ISSN 0097-4463

ANNALS of CARNEGIE MUSEUM

THE CARNEGIE MUSEUM OF NATURAL HISTORY
4400 FORBES AVENUE • PITTSBURGH, PENNSYLVANIA 15213

VOLUME 65 22 FEBRUARY 1996 NUMBER 1

CONTENTS

ARTICLES

Manuscripts, subscriptions, orders for individual numbers, and changes of address should be sent to:

Office of Scientific Publications
The Carnegie Museum of Natural History
4400 Forbes Avenue
Pittsburgh, PA 15213-4080
Phone (412) 622-3287
Fax (412) 622-8837
E-mail: schmidtm@clp2.clpgh.org

ANNALS OF CARNEGIE MUSEUM is published quarterly by The Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213-4080, by the authority of the Board of Trustees of Carnegie Institute.

THE CARNEGIE
MUSEUM OF
NATURAL HISTORY

ANNALS OF CARNEGIE MUSEUM

VOL. 65, NUMBER 1, PP. 1–12 22 FEBRUARY 1996

BIOLOGY AND IMMATURE STAGES OF SNAIL-KILLING FLIES BELONGING TO THE GENUS *TETANOCERA* (INSECTA: DIPTERA: SCIOMYZIDAE). I. INTRODUCTION AND LIFE HISTORIES OF PREDATORS OF SHORELINE SNAILS

B. A. FOOTE[1]
Research Associate, Section of Invertebrate Zoology

ABSTRACT

An overview of the taxonomic composition, geographic distribution, and general biology of the family Sciomyzidae is presented. Literature dealing with the taxonomy and biology of the genus *Tetanocera* is summarized, and collecting, rearing, and preservation techniques are discussed.

The natural histories, life cycles, and larval feeding habits of *Tetanocera fuscinervis* and *T. silvatica,* two species that prey on pulmonate snails occurring on wet shorelines, are presented.

INTRODUCTION

The acalyptrate Diptera family Sciomyzidae has a worldwide distribution and contains some 60 genera and 550 species (Knutson, 1987). The fauna of America north of Mexico consists of 21 genera and at least 175 species (Knutson et al., 1986). The biology of the family has been the focus of intensive study for over 40 years with the original impetus coming from the discovery of the snail-feeding habits of six species (Berg, 1953). Subsequently, numerous workers have described the immature stages and discussed the life histories, ecologies, and larval feeding habits of members of the family. Information is now available for over 200 species in the world, with particular attention to species occurring in the holarctic region. Larvae have been shown to prey on pulmonate aquatic snails, shoreline-inhabiting snails, terrestrial snails, snail eggs, slugs, and fingernail clams. Literature published before 1950 on the biology of Sciomyzidae has been discussed by Berg (1953) and Foote (1959). Berg (1961), Berg and Knutson (1978), and Knutson (1987) have summarized more recent findings.

The genus *Tetanocera* has a holarctic distribution and contains some 40 species, with 30 species being recorded from the Nearctic region (Knutson, 1987). Keys and descriptions of the adults of species occurring in America north of Mexico are available in Steyskal (1959) and Orth and Fisher (1982).

The present paper presents observations on the geographic distributions, habitat preferences, life histories, and larval feeding habitats of *T. fuscinervis* (Zetterstedt) and *T. silvatica* Meigen, two holarctic species having larvae that prey on pulmonate hygrophilous snails occurring in shoreline habitats. Subsequent papers will cover the biologies of species belonging to other trophic guilds, describe immature stages, and present a key to the third-instar larvae of the Nearctic species of *Tetanocera.*

---

[1] Department of Biological Sciences, Kent State University, Kent, Ohio 44240.

Submitted 10 March 1995.

REVIEW OF LITERATURE

The relatively few papers that have focused on the natural histories and larval feeding habits and/or described the immature stages of species of *Tetanocera* are discussed below.

Dufour (1849) apparently was the first worker to study the biology of a species of *Tetanocera*. He encountered a larva of *T. ferruginea* Fallén in mid-November, 1846, in floating mats of duckweed (*Lemna* sp.) and water-starwort (*Callitriche* sp.) in a small pond near Saint-Sever, France. This larva completed development in the laboratory and produced an adult on April 26, 1847. Dufour never observed larval feeding but did describe and illustrate the third-instar larva and puparium.

Grünberg (1910) described the habitat of the larvae of *T. ferruginea* in Europe as being among such aquatic plants as *Lemna* and *Callitriche* in slow-flowing water. He reported that pupae overwinter and that there are probably two or more generations a year.

Brocher (1913) illustrated a larva of *Tetanocera* and stated that it resembled larvae of another sciomyzid genus, *Sepedon,* except that it was smaller and had much shorter lobes around the posterior spiracular disc. He reported that the larva left the water before forming a puparium and that the puparium did not float. Apparently, interspiracular processes (float hairs) were absent, but it is impossible to tell from his overly stylized drawing which species was involved.

Lundbeck (1923) discovered floating puparia of 26 species of Sciomyzidae, including *T. elata* Fabricius, *T. ferruginea,* and *T. silvatica,* in marshes and ponds in Denmark during the spring months. He made no observations of the larvae, and his comment that "the larvae are phytophagous or feed on decaying vegetable matter, perhaps also being carnivorous on small objects . . ." is unfounded. Lundbeck reared parasitoids belonging to a species of Ichneumonidae (subfamily Cryptinae) and wingless species of Proctotrupidae (Hymenoptera) from puparia of *T. ferruginea.*

Johannsen (1935) described but did not illustrate the puparium of *T. ferruginea* from material collected amid vegetation along the margin of a shallow pond near Ithaca, New York. He noted the appearance of the anterior spiracles, and described the posterior spiracular disc and perianal pad (anal plate). He reported that the puparium of this species differed from those of species of *Dictya* in the appearance of the posterior spiracular disc and the length/width ratio of the perianal pad.

Bhatia and Keilin (1937) described in considerable detail the larva of an undetermined species of Sciomyzidae that was obtained from a living land snail, *Vertigo genesii* Gredler, in England. They observed swallowing of air by the larva, a common sciomyzid habit, and noted that the larva imbedded itself in the prey snail until only the posterior spiracles were visible in the aperture of the shell. Their descriptions and drawings indicate that the larva was a member of the tribe Tetanocerini. The mouthhooks possessed four accessory teeth, the number usually found in larvae of *Tetanocera,* and the rows of "sensory papillae" found on the venter of each abdominal segment are recognizable in a few species of *Tetanocera.* However, the presence of only five finger-like lobes (=papillae) on the anterior spiracles illustrated is a character not known for any *Tetanocera* larva.

Berg (1953) made observations on *T. ferruginea, T. fuscinervis* (as *unicolor* Loew), and *T. rotundicornis* Loew. Larvae of the first species were free living and preyed on aquatic and shoreline snails. Newly hatched larvae of *T. fuscinervis* fed on pieces of a freshly killed *Helisoma* (Planorbidae), but died while still a first instar. An adult of *T. rotundicornis* was reared from a larva that had infested a species of *Oxyloma* (Succineidae). He also presented evidence that overwintering occurred as pupae in *T. ferruginea* and *T. rotundicornis.* In a later paper, Berg (1961) summarized the larval feeding habits and morphology of the immature stages of 84 species of Sciomyzidae, including 16 species of *Tetanocera.*

Nielsen et al. (1954) discovered larvae of *T. robusta* Loew in wet areas in Iceland and suggested that the winter was passed as a pupa. They described and illustrated the third-instar larva.

Soós (1958) attempted to determine the number of generations produced each year for a variety of European species of Sciomyzidae by using data available on pinned specimens in museum collections. He reported that *T. arrogans* Meigen, *T. hyalipennis* Roser, and *T. silvatica* were bivoltine; whereas *T. punctifrons* Rondani and *T. fuscinervis* were univoltine. More recently, Berg et al. (1982) reported on seasonality, overwintering habits, and voltinism in north-temperate Sciomyzidae. Species of *Tetanocera* were represented in three of the five distinct groups which they recognized.

Berg and Neff (1959) discussed the use of larvae of certain predatory sciomyzids, including some species of *Tetanocera,* as biocontrol agents of aquatic snails serving as intermediate hosts of schistosome flukes that cause Schistosomiasis in man.

Foote (1961) discussed the life histories of 18 Nearctic species of *Tetanocera* and described and illustrated the eggs, larvae, and puparia of 12 species.

Disney (1964) reported that larvae of *T. ferruginea* were predators of pulmonate aquatic snails and described the larval habitat in England. He also recorded the ichneumonid wasp, *Phygadeuon elegans* Marshall, as a parasitoid of the pupa.

Rozkošny (1965) described and illustrated the mature larva and puparium of *T. ferruginea* and the puparia of *T. arrogans* and *T. elata.* Later, Rozkošny (1967) discussed the biology and larval feeding habits of several European species of Sciomyzidae, including *T. arrogans, T. elata,* and *T. ferruginea.* He also described and illustrated the eggs, mature larvae, and puparia of these species.

Although Foote (1963) briefly covered the slug-killing habits of two Nearctic species, *T. plebeja* Loew and *T. valida* Loew, the first detailed discussion of slug-killing habits in the genus was presented by Knutson et al. (1965). They presented information on the geographic distribution, habitat occurrence, life history, and larval feeding habits of *T. elata,* a Palearctic species. Other papers that discuss the biology of slug-killing species of *Tetanocera* are those of Trelka and Foote (1970) and Trelka and Berg (1977).

Knutson (1963) did an extensive literature review of sciomyzid biology and taxonomy, gave detailed information on the natural history of 26 species of nine genera occurring in the Palearctic region, described the larvae and/or puparia of 18 species, and presented a key to the mature larvae and puparia of 19 species. He included information on seven species of European *Tetanocera.* Later, Knutson (1970) summarized the natural history of sciomyzid flies occurring in Sweden, including notes on 11 species of *Tetanocera.*

Rozkošny (1966) summarized biological, ecological, distributional, and taxonomic information on the snail-killing flies of Czechoslovakia, including discussions of ten species of *Tetanocera.*

Beaver (1972) discussed the life histories and larval feeding habits of eight species of *Tetanocera* occurring in England, including four species that also occur in North America. She reported that *T. fuscinervis* and *T. silvatica* had larvae that preyed on shoreline snails, whereas larvae of *T. ferruginea* and *T. robusta* attacked aquatic snails. Beaver (1973) presented ovipositional data for six European species, and later (1974*a*, 1974*b*) discussed intra-(four spp.) and interspecific (five spp.) competition in *Tetanocera*.

Berg and Knutson (1978) reviewed the basic biology of sciomyzid flies, recognizing eight trophic guilds in the family based on the feeding habits of the larvae.

Gasc et al. (1984) described and illustrated the chorionic stucture of the egg of *T. ferruginea*, suggesting that the chorion served as a plastron in eggs that are deposited in habitats that are subject to immersion. As a result, embryonic development can continue even if eggs are completely immersed.

Vala and Haab (1984) investigated the role of temperature and photoperiod in the development of *T. ferruginea* and the induction of pupal diapause. Manguin et al. (1985, 1988*a*, 1988*b*) and Manguin and Vala (1989) investigated the predatory behavior of *T. ferruginea* with respect to its foraging strategy, prey preferences, and the influence of snail biomass on numbers of prey consumed. Manguin (1989) demonstrated sexual dimorphism in puparia and adults of *T. ferruginea*, noting that the sex of the adult could be predicted quite reliably by measuring the body length of the puparium.

Vala and Gasc (1988) attempted to correlate the structure of the posterior spiracular disc of sciomyzid larvae with their habitat preferences. They suggested that well-developed interspiracular processes (float hairs) and elongated peripheral lobes typified the aquatic predators, whereas these processes and lobes are greatly reduced in the more terrestrial species.

Ferrar (1987*a*, 1987*b*) summarized knowledge of the biology and immature stages of the family Sciomyzidae, including several species of *Tetanocera*.

MATERIALS AND METHODS

To avoid morphological descriptions and biological observations that may reflect pecularities of local races, species of *Tetanocera* were reared from as many different geographic localities as possible. Rearings were initiated from material collected in Alaska, Colorado, Idaho, Montana, New York, Ohio, and Washington. Adults collected with a standard insect sweep net were placed in 8-dram shell vials and transported alive to the laboratory. Larvae of aquatic species in shallow-water habitats were found by submerging floating and emergent vegetation and allowing the larvae and puparia to float free. Many puparia were also found by searching through floating or stranded debris. Larvae of shoreline and terrestrial species were obtained by confining large numbers of field-collected snails and slugs in shallow plastic pans for at least ten days. The pans had a substrate of moist paper toweling and were covered by cheesecloth held in place by rubber bands. The pans were examined daily for dead and dying host individuals and for larvae and puparia. Snails that appeared to be infested were isolated in small petri dishes containing moist, shredded peat moss and examined daily for larvae.

Rearings were maintained in large, well-lighted laboratories under room temperature conditions. Although relative humidities varied considerably in the laboratories, all rearings were held in small containers in which high humidities were maintained. Adults were confined in glass or plastic jars that were approximately 9.0 by 5.0 cm. The jars were covered with cheesecloth or fine screening and had a substrate of moist peat moss. Short lengths of cattail or short pieces of grass served as resting sites for the adult flies. Small living snails or slugs were placed in each jar and a small pellet of a pasty mixture of honey and brewers' yeast was appressed to the wall. In additional to the honey/yeast pellet, crushed snails were added to provide a protein source for the flies.

Breeding jars were examined daily for eggs. These were removed with a fine camel's hair brush and transferred to plastic petri dishes, with each dish receiving ten to 20 eggs. Eggs of terrestrial *Tetanocera* were placed on moist peat moss, and those of the more aquatic species were placed on short lengths of microscope slides floating in a small amount of water. Samples of eggs of each species were preserved in 10% formalin.

When eggs of the aquatic species began to hatch, several small snails (under 5.0 mm) were added to the dishes. Dead snails were removed as they appeared and then replaced with living individuals. Cast exuviae were removed when produced and preserved in 70% ethanol. Larvae of all three instars were killed in hot water and preserved in 70% ethanol. As puparia were formed, they were transferred to 8-dram shell vials containing a layer of moist peat moss and a cap of cheesecloth or fine screening.

Most external structures of the larvae were examined without dissection, but the anterior spiracles were removed and mounted on microscope slides for detailed study. The anterior spiracles were macerated for 24 hr in a 10% solution of potassium hydroxide, rinsed in acid alcohol, dehydrated in a graded series of alcohol baths, and finally mounted on microscope slides in Canada Balsam or Permount. Cephalopharyngeal skeletons were recovered from cast exuviae, dissected out of preserved larvae, or removed from puparia. The skeletons were treated as described above and either mounted on microscope slides or studied directly in 70% ethanol by use of a dissecting microscope.

All measurements were made with an American Optical Company ocular micrometer that had been calibrated with a stage micrometer. Drawings of eggs and larval structures were made by using an ocular grid of equal squares. Preliminary sketches were made on white paper that had been similarly gridded into equal-sized squares. Final drawings were made either on Strathmore drawing paper or on No. 1½ Ross stipple board.

