garrón de Doryan, 1974:26–38, 96–98). Department M of the Exposition was often referred to as the Department of Ethnology even though it included anthropology and history; the Anthropological Building contained exhibit areas devoted to ethnology, archaeology, and ancient religions, games, and folk-lore, in addition to anthropological laboratories and a library (Anonymous, 1893a; Flinn, 1893:52–59).

Much to Alfaro's displeasure, Chicago had insufficient space for the 7,000 Costa Rican artifacts displayed in Spain and 3,000 had to be shipped back to the National Museum in San José (Stone, 1956:13). Nonetheless, the antiquities actually exhibited were highly regarded and Costa Rica's exhibit is twice noted in the Exposition's official guide (Flinn, 1893:53, 134). Starr (1893) confirms that much of what Hough (1893) saw in Madrid had been reinstalled in Chicago and his report not only lauds the overall exhibit, but also recognizes Alfaro and Peralta by name.

Costa Rica's participation at the World's Columbian Exposition was a fortuitous circumstance for Hartman:

After the conclusion of Dr. Lumholtz' first expedition [what Lumholtz terms the second expedition, ending in 1893] I went with him to the Columbian Exhibition [sic] at Chicago, where I remained six months in the Anthropological Department, arranging exhibits and assisting in the purchase and packing of ethnological collections. (Hartman Archives, letter, February 20, 1903, C. V. Hartman to W. J. Holland).

It is likely that Lumholtz either arranged for or facilitated Hartman's employment at the World's Columbian Exposition. Hartman's presence there directly influenced his career change to anthropology because he met Alfaro and Peralta and observed Costa Rican antiquities for the first time. Both events would affect his life dramatically within a short time.

The Hartman Archives contain an interesting commentary concerning an attempt to secure Costa Rican artifacts for the Columbian Exposition. Fourteen years after the event, in a letter to the Chairman of the Carnegie Museum Committee, Hartman wrote:

Other collectors, but with less practical training, have tried the Costa Rican field but with little success. During the preparations for the World's Fair in Chicago a collector was dispatched by Professor Putnam and provided the means for securing archeological material from Costa Rica. He spent several months in the country but was able to pick up a few specimens here and there, altogether two or three small boxes. (Hartman Archives, letter, May 27, 1907, C. V. Hartman to C. C. Mellor).

Putnam's attempt to obtain other Costa Rican artifacts seems unwarranted in view of the large exhibition Alfaro mounted subsequently in Chicago. His effort makes more sense, however, when one remembers that many of the artifacts he assembled for the Exposition eventually formed the Field Columbian Museum's anthropological collections. Alfaro's artifacts would be unavailable to the museum because they were going back to Costa Rica.

The Columbian Exposition provided Hartman with the chance to become acquainted with major figures in the field, among them Putnam and his assistant Franz Boas. The concurrent International Congress of Anthropology, convening in Chicago from August 28 to September 2, afforded an even greater opportunity to meet anthropologists and hear them lecture on a wide range of topics. Lumholtz must have willingly acquainted his colleagues with his longest serving field assistant, whom he had just accompanied from Mexico to Chicago. The Mexican expedition was the subject of Lumholtz's lecture, "Cave Dwellers of the Sierra Madre" (Holmes, 1893:427). Among the many North Americans attending the Congress, aside from Putnam and Boas, were Daniel G. Brinton, Otis T. Mason, Zelia Nuttall, Frank Cushing, Alice C. Fletcher, George A. Dorsey, W. H. Holmes, Stewart Culin, and Walter Hough; Latin America was represented by M. A. Muniz and Emilio Montes (Peru), Emil Hassler (Paraguay), Manuel M. de Peralta (Costa Rica), and A. Ernst (Venezuela) (Anonymous, 1893*b*). Fowler (2000:211) mentions that A. M. Stephen presented a paper in Chicago, although at the International Folk-Lore Congress, not at the Congress of Anthropology. It thus seems likely that Hartman, Lumholtz, and Stephen were together again at least one time after the Lumholtz expedition ended.

Hartman benefited from this Exposition in other ways. He gained practical experience in the mounting of anthropology exhibits. His previous anthropological background was restricted to fieldwork and his familiarity with archaeology limited to northwest Mexico, but by the time he returned to Sweden in 1894, his anthropological experience was broader and his network of personal contacts wider. A Swedish scholar attests to the central role this played in broadening Hartman's exposure to anthropology, in stating that his "... interest in the region [Spanish America] was further strengthened at the World's Fair in 1893 in Chi-

cago, where New World archaeology and ethnography were given considerable attention" (Brunius, 1985:152).

Louisiana Purchase Exposition

Hartman attended the Louisiana Purchase International Exposition in St. Louis in September 1904, while employed as a curator at Carnegie Museum, and the activities in which he participated are detailed in his report to the Director:

. . . I spent one week in St. Louis, where I studied the various ethnological exhibits and attended the meetings of the Ethnological and Archaeological sections of the "Congress of Arts and Science." At one of the meetings I read a paper on "Recent archaeological investigations on the Pacific Coast of Costa Rica." For the Museum I purchased from the Coco-Maricopa Indians at the Fair (for \$3) a small collection of their pottery and the peculiar implements they use for its manufacture. (Hartman Archives, Report from the Ethnological Department for the month of September 1904, C. V. Hartman to W. J. Holland).

Hartman probably referred to the Cocopa Indians, a group from Baja California forming ". . . a part of the anthropological exhibit . . ." (Louisiana Purchase Exposition Co., 1904:285), although the Maricopas also were present (Fowler, 2000: 215). W J McGee (he did not use periods after his initials), formerly with the Bureau of American Ethnology and known to Hartman from previous meetings, had become head of the Anthropology Department at the St. Louis exposition by 1903 (Watters and Fowler, 2002). Rydell, Findling, and Pelle (2000:54) claim that this exposition had the most anthropological exhibits of any world's fair and credit McGee, a believer in living exhibits, with creating an "outdoor laboratory for anthropological fieldwork."

Hartman's standing as an anthropologist was enhanced by the eminent German anthropologist, Eduard Seler, who lauded his Costa Rican research in an invited paper, "The Problems of Archeology," which reviewed the status of archaeology across the Americas. He stated:

A limited region, including the old settlements on the slopes of the volcano of Irazú and certain groups of hills which extend down into the Atlantic lowlands, has lately been investigated in a really exemplary manner by E. [sic] V. Hartman . . . Outside of this, to be sure, we still lack excavations [in Central America] undertaken in a scientific manner and authenticated by documents. (Seler, 1906:536).

Hartman had known Seler for at least a decade before the St. Louis meeting. Seler (1904) reviewed Hartman's first Costa Rican monograph and provided one of the "excellent testimonials" that Hartman submitted to Holland while negotiating employment in 1903. McGee and Boas also were invited speakers.

Our research has been unable to confirm that Hartman actually read his paper at the Congress. Rogers (1905–1907) produced an eight-volume set of proceedings of the Congress of Arts and Science. The volumes relevant to invited anthropological papers, in volume V (Rogers, 1906:513–571), and "short papers," in volume I (Rogers, 1905:82–84), do not mention a paper by Hartman; nor does his name appear in volume VIII (Rogers, 1907), the index compiled for the eight-volume set. It seems that despite his claim to Holland, he did not "read" his

paper (in a formal, officially sanctioned sense), although he may have informally discussed or otherwise provided information about his Costa Rican research while at the Louisiana Purchase Exposition. Nevertheless, he once again effectively used his involvement with an exposition as a means of interacting with major figures in anthropology.

ASSOCIATIONS

Hartman's development as a professional anthropologist was enhanced by his involvement with three scholarly associations, two of which were national organizations but with extensive links abroad and one that was explicitly international in scope. His talks at their meetings covered archaeological, ethnographic, and linguistic topics and his articles, sometimes published in their proceedings and journals, dealt almost exclusively with his anthropological research in the western hemisphere.

Swedish Society for Anthropology and Geography

The Svenska Sällskapet för Antropologi och Geografi (SSAG) was the primary scholarly association promoting the interests and interactions of Americanist researchers in Sweden during Hartman's career. His involvement with the SSAG occurred at a time crucial for his transition from botanist to anthropologist in the mid-1890s and gave him access to influential Swedish Americanists who would guide his career. Hjalmar Stolpe, who in 1873 enthusiastically endorsed the founding of this society, then known as the Antropologiska Sällskapet (Brunius, 1990), played significant roles in mentoring Hartman and advancing his anthropological career two decades later. The SSAG was involved with the General Ethnographic Exposition organized by Stolpe in Stockholm in 1878–79 and the Madrid Exposition of 1892, along with its antecedent 9th Session of the International Congress of Americanists held in Huelva, Spain (Alvarsson and Brunius, 1994:43; Brunius, 1990, 1992).

The SSAG served as titular sponsor of the Central American expedition (1896–99) funded by Åke Sjögren. Hartman served as an SSAG delegate at the 13th, 16th, and 18th Sessions of the International Congress of Americanists; at the 15th Session he is listed as the Swedish government delegate though not specifically the SSAG representative.

Hartman published three (1895, 1901*b*, 1902) of his first five articles on anthropological topics as well as lesser contributions such as book reviews, obituaries, and meeting reports in *Ymer*, the SSAG journal, (Franzén, 1969). The SSAG appointed W. J. Holland a corresponding member within a year of his having hired Hartman at Carnegie Museum (Anonymous, 1904*a*).