LIFE HISTORY STUDIES

Tetanocera fuscinervis (Zetterstedt), 1838; Insecta Lapponica Descripta: 737

Tetanocera fuscinervis is holarctic, occurring in Europe and Siberia as well as in North America. In the Nearctic region (Fig. 1), it is recorded from Newfoundland west to Alaska, and south to New York, Iowa, and Arizona (Knutson et al., 1986). Earlier American literature (e.g., Steyskal, 1959) referred to this species as *T. unicolor* Loew, 1847.

In central New York, adults and puparia were found only in stands of emergent vegetation growing at the south end of the White Church Marsh located south of Ithaca. Adults were swept from a borrow pit bordering the abandoned railroad as well as along the south shore of the main marsh. Puparia were taken most abundantly floating amid the emergent sedges in the borrow pit. In northeastern Ohio, adults were taken only in an unshaded fen located in the Herrick Preserve in Portage County. In Colorado (three localities near Florissant in Teller County), Idaho (several localities in the northern half of the state), and Alaska (the Matanuska Valley and south of Anchorage), adults were collected in open or partially

Fig. 1.—Distribution of *Tetanocera fuscinervis* in North America.

shaded marshes containing little water but supporting dense stands of emergent vegetation, especially species of *Carex.*

This species was used in the first attempt to initiate a rearing of any sciomyzid by confining wild-caught flies for oviposition (Berg, 1953). Adults of *T. fusci-*

nervis (=*T. unicolor*) collected by Berg in an unshaded grass-sedge marsh five miles south of Anchorage, Alaska, on July 2, 1952, were confined in an experimental model of what has now evolved as a standard breeding jar. They mated soon after confinement and laid eggs on July 3 and 4, attaching them to damp sphagnum moss at the bottom of the container. Although motion inside the egg membranes was noticed on July 8, no hatching occurred on that day nor on the next. Some eggs had hatched by the morning of July 10; all, by noon of July 11. As there was then no knowledge that the minute first-instar larvae attack and kill living snails, they were offered pieces of freshly killed and chopped *Helisoma subcrenatum* (Carpenter). They fed sparingly and showed little evidence of development. Although the larvae survived well (up to 14 days), all died without molting into the second instar (Berg, 1953).

Rearings were initiated by the present author from puparia taken at the White Church Marsh during March and April 1956 and from adults taken in June and early July 1958–60 in a small, partially shaded marsh located eight miles north of Sandpoint, Bonner County, Idaho (see Foote, 1961:148 for description of the Idaho site). Another rearing was initiated from adults collected on July 24, 1993, in an open grass–sedge marsh located one mile west of Florissant, Colorado.

Many eggs were obtained from laboratory-reared and wild-caught females. On March 14, 1956, two females and a male that had emerged on March 13 were placed in a breeding jar. Mating was noticed first on March 19 and was seen frequently thereafter. Females began ovipositing on March 21, but laid only 16 eggs before dying on March 23. Another laboratory-reared female deposited 33 eggs between June 21 and July 1, 1958. Each of the females collected in nature in Idaho during June and early July produced between 70 and 204 eggs during periods ranging from eight to 13 days. Colorado-reared adults lived in the breeding jars from three to 21 days but did not oviposit.

In the breeding jars, eggs were placed low on the glass jars, within two centimeters of the moss, on projecting sprigs of moss, and on shells of living and dead snails. One female deposited 95 eggs on the jar, 66 on projecting bits of moss, and 34 on shells of living *Fossaria obrussa* (Say). Those placed on moss were closely clustered in amorphous masses containing up to 30 eggs each. Eggs laid on the sides of breeding jars were more scattered and usually did not touch each other. Another female laid 108 eggs on the jar, three on shells, and none on moss. Under laboratory conditions, the incubation period was four to six days in the specimens collected in New York and Idaho but seven days in those from Alaska (n = 79: New York, 10; Idaho, 57; Alaska, 12).

Larvae fed on small *Gyraulus parvus* (Say) and *Helisoma* spp. but developed more slowly than did other predaceous sciomyzid larvae reported in the literature. A larva that hatched on June 24 destroyed several small *Helisoma,* but did not molt into the second instar until July 1. Seven other larvae remained in the second instar for nine to 11 days. Very few larvae reached the second instar, only four attained the third instar, and none formed a puparium. The causes of this heavy mortality rate are unknown. Knutson (1963) reared larvae of a European strain of *T. fuscinervis* (as *T. unicolor*) from hatching to pupariation, and did not mention a high mortality rate. However, only one adult emerged from his 19 puparia, and the puparia that were dissected contained mummified or decaying bodies.

The 17 puparia found floating at the White Church Marsh from early March to April produced adults 11 to 16 days after being brought into the heated laboratory. Greatest emergence occurred in 11 to 12 days.

In central New York, the earliest seasonal record for adults is June 10; the latest, September 2. Adults were collected occasionally throughout the summer months. Puparia were taken from early March to early April. In northern Idaho, the earliest record for adults is June 1; the latest, August 11. Because of the comparatively slow growth of the larvae, *T. fuscinervis* may have only one generation per year. Overwintering evidently occurs in the pupal stage. Living puparia were collected on March 1 (more than three months before the earliest record for adults in this region) by breaking through the ice at the White Church Marsh.

Two of eight puparia collected on March 12 produced ichneumonid wasps of an undetermined species on March 24.

Tetanocera silvatica Meigen, 1830; Systematische Beschreibung der bekannten eüropaischen zweiflügeligen Insekten: 41.

Tetanocera silvatica is a holarctic species that has a transcontinental distribution in Canada and the northern United States (Knutson et al, 1986), ranging from Alaska to Newfoundland and south to Minnesota, Colorado, and Arizona (Fig. 2).

Adults of this species were most commonly encountered in permanent marshes or in marshy areas surrounding lakes. Other adults were taken in more temporary herbaceous wetlands, but none were encountered in wooded habitats. Near Florissant, Colorado, adults were taken on July 24, 1993, in association with *T. fuscinervis, Dictya montana* Steyskal, *Renocera johnsoni* Cresson, *Sepedon fuscipennis* Loew, and *Limnia sandovalensis* Fisher and Orth from a small (ca 1 acre), unshaded sedge marsh in which water levels had dropped noticeably as summer advanced. Adults of *T. silvatica* were especially common in somewhat drier, marginal areas of the marsh. In Banff National Park on August 10, four adults that served as the basis of a laboratory rearing were swept from herbaceous vegetation growing in a floodplain marsh partially shaded by spruces. Small pools of open water one-half to one meter deep were scattered across the marsh. Three third-instar larvae of *T. silvatica* were found in shoreline debris around the shallow pools. Small aquatic snails of the genera *Helisoma, Physella,* and *Gyraulus* were abundant, and several individuals were crawling over the wet shoreline bordering the pools. Amphibious snails of the genera *Catinella* and *Oxyloma* were abundant on the shoreline vegetation. Another indication that the larvae are usually associated with shoreline habitats was my failure to recover larvae from floating vegetation in western Alberta, central New York, northwestern Idaho, and central Colorado despite repeated attempts.

Numerous matings in the breeding jars were noted at various times during the day between 10:00 A.M. and 9:30 P.M. The male's position was similar to that observed in other species of the genus, except that his fore tarsi were placed close together on the middle of the female's frons rather than lying along her eye orbits. The first 24 eggs were obtained on August 16 from the two females collected in nature on August 10. Seven eggs were affixed close together on the umbilical surface of a dead *Helisoma,* two were on the shell of a dead *Lymnaea,* six were placed on peat moss near a living *Lymnaea,* and the remaining nine eggs were scattered over the glass walls of the jar. A total of 71 eggs was deposited by these two females between August 16 and September 5.

The incubation period lasted two to three days ($n = 18$), and newly hatched larvae were given small living *Gyraulus* and *Lymnaea* snails. As in *T. fuscinervis,* larval development in this species was somewhat prolonged, with the first stadium

Fig. 2.—Distribution of *Tetanocera silvatica* in North America.

lasting four to five days ($n = 6$). Another behavior that was somewhat unusual for species of *Tetanocera* was a tendency for the newly hatched larvae to feed gregariously within individual snails, with up to four larvae feeding together in a single *Gyraulus*. In contrast, second and third instars were more solitary in their feeding habits and did not occur together in any one snail. The second stadium was completed in five to six days ($n = 3$), but no larva managed to pupariate. Another rearing initiated by two females collected on July 24 in the marsh near Florissant, Colorado, was somewhat more successful in that adults emerged from two puparia obtained in the laboratory rearing. As in the earlier rearing, the newly hatched larvae commonly fed gregariously in such snails as small species of *Gyraulus, Helisoma, Lymnaea,* and *Oxyloma,* whereas older larvae fed singly. Between six and eight snails were consumed by two larvae during feeding periods of 22 and 27 days, respectively. The first stadium lasted four to six days ($n = 3$); the second, five days ($n = 2$); and the third, ten to 11 days ($n = 2$). The pupal period for a female was 17 days, whereas that of a male was 21 days. Mating among these reared adults began within three days after emergence, but no eggs were deposited.

The earliest seasonal record for adults was obtained on May 20 (Minnesota); the latest, on August 17 (Alaska). Adults have been taken throughout the summer months in several localities, and it is probable that *T. silvatica* is at least bivoltine. The duration of the egg-to-egg period in the laboratory was 46 to 55 days, and there was no indication of diapause in any life stage.

DISCUSSION

The habitat distribution of these two species of *Tetanocera* is quite similar in that both occur in open, largely unshaded herbaceous marshes with fluctuating water levels. More specifically, their larvae are associated with shorelines and can be found preying on stranded pulmonate aquatic and hygrophilic snails occurring in such situations. By frequenting shoreline habitats, the larvae probably escape competition from the more aquatic species of *Tetanocera* and other genera of Sciomyzidae. They probably do encounter competition from larvae belonging to other shoreline-dwelling genera of the family, such as species of *Pherbellia,* as well as from larvae of other species of *Tetanocera.* However, the specialization of the other species of shoreline *Tetanocera* on particular assemblages of gastropods probably mitigates interspecific competition within the genus. In contrast to such trophically specialized shoreline-dwelling species that prey on succineid snails (*T. melanostigma* Steyskal, *T. oxia* Steyskal, *T. rotundicornis*) or slugs (*T. plebeja*), larvae of *T. fuscinervis* and *T. silvatica* are rather generalized predators, frequently attacking stranded individuals of more aquatic species of Gastropoda.

Competition for a limiting resource (stranded aquatic snails) may occur occasionally between *T. fuscinervis* and *T. silvatica.* Adults of the two species commonly occur in the same marsh at the same time, although the first species usually is more abundant. For example, the acre-sized marsh near Florissant, Colorado, supported a large population of *T. fuscinervis,* but a relatively small population of *T. silvatica.* Perhaps biotic (enemies) and abiotic (weather conditions) factors maintain populations of one or both species of *Tetanocera* below the carrying capacity of the marsh habitat such that there is only rarely a shortage of larval food.

ACKNOWLEDGMENTS

Research was supported by grants from the National Science Foundation, National Institute of Allergy and Infectious Diseases, National Geographic Society, and the American Philsophical Society. Appreciation is expressed to G. C. Steyskal of Gainesville, Florida, for his expert help in determining species of *Tetanocera.*

This paper is dedicated to the memory of Dr. C. O. Berg, formerly of the Department of Entomology at Cornell University in Ithaca, New York.

LITERATURE CITED

BEAVER, O. 1972. Notes on the biology of some British sciomyzid flies (Diptera: Sciomyzidae). II. Tribe Tetanocerini. The Entomologist, 105:284–299.

———. 1973. Egg laying studies on some British sciomyzid flies (Diptera: Sciomyzidae). Hydrobiologia, 43:1–12.

———. 1974*a*. Laboratory studies on competition for food of the larvae of British sciomyzid flies (Diptera: Sciomyzidae. I. Intra-specific competition. Hydrobiologia, 44:443–462.

———. 1974*b*. Laboratory studies on competition for food of the larvae of some British sciomyzid flies (Diptera: Sciomyzidae). II. Inter-specific competition. Hydrobiologia, 45:135–153.

BERG, C. O. 1953. Sciomyzid larvae (Diptera) that feed on snails. Parasitology, 39:630–636.

———. 1961. Biology of snail-killing Sciomyzidae (Diptera) of North America and Europe. Verhandlung der XI International Kongress für Entomologie, 1:197–202.

BERG, C. O., AND L. V. KNUTSON. 1978. Biology and systematics of the Sciomyzidae. Annual Review of Entomology, 23:239–258.

BERG, C. O., AND S. E. NEFF. 1959. Preliminary tests of the ability of sciomyzid larvae (Diptera) to destroy snails of medical importance. Bulletin of the American Malacological Union, 25:11–13.

BERG, C. O., B. A. FOOTE, L. KNUTSON, J. K. BARNES, S. L. ARNOLD, AND K. VALLEY. 1982. Adaptive differences in phenology in sciomyzid flies. Memoir of the Entomological Society of Washington, 10:15–36.

BHATIA, M. L., AND D. KEILIN. 1937. On a new case of parasitism of a snail (*Vertigo genesii* Gredl.) by a dipterous larva. Parasitology, 29:399–407.

BROCHER, F. 1913. L'Aquarium de Chamber. Libraire Payot, Paris, 451 pp.

DISNEY, R. H. L. 1964. A note on diet and habitats of the larva and an ichneumonid parasite of the pupa of *Tetanocera ferruginea* Fall. (Dipt., Sciomyzidae). Entomologist's Monthly Magazine, 25: 88–90.

DUFOUR, L. 1849. Histoire des metamorphoses du *Tetanocera ferruginea*. Annals of the Entomological Society of France, 7:67–79.

FERRAR, P. 1987*a*. A Guide to the Breeding Habits and Immature Stages of Diptera Cyclorrhapha. Entomograph 8, Part 1: Text. E. J. Brill/Scandinavian Science Press, Copenhagen, 478 pp.

———. 1987*b*. A Guide to the Breeding Habits and Immature Stages of Diptera Cyclorrhapha. Entomograph 8, Part 2: Figures. E. J. Brill/Scandinavian Science Press, Copenhagen, 429 pp.

FOOTE, B. A. 1959. Biology and life history of the snail-killing flies belonging to the genus *Sciomyza* (Diptera: Sciomyzidae). Annals of the Entomological Society of America, 52:31–43.

———. 1961. Biology and immature stages of snail-killing flies belonging to the genus *Tetanocera* (Diptera: Sciomyzidae). Unpublished Ph.D. dissert., Cornell University, Ithaca, New York, 190 pp. Order No. 62–105, University Microfilms, Ann Arbor, Michigan (Dissertation Abstracts, 22: 3302–3303).

———. 1963. Biology of slug-killing *Tetanocera* (Diptera: Sciomyzidae). Proceedings of the North-central Branch of the Entomological Society of America, 18:97.