International Congress of Americanists

If one factor were to be singled out as the most important influence in advancing Hartman's anthropological career, it would be his participation in the International Congress of Americanists (ICA), a scholarly association with which he remained involved for thirty years. It seems fitting that he attended his first and last ICA sessions in Sweden. At his first Session, the 10th ICA in Stockholm in 1894, he was a relatively young person (32 years old) about to embark on a new profession. By his final Session, the 21st ICA held in Göteborg in 1924, he

was 62 years old and had enjoyed a career that was international in scope, intimately linking Sweden with Central and North America.

Hartman's participation in ICA Sessions, in a variety of roles, was tracked by reviewing the pertinent proceedings, and his publications therein were checked against the enormously valuable ICA centenary volume compiled by Comas (1974). The formal convening of the International Congress of Americanists is termed a Session. Sessions and their proceedings are numbered sequentially since the 1st Session was held in Nancy, France in 1875 (see Comas, 1974:14, 117–132, for lists of the sessions and proceedings). For convenience and brevity, we have opted in this paper to drop the word Session and use the numerical designator and the abbreviation ICA when referring to a particular Session (e.g., 13th ICA). Depending on the roles played, an individual's name can recur in various categories in the proceedings—Committee of Organization, Delegates of Governments, Delegates of Scholarly Societies, Members of Congress, and Subscribers—although one category sometimes subsumes another in certain proceedings. A Member who actually attended a Session can be confirmed, but only for selected proceedings, by the presence of an asterisk beside the name. Most of the earlier proceedings fortunately include titles of all papers presented at a Session (sometimes even those read “by title” only), irrespective of whether they later were published in the volumes. With these constraints in mind, it is feasible to document fairly completely Hartman's involvement with the International Congress of Americanists.

10th International Congress of Americanists (Stockholm, 1894).—The 10th ICA was held in August of the same year Hartman returned to Sweden, having completed his first anthropological fieldwork with Lumholtz and participated in his first international exposition in Chicago. He was fortunate to be in Sweden because Lumholtz, who was in Mexico on his third expedition, declined an invitation to attend this Session and asked him to be his substitute and speak about their Sierra Madre fieldwork. His first anthropological paper, “The Indians of North-Western Mexico,” was presented to an international audience of anthropologists and published in Swedish and English (Hartman 1895, 1897). The 10th ICA proceedings volume (p. xvi) lists him as a *naturaliste voyageur* in the roster of Swedish members, implying he was not yet regarded as an anthropologist.

Personal contacts he made at this ICA Session ultimately became more important than his paper for his anthropological career. Costa Rican participants included Anastasio Alfaro and Manuel M. de Peralta, whom he had met just the year before in Chicago, and Bernardo Augusto Thiel, a Bishop who had assembled a large collection of antiquities while serving in that country. German members included H. Polakowsky, who had traveled to Costa Rica and written about its antiquities, and the anthropologists Seler, Adolph Bastian, and Rudolph Virchow. Americans included Brinton, Nuttall, and the Duc de Loubat. However, it was the Swedish members, especially Hjalmar Stolpe and to a lesser degree Carl Bovalius, collector of the Talamanca ethnographic materials exhibited in Madrid in 1892, who most directly influenced Hartman's transition. Hjalmar Sjögren is listed as a member from Sweden but his son, Åke Sjögren, is not. However, Åke Sjögren later was appointed Interim Secretary General and it fell to him to assemble the proceedings and write its forward. Hartman departed on the Åke Sjögren-funded Swedish expedition to Central America less than two years after the 10th ICA ended.

13th International Congress of Americanists (New York City, 1902).—Hartman established his stature as a professional anthropologist in the eight years elapsing between the International Congress of Americanists meetings in Stockholm and New York. The 13th ICA proceedings reveal that he was no longer regarded as a *naturaliste voyageur*. Instead, he and Åke Sjögren are listed as official representatives of the Swedish Society of Anthropology (actually SSAG by then); Hjalmar Stolpe was the delegate of the government of Sweden and a Vice President of the ICA. W. J. Holland was a delegate of the United States and C. C. Mellor, Chair of the Museum Committee, was listed as a subscriber (Watters, 2002a). Holland spoke about Carnegie Museum, then in its “infancy,” issued an invitation for delegates to visit Pittsburgh, and presented a paper on petroglyphs in Pennsylvania (Holland 1905a, 1905b). Delegates or members from Costa Rica included Henri Pittier de Fabrega and Juan Fernández Ferraz. Delegates representing French societies included the Duc de Loubat for the Société des Américanistes de Paris, and Yale University professor George Grant MacCurdy, for the Société d’Anthropologie de Paris. Seler was a German delegate. Franz Boas, Stewart Culin, J. Walter Fewkes, Walter Hough, A. L. Kroeber, Otis T. Mason, W. J. McGee, Zelia Nuttall, George Pepper, and F. W. Putnam were among the many members (either delegates or subscribers) representing anthropology in the United States.

His participation in the 13th ICA strengthened relations with some major figures in anthropology and introduced him to other persons important to his career. Along with Boas, Pittier de Fabrega, Fernández Ferraz, Holland, MacCurdy, and Seler, among others, he served on the Council of the Commission of Organization. The Duc de Loubat was its Honorary President; Stolpe and Putnam were Vice Presidents.

The 13th ICA proceedings (pp. lxvi–lxvii) disclose that he read one paper, “Archaeological Researches in Costa Rica,” in full, and a second paper, “The Aztecs of Salvador,” by title only. Neither was published in the proceedings.

Hartman’s status as a professional anthropologist was enhanced greatly when it was made known that he had been awarded the prestigious Duc de Loubat prize by the Royal Academy of Belles Lettres, History and Antiquities of Sweden. Hjalmar Stolpe (1905) announced this award in a speech to the 13th ICA members, which appears in the proceedings. The Loubat award was bestowed for *Archaeological Researches in Costa Rica*, Hartman’s monograph (1901a) based on the Swedish expedition. This sumptuous volume, the cost of which had been borne by Hartman’s benefactor, Åke Sjögren, subsequently was “laid upon the table” for the Congress to examine.

After Stolpe’s speech, Putnam called for a resolution of congratulations for Hartman. The resolution’s text is not included in the proceedings but selected passages were extracted by Hartman and included in his letter to Mellor five years later:

Resolved, that the Members of the 13th International Congress of Americanists, assembled in New York, hereby express their hearty appreciation of the results obtained by the Archaeological Expedition to Costa Rica under the direction of C. V. Hartman . . . and they congratulate Mr. Sjögren upon the magnificent manner in which the Report has been published. [They further characterize this volume as] . . . the most painstaking and elaborate Report of the exploration of ancient graves in Cen-



Visitors From All Over the Continent Caught by The Dispatch Staff Photographer in Front of Hotel Schenley.

Fig. 3.—Photograph from the *Dispatch* (October 30, 1902 edition, page 8) of the visiting delegation of the International Congress of Americanists at the Hotel Schenley. (Carnegie Museum of Natural History Archives, Holland newspaper clipping scrapbook).

tral America which has ever been undertaken . . . [and add] . . . the beautiful volume will always serve as a model for this class of archaeological work. (Hartman Archives, letter, May 27, 1907, C. V. Hartman to C. C. Mellor, citing passages extracted from the Putnam resolution).

According to Hartman, the resolution was proposed by Putnam, seconded by Boas, and adopted unanimously by the Congress. Being recognized personally and having his research honored in this manner by his fellow anthropologists surely was enormously satisfying for Hartman who had commenced his transition to anthropology with the fieldwork he conducted on the Lumholtz expedition only twelve years before.

The 13th ICA proceedings volume discloses that a delegation traveled “. . . on an excursion to Chicago, including visits to Philadelphia, Washington, Pittsburgh[h], and ‘Fort Ancient,’ in southern Ohio and Cincinnati” (p. lxxvii) the week after the Congress. Hartman, Stolpe, Pittier de Fabrega, Fernández Ferraz, and Seler were among the delegation of foreigners (Fig. 3) welcomed by Holland when they visited Pittsburgh on October 29, 1902. Pittsburgh newspapers disclose that 31 dignitaries arrived in the city, toured Carnegie Institute, and heard Holland speak of his vision for Carnegie Museum, and further state that the excursion was to be extended to St. Louis following the visit to Chicago (Watters, 2002a).

15th International Congress of Americanists (Québec City, 1906).—Canada’s hosting of the 15th ICA resulted from a resolution adopted six years earlier, at the 12th ICA in Paris, whereby Sessions were to alternate between venues in Europe and the Americas, with the 13th ICA in New York inaugurating this scheme in 1902. Hartman’s presence in Pittsburgh caused him to miss the 14th ICA in Stuttgart, Germany but, conversely, facilitated his attendance at the 15th ICA in Québec.

The 15th ICA proceedings list Hartman as the lone delegate for the government of Sweden, a member of the Council, and a curator of Carnegie Museum. Seler

again was a delegate of the government of Germany (actually listed as Prussia) and a Vice President of the ICA. Delegates from scholarly organizations in the United States included Boas, W. H. Holmes, and Clark Wissler. Fewer international members were present and fewer countries represented at Québec than at the New York Session of 1902. Costa Rica and many other Latin American countries had no representation.

At the 15th ICA, Hartman informed the Congress of the death of his mentor and friend, Hjalmar Stolpe, who had died the year before (Culin, 1906), and it seems that eulogizing Stolpe was the major reason he attended. He participated in meetings of the Council and presided over one morning session, but seems not to have presented a paper since none is listed in the 15th ICA proceedings.

16th International Congress of Americanists (Vienna, 1908).—Hartman's return to Sweden in 1908 following his resignation from Carnegie Museum explains his attendance at the next European venue of the ICA, at the 16th Session held in Vienna, Austria in September. After this final trans-Atlantic move, Hartman's employment and professional life forever after were centered in Sweden.

His participation in the Vienna Session, as the delegate of the government of Sweden, representative of the SSAG, an attending Member, and, for the first time, a Vice President (along with Seler), facilitated his reentry into European anthropology and museology.

He presented two papers. "Some features of Costa Rican Archeology" compared the architectural forms and geographic distributions of four kinds of graves investigated during his two expeditions. The second paper dealt with a sound recording device called the photographone, invented by his fellow Swede, Sven Berglund. Both papers were published in the 16th ICA proceedings (Hartman, 1910*a*, 1910*b*). His Costa Rica article is listed as "an abstract" and unquestionably was an abbreviated version of a longer lecture illustrated with lantern-slides. He never published the full version of this paper to the enduring frustration of persons interested in his Costa Rica research. He also laid upon the table for examination by the Congress his two recent publications, the second Costa Rican monograph, published by Carnegie Museum, and his article in *American Anthropologist* (Hartman, 1907*a*, 1907*b*).

Other International Congress of Americanists Sessions.—Hartman attended later Sessions of the International Congress of Americanists but participated less actively than in the past, possibly due to deteriorating health. He had experienced health problems while at Carnegie Museum and in several monthly reports to the Director he mentioned missing work because of illness. The underlying cause of his impaired health may have been malaria. In his 1907 letter to C. C. Mellor, he mentions his outlays for bills from doctors resulting from his anemic condition caused by months of work in malarial regions during the rainy season. Comments in the 18th and 19th ICA proceedings suggest deteriorating health, and we know he was granted a medical leave of absence from the Ethnological Section in 1923, five years before he retired (Lindblom, 1941).

At the next European Session (18th ICA), in London in 1912, he is listed as a delegate for the government of Sweden and for the SSAG, an attending Member, and a Council member. However, the 18th ICA proceedings, without further explanation, state (p. xl): "Professor C. V. Hartman, Stockholm, was unable to present his paper 'Physical Anthropology of the Aztecs of Salvador.'" Immediately after the ICA, he stayed on in London to attend an International Conference



Fig. 4.—The Carnegie Institute building (left), which contained Carnegie Museum, and the Hotel Schenley (right) were situated in the predominantly rural setting of the Oakland district of Pittsburgh when Hartman was Curator. The twin towers, features of the original (1895) building, were removed during the 1907 addition. (Carnegie Museum of Natural History Archives).

in which a proposal for an International Anthropological Congress was being debated. No remarks are attributed to him in the summary of that meeting in the 18th ICA proceedings.

Hartman did not attend the 19th ICA in Washington, D.C., which took place in 1915 when Europe was embroiled in World War I but before the United States entered. In the proceedings, the Swedish delegate, Amandus Johnson, extended his well wishes to the Congress and added (p. xlvi): “Professor Hartman would have been with us except for his health and the unfortunate state of affairs in Europe.”

The 21st ICA included two Sessions held in August 1924, first at The Hague in the Netherlands and then at Göteborg in Sweden. Hartman attended the Göteborg Session and was listed as a member of the Commission of Organization, a member of the Council, and an attending member, but no longer as a delegate of the government of Sweden or the SSAG. Comas (1974) lists no Hartman papers or publications for the 21st ICA, at either session. The 1924 Göteborg Session, the final one he attended, occurred thirty years after his first Congress, the 10th, in Stockholm.

American Anthropological Association

The American Anthropological Association (AAA) convened its founding meeting on June 30, 1902 in the Oakland Methodist Episcopal Church in the Oakland district of Pittsburgh (Fig. 4), almost exactly four months prior to Hartman’s visit to Pittsburgh on the excursion following the 13th ICA in New York City. The AAA founding meeting was held in conjunction with the 51st annual meeting of the

American Association for the Advancement of Science (AAAS), which was being attended by anthropologists from its Section H (Anthropology) (Watters, 2002*b*; Watters and Fowler, 2002). W. J. Holland's courtesy to Section H, by arranging for Carnegie Museum to exhibit a Mexican sculpture discussed by Marshall Saville in the scientific sessions, was acknowledged by Smith (1902:210) and McGee (1902:477). Holland did not participate in the founding meeting but soon afterward was accredited as being an AAA founder (Anonymous, 1903:191).

Hartman became involved with the American Anthropological Association during his tenure at Carnegie Museum but the Hartman Archives contain few details about the extent of his participation. His attendance is documented so far only for the AAA meeting in 1905, held from December 27–29 at Cornell University in Ithaca, New York. The meeting provided Hartman with an excellent opportunity to broaden his network of contacts, because it was held jointly with the Archaeological Institute of America, American Folk-Lore Society, and American Philological Association. Prior to his departure, he informed Holland of his planned activities:

With the Director's kind permission, I leave the 25th for Ithaca, where I at the meeting of the Am. Anthropological Association will read a paper entitled "Use and ornamentation of the tree-calabash in tropical America." I will also attend the sessions of the "Committee for the preservation of the antiquities of the United States," which has honored me with membership. (Hartman Archives, Report from the Section of Ethnology for the month of December 1905, C. V. Hartman to W. J. Holland).

His paper, one of only nine read in full at the AAA meeting, was published subsequently in the Boas Anniversary Volume (Hartman, 1906). He illustrated his talk with the stereopticon and exhibited a number of calabash specimens according to MacCurdy's (1906) summary of the meeting. Participants he already knew included Boas, who presided in the absence of AAA President Putnam, and MacCurdy, the AAA Secretary, and immediately following the Ithaca meeting, he traveled to New York and New Haven to consult with them about his Costa Rican research. MacCurdy (1906) also reported at the Ithaca meeting on the plans for AAA participation at the 16th ICA in Québec. The AAA provided European anthropologists in Québec with voluminous information about "Recent Progress in American Anthropology" (Anonymous, 1906).

Hartman served on the American Anthropological Association's Committee for the Preservation of American Antiquities, one of the committees that ultimately lobbied successfully for enactment of the Antiquities Act of 1906. He published two articles in *American Anthropologist* (1907*b*, 1907*c*), one on his Costa Rican research and the other on engraved shell artifacts from Tennessee in the Carnegie Museum collections.

MUSEUMS

Hartman's anthropological career was centered in museums, not in universities. He was employed in museums; his two monographs on Costa Rican archaeology were museum publications; field methods he used in Costa Rica were learned from a museum anthropologist; and his professional colleagues were anthropologists associated primarily with museums (including university museums). The Hartman Archives reveal that he performed the full gamut of museum duties relating to exhibition and collections while at Carnegie Museum. However, his

five-year (1903–1908) term of employment is more appropriately perceived as a time span intervening between periods of employment at the Naturhistoriska Riksmuseet (Royal Museum of Natural History) in Sweden.

Ethnographical Department of the Royal Museum of Natural History of Sweden

Hjalmar Stolpe was the key person responsible for mentoring Hartman in museum anthropology and for involving him with the Swedish Museum of Natural History. Both were trained in the natural sciences, Stolpe in zoology and Hartman in botany, yet each later embraced anthropology as his life's work and ultimately ended his career as a museum administrator, rightfully having achieved recognition as an archaeologist as well as an ethnologist (Brunius, 1984; Culin, 1906; Lindblom, 1941). Hartman's association with Stolpe began at least as far back as 1894, when both participated in the 10th ICA in Stockholm.

Soon after the 10th ICA, Stolpe introduced Hartman to Åke Sjögren and it is clear that Sjögren's interest in Costa Rica's archaeology was the determining factor in Hartman's decision to conduct research in that country (Stolpe, 1905). Undoubtedly even more compelling was Sjögren's willingness to fund the expanded (in anthropological and geographical scope) Central American expedition of 1896–1899. Hartman modeled his field methods for excavating Costa Rican burial grounds on Stolpe's meticulous excavation and mapping of Swedish Iron Age cemeteries at Björko and Vendel (Alvarsson and Brunius, 1994:43–45; Brunius, 1984; Rowe, 1959). He acknowledged this debt: "Having received thorough instructions from Dr. Hj. Stolpe in the investigation of graves, according to his well-known method for similar research in Sweden, I started for Costa Rica in the spring of 1896" (Hartman, 1901a:1). After the Central American expedition concluded, Hartman traveled for six months in the United States visiting the major museums in order to prepare himself for museum work.

Hartman's return to Sweden in 1899, following the three-year Central American expedition, was auspicious because Stolpe was achieving his long-term goal of creating a separate Ethnographical Department (sometimes termed Ethnographical Museum) within the Royal Museum of Natural History. The department came into being in 1900 and Stolpe was appointed its Director (Brunius, 1990). Stolpe hired Hartman as his assistant, a position affording him opportunities to perform curatorial duties, develop exhibits, catalog collections, and write up his research. This appointment provided Hartman with his first true museum experience, although he had been involved earlier in exhibit development at the World's Columbian Exposition.