GASC, C., J. VALA, AND J. REIDENBACH. 1984. Étude comparative au microscope électronique a balayage structures chorioniques d'oeufs de cinq espèces de Sciomyzidae à larves terrestres et aquatiques (Diptera). Annals de la Société Entomologie de France, 20:163–170.

GRÜNBERG, K. 1910. Diptera, Zweiflüger. Pp. 1–312, *in* Die Süsswasserfauna Deutschlands. Heft 2A (A. Brauer, ed.), Jena.

JOHANNSEN, O. A. 1935. Aquatic Diptera II. Orthorrhapha-Brachycera and Cyclorrapha. Memoir of the Cornell University Agricultural Experiment Station, 177:1–62.

KNUTSON, L. V. 1963. Biology and immature stages of snail-killing flies of Europe (Diptera: Sciomyzidae). Unpublished Ph.D. dissert., Cornell University, Ithaca, New York, 390 pp. Order No. Mic 63–4822, University Microfilms, Ann Arbor, Michigan (Dissertation Abstracts, 24:445–446).

———. 1970. Biology of snail-killing flies in Sweden (Dipt., Sciomyzidae). Entomologica Scandinavica, 1:307–314.

———. 1987. 84. Sciomyzidae. Pp. 927–940, *in* Manual of Nearctic Diptera, Volume 2 (J. F. McAlpine, B. V. Peterson, G. E. Shewell, H. J. Teskey, J. R. Vockeroth, and D. M. Wood, coords.), Research Branch, Agriculture Canada Monograph 28, Ottawa, 675–1332 pp.

KNUTSON, L. V., J. W. STEPHENSON, AND C. O. BERG. 1965. Biology of a slug-killing fly, *Tetanocera elata* (Diptera: Sciomyzidae). Proceedings of the Malacological Society of London, 36:213–220.

KNUTSON, L. V., R. E. ORTH, T. W. FISHER, AND W. L. MURPHY. 1986. Catalog of Sciomyzidae (Diptera) of America north of Mexico. Entomography, 4:1–53.

LUNDBECK, W. 1923. Some remarks on the biology of Sciomyzidae, together with the description of a new species of *Ctenulus* from Denmark (Dipt.). Viddenskabelige Meddelelser fra Dansk Naturhistoriske Forening I København, 76:101–109.

MANGUIN, S. 1989. Sexual dimorphism in size of adults and puparia of *Tetanocera ferruginea* Fallén (Diptera: Sciomyzidae). Proceedings of the Entomological Society of Washington, 91:523–528.

MANGUIN, S., AND J. VALA. 1989. Prey consumption by larvae of *Tetanocera ferruginea* (Diptera: Sciomyzidae) in relation to number of snail prey available. Annals of the Entomological Society of America, 82:588–592.

MANGUIN, S., J. C. VALA, AND J. M. REIDENBACH. 1985. Prédation de mollusques dulçaquicoles par les larves malacophages de *Tetanocera ferruginea* Fallén, 1820 (Diptera, Sciomyzidae). Canadian Journal of Zoology, 64:2832–2836.

———. 1988*a*. Action prédatrice des larves de *Tetanocera ferruginea* (Diptera: Sciomyzidae) dans des systèmes à plusieurs espècies de mollusques-proies. Acta Oecologica/Oecologia Applicata, 9: 249–259.

———. 1988*b*. Détermination des préferénces alimentaires des larves de *Tetanocera ferruginea* (Diptera: Sciomyzidae), prédateur de mollusques dulçaquicoles. Acta Oecologica/Oecologica Applicata, 9:353–370.

NIELSEN, P. O., O. RINGDAHL, AND S. L. TUXEN. 1954. The Zoology of Iceland. Volume III, Part 48a: Diptera I. Ejnar Munksgaard, Copenhagen, 189 pp.

ORTH, R. E., AND T. W. FISHER. 1982. A new species of *Tetanocera* Dumeril from Colorado (Diptera: Sciomyzidae). Proceedings of the Entomological Society of Washington, 84:685–689.

ROZKOŠNY, R. 1965. Neue Metamorphosestadien mancher *Tetanocera*-arten (Sciomyzidae, Diptera). Zoologische Listy, 14:367–371.

———. 1966. Ceskoslovenske druhy malakofagni celedi Sciomyzidae (Diptera) (The Czechoslovakian species of the malacophagous family Sciomyzidae). Folia Facultatis Scientiarum Naturalium Universitatis Purkynianae Brunensis Biologia, 7:1–111.

———. 1967. Zur Morphologie und Biologie der Metamorphosestadien mitteleuropaischer Sciomyziden (Diptera). Acta Scientiarum Naturalium Academiae Scientiarum Bohemoslovacae Brno I, 4:117–160.

SOÓS, A. 1958. Ist das Insektenmaterial der Museen für ethologische und ökologische Untersuchungen verwandbar? Angaben über die Flugzeit und die Generationszahl der Sciomyziden (Diptera). Acta Entomologische Museum National Prague, 32:101–150.

STEYSKAL, G. C. 1959. The American species of the genus *Tetanocera* Dumeril (Diptera). Papers of the Michigan Academy of Science, Arts, and Letters, 44:59–91.

TRELKA, D. G., AND C. O. BERG. 1977. Behavioral studies of the slug-killing larvae of two species of *Tetanocera*. Proceedings of the Entomological Society of Washington, 79:475–486.

TRELKA, D. G., AND B. A. FOOTE. 1970. Biology of slug-killing *Tetanocera*. Annals of the Entomological Society of America, 63:877–895.

VALA, J., AND C. GASC. 1988. Ecological adaptations and morphological variation in the posterior disc of larvae of Sciomyzidae (Diptera). Canadian Journal of Zoology, 68:517–521.

VALA, J., AND C. HAAB. 1984. Étude expérimentale du developement larvaire de *Tetanocera ferruginea* Fallen, 1820. Influences de la température et de la photopériode, diapause pupale, biomasse alimentaire (Diptera: Sciomyzidae). Bulletin et Annales de la Société Royale Entomologie de Belgique, 120:165–178.

ANNALS OF CARNEGIE MUSEUM
Vol. 65, Number 1, Pp. 13–16 22 February 1996

NEW SPECIES OF *RHYACOPHILA* FROM VIRGINIA (INSECTA: TRICHOPTERA: RHYACOPHILIDAE)

Jan L. Sykora
Research Associate, Section of Invertebrate Zoology

Declan J. McCabe[1]

Abstract

A new species of rhyacophilid caddisfly from Virginia, *Rhyacophila tricornuta* is described and figured. This new species is related to *R. nigrita,* but differs from all other known species of *R. nigrita* subgroup mainly by the shape of the dorsoapical section of Segment IX bearing three short and rounded lobes.

Introduction

The genus *Rhyacophila* is widely distributed throughout the holarctic region. The Nearctic region supports rich and diverse populations of *Rhyacophila* that are included in several indigenous groups and complexes. One-hundred-twenty-six species were reported from North America including Greenland and Mexico (Morse, 1993). The *R. invaria* group includes 14 species all restricted to the eastern United States. Larvae in this group inhabit small, cold rivers and streams in the Appalachian region. According to Schmid (1970) within this group two subgroups could be easily distinguished, the *R. invaria* subgroup and the *R. nigrita* subgroup. Until now the *R. nigrita* subgroup included six closely related species that could be identified based on male genitalia characterized by transverse and high-crested abdominal Segment X, absence of horizontally produced lateral winglets on anal sclerites, and notched dorsoapical margin of Segment IX. In collections from Smyth County, Virginia, a new species of *Rhyacophila* in the *R. nigrita* subgroup has been recently discovered, and is described in this paper.

Systematic Entomology

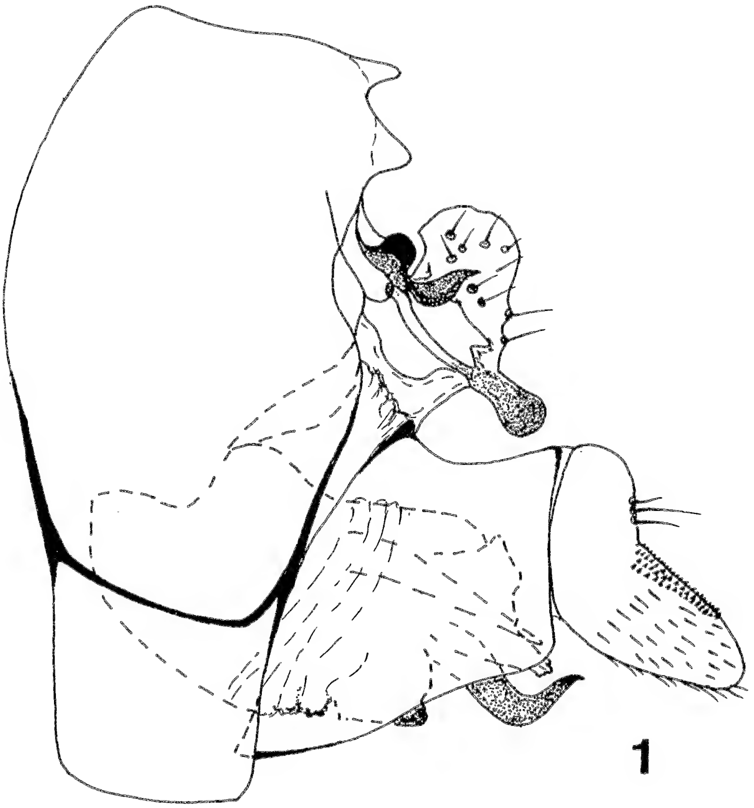
Rhyacophila tricornuta, **new species**
(Fig. 1–3)

Diagnosis.—This species is characterized by its male genitalia. The unique features separating this species from other American *Rhyacophila* are three dorsoapical, rounded lobes on Segment IX and a dark, rounded process extended into an "undulated" apicolateral section located at the base of the anal sclerites.

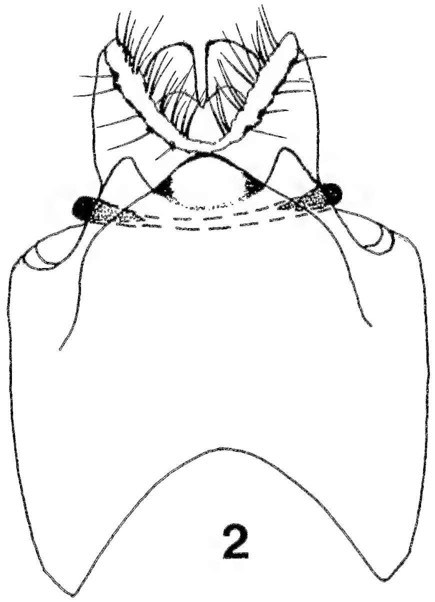
Description.—Male: length 12 mm. General appearance of specimen in alcohol brown. Head, thorax, and antennae black; legs yellowish; abdomen brown with darker terminal Segments VII, VIII, and IX. Ventromesal projection on Segment VII very short and smaller than in *R. nigrita,* corresponding in size to ventral

---

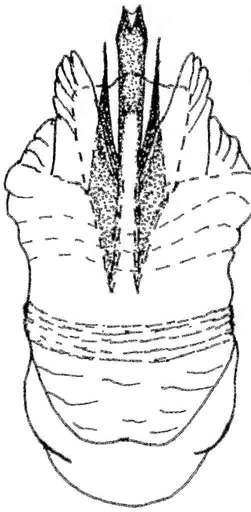
[1] Department of Biological Sciences, University of Pittsburgh, Pittsburgh, Pennsylvania 15260; current address: Department of Biology, University of Vermont, Burlington, Vermont 05405.
Submitted 19 April 1995.



1



2



3

"dent" found on Segment VI in the latter species. Wing venation and general structure typical for genus.

Male genitalia: Segment IX annular, narrow ventrally, wide dorsal section with double emargination forming lateral notch producing pair of dorsolateral lobes and very short, rounded dorsoapical process not reaching base of Segment X. Segment X with emarginated dorsoapical section resulting in V-shaped, triangular notch; from lateral view forming high-crested, rounded lobes covered with short bristles. Base of Segment X narrow with heavily sclerotized small, dark lateral lobes extending dorsoapically into an "undulated," dark brown sclerite. Anal sclerites similar to those of *R. nigrita* with rounded apices from lateral and dorsal views. Inferior appendages each with basal segment as broad as long, apical segment bilobed; tapered ventral lobe bearing narrow band of conspicuous dark spicules on dorsoapical margin; the ventral lobe 2.5 times as long as apically rounded dorsal lobe.

Phallic apparatus large, mostly membranous, and similar to that of *R. nigrita*; the spiniform parameres straight and long; aedeagus sinuous, sclerotized and upturned at apex.

Female: unknown.

Type Specimen.—Holotype, male, Virginia: Smyth Co., Mount Rodgers National Recreation Area, Hurricane Campground next to Hurricane Creek, May 22, 1994, Declan J. McCabe. The holotype is deposited at the Carnegie Museum of Natural History.

Etymology.—Latin, meaning "three horns."

DISCUSSION

Rhyacophila tricornuta is a member of the *R. invaria* group and closely related to species included in the *R. nigrita* subgroup. This is based on similarity of several morphological features but especially on the shape of Segment X with transverse high crest and inferior appendages similar to those in *R. nigrita* and *R. acutiloba* (Schmid, 1970; Morse and Ross, 1971). However, the characteristic which separates this new species from all members of the *R. nigrita* group is the shape of the dorsoapical margin of Segment IX which in the *R. invaria* subgroup is extended into a single, solid or more-or-less forked dorsomesal lobe. In six species of the *R. nigrita* subgroup the dorsoapical margin of Segment IX is notched posteriorly in the center with no distinct lobes or projections. It is also of interest that the ventromesal projection on Segment VII is extremely short in *R. tricornuta* (30 μm). In males of *R. nigrita* the same process is usually over 60 μm in length while the rudimentary ventromesal projection on Segment VI is approximately 20 μm long. This process is missing on Segment VI of *R. tricornuta.*

These morphological characteristics, especially the three-lobed Segment IX, set *R. tricornuta* apart from any other known species in the *R. invaria* group. However, in order to define the placement of this species within *R. nigrita* subgroup, additional information on female morphology and possibly on immature stages is needed.

←

Fig. 1–3.—Male genitalia of *Rhyacophila tricornuta,* n. sp. 1, left lateral view; 2, dorsal view; 3, phallic apparatus, ventral view.

A single specimen of *R. tricornuta* was captured in a black-light trap near the confluence of two second-order streams—an unnamed tributary and Hurricane Creek. Hurricane Creek flows east in the valley formed between Hurricane Mountain and Bear Ridge while the unnamed creek flows west in the valley formed between Hurricane Mountain and Bobbys Ridge. The two combine at 36°42′45″N 81°42′45″W, and the resulting third order stream is called Comers Creek which flows north between Bobbys Ridge and Bear Ridge. The confluence is at elevation 852 m (2795 ft) in the Iron Mountains. The trap was operated continuously from shortly before nightfall until midnight. Additional Trichoptera species collected in the light trap included *Goera fuscula* Banks, *Glossosoma nigrior* Banks, and *Dolophilodes distinctus* (Walker). The following caddisfly larvae were collected by hand from the creeks in the sampling area: *Rhyacophila carolina* Banks, *R. fuscula* Banks, *Agapetus* sp., *Neophylax* sp., *Dolophilodes distinctus* (Walker), and *Pycnopsyche luculenta* Betten. The streams in the area also supported a diverse population of stoneflies, mayflies, and blephariceríd flies including species of *Acroneuria, Peltoperla, Isoperla, Ephemerella, Epeorus,* and *Blepharicera.*

Based on this information the larvae of this new species inhabit second-order streams or seepage areas at higher elevations of the Appalachians in Virginia.