Hartman acknowledged his indebtedness for Stolpe's training:

In Stockholm I undertook new training in the various duties of a museum worker under the immediate supervision of Professor Hjalmar Stolpe. I classified, arranged and labelled anew my collections and wrote descriptive catalogues. At the same time I had the opportunity day after day of following in detail the work Dr. Stolpe was doing in the different departments, at that time especially valuable and instructive, on account of the complete reorganization of the institution then going on, according to thorough scientific and systematic plan. Although the experience thus gained during the three years of daily intercourse with Professor Stolpe does not seem to cover a very long time I consider the same really valuable, because my instructor is undoubtedly one of the fore-

most museum men of Europe, having worked some 30 years inside the walls of the National Museum in Stockholm . . . and having studied nearly all the museums of Europe, North & South America, and Asia. (Hartman Archives, letter, February 20, 1903, C. V. Hartman to W. J. Holland).

Within a single decade, the 1890s, Hartman had transformed himself from a botanist on the Lumholtz expedition to a professional anthropologist employed at a major natural history museum in Europe. Within a year of his museum employment in Sweden, he mounted a major exhibit of the Central American archaeological and ethnographic materials that his benefactor, Åke Sjögren, by then had donated to the Ethnographical Department (Anonymous, 1900). By 1902, he (1901*a*, 1901*b*, 1902) had produced a monograph in English and two articles in Swedish about his Costa Rican archaeological and Salvadoran ethnographic research and had been honored with the Duc de Loubat award.

His research had been focused almost exclusively in the New World, yet his museum employment remained firmly rooted in the Old World until Carnegie Museum hired him in 1903. Five years later he returned to Sweden to take over the position of Director of the Ethnographical Department, vacant since the death of his mentor, Hjalmar Stolpe in 1905. Thereafter, he became a full-time museum administrator whose duties precluded further productivity in the realms of research and publication. While it is clear that he planned to publish more about his research in Costa Rican archaeology and Central American ethnology, these plans failed to come to fruition for the most part. He took a medical leave of absence from the Ethnographical Department in 1923, from which he entered retirement in 1928; he died in 1941 (Lindblom, 1941).

Carnegie Museum of Carnegie Institute

Hartman attended the 13th ICA with the intent of seeking a position at a museum in the United States. During the succeeding three months, he used his network of contacts with American anthropologists to explore employment opportunities at museums in New York, Washington, and Philadelphia before he approached Carnegie Museum. He was seeking a museum position at the same time Holland (Fig. 5) sought an anthropology curator, yet neither was the first choice of the other. Holland had been unsuccessful in his effort to woo Stewart Culin from the Museum of the University of Pennsylvania in Philadelphia; instead, Culin went to the Brooklyn Institute of Arts and Sciences, now the Brooklyn Museum, as its first Curator of Ethnology (Fane, 1991). Culin declined Holland's offer during the first week of February 1903, thus opening the door for his serious consideration of Hartman's application letter of January 28. Thereafter, negotiations progressed rapidly and Hartman was employed exactly one month later (Watters and Fonseca Zamora, 2001*b*).

Holland's assessment of Hartman's qualifications for becoming Curator of the Section of Ethnology and Archaeology was quite favorable. In his Monthly Report to the Museum Committee, delivered February 28, 1903, Holland wrote:

Dr. C. V. Hartmann [sic], whose acquaintance I formed at the recent Congress of Americanists, is in the building, and I shall take pleasure in presenting him to you at sometime this evening. He has had experience in Museum work, having been associated with Dr. Stolpe, the celebrated Swedish ethnologist, whose assistant he was at Stockholm.

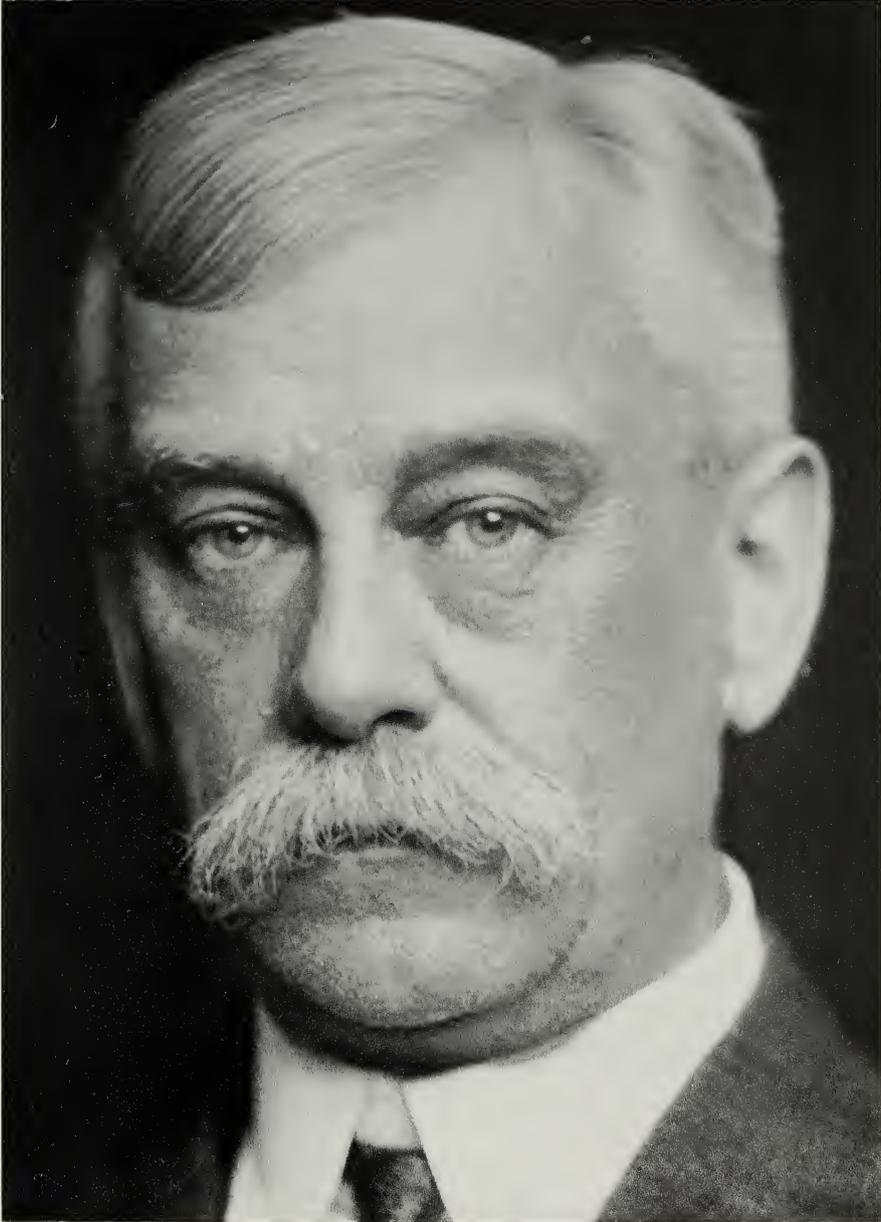


Fig. 5.—William Jacob Holland was Director of Carnegie Museum during Hartman's tenure (1903–1908). (Carnegie Museum of Natural History Archives).

He was for a long time with Dr. Lumholtz in Mexico and has written extensively upon the ethnology of Costa Rica. It may be that he is the man, for whom we are looking. He produces excellent testimonials. (Holland Archives, Monthly Reports of the Director to the Museum Committee, volume 1, March 1, 1903).

Among those “excellent testimonials” were letters from Boas at the American Museum of Natural History, McGee at the Bureau of American Ethnology, Smithsonian Institution, and German anthropologists Eduard Seler and A. B. Meyer. Holland offered and Hartman (who had traveled to Pittsburgh) accepted employment on February 28, the same day the Committee approved Holland’s recommendation to hire.

In his speech at the 13th ICA in 1902, Holland (1905*a*) alluded to Carnegie Museum, then in existence for six years, being in its “infancy” (Watters, 2002*a*). Thus, acquiring collections was a priority for Holland. Hartman, being aware of the Director’s desire, emphasized during their negotiations his personal knowledge of Costa Rican collections available for purchase (Fig. 6). He likewise was aware of the plans afoot for the new Carnegie Museum, having heard Holland expound upon his vision at the 13th ICA and afterward in Pittsburgh with the visiting delegation. He contributed to the realization of that vision when the new facility was inaugurated in 1907. His Costa Rican artifacts, displayed prominently in the new Gallery of Archeology, were one of only two archaeology collections mentioned in the booklet (Fig. 7) prepared for that dedication (Carnegie Institute, 1907). In his letter to Mellor soon after the dedication, Hartman estimated about 2,000 Costa Rican artifacts were on exhibit in 1907.

Holland and Hartman experienced differences of opinion within a few months of the hiring, and the difficulties resurfaced at various times during Hartman’s employment. The fundamental issue lay in how each conceived of the curatorial position. In Holland’s view, acquisition of collections and preparation of exhibits were the priorities. Hartman consistently emphasized research, from the resumption of his fieldwork in Costa Rica to conducting comparative studies at other museums. The situation escalated on May 27, 1907 when Hartman wrote a twenty-page letter stating his case for a salary increase to C. C. Mellor, Chairman of the Museum Committee. The Committee referred the letter to Holland for action; Holland’s response to the Committee was less than enthusiastic. Although a year was to pass before Hartman resigned, he began to lay the groundwork for that move soon after his request for a salary increase. In July 1907, he used his accumulated vacation to visit Sweden for three months, after which he returned to Pittsburgh for about six months, resigned from Carnegie Museum on May 1, 1908, and soon thereafter moved back permanently to Sweden, where he assumed the directorship of the Ethnographical Department.

Hartman took advantage of the professional enhancements afforded by Carnegie Museum, including his trips to the Louisiana Purchase Exposition in St. Louis, the 15th ICA in Québec, and the AAA meeting in Ithaca. He interacted with anthropologists in the United States through a series of trips authorized by Holland to facilitate access to library and collection resources not available at Carnegie Museum. He reported on one trip:

Nearly whole the month of January I have spent in New York at the private libraries of Professors M. H. Saville and A. F. Bandelier of the American Museum of Natural History and at the Lennox library, in order to look up references regarding Spanish-American archaeology and history. I have also consulted the collections from said countries in the Museums of New York, Cambridge, New Haven, and Philadelphia. (Hartman Archives, Monthly Report of the Section of Ethnology, January 1905, C. V. Hartman to W. J. Holland).

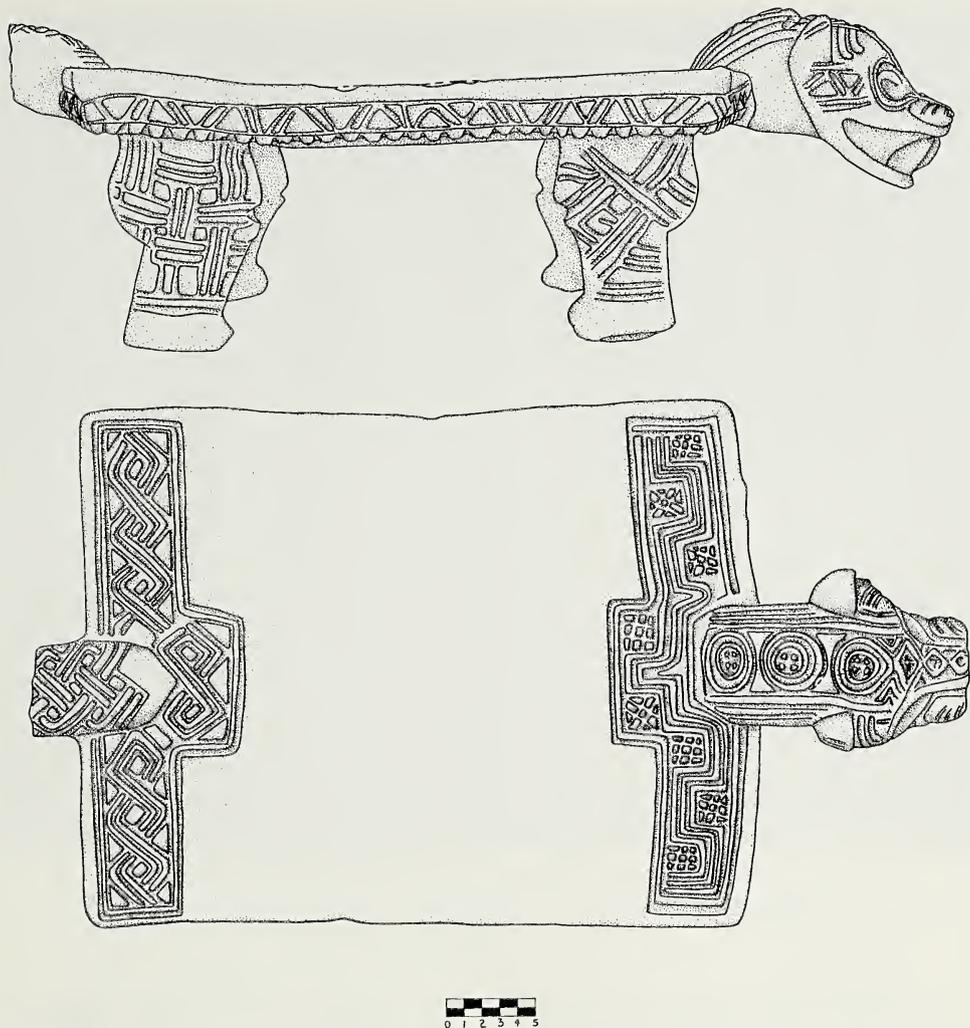


Fig. 6.—An elaborately decorated “jaguar metate” obtained by Hartman in Costa Rica in 1903 (Accession #2793/2076).

Other museum trips include visits to New York and Philadelphia in March 1904; to the Bureau of American Ethnology, Washington, D.C. in August 1905; to New York, New Haven, Washington, D.C., and Philadelphia from December 1905 through March 1906; and to New York in September 1906 after the 15th ICA in Québec.

The tension between Holland and Hartman surfaced during the latter’s lengthy absence, between late December 1905 and March 1906, when he conducted research at the American Museum of Natural History and Yale Peabody Museum in consultation respectively with Boas and MacCurdy. Hartman requested and Holland approved, albeit reluctantly, an extension to this trip. However, his pro-

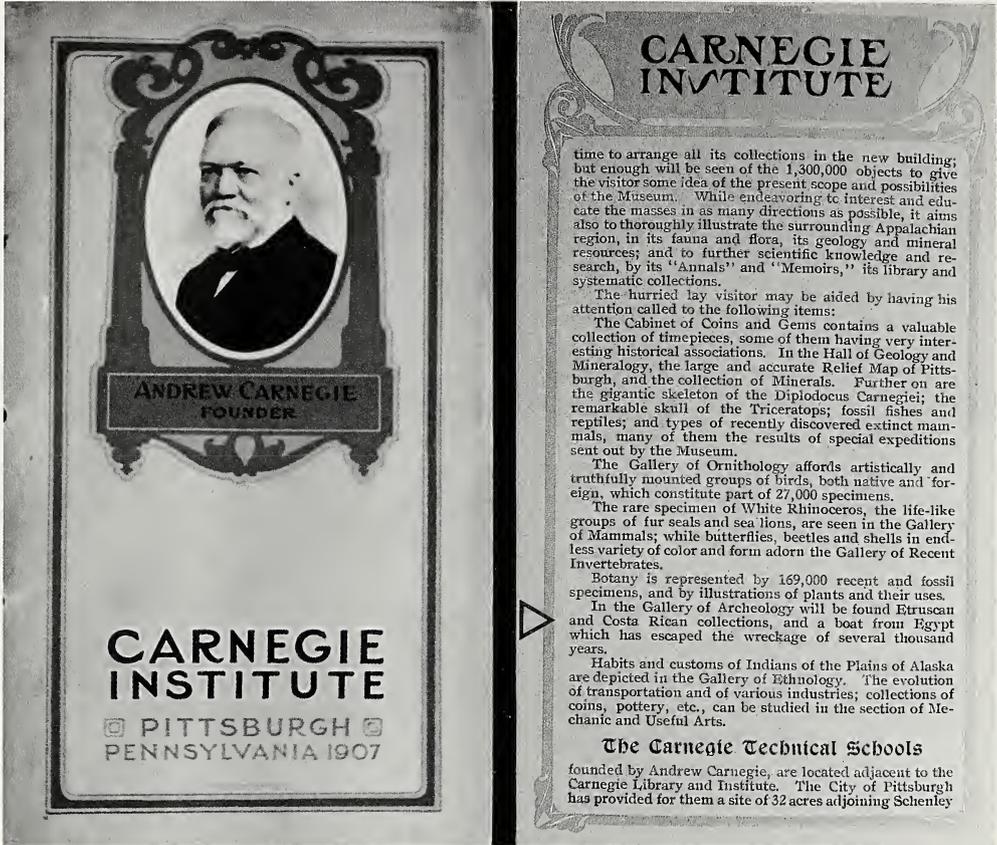


Fig. 7.—The cover of the 1907 dedication booklet and the page mentioning the Costa Rican collection exhibited in the Gallery of Archeology.

tracted stay increasingly annoyed Holland, to the point that in early March he ordered him to return to Pittsburgh. Between that trip and his resignation in 1908, Hartman never again traveled under Carnegie Museum auspices to any museum except for the brief visit to New York in September 1906 after attending the 15th ICA. Ironically, besides conducting collection research, Hartman actually was complying with Holland's mandate to acquire collections. While visiting Clark Wissler at the American Museum of Natural History, he made arrangements for a major exchange of artifacts between the two museums.

Carnegie Museum published Hartman's (1907a) second Costa Rican monograph in its *Memoirs* series and it is clear that Holland expected to publish more monographs. When departing Carnegie Museum, Hartman promised he would submit from Sweden the manuscript for his second *Memoirs* monograph dealing with ceramic artifacts from Costa Rica, a text that was well along and possibly even nearly completed. However, he never sent the manuscript and no draft versions are present in the Hartman Archives. A third *Memoirs* monograph was planned or at least under consideration before he left Carnegie Museum.

His presence at Carnegie Museum afforded him the opportunity to expand his

contacts within the field of museology and this network gained importance when he was appointed Director of the Ethnographical Department in Sweden. He was in Pittsburgh when the newly founded American Association of Museums (AAM) met there in June 1907 to celebrate the dedication of the new Carnegie Institute and in May 1908 he attended the AAM annual meeting in Chicago.