ACKNOWLEDGMENTS

We are grateful to Dr. John S. Weaver III for reviewing the figures.

LITERATURE CITED

MORSE, J. C. 1993. A checklist of the Trichoptera of North America including Greenland and Mexico. Transactions of the American Entomological Society, 119:4–93.

MORSE, J. C., AND H. H. ROSS. 1971. Two new species of *Rhyacophila* from eastern North America. Journal of the Kansas Entomological Society, 44:403–405.

SCHMID, F. 1970. Le genre *Rhyacophila* et la famille des Rhyacophilidae (Trichoptera). Mémoires de la Société Entomologique du Canada, 60:1–230.

ANNALS OF CARNEGIE MUSEUM
VOL. 65, NUMBER 1, PP. 17–25 22 FEBRUARY 1996

NEW SPECIES OF MICROCADDISFLIES FROM THE EASTERN UNITED STATES (INSECTA: TRICHOPTERA: HYDROPTILIDAE)

STEVEN C. HARRIS[1]
Research Associate, Section of Invertebrate Zoology

JAN L. SYKORA
Research Associate, Section of Invertebrate Zoology

ABSTRACT

Three new species in the genus *Hydroptila* and one in the genus *Mayatrichia* from the eastern United States are described and illustrated: *Hydroptila koryaki* and *H. fowlesi* from West Virginia, *H. homochitta* from Mississippi, and *M. tuscaloosa* from Alabama.

INTRODUCTION

Although the caddisfly fauna of the eastern United States has been fairly well studied, ongoing collecting continues to reveal undescribed species. This paper describes four new species of microcaddisflies from West Virginia, Mississippi, and Alabama, three in the genus *Hydroptila* and one in the genus *Mayatrichia.* The Hydroptilidae, or microcaddisflies, include the smallest species of Trichoptera, ranging in size from 1.2 to 6 mm. They are also the most speciose of all North American families with over 300 species (Morse, 1993), nearly one-third of which are in the genus *Hydroptila.* The genus *Mayatrichia* is much less species-rich with only five species known from North America (Morse, 1993).

Terminology used in the descriptions follows that of Marshall (1979). Specimen length was measured from the tip of the head to the end of the wings and is given as a range when more than one specimen was available. Type material will be deposited at the Carnegie Museum of Natural History (CMNH); the National Museum of Natural History, Smithsonian Institution (NMNH); the Illinois Natural History Survey (INHS); the Florida State Collection of Arthropods (FSCA); Mississippi State University, Department of Entomology (MSU); and the collections of the authors (SCH and JLS).

SYSTEMATIC ENTOMOLOGY

Hydroptila koryaki, new species
(Fig. 1–4)

Diagnosis.—This species, a member of the *H. waubesiana* group, superficially resembles *H. ouachita* Holzenthal and Kelley and *H. cheaha* Harris in the spinose eighth segment and forked tenth tergum. Members of the *H. waubesiana* group, in general, are characterized by a short ventromesal process on Segment VII and a highly modified tenth tergite which may bear sclerotized hooks, elongate processes, curved rods, or sclerotized strips. The new species is easily recognized by

---

[1] Department of Biology, Clarion University, Clarion, Pennsylvania 16214.

Submitted 28 April 1995.

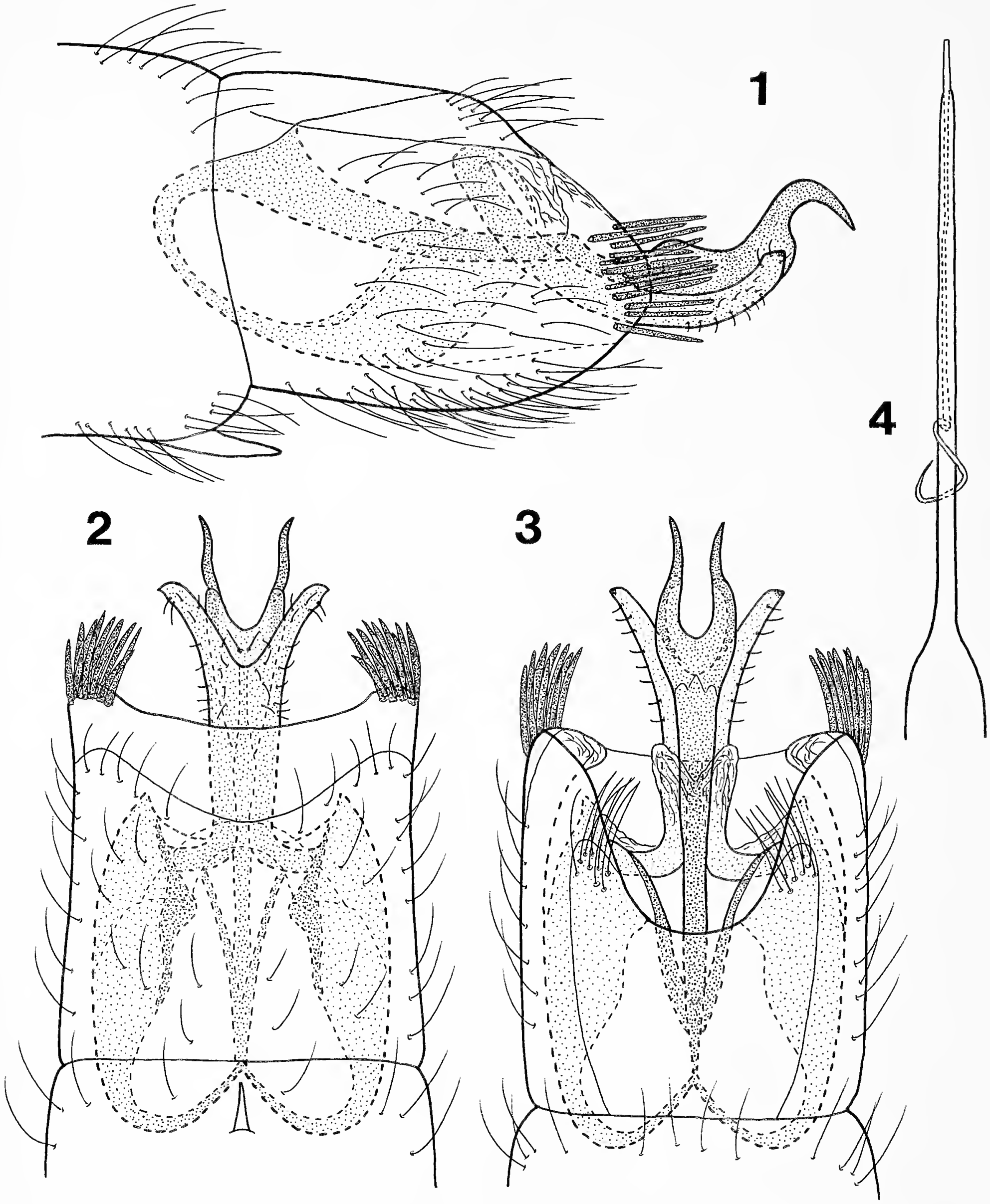


Fig. 1–4.—*Hydroptila koryaki* n. sp., male genitalia. 1, left lateral view; 2, ventral view; 3, dorsal view; 4, phallus, ventral view.

the thin, curved inferior appendages which are fused mesally and the elongate tenth tergum which is hooked in lateral aspect.

Description.—Male: length 2.6 mm. Antennae 26-segmented. Color brown in alcohol. Sternite of abdominal Segment VII with short apicomesal process. Segment VIII narrowing posteriorly in lateral view, bearing numerous heavy setae at the apical margin; slightly emarginate in ventral view; deeply incised dorsally with pair of small setose lobes, heavy spines laterally. Segment IX completely retracted within Segment VIII, generally quadrate in shape, incised slightly both anteriorly and posteriorly. Segment X elongate, extending nearly to posterior Segment VII; in lateral view narrowing apically to sclerotized, downturned hook, with dorsal hump subapically; in dorsal view narrow basally, divided apically into pair of thin, sinuate processes. Inferior appendages thin and elongate in lateral aspect, curving dorsad; in ventral view fused mesally, narrow basally, divided into two diverging arms distally each with sclerotized point on outer apical margin, pair of stout setae subapically; in dorsal view basally with narrow sclerotized bands laterally which join anteriorly. Phallus long and narrow, paramere encircling shaft before midlength; ejaculatory duct protruding at apex.

Female: unknown.

Type Specimens.—Holotype, male (CMNH): West Virginia, Lewis County, Right Fork of the West Fork River, Walkersville, 17 July 1993, light trap, J. L. Sykora. Paratypes: same, 13 July 1992, Shawn Campbell, 3 males (NMNH, SCH, JLS).

Etymology.—Named for Michael Koryak from the U. S. Army Corps of Engineers who selected the site where this species was collected.

Remarks.—Under the dissecting microscope (50×), Segment VIII in lateral view appears to narrow distally much as in *H. waubesiana* Betten, but this is an illusion created by the lateral curving of the segment. The species was collected adjacent to a small, slow-flowing stream composed mostly of pools with very few riffles. The stream is affected by human activity as it flows through a rural community and by farming activites, as evidenced by open grazing, erosion, and possibly animal wastes. Other species of *Hydroptila* collected at this site included *H. amoena* Ross, *H. grandiosa* Ross, *H. hamata* Morton, and *H. fowlesi* n. sp.

Hydroptila fowlesi, **new species**

(Fig. 5–8)

Diagnosis.—This species, a member of the *H. tineoides* group of Marshall (1979), is most similar to *H. sandersoni* Mathis and Bowles and other members of the *H. amoena* complex. Members of this complex have in common a long apicomesal process from the seventh sternum, beak-like inferior appendages, and a phallus divided into two apical processes. The new species is distinguished by the triangular shape of the tenth tergum and by the structure of the phallus, which is divided into apical processes unequal in length.

Description.—Male: length 2.8 mm. Antennae 27-segmented. Color brown in alcohol. Venter of abdominal Segment VII with long apicomesal process. Segment VIII annular, with venter longer than dorsum. Segment IX deeply excised anteriorly in dorsal and ventral views; laterally with thin posterior lobe bearing numerous setae along posterodorsal and ventral margins, apodeme long and narrow extending to middle of Segment VII; square in dorsal view, incised at margins; in ventral view shallowly incised on posterior margin, bearing numerous setae laterally and submesally; internally with bilobed process bearing pair of setae posteriorly. Tergite X triangular, wide basally tapering to rounded apex, anteriorly fused to Segment IX; in lateral view sharply upturned basally. Inferior appendages beak-like, each with dorsolateral thumb-like projection bearing three setae on posterior margin, ventral projection tapering ventrad to sharp apex; fused along meson with wing-like lateral extensions in ventral view. Phallus with basal and

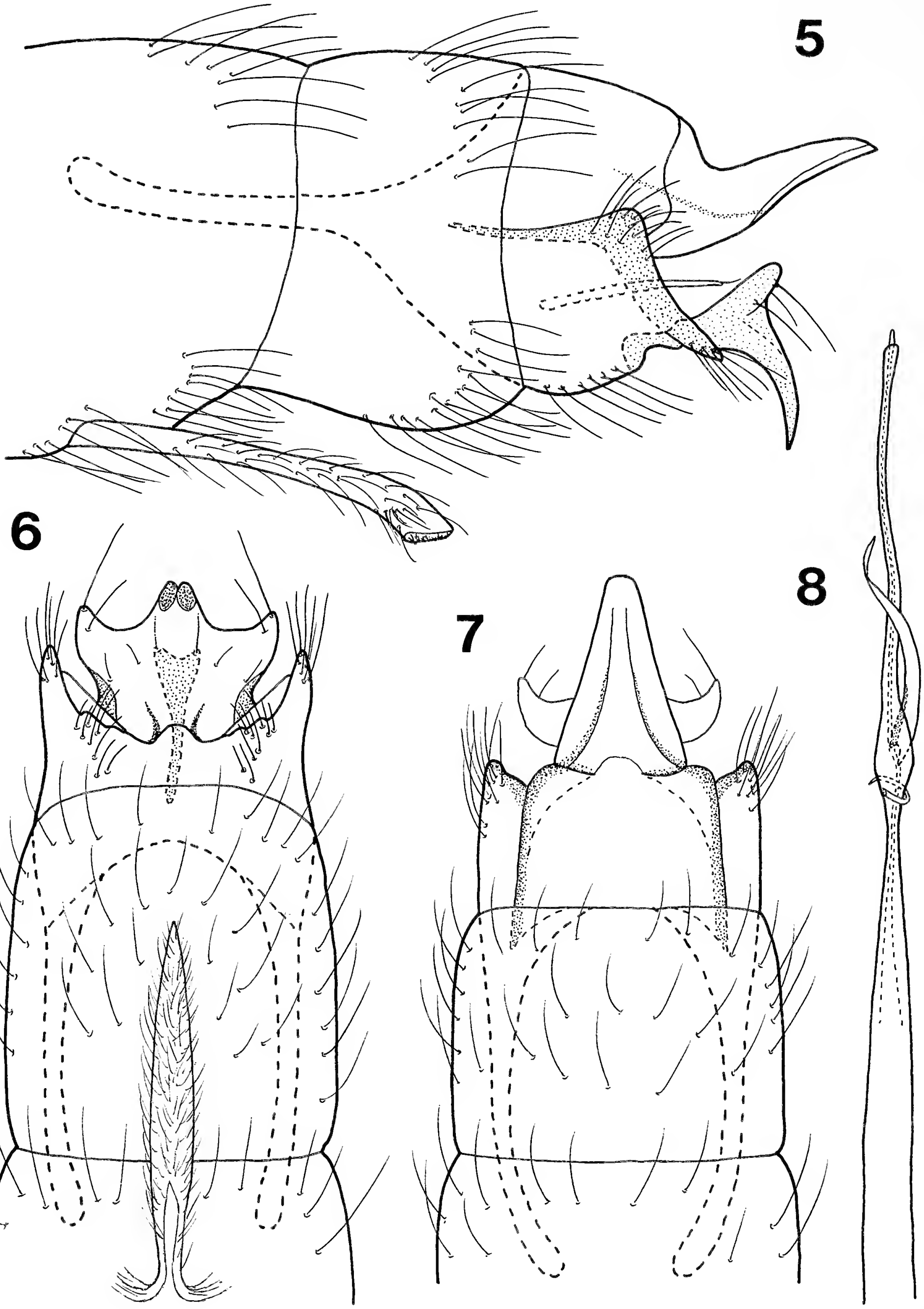


Fig. 5–8.—*Hydroptila fowlesi* n. sp., male genitalia. 5, left lateral view; 6, ventral view; 7, dorsal view; 8, phallus, ventral view.

apical portions equal in length, with short paramere making nearly one revolution at midlength, apical portion divided into two thin processes; process bearing protruding ejaculatory duct straight and twice as long as sheath-like second process.