National Museum of Costa Rica

Hartman interacted with personnel at the Museo Nacional de Costa Rica (MNCR) during the Swedish expedition (1896–1897) and Carnegie expedition (1903). Anastasio Alfaro, known to Hartman through the World's Columbian Exposition and the 10th ICA in Stockholm, headed the MNCR during the first visit. Juan Fernández Ferraz, whom he had known since the Swedish expedition, succeeded Alfaro in 1898 and headed the MNCR until 1904, according to Kandler (1987:28). Henri Pittier de Fabrega, Swiss by birth, was Director of Costa Rica's Instituto Físico-Geográfico (IFG) and had been associated with the MNCR since 1888, being one of the first persons appointed to serve on its Board of Directors. Fernández Ferraz and Pittier de Fabrega represented Costa Rica at the 13th ICA in New York, thereafter visited Pittsburgh with Hartman during the post-Congress excursion, and were the recipients of the letters of introduction that Holland wrote on Hartman's behalf for the Carnegie Museum expedition (Watters, 2002*a*). Fernández Ferraz, a Spaniard, and Pittier de Fabrega, Swiss, exemplify the many foreigners who moved to Costa Rica for career advancement (González Flores, 1921).

A shared interest in and involvement with scientific research allied the MNCR and IFG. Although normally independent entities, they were on occasions consolidated during various reorganization schemes (Anonymous, 1904*b*; Conejo Guevara, 1975:26, 149–150; Stone, 1956:17). One such reorganization scheme had taken place not long before the Carnegie expedition began:

A great advantage for me just now is, that one of my most intimate friends, Professor H. Pittier de Fabrega, the head of the "Instituto Physico-Geographico" [sic] in San José has recently, when Dr. Juan Ferraz was discharged, got the arch. museum affiliated with his institution. At the Congress in N.Y. he urged me ardently to try to go down to C.R. again. He has no time for arch. and he wants me during the rainy season to arrange and classify the somewhat heterogenous [sic] collections in the museum. (Hartman Archives, letter, January 28, 1903, C. V. Hartman to W. J. Holland).

Hartman's statement discloses that the IFG under Pittier de Fabrega "affiliated" the MNCR in 1903, a point conflicting with Kandler's (1987:28) contention that Fernández Ferraz headed the MNCR until 1904. His statement would indicate that it was Pittier de Fabrega, not Fernández Ferraz, who arranged access to the MNCR archaeological collections studied and photographed by Hartman in the midst of the Carnegie expedition (Fig. 8). He used images of some MNCR artifacts for comparative purposes in his 1907 monograph. He also used his acquaintance with MNCR scientists (e.g., entomologist P. Biolley) to obtain botanical and zoological specimens that Holland desired for Carnegie Museum.

Pittier de Fabrega links with Hartman and with Costa Rican anthropology in other ways. He wrote reports on languages and customs of Costa Rica's indigenous peoples (Conejo Guevara, 1975:157) and was involved with mapping Costa



Fig. 8.—Artifacts photographed by Hartman in 1903 in the collection of the Museo Nacional de Costa Rica. (Section of Anthropology glass-plate negative G484).

Rica, a project in the course of which he explored the entire country and routinely encountered archaeological sites. Hartman attests to the close ties he maintained with Pittier de Fabrega:

In case I can continue the investigations even during the following dry season Professor P. [Pittier de Fabrega] places all his knowledge about ancient remains, rockcarvings, idols, etc. at my disposition. While engaged since 20 years ago on the work on the map of C. R. he has travelled almost all over the Republic. All arch. work that can be done in C.R. ought to be carried out soon before the rush of laborers to Panama [for canal construction] begins and wages rise. (Hartman Archives, letter, January 28, 1903, C. V. Hartman to W. J. Holland).

Hartman's mounting of the expedition in 1903 was fortuitous because Pittier de Fabrega soon thereafter left Costa Rica, having lived there for seventeen years, and moved to the United States, where he worked for the U. S. Department of

Agriculture starting in 1905 (Chase, 1950; Standley, 1950). Pittier de Fabrega is accredited as a founding member of the American Anthropological Association (Anonymous, 1903:191; recorded incorrectly as Fabrega, H. P. de).

Though not connected to the MNCR, other foreigners residing in Costa Rica were a valuable link for Hartman. He explained the ways they assisted his expedition:

My success in the excavations during this short period [the Carnegie Museum expedition], I attribute in the first hand to my own local experience in the field; second, to the valuable friendships, previously made both among the foreigners, Scandinavians, Americans and Germans, as well as among the natives in various places. Through their generous help and disinterested assistance I was enable to obtain permission from the owners of the land to excavate in various localities; and owing to the hospitality and courtesy of various of these gentlemen, my expenses were considerably lowered. (Hartman Archives, letter, May 27, 1907, C. V. Hartman to C. C. Mellor).

Minor C. Keith, the American entrepreneur who built railroads in Costa Rica, was an avid collector of antiquities and assembled a large collection while living there (Stewart, 1964:160–168). Keith obtained antiquities from various sources but especially at the site of Las Mercedes, situated on land he owned on the Atlantic coastal plain (Mason, 1945; Spinden, 1915). With Keith's authorization, Hartman (1901a:7–39) excavated part of Las Mercedes during the Swedish expedition and later brought back to Carnegie Museum a number of sculptures from that site. He reciprocated by providing Keith (as well as Pittier de Fabrega and Ferraz) with a copy of his 1901 monograph.

The Hartman and Holland Archives disclose the intriguing story of one foreigner, German consul Felix Wiss, who assisted Hartman in an unusual way. It was Wiss who informed him that the estate of Señor Juan Ramón Rojas Troyo was preparing to sell a major collection of antiquities. When Hartman acquired this Troyo collection in October 1903, just before departing Costa Rica, he used monies borrowed from Wiss since he had depleted his Carnegie Museum field funds. Thus, the German consul advanced funds to a Swedish archaeologist to purchase Costa Rican antiquities on behalf of an American museum. Holland, ever pleased with acquiring yet one more collection, willingly reimbursed the German consul's loan the following month.

DISCUSSION

Hartman transformed his career from botany to anthropology within a single decade, the 1890s; within another decade, the 1900s, he had achieved recognition as a professional anthropologist by colleagues on both sides of the Atlantic. Our analysis of the four entities—expeditions, expositions, associations, and museums—structuring this transition provides the framework for tracking his career change. However, the sequence of events and inter-relations among the activities during those two decades are masked by our focus on each entity individually. In the Appendix, we have presented these events chronologically and linked them to individuals who had roles in developing and in promoting his anthropological career. Our strategy follows Givens' ideas of the desirable content for an archaeological biography: “. . . the outline of a subject's life, relationships between the

subject and colleagues and supporting institutions, and the character's role in expanding professional and public knowledge of archaeology" (Givens, 1992:59).

Hartman began his transition to anthropology during the Lumholtz expedition and expanded his knowledge of the discipline and his network of contacts during the World's Columbian Exposition. In the mid-1890s, he presented and published the results of his anthropological fieldwork in Mexico, learned archaeological field methods, and initiated his first research in Central America. By 1900, he had completed archaeological and ethnographic research in Central America, visited museums in the United States, been hired in his first museum job, prepared an exhibit, and was writing up the research in his soon to be published articles and first monograph. By 1903, he had been awarded the Duc de Loubat prize, been honored by his peers at the 13th ICA, moved to the United States and been employed at Carnegie Museum, and completed his second expedition. By 1908, he had published his second monograph and a number of articles, served five years as Curator, mounted another exhibition, attended the 15th and 16th ICA Sessions, American Anthropological Association annual meeting, two meetings of the American Association of Museums, and the St. Louis exposition, served as a member of the Committee for the Preservation of American Antiquities, visited colleagues at various museums in the United States, and resigned his position at Carnegie Museum. By 1910, he had directed the Ethnographical Department of the Swedish Museum of Natural History for two years, and already was experiencing a decline in his research and publication productivity.

With respect to his enduring links to Costa Rica, Hartman's involvement can be traced from his first exposure to that country's antiquities and his first acquaintance with Alfaro and Peralta at the World's Columbian Exposition in 1893, to his renewal of their acquaintance at the 10th ICA and his introduction to Åke Sjögren, to Sjögren's conceiving of the Central American expedition. During the latter half of the 1890s, the connections continue through his archaeological fieldwork in Costa Rica, his meeting of Fernández Ferraz and Pittier de Fabrega at the Museo Nacional, his analysis and publication of archaeological materials from the first expedition, and his mounting of the first Costa Rican exhibition. In the first decade of the twentieth century, he renewed relations with Fernández Ferraz and Pittier de Fabrega at the 13th ICA, excavated sites and purchased antiquities during the Carnegie expedition, studied collections at the Museo Nacional, and completed his second monograph and second exhibition about Costa Rican antiquities (Fig. 9).