Female: unknown.

Type Specimen.—Holotype, male (CMNH): West Virginia, Lewis County, Right Fork of the West Fork River, Walkersville, 13 July 1992, light trap, Shawn Campbell.

Etymology.—Named for J. M. Fowles from the U. S. Army Corps of Engineers who organized the light trap sampling program.

Remarks.—That several species having a phallus divided into two straight apical processes would key to *H. amoena* was first recognized by Harris (1985) with the description of two closely related species. Two additional species were described by Mathis and Bowles (1990), who also presented a key to the five species in the complex and discussed characteristics separating the species. With the addition of another species, the key of Mathis and Bowles is appended as follows:

Amended Key to *H. amoena* complex

1. Aedeagus short, less than one-third as long as abdomen; phallic process lacking ejaculatory duct with apex flattened and pointed (Mathis and Bowles, 1990:fig. 4) . . . . *H. artesa*

1a. Aedeagus longer, greater than one-third as long as abdomen; apical process not as above (Fig. 8) 2

2. Apex of Tergite X entire (Fig. 7) 2a

Apex of Tergite X excised (Harris, 1985:fig. 8E) 3

2a. Tergite X narrow, nearly parallel-sided basally in dorsal view (Mathis and Bowles, 1990:fig. 9); Segment X directed caudad in lateral view (Mathis and Bowles, 1990:fig. 10); phallus with distal portion at least twice as long as base, apical processes equal in length (Mathis and Bowles, 1990:fig. 11) . . . . *H. sandersoni*

2b. Tergite X wide basally, tapering distally in dorsal view (Fig. 7); Segment X upturned in lateral view (Fig. 5); phallus with distal portion equal in length to base, apical processes unequal in length (Fig. 8) . . . . *H. fowlesi*

Hydroptila homochitta, **new species**

(Fig. 9–12)

Diagnosis.—This species, a member of the *H. waubesiana* group of Marshall (1979), is distinguished from the similar *H. cretosa* Harris and *H. lonchera* Blickle and Morse by the long, thin processes from the venter of Segment X. Such intermediate appendages are found in several southeastern members of the *H. waubesiana* group, including *H. oakmulgeensis* Harris, *H. tridentata* Holzenthal and Kelly, and *H. poirrieri* Holzenthal and Kelley, but in these species the structures tend to be sickle-shaped rather than long and narrow as in *H. homochitta.* The club-shaped, serrate apex of the tenth tergum is also diagnostic for the new species.

Description.—Male: length 2.3–2.6 mm. Antennae 25-segmented. Color brown in alcohol. Venter of Segment VII with short, posteromesal process. Segment VIII rounded posteriorly in lateral view; in dorsal view deeply emarginate posteriorly; slightly emarginate on posterior margin in ventral aspect. Segment IX retracted within Segment VIII, rounded anteriorly in lateral view; in dorsal and ventral view anterior margin deeply incised, truncate posteriorly, and fused with Segment X. Tergum X rectangular in dorsal view, cleft distally with sclerotized spinal process at apex; in lateral view wide basally, narrowing at midlength, then widening to rounded apex with numerous sclerotized serrations on posterodorsal mar-

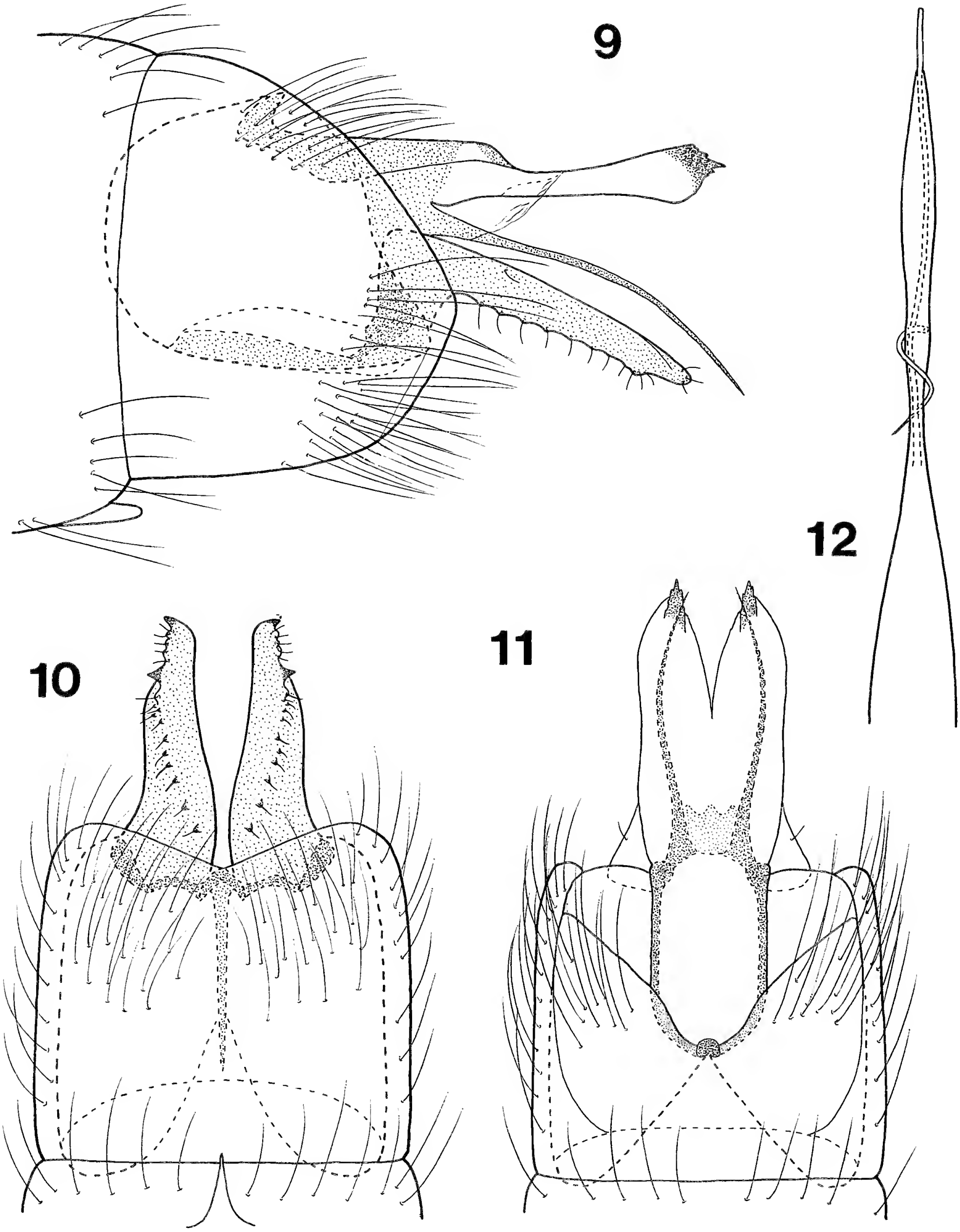


Fig. 9–12.—*Hydroptila homochitta* n. sp., male genitalia; 9, left lateral view; 10, ventral view; 11, dorsal view; 12, phallus, ventral view.

gin, ventral margin produced into thin, elongate sclerotized processes (intermediate appendages) extending beyond Tergum X and curving ventrad. Inferior appendages lightly sclerotized; in lateral view nearly parallel-sided, dorsal margin straight, ventral margin irregular and bearing numerous setae, narrowing apically to rounded tip; in ventral view wide basally and gradually tapering distally, sclerotized points apically and subapically on outer margin, series of stout setae directed laterad on ventral surface. Phallus long and narrow, widening basally and subapically, ejaculatory duct protruding at apex, thin paramere encircling shaft at midlength.

Female: unknown

Type Specimens.—Holotype, male (CMNH): Mississippi, Franklin County, Porter Creek, (T5N, R4E, S8NW), 29 June 1992, T. Schiefer and R. Fontenot. Paratypes, same, 16 males (NMNH, INHS, CMNH, MSU, SCH, JLS); same, but 27 July 1992, 7 males (NMNH, INHS, FSCA); Franklin County, Tributary to McGehee Creek, (TGN, R4E, S26SW), 1 June 1992, T. Schiefer and R. Fontenot, 1 male, (NMNH).

Etymology.—Named for the Homochitto National Forest, collection locality for the species.

Remarks.—The streams of the Homochitto National Forest where the new species was collected are all small, clear, and sandy-bottomed, flowing through relatively undisturbed mixed hardwood forests.

Mayatrichia tuscaloosa, **new species**

(Fig. 13–16)

Diagnosis.—Although similar to *M. ponta* Ross in the structure of the inferior appendages with three heavy setae at the apex, *M. tuscaloosa* differs in the bracteoles being entire posteroventrally; a character which is shared with *M. illobia* Harris and Holzenthal and *M. ayama* Mosely. The new species is separated from the widespread *M. ayama* and *M. illobia,* which is only known from Costa Rica, on the basis of the rectangular inferior appendages.

Description.—Male: length 2.3–2.4 mm, antennae 18-segmented. Color brown in alcohol. Sternum VI with short posteromesal process. Segment VIII annular. Segment IX tapering anteriorly in lateral view; posterolateral processes (bracteoles) narrow; ventral margin straight, entire; dorsal margin rounded; in dorsal view, Tergum IX deeply emarginate posteriorly, line of setae at margin, anteriorly with shallow, rounded incision; in ventral view bracteoles elongate and narrow, curving inward distally. Tergum X membranous, rounded apically; in lateral view triangular, indistinct. Inferior appendages in lateral aspect wide basally, narrowing distally, each bearing elongate setae; in ventral view nearly parallel-sided, each with three teeth bearing stout, elongate setae. Subgenital plate with posteromesal process directed ventrad; in ventral view truncate, slightly emarginate mesally, bearing pair of small setae on posteromesal margin. Phallus long and narrow, apex with small, dorsal projection.

Female: unknown.

Type Specimens.—Holotype, male (CMNH): Alabama, Tuscaloosa County, Big Sandy Creek at 4.5 mi south of Coaling on an unnumbered county road, 20 March 1991, S. Harris and T. Shepard. Paratype: same, 1 male (NMNH).

Etymology.—Named for Tuscalosa County, Alabama.

Remarks.—The species was found only in a single early spring collection. A

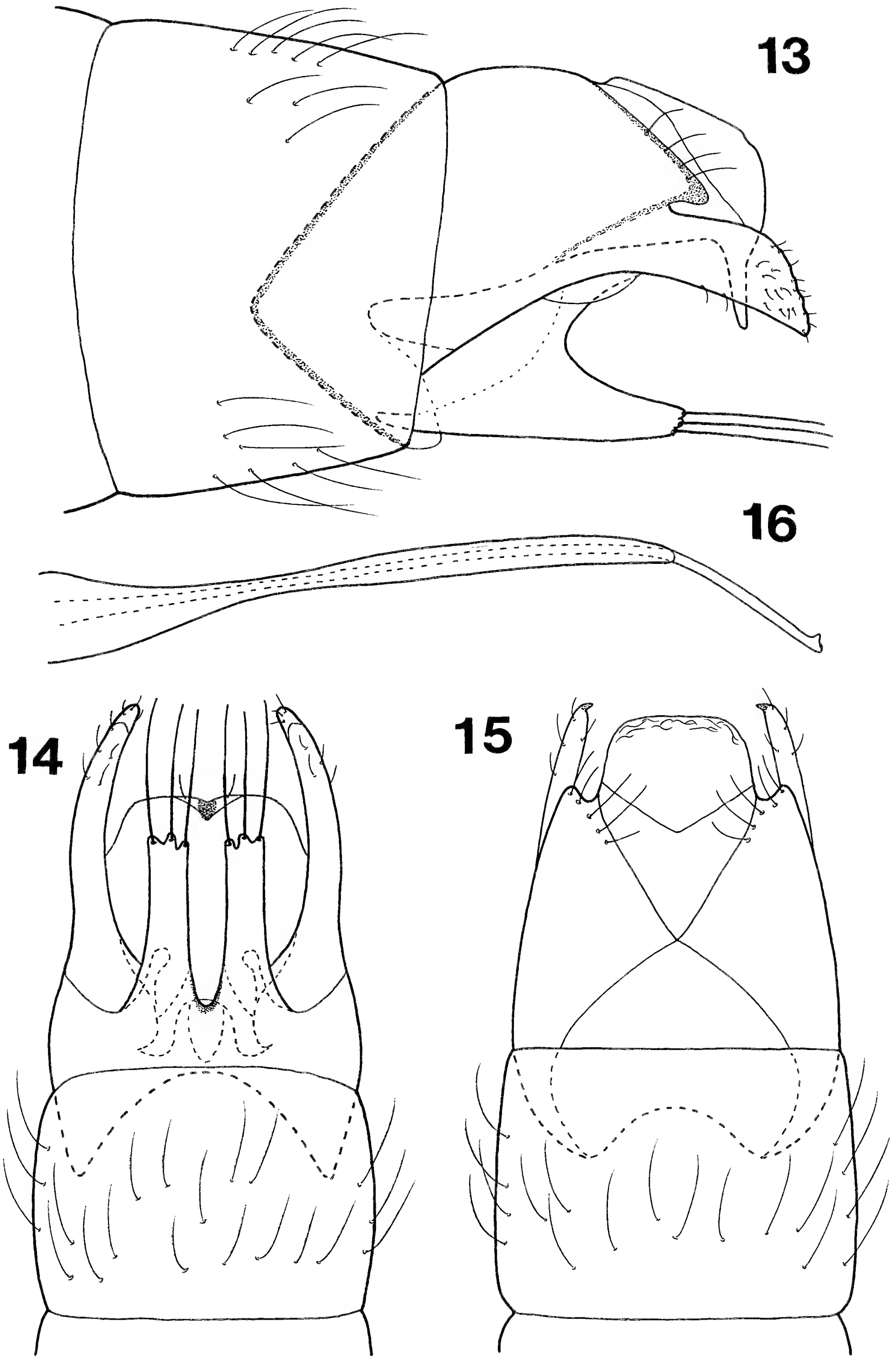


Fig. 13–16.—*Mayatrichia tuscaloosa* n. sp., male genitalia. 13, left lateral view; 14, ventral view; 15, dorsal view; 16, phallus, lateral view.

collection made the following night and monthly collections through October at the same site failed to collect additional specimens. Collections made in March and April of the following year were also unsuccessful. The collection locality was at the headwaters of Big Sandy Creek in a transition zone where the stream emerged from a springfed limestone region out onto the coastal plain.

ACKNOWLEDGMENTS

Mississippi specimens were obtained from Richard L. Brown of Mississippi State University and were collected as part of NSF grant BSR-9200856. West Virginia specimens were collected as part of contract DACW 59-92-M-0422 to JLS by the U. S. Army Corps of Engineers. The help of Tom Shepard of the Geological Survey of Alabama in the collection of the Alabama specimens is gratefully acknowledged.

LITERATURE CITED

HARRIS, S. C. 1985. New microcaddisflies (Trichoptera: Hydroptilidae) from Alabama. Proceedings of the Entomological Society of Washington, 87:606–621.

MARSHALL, J. E. 1979. A review of the genera of the Hydroptilidae (Trichoptera). Bulletin of the British Museum of Natural History (Entomology), 39:135–239.

MATHIS, M. L., AND D. E. BOWLES. 1990. Three new species of microcaddisflies (Trichoptera: Hydroptilidae) from the Ozark Mountains, U.S.A. Proceedings of the Entomological Society of Washington, 92:86–92.

MORSE, J. C. 1993. A checklist of the Trichoptera of North America, including Greenland and Mexico. Transactions of the American Entomological Society, 119:47–93.

ANNALS OF CARNEGIE MUSEUM

Vol. 65, Number 1, Pp. 27–88 22 February 1996

A PHYLOGENETIC REASSESSMENT OF THE TADORNINE–ANATINE DIVERGENCE (AVES: ANSERIFORMES: ANATIDAE)

Bradley C. Livezey
Associate Curator, Section of Birds

Abstract

Phylogenetic analysis of eight problematic genera of waterfowl (*Stictonetta Plectropterus, Sarkidiornis, Hymenolaimus, Tachyeres, Merganetta, Malacorhynchus,* and *Salvadorina*) and representatives of other tadornine genera and anatine tribes was undertaken using 114 morphological characters (39 skeletal, four tracheal, 11 natal, and 60 of the definitive integument) and a variety of weighting schemes, in an attempt to clarify relationships in the most poorly understood segment of the phylogeny of Anseriformes (Livezey, 1986*a*). Under equal weighting of characters, 40 equally parsimonious trees were found that shared the following findings: (1) a sister-group relationship of *Stictonetta* to a clade comprising the Tadorninae and Anatinae; (2) a sister-relationship between *Plectropterus* and *Sarkidiornis*; (3) monophyly of the typical shelducks and sheldgeese (*Tadorna, Cyanochen, Alopochen, Neochen,* and *Chloephaga*); (4) monophyly of *Hymenolaimus, Tachyeres,* and *Merganetta*; and (5) a sister-relationship between *Salvadorina* and *Malacorhynchus.* An analysis wherein skeletal characters were given twice the weight of other character groups resulted in four shortest trees which, in addition to the findings under equal weighting, indicated that: (1) *Plectropterus* + *Sarkidiornis* represent the sister-group of the typical shelducks and sheldgeese; (2) a sister-relationship between the clade comprising *Hymenolaimus, Tachyeres,* and *Merganetta* and the preceding clade, collectively constituting the "tadornine" clade; and (3) a sister-relationship between *Malacorhynchus* + *Salvadorina* and an "anatine" clade comprising the remaining tribes and subtribes (Cairineae, Nettapodeae, Anateae, Aythyini, Mergini, and Oxyurini). An analysis in which skeletal, tracheal, natal, and definitive characters were assigned weights of four, three, two, and one, respectively, produced identical results to the preceding weighting scheme. Successive weighting by rescaled consistency indices produced two shortest trees that resembled those found under the two preceding protocols except: (1) the Mergini were placed as the sister-group of the "tadornine" clade defined above; and (2) the Cairineae (*Cairina, Pteronetta,* and *Aix*) were placed as the sister-group to *Plectropterus* + *Sarkidiornis.* Based on the comparative strengths of hypothesized homologies of skeletal characters and assessments of topological support (including bootstrapping, decay indices, and near-shortest trees) for all weighting schemes, a conservative classification was based on the *a priori* weighting schemes favoring skeletal characters. Maps of selected ecomorphological attributes on this phylogenetic tree revealed several distinct evolutionary trends, but incompletely resolved relationships among these diverse genera and within suprageneric taxa limited inferences. Additional promising areas for anatomically based systematic study are identified, and the need for continued cladistic study of this poorly resolved but topologically critical segment of the phylogeny of Anseriformes is emphasized.

Introduction

Greater diversity of opinion has attended the classification of the following eight southern-hemisphere genera of waterfowl than in any assemblage of similar size in the Anseriformes: *Stictonetta, Plectropterus, Sarkidiornis, Hymenolaimus, Tachyeres, Merganetta, Malacorhynchus,* and *Salvadorina* (Table 1). Early taxonomists typically included these genera within larger, more-familiar groups of waterfowl on the basis of superficial comparisons and very limited material (Eyton, 1838; Gray, 1841, 1871; Bonaparte, 1856; Sclater, 1880; Salvadori, 1895; Phillips 1922, 1923, 1925, 1926).

In recent decades, taxonomic classifications of the Freckled Duck (*Stictonetta*

Submitted 16 June 1995.

Table 1.—*A century of taxonomic classifications of eight taxonomically problematic genera of Anatidae.*

Genus	Salvadori (1895)	Phillips (1922–1925)	Peters (1931)
Stictonetta	Anatinae, between *Marmaronetta* and *Heteronetta.*	Anatinae[a], between *Anas* and *Heteronetta.*	Anatinae, between *Casarca* and *Tadorna.*
Plectropterus	Plectropterinae, before *Cairina* and *Sarkidiornis.*	Plectropterinae, before *Cairina* and *Sarkidiornis.*	Plectropterinae, with *Anseranas.*
Sarkidiornis	Plectropterinae, between taxa currently merged into *Cairina.*	Plectropterinae, between taxa currently merged into *Cairina.*	Anatinae, between *Neochen* and *Cairina.*
Hymenolaimus	Merganettinae, between *Salvadorina* and *Merganetta.*	Merganettinae, between *Salvadorina* and *Merganetta.*	Nyrocinae[a], between *Polysticta* and *Salvadorina.*
Tachyeres	Fuligulinae[a], between *Aythya* and *Bucephala.*	Fuligulinae[a], between *Aythya* and *Bucephala.*	Nyrocinae, between *Aythya* and *Bucephala.*
Merganetta	Merganettinae, with *Salvadorina* and *Hymenolaimus.*	Merganettinae, with *Salvadorina* and *Hymenolaimus.*	Merganettinae (monotypic), after "Merginae" (mergansers).
Malacorhynchus	Anatinae[a], between *Anas* (part) and *Marmaronetta.*	Anatinae[a], between *Anas* (part) and *Aix.*	Anatinae, between *Anas* (part) and *Rhodonessa.*
Salvadorina	Merganettinae, with *Hymenolaimus* and *Merganetta.*	Merganettinae, with *Hymenolaimus* and *Merganetta.*	Nyrocinae, with *Polysticta* and *Hymenolaimus.*

[a] Generic taxa used by author(s) are replaced by currently accepted synonyms.
[b] Johnsgard (1979) listed no tribes within subfamilies.
[c] *Salvadorina* merged with *Anas* by author.
[d] Skeletal specimens of *Salvadorina* not examined by Woolfenden (1961).

naevosa) have included placements as: an aberrant dabbling duck (Delacour, 1938; Delacour and Mayr, 1945) or shelduck (Boetticher, 1942, 1952); the sole member of a tribe or higher taxon closely related to the true geese (Verheyen, 1953, 1955; Frith, 1964*a,* 1964*b,* 1965, 1967; Johnsgard, 1978); a very primitive sister-group of the majority of modern ducks, geese, and swans (Frith, 1967; Olson and Feduccia, 1980; Madsen et al., 1988; Sibley and Ahlquist, 1990; Sibley and Monroe, 1990); or as both very primitive and a close relative of the stiff-tailed ducks (Fullagar et al., 1990; Marchant and Higgins, 1990). Also, assignments of single species to monogeneric higher taxa has led to the phylogenetically misleading conclusion that each has, like *Stictonetta,* "no near living relatives" (e.g., Johnsgard, 1978:xx) or "is not closely related to any other tribe" (e.g., Edkins and Hansen, 1972:105). However, under an assumption of the monophyly of the biota of the earth, any species is the sister-group (i.e., closest relative) of some other group of organisms. At present, there is a consensus among most systematists that *Stictonetta* should be excluded from the true ducks (Anatinae), although other details of its relationships within the Anseriformes remain in dispute (Wolters, 1976; Johnsgard, 1979; Livezey, 1986*a*; Madsen et al., 1988; Sibley and Monroe, 1990).

The Spur-winged Goose (*Plectropterus gambensis*) and Comb Duck (*Sarkidiornis melanotus*), traditionally considered to be members of an assemblage termed the "perching ducks," or formally the Subfamily Cairininae or Tribe Cairinini (e.g., Delacour, 1938, 1959, 1964; Delacour and Mayr, 1945; Boetticher,

Table 1.—*Extended.*

Delacour and Mayr (1945)	Boetticher (1952)	Delacour (1954–1959)
Anatinae, Anatini, as "aberrant."	Anatinae, Tadornini, in monotypic "section."	Anatinae, Anatini, after *Hymenolaimus,* and *Merganetta.*
Anatinae, Cairinini, after *Sarkidiornis* and *Cairina.*	Anatinae, Cairinini, before *Cairina* and *Sarkidiornis.*	Anatinae, Cairinini, after *Sarkidiornis* and *Cairina.*
Anatinae, Cairinini, between *Nettapus* and *Cairina.*	Anatinae, Cairinini, between *Cairina* and *Nettapus.*	Anatinae, Cairinini, between *Nettapus* and *Cairina.*
Anatinae, Anatini, as "aberrant."	Anatinae, anatini, after *Malacorhynchus.*	Anatinae, Anatini, between *Malacorhynchus* and *Merganetta*
Anatinae, Tadornini, as "aberrant."	Anatinae, Tachyerini, monogeneric.	Anatinae, Tadornini, after *Lophonetta.*
Anatinae, Merganettini (monotypic), after Oxyurini.	Anatinae, Oxyurini, after *Heteronetta.*	Anatinae, Anatini, between *Hymenolaimus* and *Stictonetta.*
Anatinae, Anatini, as "aberrant."	Anatinae, Anatini, before *Hymenolaimus.*	Anatinae, Anatini, between *Rhodonessa* and *Hymenolaimus.*
Anatinae, Anatini, merged with *Anas.*	Anatinae, Anatini, between taxa currently merged into *Anas.*	Anatinae, Anatini, merged with *Anas.*

1952; Johnsgard, 1965*a,* 1978), were reassigned to a monotypic subfamily (Plectropterinae) and the shelducks (Tadorninae), respectively, by Livezey (1986*a*). Similarly, steamer-ducks (*Tachyeres* spp.; Livezey and Humphrey, 1992) and the Torrent Duck (*Merganetta armata*), for which persistent doubts concerning phylogenetic relationships were finessed by some through allocations to monotypic tribes (Delacour and Mayr, 1945; Verheyen, 1953; Johnsgard, 1965*a,* 1966, 1978), also were included in the poorly resolved Tadorninae by Livezey (1986*a*).

The Blue Duck (*Hymenolaimus malacorhynchos*) and the Pink-eared Duck (*Malacorhynchus membranaceous*), traditionally considered to be aberrant members of the dabbling ducks (Delacour, 1938; Delacour and Mayr, 1945; Boetticher, 1952; Delacour, 1956; Johnsgard, 1965*a,* 1965*b,* 1978, 1979; Kear and Steel, 1971; Sibley and Monroe, 1990), were included as well among the tadornines by Livezey (1986*a*). However, Olson and Feduccia (1980:22) suggested that *Malacorhynchus,* together with *Stictonetta* and perhaps *Merganetta,* were "primitive relicts of an early anatid radiation and may be only distantly related to the remainder of the Anatidae." Salvadori's Duck (*Salvadorina waigiuensis*), for which skeletal and tracheal specimens were not available in the analysis performed by Livezey (1986*a*), also has been classified in recent decades as an unusual member of the dabbling ducks, and often merged with the genus *Anas* (Mayr, 1931; Delacour and Mayr, 1945; Delacour, 1956; Johnsgard, 1965*a,* 1978, 1979). Subsequent behavioral comparisons (Kear, 1975) and limited osteological data (Mlíkovský, 1989), however, indicate that the species may be more closely related to other waterfowl variably specialized for lotic habitats (*Merganetta* and *Hymenolaimus*) or to the unique *Malacorhynchus.* Based in large part on these data, Livezey (1991) tentatively included the genus among the shelducks and allies

Table 1.—*Continued.*

Genus	Woolfenden (1961)	Johnsgard (1965[a])	Wolters (1976)
Stictonetta	Anserinae, Dendrocygnini (not examined).	Anserinae, Stictonettini (monotypic), after Anserini.	Stictonettinae (monotypic), between Dendrocygninae and Anserinae.
Plectropterus	Anatinae, Tadornini, before *Chloephaga* and *Cyanochen.*	Anatinae, Cairinini, before *Cairina* and *Sarkidiornis.*	Plectropterinae (monotypic), between Tadorninae and Anatinae.
Sarkidiornis	Anatinae, Anatini, before *Pteronetta* and *Cairina.*	Anatinae, Cairinini, between *Cairina* and *Pteronetta.*	Anatinae, before *Cairina* and *Pteronetta.*
Hymenolaimus	Anatinae, Anatini, between *Malacorhynchus* and *Tachyeres.*	Anatinae, Anatini, before *Merganetta* and *Anas.*	Anatinae, between *Malacorhynchus* and *Tachyeres.*
Tachyeres	Anatinae, Anatini, after *Malacorhynchus* and *Hymenolaimus.*	Anatinae, Tachyerini, between Tadornini and Cairinini.	Anatinae, between *Hymenolaimus* and *Marmaronetta.*
Merganetta	Anatinae, Merganettini, monotypic.	Anatinae, Anatini, between *Hymenolaimus* and *Anas.*	Anatinae, between *Lophonetta* and *Salvadorina.*
Malacorhynchus	Anatinae, Anatini, between *Salvadorina* and *Hymenolaimus.*	Anatinae, Anatini, between *Anas* and *Marmaronetta.*	Anatinae, between *Salvadorina* and *Hymenolaimus.*
Salvadorina	Anatinae[d], Anatini, between *Anas* and *Malacorhynchus.*	Anatinae, Anatini, as monotypic subgenus of *Anas.*	Anatinae, between *Merganetta* and *Malacorhynchus.*

(Tadorninae). Thirteen representative classifications of these eight genera spanning the last century are summarized in Table 1.