Hjalmar Stolpe was the individual with most influence on Hartman's anthropological career. He mentored Hartman in archaeological field methodology prior to the Swedish Central American expedition and in museum anthropology thereafter. Hartman modeled his fieldwork at Costa Rican burial grounds (Fig. 10) after Stolpe's mapping and excavation techniques developed in Sweden. Stolpe introduced Hartman to Åke Sjögren, who conceived and funded the Swedish expedition and donated the Costa Rican artifacts to the Museum of Natural History, thereby allowing Hartman to mount his first anthropological exhibit in 1900. He also paid for publication of Hartman's first monograph. Stolpe hired Hartman in his first museum position, from which he gained experience in performing curatorial duties, cataloging collections, developing exhibits, and writing up his research. He also connects to Hartman through the Swedish Society for Anthropology and Geography, the Museum of Natural History of Sweden (and later its Ethnographical Department), the 10th, 13th, and 15th International Congress of

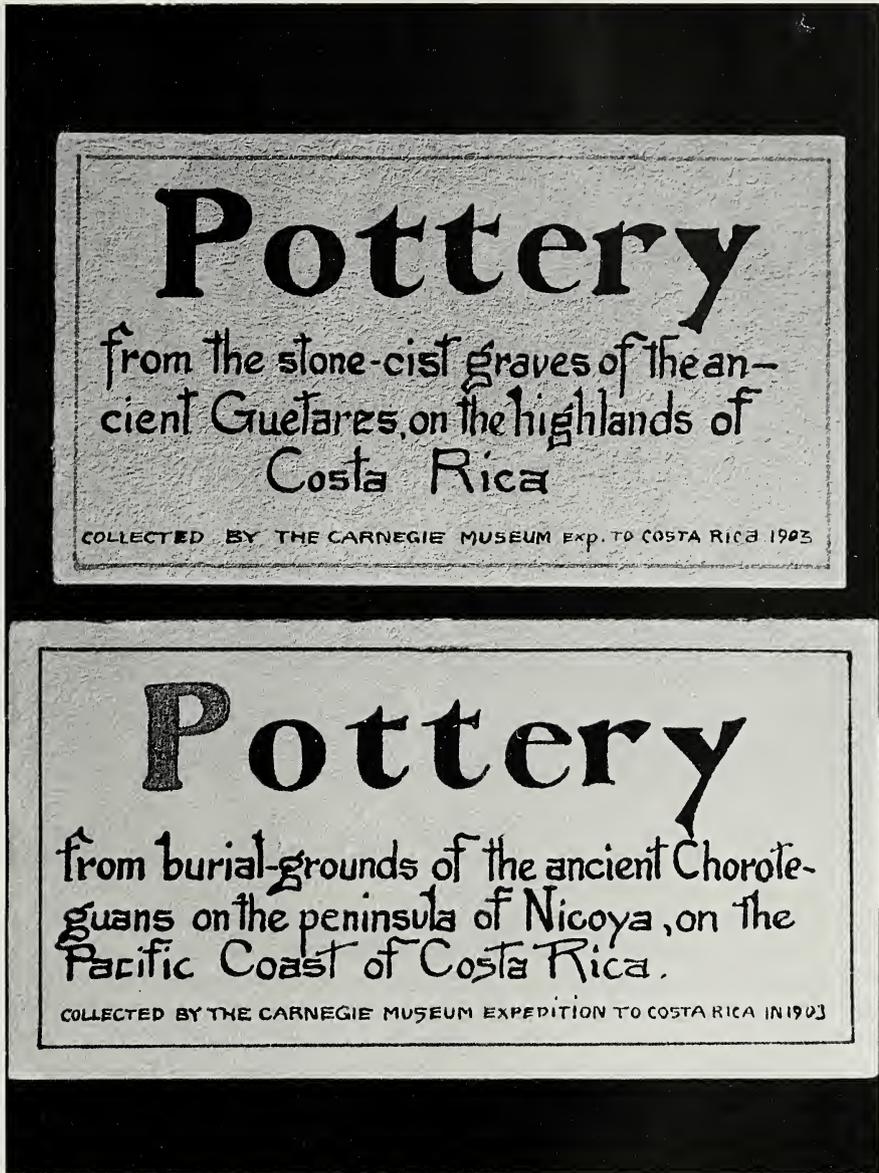


Fig. 9.—Two of the original labels (1907 exhibit) disclose that Hartman used pottery variability to distinguish between the “Guetares” of the Central Highlands and the “Choroteguans” (= Chorotegas) of the Pacific coast.

Americanists, the Duc de Loubat award, Åke Sjögren and the Swedish Central American expedition, and W. J. Holland during the post-13th ICA excursion to Carnegie Museum.

Henri Pittier de Fabrega was Hartman’s principal contact in Costa Rica. They were linked through the Swedish Central American expedition and Carnegie Museum expedition, the Museo Nacional de Costa Rica where Pittier de Fabrega



Fig. 10.—C. V. Hartman (at rear, behind stake, holding tape measure) and field crew installing grid stakes at the Chinchilla site in 1903. (Section of Anthropology glass-plate negative G964).

arranged for Hartman's study of the collections, the 13th International Congress of Americanists and the excursion to Pittsburgh, their mutual acquaintance with W. J. Holland, the American Anthropological Association, and Pittier de Fabrega's mapping project during which Costa Rican archaeological sites were identified. One probable connection we have not yet been able to verify is their continued interaction after 1905, when Hartman was still at Carnegie Museum and Pittier de Fabrega was employed in Washington, D.C.

W. J. Holland links to Hartman mainly through the Carnegie Museum connection, including his employment as Curator, the Carnegie Costa Rica expedition, publication of the second monograph, acquisition of Costa Rican collections, and installation of artifacts in the 1907 building. External links include attendance at the 13th ICA and the post-Congress excursion, their mutual acquaintance with Pittier de Fabrega, Fernández Ferraz, and Stolpe, their mutual involvement with the American Anthropological Association, Hartman's presence at the 15th ICA in Québec, and Holland's election as a corresponding member of the Swedish Society for Anthropology and Geography. It also was Holland who authorized Hartman's visit to other North American museums, which resulted in his expanded interaction with anthropological colleagues.

The two decades (1890–1910) spanning Hartman's transition to and most active involvement with anthropology coincide with a period of significant developments

in the discipline in the Americas and Europe. Foremost among these developments in North America was the move toward “professionalization” of the discipline, a process or set of processes in which Franz Boas played a key role (Stocking, 1960). Other activities linked to professionalization included establishing a national journal, *American Anthropologist*, and founding a national organization, the American Anthropological Association, with an “inclusive” membership policy (Darnell, 1998:246–251). An important development in Costa Rica during Hartman’s times was the use of archaeology to support a nationalistic agenda (Corrales Ulloa, 1999; Viales Hurtado, 1997), a movement that was widespread in Latin America under the “State Archaeology” phase of nationalism (Oyuela-Cayedo, 1994:13–16).

Another North American trend in progress but not completed during this formative period was a gradual transition in the venue where anthropology students were trained, moving from the museum setting to the university academic department where the four-field approach to the discipline was emphasized (Collier and Tschopik, 1954; Darnell, 1998:97–175). Darnell (1998:5) distinguishes two paradigms in the history of American anthropology, the first paradigm (“old school”) revolving around John Wesley Powell and colleagues at the Bureau of American Ethnology and the second paradigm (Boasian anthropology) developing around Franz Boas at Columbia University. Boas’ own career exemplifies the intellectual issues underlying this paradigm shift, when he chose to resign as curator at the American Museum of Natural History in 1905, in favor of concentrating his efforts on his professorship at Columbia (Cole, 1999:223–260; Jacknis, 1985). The transition between paradigms already was underway, albeit in incipient form, by the time Hartman attended the 13th ICA in 1902.

Hartman transformed himself into a credible “old school” anthropologist by about 1900, but the timing of his only employment as an anthropologist at a North American institution coincided with the onset of the Boasian anthropology paradigm. He unquestionably was cognizant of the four-field Americanist orientation to anthropology, despite having had no formal training in the holistic orientation to the discipline. However, he went beyond merely recognizing to actually researching in the four fields during his Central American projects. Although his archaeological publications predominate, he did publish some of his ethnographic and ethnobotanical research and, to a lesser degree, his linguistic and anthropometric studies. The recent Spanish translation (Hartman, 2001) of his century-old article originally published in Swedish, attests to the enduring value of his ethnographic research. Further evidence of his wide-ranging anthropological interest is disclosed in the proceedings of Sessions of the International Congress of Americanists, which list papers he presented but did not publish as well as papers he planned to present but did not. Among the latter was “Physical Anthropology of the Aztecs of Salvador,” a paper which he was unable to present at the 18th ICA in London in 1912, perhaps because of his health problems or the burden of administrative duties.

CONCLUSIONS

C. V. Hartman’s career as an Americanist anthropologist was international in scope, spanning the Old and New Worlds, and his anthropological research in the western hemisphere, covering the fourteen-year period between 1890 and 1903, included three expeditions embracing about six years of fieldwork, encompassed

northwest Mexico and three Central American countries, and involved archaeological, ethnographic, linguistic, and anthropometric studies. He was employed in the New World for six months at the World's Columbian Exposition in 1893 and five years at Carnegie Museum (1903–1908); he spent an additional six months visiting North American museums in 1899 and another four months seeking a job after the 13th ICA. In all, he resided in the Americas for about thirteen years between 1890 and 1908, from the start of the Lumholtz expedition to when he left Carnegie Museum. He lived in Sweden only five years.

The defining attributes of C. V. Hartman's anthropological career are captured in two statements, written almost fifty years apart, concerning the history of anthropology. "Anthropology grew out of expeditions and museums . . ." (Kroeber, 1954:764). "Prior to the establishment of academic anthropology, practitioners were self-taught and self-identified" (Darnell, 1998:12). Hartman transformed himself into an anthropologist not through university training, but instead through self-directed fieldwork conducted mainly on expeditions associated with museums.

The twenty years spanning his most active involvement occurred at a time when museum-based anthropology still strongly influenced the field, and when the "old school" paradigm was the traditional career route for most practitioners on both sides of the Atlantic. His dual background in botany and anthropology reflects another issue prevalent at that time, whether anthropology should be linked to the natural or social sciences within academia (Kroeber, 1954). This period also coincided with intellectual issues associated with patron-driven projects in museums (Snead, 1999). "As long as museum goals were set by patrons and administrators, anthropology *as a science* was subordinated" (Darnell, 1998:100; emphasis in original). The contradictory viewpoints of Hartman and Holland, respectively emphasizing field research and collection acquisition, exemplify the tensions inherent in museums at the time.