Woolfenden (1961) presented the first study of the comparative osteology of waterfowl from the perspective of (phenetic) assessments of relationships. Livezey (1986*b*) presented a species-level phylogenetic analysis of *Tachyeres* based on morphological comparisons, one which compared favorably with an assessment of genetic distances in the group (Corbin et al., 1988) and biochemical patterns in secretions from the uropygial glands (Livezey et al., 1986). Other contributions to the knowledge of the anatomy of these genera include, by genus: *Stictonetta* (Campbell, 1899; Frith, 1964*b*; Olson and Feduccia, 1980), *Plectropterus* (Rand, 1954; Möller, 1969), *Sarkidiornis* (Garrod, 1875), *Hymenolaimus* (Kear and Burton, 1971), *Tachyeres* (Livezey and Humphrey, 1986, 1992), *Merganetta* (Niethammer, 1952; Weller, 1968; Raikow, 1970), *Malacorhynchus* (Frith, 1955, 1967), and *Salvadorina* (Rothschild, 1895; Mayr, 1931; Kear, 1975; Mlíkovský, 1989). Tyler (1964) included several of these genera in a comparison of the microanatomy of anseriform egg shells. Fossils assignable to any of these eight genera are limited to Pleistocene material of *Sarkidiornis* and subfossil material of *Malacorhynchus* (Brodkorb, 1964; Howard, 1964*a*; Olson, 1977, 1985; Worthy, 1995).

Table 1.—*Extended.*

Johnsgard (1978)	Johnsgard (1979)[b]	Livezey (1986[a])	Sibley and Monroe (1990)
Anserinae, Stictonettini (monotypic), after Cereopsini (monotypic).	Anserinae, between *Cereopsis* and Tadorninae.	Stictonettinae (monotypic), between Anserinae and Plectropterinae.	Stictonettinae (monotypic), between Oxyurinae and Cygninae.
Anatinae, Cairinini, before *Cairina* and *Sarkidiornis.*	Anatinae, before *Cairina* and *Pteronetta.*	Plectropterinae (monotypic), between Stictonettinae and Tadorninae.	Anatinae, Anserini, between *tachyeres* and *Cairina.*
Anatinae, Cairinini, between *Cairina* and *Pteronetta.*	Anatinae, between *Pteronetta* and *Nettapus.*	Tadorninae, Sarkidiornithini (taxon amended; monotypic).	Anatinae, Anserini, between *Pteronetta* and *Nettapus.*
Anatinae, Anatini, before *Salvadorina*[c].	Anatinae, between *Merganetta* and *Salvadorina*[c].	Tadorninae, Tadornini, in subtribe with *Merganetta* and *Tachyeres.*	Anatinae, Anatini, between *Merganetta* and *Salvadorina*
Anatinae, Tachyerini, between Tadornini and Cairinini.	Tadorninae, after *Tadorna* as last included genus.	Tadorninae, Tadornini, in subtribe with *Hymenolaimus* and *Merganetta.*	Anatinae, Anserini, between *Tadorna* and *Plectropterus.*
Anatinae, Merganettini, between Cairinini and Anatini.	Anatinae, between *Amazonetta* and *Hymenolaimus.*	Tadorninae, Tadornini, in subtribe with *Hymenolaimus* and *Tachyeres.*	Anatinae, Anatini, between *Amazonetta* and *Hymenolaimus.*
Anatinae, Anatini, between *Anas* and *Marmaronetta.*	Anatinae, between *Anas* and *Marmaronetta.*	Tadorninae, Tadornini, as subtribe between *Tadorna* and sheldgeese.	Anatinae, Anatini, between *Anas* and *Marmaronetta.*
Anatinae, Anatini, after *Hymenolaimus* as first member of *Anas.*	Anatinae, after *Hymenolaimus* as first member of *Anas.*	Anatinae[d], Anatini, pro visionally included in *Anas.*	Anatinae, Anatini, between *Hymenolaimus* and *Anas.*

Phylogenetic analyses using molecular characters are considered by some to hold potential for especially reliable inferences of phylogeny, but an assumption of inherent superiority lacks empirical support (Hillis, 1987; Sanderson and Donoghue, 1989; Moritz and Hillis, 1990). Moreover, comparisons of studies based on molecular and morphological data, even where fundamentally phenetic methodologies were applied, share broad areas of agreement (e.g., Bledsoe and Raikow, 1990; Omland, 1994; see also Swofford, 1991). Unfortunately, most of the larger studies of Anseriformes employing molecular techniques included none of the eight genera considered here (Kessler and Avise, 1984; Patton and Avise, 1985; Scherer and Sontag, 1986). Numachi et al. (1983) included but a single member of this group of genera, *Sarkidiornis,* precluding any tests of relationships among members. Bottjer (1983) included *Plectropterus* and *Sarkidiornis* in his immunological comparisons; one especially distinctive finding was the low similarity between *Plectropterus* and the "perching ducks" *Cairina, Chenonetta,* and *Aix.* The electrophoretic comparisons of egg-white proteins by Sibley and Ahlquist (1972:fig. 10–12) included *Plectropterus, Sarkidiornis, Hymenolaimus,* and *Malacorhynchus,* but not even a phenetic analysis of the intriguing patterns was presented. Other molecular analyses including two or more of these taxa also were phenetic in methodology, and therefore any inferred associations represent assessments of overall similarity rather than direct indications of phylogenetic relationship (Jacob and Glasser, 1975; Brush, 1976; Jacob, 1982; Jacob and Hoerschelmann, 1993). Of the latter, the comparisons of feather proteins by Brush (1976) included six of the eight genera of interest here, but the resultant banding patterns proved difficult to interpret phylogenetically and rendered tribal assignments problematic for *Stictonetta, Hymenolaimus, Merganetta,* and *Malacorhynchus.*

The analyses by Sibley and Ahlquist (1990) using DNA hybridization, and the related classification (Sibley et al., 1988; Sibley and Monroe, 1990), also lacked any samples from these eight genera. The placement of *Stictonetta* by Madsen et al. (1988) in an analysis of 13 species of Anseriformes using DNA hybridization must be viewed with caution in light of criticisms of this general methodology (Cracraft, 1987; Houde, 1987; Sarich et al., 1989; Springer and Krajewski, 1989), poor representation of taxa, and unfavorable metric properties evident in the comparisons.

The primarily osteological study by Livezey (1986*a*) remains the only work in which even a majority of these problematic "tadornine" genera were analyzed. However, support for inferences in the topological vicinity of the divergence of the "shelducks" (Tadorninae) and the "surface-feeding ducks" (Anatinae) in the preliminary analysis by Livezey (1986*a*), should be considered tentative. This assessment stems from several concerns: (1) the polychotomous topology depicted for the genera included in the tadornines (Livezey, 1986*a*:fig. 1, 3); (2) the limited numbers of characters supporting groupings within this segment of the tree, e.g., those uniting *Cyanochen* with *Hymenolaimus, Merganetta,* and *Tachyeres*; (3) the impossibility of an assessment of support (e.g., bootstrapping of characters or consideration of suboptimal topologies) or the treatment of polymorphic character states at the time of the analysis; (4) three characters used by Livezey (1986*a*) to support clades in the tadornines—characters 15, 33, and 61—were judged unreliable for these taxa based upon further study (Livezey, unpublished data); (5) several of the characters of the pelvic limb (including characters 56 and 69) show significant homoplasy evidently associated with diving habit (Livezey, 1986*a*; Faith, 1989), therefore groups united in part by these characters (e.g., *Hymenolaimus, Tachyeres,* and *Merganetta*) merit confirmation; and (6) the profound limitations of software and computing platform increased the likelihood of suboptimal solution sets (e.g., retention of more than 50 trees in memory for this data set typically caused a "crash" of the analysis).

Livezey (1986*a*) indicated several areas of poor resolution and marginal support in the resultant phylogenetic hypothesis, and subsequent study discovered alternative solutions to at least the basal segment of the tree (Livezey, 1989). In addition, reanalysis of the original data matrix compiled by Livezey (1986*a*) using improved versions of analytical software discovered multiple, slightly shorter alternative trees including several distinct topologies (J. Harshman, personal communication), the majority of which were the result of poorly resolved relationships in the vicinity of the divergence of "tadornine" and "anatine" genera. With respect to the eight genera of concern here, these alternative trees shared the following elements: (1) paraphyly of *Stictonetta* and *Plectropterus* to "tadornine" and "anatine" genera (as inferred by Livezey, 1986*a*); and (2) placement of *Malacorhynchus,* Blue-winged Sheldgoose (*Cyanochen cyanopterus*), true shelducks (*Tadorna*) and other sheldgeese (*Alopochen, Neochen,* and *Chloephaga*), *Sarki-*

diornis, and the clade comprising *Hymenolaimus, Merganetta,* and *Tachyeres* as paraphyletic to the genera included in the Anatinae by Livezey (1986*a*).

Contradictory assessments of relationships in this group of genera "transitional" between the anseriform subfamilies Tadorninae and Anatinae, as well as shortcomings in analyses to date, justify a renewed effort to recover phylogenetic structure in this important group of waterfowl. Because of the phylogenetically central position of these genera, i.e., their topological proximity to the divergences of the tribes of the Anatinae (Livezey, 1986*a,* 1991), a study of this kind provides an opportunity to assess available morphological evidence concerning the relationships among the anatine tribes as well. This paper, one of a series of finer-scale analyses of the major subparts of the phylogeny of waterfowl (Livezey, 1991, 1995*a,* 1995*b,* 1995*c,* in press *a,* in press *b,* in press *c*), presents a phylogenetic analysis of the eight aforementioned genera and representatives of related tribes, using an enlarged set of morphological characters and improved analytical algorithms. This analysis is followed by ancillary considerations of morphological evolution, phylogenetic patterns of behavior and ecology, implications for historical biogeography, and promising areas for future study for this most challenging aspect of the phylogeny of Anseriformes.

MATERIALS AND METHODS

Taxonomy

Composition of the Ingroup.—Determination of the broad limits of the comparatively derived members of the Anseriformes, based on the cladistic analyses by Livezey (1986*a,* 1995*a,* in press *c*), conservatively included representatives of all groups exclusive of the screamers (Anhimidae), Magpie Goose (Anseranatidae: *Anseranas semipalmata*), whistling ducks and allies (Dendrocygninae), and true geese and swans (Anserinae). Comparisons included representatives of all taxa included in the eight genera of primary interest—*Stictonetta, Plectropterus, Sarkidiornis, Hymenolaimus, Tachyeres, Merganetta, Malacorhynchus,* and *Salvadorina.* Representatives of other "tadornine" genera (*Cyanochen, Alopochen, Neochen, Chloephaga,* and *Tadorna*), also were included, which were inferred to constitute a monophyletic group in this series of phylogenetic analyses (Livezey, in press *a*). The Cape Barren Goose (*Cereopsis novaehollandiae*), considered by some to be an aberrant sheldgoose or an evolutionary "link" between the true geese and the sheldgeese (Delacour and Mayr, 1945; Delacour, 1954; Johnsgard, 1961*a,* 1978; Woolfenden, 1961; Frith, 1967; Kear and Murton, 1973), is excluded from this study on the basis of its inclusion among the true geese and swans (Livezey, 1986*a,* 1989, in press *c*).

Also included are "basal" representatives (see below for methods of characterization) of the major clades of Anatinae: three subtribes of dabbling ducks or Anatini (Cairineae, Nettapodeae, and Anateae; Livezey, 1991), as well as the pochards (Aythyini; Livezey, in press *b*), seaducks (Mergini; Livezey, 1995*b*), and stiff-tailed ducks (Oxyurini; Livezey, 1995*c*). Inclusion of the separate subtribes of Anatini defined by Livezey (1991) in the analysis was necessitated by variation among the subgroups in characters determined to be informative as well among "tadornine" genera. Under the taxonomy proposed by Livezey (1991), the three subtribes of Anatini comprise the following genera: Cairineae (*Cairina, Pteronetta,* and *Aix*), Nettapodeae (*Chenonetta* and *Nettapus*), and Anateae (*Amazonetta, Callonetta, Lophonetta, Speculanas, Mareca,* and *Anas*).

Composition of Included Genera.—Five of the eight genera of primary interest in this analysis are considered to comprise single species by most taxonomists: *Stictonetta, Plectropterus, Sarkidiornis, Hymenolaimus,* and *Merganetta* (e.g., Delacour and Mayr, 1945; Delacour, 1954, 1956, 1959; Johnsgard, 1961*a,* 1965*a,* 1965*b,* 1978, 1979; Wolters, 1976). Segregation of Salvadori's Duck in the genus *Salvadorina* (Woolfenden, 1961; Kear, 1975; Wolters, 1976; Mlíkovský, 1989; Sibley and Monroe, 1990; Livezey, 1991), instead of inclusion of the species within *Anas* (e.g., Delacour and Mayr, 1945; Boetticher, 1952; Delacour, 1956; Johnsgard, 1965*a,* 1978), delimits another monotypic genus in this group.

Two of these purportedly monotypic genera—*Sarkidiornis* and *Merganetta*—include two or more qualitatively distinct taxa that might be accorded species rank. For example, in light of plumage differences and geographical isolation (Madge and Burn, 1988), partitioning of *Sarkidiornis* into a nominate African species *S. melanotus* and a Neotropical species *S. sylvicola* is consistent with both the emphasis of the "minimal diagnosable unit" under the phylogenetic species concept, and the requirements of distinct historical "identities" and independent evolutionary "tendencies" and "fate" under the evolutionary species concept (Wiley, 1978; Cracraft, 1983, 1988; McKitrick and Zink, 1988; Frost and Hillis, 1990). In practice, application of the phylogenetic species concept can approximate the lineages conceptualized under the evolutionary species concept (Frost and Kluge, 1994). Numerous synapomorphies demonstrate the monophyly of *Sarkidiornis* (see beyond), however, and the included species were identical for the characters coded here; therefore the species-level taxonomy of the genus is not germane to this analysis. Similarly, substantial support for monophyly of *Merganetta* (see beyond) and identical states of analyzed characters render inconsequential any species-level interpretation one might impose on this poorly understood complex of three to six recognized forms for purposes of this analysis (Conover, 1943; Delacour, 1956; Johnsgard, 1978; Madge and Burn, 1988). The steamer-ducks (*Tachyeres*) are treated as a single generic taxon for this analysis; the genus comprises four confusingly similar species (Livezey and Humphrey, 1992), is demonstrably monophyletic (Livezey, 1986*a,* 1986*b,* present study), members of the genus were identical for included characters, and the phylogeny of included taxa has been examined elsewhere (Livezey, 1986*b*; Corbin et al., 1988).

The Spur-winged Goose (*Plectropterus gambensis*) currently is considered to comprise two poorly differentiated subspecies (northern, comparatively pale *gambensis* and southern, comparatively dark *niger*) having a broad area of intergradation; the two forms are considered as a single analytical taxon here (Delacour, 1959; Johnsgard, 1978; Brown et al., 1982; Madge and Burn, 1988). No diagnosable populations have been detected within the other four critical genera—*Stictonetta, Hymenolaimus, Malacorhynchus,* and *Salvadorina* (Delacour, 1956, 1959; Johnsgard, 1978, 1979).

Specimens and Related Data

Specimens Examined.—Study skins of adult birds were compared for determination of plumage pattern and general structure of the externum in the collections of several major museums, most importantly the National Museum of Natural History and the American Museum of Natural History. Colors of the irides, bill, tarsi, and feet of adults also were characterized using study skins, but colors of unfeathered integument are not always reliably coded using dried specimens; consequently, colors of soft parts were confirmed using published descriptions (see below), notes on specimen labels, photographs of living individuals, and direct observation of living birds in avicultural collections or in the wild. Plumage patterns of downy young, specimens of which are comparatively rare in museum collections, were ascertained by comparisons of study skins (including an important collection at the Wildfowl and Wetlands Trust) and fluid-preserved specimens.