Our study has been able to reconstruct the major activities, organizations, events, and individuals influencing C. V. Hartman's anthropological career. There are, however, unresolved or poorly understood issues deserving of further study. Why did Lumholtz select Hartman as his botanist on the expedition to Mexico? Where was Hartman when he left Lumholtz for eight or so months in late 1892 and early 1893? In what specific activities was he engaged at the World's Columbian Exposition? Which North American museums did he visit for the six months after the Swedish Central American expedition? Why was he unable to obtain employment in the museums he investigated before approaching Carnegie Museum? Was his limited publication productivity in Sweden due to his health or to administrative responsibilities? Did he return to Sweden because he was a museum-based "old school" traditionalist who disapproved of or disagreed with the transition to the university setting that was starting in American anthropology?

Hartman is remembered for the high standards of fieldwork he introduced into Costa Rican archaeology, the meticulous nature of which was demonstrated in his two monographs resulting from the Swedish and Carnegie Museum expeditions. Willey and Sabloff (1993:85) regard his research to be worthy of special note, and Rowe (1959) explicitly acknowledges the importance of his field training under Stolpe. He photographically documented his excavations to an extent that is neither widely known nor adequately appreciated. Carnegie Museum of Natural History is fortunate to possess a Hartman photographic legacy, in the form of some 120 glass-plate negatives and old prints revealing his fieldwork

during the 1903 expedition (see Figures 1, 2, and 10 herein, as well as Watters and Fonseca Zamora, 2001a). A century ago his peers acclaimed his high standards in fieldwork and publication. Yet, soon thereafter Hartman's pioneering work began to be forgotten, and more than fifty years would pass before Rowe (1959) initially resurrected his reputation and Baudez (1967) credited his research with a key role in the establishment of Costa Rica's regional chronologies.

Hartman deserves greater recognition for his anthropological contributions in the Americas than he has been accorded to date. This paper furthers that recognition by analyzing the four entities that structured his career change and by placing them in broader historical context, but we regard this study to be an ongoing work and by no means the final say on the anthropological career of C. V. Hartman.

ACKNOWLEDGMENTS

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A NOTE ON SOURCES

The time span covered in this study encompasses the transitions from "old series" to "new series" for two journals, *Science* and *American Anthropologist*. In each instance, we indicate the old series by "o.s." but do not specifically designate the new series (for example, see the citations under Anonymous in Literature Cited). Also, when Hartman served at Carnegie Museum, the officially sanctioned spelling of the city was Pittsburg, the "h" having been dropped following a decision by the U.S. Geographic Names Board in 1890 (rescinded in 1911, after protest), although both spellings were in common use. We retain the city's spelling in the Literature Cited section as the author (e.g., McGee, 1902) originally presented it.

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APPENDIX

Chronology of significant events in C. V. Hartman's Anthropological Career (1890–1910).

1890–1892 (and several months in 1893)—Lumholtz expedition to Mexico

First experience in ethnographic and archaeological fieldwork
Carl Lumholtz, A. M. Stephen

1893 (six months)—World's Columbian Exposition (Chicago)

First experience in exhibiting anthropological materials
Met eminent anthropologists at International Congress of Anthropology
First observed Costa Rican antiquities
Broadened knowledge of New World anthropology
Carl Lumholtz, F. W. Putnam, Franz Boas, Anastasio Alfaro, Manuel de Peralta, W. H. Holmes

1894 (August)—10th International Congress of Americanists (Stockholm)

Presented first anthropological paper (as a stand-in for Lumholtz)
Subsequently published Swedish and English versions of the paper
Established contact with Swedish and European anthropologists
Anastasio Alfaro, Manuel de Peralta, Bishop Thiel, Eduard Seler, H. Polakowsky, Hjalmar Stolpe, Åke Sjögren, Carl Bovallius

1895—Swedish Iron Age archaeological sites

Learned “grid and square ruled paper” archaeological field techniques
Developed plans for the Swedish Costa Rican expedition
Hjalmar Stolpe, Åke Sjögren

1896–1899—Swedish Central American Expedition

Seventeen months (May 1896–September 1897) archaeological research in Atlantic plain and Central Highlands of Costa Rica
Implemented Stolpe's field methods in various excavations
Involved with persons and collections at the Museo Nacional de Costa Rica
Collections presented to Åke Sjögren who donated them to Museum of Natural History of Sweden
Conducted ethnographic and linguistic research in El Salvador and Guatemala (September 1897–spring 1899)
Expedition nominally sponsored by Swedish Society for Anthropology and Geography (SSAG)
Åke Sjögren, Anastasio Alfaro, Juan Fernández Ferraz, Henri Pittier de Fabrega

1899—North America

Visited museums in the United States for six months
 Returned to Sweden after being away three and a half years

1899–1902—Ethnographical Department of the Museum of Natural History of Sweden

Served as an assistant to the Director of the Ethnographical Department
 First experience in museum anthropology performing various curatorial duties
 Mounted first exhibition of Costa Rican artifacts
 Published first monograph on Costa Rican archaeology and articles on Central American ethnography and archaeology in *Ymer*, the SSAG journal
 Honored by the Swedish Royal Academy with the Duc de Loubat award for his monograph
 Hjalmar Stolpe, Åke Sjögren

1902 (October)—13th International Congress of Americanists (New York City)

Presented papers on Costa Rican archaeological research and (by title only) ethnographic research in El Salvador
 SSAG representative to Congress
 Introduction by Stolpe regarding the Duc de Loubat award, and afterward honored with a resolution of congratulations by the Congress
 First met W. J. Holland
 Post-Congress excursion to Pittsburgh and Carnegie Museum
 Followed by a three-month period visiting museums in search of employment
 Hjalmar Stolpe, Åke Sjögren, Eduard Seler, W. J. Holland, F. W. Putnam, Franz Boas, Juan Fernández Ferraz, Henri Pittier de Fabrega, George Grant MacCurdy, W. H. Holmes, W. J. McGee, Duc de Loubat

1903 (January–March)—Carnegie Museum Hiring

Exchange of letters with W. J. Holland while negotiating for a curatorial position
 Hired as Carnegie Museum's first Curator of Ethnology and Archaeology on February 28
 Reported for duty on March 17 and departed for Costa Rica two weeks later
 W. J. Holland, Franz Boas, Eduard Seler, W. J. McGee

1903 (April–November)—Carnegie Museum Costa Rican Expedition

Excavated archaeological sites in the Central Highlands and Pacific coast
 Purchased collections of antiquities from various individuals
 Photographed and researched collections in the Museo Nacional de Costa Rica
 Shipped anthropological, zoological, and botanical specimens to Carnegie Museum
 Henri Pittier de Fabrega, Juan Fernández Ferraz, W. J. Holland

1903–1908—Carnegie Museum Curatorship

Performed curatorial duties related to museum anthropology
 Developed second exhibition of Costa Rican antiquities in the new (1907) Carnegie Institute building
 Cataloged, researched, and photographed the Costa Rican collections he had obtained
 Published his second monograph on Costa Rican archaeology and several other articles
 Attended the annual meetings of the American Association of Museums in 1907 and 1908
 Visited anthropologists at museums in the United States for comparative collection research and to arrange exchanges
 Resigned as Curator on May 1, 1908
 W. J. Holland, Franz Boas, George Grant MacCurdy, Marshall H. Saville, A. F. Bandelier, W. H. Holmes, Clark Wissler

1904 (September)—Louisiana Purchase Exposition (St. Louis)

Attended the Congress of Arts and Science and (perhaps) informed his colleagues about his Costa Rican archaeological research
 Had his research efforts lauded by Eduard Seler
 Heard lectures by McGee and Boas
 Studied the ethnological exhibitions and purchased collections
 Eduard Seler, W. J. McGee, Franz Boas

1905 (December)—American Anthropological Association (Ithaca)

Presented a paper on the tree-calabash
 Served on the Committee for the Preservation of American Antiquities
 Franz Boas, George Grant MacCurdy

1906 (September)—15th International Congress of Americanists (Québec City)

Served as the lone representative of the government of Sweden
 Served on the Council and chaired one scientific session
 Announced the death of his mentor Hjalmar Stolpe in 1905
 George Grant MacCurdy, Franz Boas, W. H. Holmes, Clark Wissler, Eduard Seler

1908–1910—Ethnographical Department of the Museum of Natural History of Sweden

Served as Director of Ethnographical Department
 Reduction in productivity with respect to his anthropological research due to administrative responsibilities

1908 (September)—16th International Congress of Americanists (Vienna)

Presented papers on his comparative study of grave forms in Costa Rica and the photographone
 (both published in the 1910 proceedings volume)
 Laid upon the table his second Costa Rican monograph, published by Carnegie Museum
 Attendance facilitated his reentry into European anthropology and museology
 Served as an ICA Vice-President and a delegate of the government of Sweden and the Swedish
 Society for Anthropology and Geography
 Eduard Seler, George Grant MacCurdy, Franz Boas

1910–1928—Concluding his career

Continued as Director of the Ethnographical Department until he took a medical leave of absence
 in 1923 and ultimately retired in 1928
 Attended but participated little in the 18th ICA (London, 1912) and 21st ICA (Göteborg, 1924)
 Very little productivity in researching and publishing his Central American anthropological investigations

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