Prepared skeletal specimens of adults were used for osteological comparisons. Numbers of prepared skeletons available varied significantly among taxa. Large series of skeletons (100 or more) were available for several groups (*Tachyeres, Anas*), whereas fewer than five were available for several others (*Hymenolaimus, Merganetta*); at least five skeletons were studied for other taxa, with the exception of *Salvadorina* (for which no complete skeletal specimen exists). Tracheal characters were determined using ossified elements in skeletal specimens and complete tracheae removed from fluid-preserved specimens (some previously mounted and dried).

Published Data.—Published descriptions and illustrations of adult and subadult plumages supplemented data collected from direct study (Conover, 1943; Delacour, 1954, 1956, 1959, 1964; Johnsgard, 1965*a,* 1978; Weller, 1968; Todd, 1979; Humphrey and Livezey, 1982; Madge and Burn, 1988; Marchant and Higgins, 1990; Hoyo et al., 1992). Preliminary study of variation in natal plumages was accomplished using the illustrations and descriptions of downy young provided by Delacour and Mayr (1945, 1946), Delacour (1954, 1956, 1959, 1964), Frith (1955, 1964*b*), Pengelly and Kear (1970), Kear (1972, 1975), and Humphrey and Livezey (1985). Variation and alternative interpretations of skeletal characters, most of which were based on my earlier analyses (Livezey, 1986*a,* 1989, 1991), were made using the works by Shufeldt (1909), Verheyen (1953), Rand (1954), Woolfenden (1961), Humphrey and Clark (1964), Cracraft (1968), Weller (1968), Möller (1969), and Raikow (1970). The few skeletal characters determinable for *Salvadorina* were coded using the descriptions of a few elements by Mayr (1931) and Mlíkovský (1989). Additional information on the tracheal anatomy of waterfowl was taken from Yarrell (1827), Garrod (1875), Campbell (1899), Mayr (1931), Niethammer (1952), Johnsgard (1961*b,* 1971), and Humphrey and Clark (1964).

Definition of Characters

Theory and Objectives.—Characters used in this phylogenetic analysis are distinct morphological features, hypothesized to be homologous (de Pinna, 1991; Lipscomb, 1992; Hall, 1994), that comprise two or more states within the ingroup or differ between the ingroup and outgroups. Of the states defined, one is hypothesized as the primitive or plesiomorphous state based on outgroup comparisons (see below), and the other(s) as the derived or apomorphic state(s). Definition of characters and included states are essential to any cladistic analysis, but recognition of homology and description of the implicit distinctions between states remain the most challenging and influential aspect of phylogenetic inference (Pogue and Mickevich, 1990).

Given that shared derived characters (synapomorphies) constitute the only empirical support for the delimitation of hierarchically nested sets of closest relatives (clades), the primary objective of character analysis is the discovery of such changes in states (transformation series) germane to the group of interest. Autapomorphies, character changes that are unique to terminal taxa, cannot contribute to the resolution of such groupings of included taxa (Wiley, 1981), although such differences traditionally have been accorded considerable weight in previous attempts at classification (e.g., Delacour, 1954; Johnsgard, 1961*a,* 1965*a,* 1978). However, autapomorphies of the key eight genera of interest were included in this analysis for several reasons: (1) inclusion of autapomorphic divergence in cladistically based phylograms can provide insights into relative evolutionary rates, (2) autapomorphic characters of polytypic genera also are synapomorphic for included members, and (3) autapomorphic divergence can be depicted in phylogenetic trees independently of the character changes supporting topological structure and associated summary statistics.

Characters Defined.—A total of 114 morphological characters were defined for this analysis: 39 characters of the skeleton, four of the trachea and syrinx, 11 of the natal plumage, and 60 of the definitive plumage and soft parts (Appendix 1). Most skeletal characters were adapted from those described by Livezey (1986*a*), with lesser numbers from Livezey (1989, 1991); for this analysis, states of these characters were restricted to those represented by the ingroup. This more detailed consideration of tracheosyringeal anatomy obviated the *ad hoc* weighting of the single (composite) syringeal transformation series defined in the analysis by Livezey (1986*a*).

Behavioral patterns, especially courtship displays, have received considerable study in waterfowl (Delacour and Mayr, 1945; Delacour, 1954, 1956, 1959; Johnsgard, 1960*a,* 1961*a,* 1962, 1965*a,* 1978). Such ethological data have provided insights into phylogenetic relationships of waterfowl (e.g., Johnsgard, 1961*a*) and have been shown to be comparable in consistency to morphological and molecular characters (de Queiroz and Wimberger, 1993). Formal inclusion of such data in the phylogenetic analysis, however, was precluded by numerous missing data, problems of coding behavioral characters termed "rare" or "uncommon" in a discrete scheme, and questions of homology and polarity not addressable from published descriptions.

Each character was coded for the 19 members of the ingroup and a hypothetical "ancestor" (see below), producing a data matrix of dimension 20 × 114 (Appendix 2). Missing data were as follows: 28 entries for skeletal characters of *Salvadorina* were coded as "missing"; two natal characters for the "hypothetical ancestor" were coded as "missing," indicating an unknown polarity; and one entry for character 44, three entries for character 46, single entries for characters 47 and 48, and two entries for character 77 were treated as "missing" because of problematic comparability of states. In total, there were 38 matrix entries coded as "missing" (1.7% of matrix). The impact of missing data on phylogenetic inference has been considered by Nixon and Davis (1991) and Platnick et al. (1991).

Fourteen characters were "multistate" (i.e., included two or more derived states), of which two (characters 29 and 78) were ordered, i.e., a particular ordination of derived states was considered more probable on structural or developmental grounds (Wilkinson, 1992). Analytical implications of multistate characters and ordering attract continuing controversy and empirical study (Hauser and Presch, 1991; Mickevich and Lipscomb, 1991; Lipscomb, 1992; Barriel and Tassy, 1993; Slowinski, 1993). Consequently, an assessment of the analytical impact of these two orderings was made by comparison with analyses in which all characters were treated as unordered.

Characterization of Generic Vectors.—Coding of states for characters found to be uniform among members of genera was straightforward. Most character states for the "typical" tadornines—*Cyanochen, Alopochen, Neochen, Chloephaga,* and *Tadorna*—were based largely on a separate species-level analysis (Livezey, in press *a*). Several characters for the polyspecific genera in this group (*Chloephaga, Tadorna*) varied among species. Similarly, character states for the "composite" vectors for the seven major subgroups of Anatinae, where invariant within groups, were made on the basis of the present study or taken from Livezey (1991). Where determinable on the basis of distribution of states within the species-level analyses of these genera (Livezey, 1991, 1995*b,* 1995*c,* in press *b*), the "basal" state (therefore presumptive locally ancestral state) was used to characterize the genus in this analysis. Where variation and distribution of states within a genus precluded such a determination, the state was coded as polymorphic (character 4 for Cairineae, character 8 for the genera of Tadornini, character 82 for Anateae, and character 91 for Nettapodeae).

Determination of Basal Polarities

Outgroup Comparisons.—Basal polarities of characters, i.e., the states of characters judged to be ancestral for the ingroup under analysis, were inferred by reference to outgroups (Watrous and Wheeler, 1981; Maddison et al., 1984), as opposed to ontogenetic criteria (de Queiroz, 1985; Mabee, 1989; Wheeler, 1990; Williams et al., 1990). Based on the analysis by Livezey (1986*a*), the most informative outgroups for study were the taxa of Anseriformes paraphyletic to the clade comprising *Stictonetta, Plectropterus,* Tadorninae, and Anatinae. Characters were compared against representative members of each of the subfamilies and tribes, with primary exemplars given in parentheses: Anseranatinae (*Anseranas semipalmata*), Dendrocygninae (*Dendrocygna autumnalis* and *Thalassornis leuconotus*), and Anserinae (*Cereopsis novaehollandiae, Branta canadensis, Anser anser, Coscoroba coscoroba,* and *Cygnus olor*). Character states that were found in successive outgroups were considered plesiomorphous and used to define the states presumed to be ancestral for the ingroup.

Hypothetical Ancestor.—A hypothetical ancestor, the set of character states judged to be primitive based on outgroup comparisons, was used to root the phylogenetic tree(s). This method provided a single, simple root for the ingroup without explicitly including representative outgroup taxa in this study, thereby avoiding ancillary analytical digressions concerning relationships among outgroups, considered elsewhere (Livezey, 1986*a,* 1989, 1995*a,* in press *c*; Livezey and Martin, 1988). Monophyly of the ingroup under study here was demonstrated by Livezey (1986*a*), and is further substantiated in the present analysis if one or more unambiguous synapomorphies for the taxa exclusive of the hypothetical ancestor are discovered; a less stringent criterion is a basal branch with positive length.

Derivation of Trees

Global Parsimony and Search Algorithms.—Phylogenetic reconstruction was based on the cladistic principle of grouping taxa on the basis of shared derived characters (synapomorphies), and the set of trees that accomplished this with a minimum number of hypothesized character transformations in the entire tree was sought (i.e., in accordance with the criterion of global parsimony). This approach was first formulated by Hennig (1966) and has been reviewed by Wiley (1981) and Wiley et al. (1991). Exhaustive searches of all possible trees were prohibited by the size of the data matrix; use of the branch-and-bound algorithm, a method guaranteed to discover all most-parsimonious trees (Hendy and Penny, 1982), also was not practical for a problem of this moderately large size (Swofford, 1993). Consequently, topological searches were undertaken using global branch swapping (a heuristic technique), the retention of ten trees at each step, using options for both simple and random order of entry of taxa (ten replications), and the retention of multiple equally parsimonious trees throughout the search. Also, three alternative branch-swapping methods (nearest-neighbor interchanges, tree-bisection-reconnection, and subtree-pruning-regrafting) were used to avoid local optima or "islands" of suboptimal topologies (Maddison, 1991; Page, 1993).

Several summary statistics were used to quantify the evidence supporting phylogenetic trees (Kluge and Farris, 1969; Farris, 1989): total tree length; consistency index, both including (CI) and excluding uninformative characters (CI*); homoplasy index, both including (HI) and excluding uninformative characters (HI*); retention index (RI); and rescaled consistency index (RC). All phylogenetic analyses were performed using the software PAUP version 3.1 (Swofford, 1993) and MacClade version 3.0 (Maddison and Maddison, 1992) on a Macintosh Quadra 800.

Weighting of Characters.—In addition to the equal (unit) weighting of characters employed in the baseline analyses, several alternative weighting schemes were used. Use of differential weighting in phylogenetic analysis remains controversial (Neff, 1986; Wheeler, 1986; Chippindale and Weins, 1994), but was included here to explore the impact of preconceived and *post facto* inferences concerning relative reliability of different character types. Two *a priori* differential weighting schemes were used: (1) "*two-group*" *scheme*—skeletal characters, considered here to be evolutionarily more conservative than more-superficial morphological features based on studies by Livezey (1986*a*, 1991, 1995*a*, 1995*b*, 1995*c*, in press *a*, in press *b*, in press *c*), were given a weight of two whereas other character groups were given a weight of one; and (2) "*four-group*" *scheme*—in which skeletal, tracheal, natal integumentary, and definitive integumentary characters were given weights of four, three, two, and one, respectively. Weighting of skeletal characters over those of the integument in this analysis was prompted further by the marginal confidence held in the homologies and the comparatively greater difficulties of variation and sexual dimorphism in several plumage characters included here (Appendix 1). Finally, I employed an *a posteriori* weighting method—successive weighting (Farris, 1969; Carpenter, 1988)—in which characters are iteratively reweighted (base weight of 2) on the basis of rescaled consistency indices of characters.

Consensus Trees.—Where multiple, equally parsimonious trees were discovered using the same set of analytical options, two consensus methods were employed to summarize graphically the topological regions given support by the set of shortest trees: strict consensus trees (showing only those nodes shared by all equally parsimonious trees; Sokal and Rohlf, 1981) and majority-rule consensus trees (Margush and McMorris, 1981). The utility of consensus trees does not enjoy unanimous recognition (e.g., Barrett et al., 1991), and it has been shown that such summary trees are seldom interpretable in the same ways as the actual trees from which they are compiled (Swofford, 1991; Wiley et al., 1991). Accordingly, consensus methods were used simply to summarize areas of congruence among equally parsimonious trees.

Assessment of Support

Bootstrapping of Characters.—Standard summary statistics (e.g., consistency index) are flawed measures of empirical support for phylogenetic trees, because most are conditional in part on the number of taxa analyzed (Brooks et al., 1986; Archie, 1989*a,* 1989*b,* 1990; Sanderson and Donoghue, 1989; Faith and Cranston, 1991; Meier et al., 1991). Consequently, stability of nodes in minimal-length trees in this analysis was assessed using bootstrapping, although the limitations of this method in phylogenetic contexts remain controversial (Carpenter, 1992; Davis, 1993; Hillis and Bull, 1993; Penny et al., 1994). Applications involved generating 100 bootstrapped replicates using the same heuristic methods employed in the primary analyses, and summarizing those branches robust to this procedure through majority-rule consensus trees. The nature of the characters analyzed violates the assumption of statistical independence required for the bootstrapped percentages to be viewed as statistically rigorous levels of confidence (Felsenstein, 1985*a*; Sanderson, 1989), therefore the procedure was employed here as one of several quantitative indices to empirical support for branches (Bremer, 1994).

Phylogenetic "Signal" and Suboptimal Trees.—One measure of the phylogenetic "signal" of a data set is the skewness statistic for the distribution of resultant tree lengths (Hillis, 1991; Huelsenbeck, 1991; Hillis and Huelsenbeck, 1991; Källersjö et al., 1992). Exhaustive generation of tree lengths was not feasible for a data set of this size, therefore the skewness statistics (g_1) for random samples of 1000 trees (excluding the hypothetical ancestor) under each of the three *a priori* weighting schemes were calculated as an index to "phylogenetic signal" (Archie and Felsenstein, 1993). Values of g_1, however, provide poorly focused indices to phylogenetic informativeness, distributional characteristics of g_1 remain poorly known, and values can be subject to significant bias (Källersjö et al., 1992).

An alternative measure of support proposed by Bremer (1988), later dubbed the "decay index" by Donoghue et al. (1992), is the relative stability of nodes with respect to increased homoplasy (*sensu lato,* including both convergence and reversals). Specifically, the "decay index" for a given node is the minimal number of additional steps in tree length at which topologies not supporting the node are discovered. Estimates of the "decay index" were made for selected clades found to be robust under bootstrapping and various weighting regimes using exclusionary constraints in heuristic searches in PAUP.

Topologically Constrained Analyses.—The impact of particular topological constraints on the lengths of the shortest trees permissible for this matrix (i.e., the increases in total length) were estimated by performing searches constrained to preserve the specific phylogenetic relationship in question (while allowing topological modifications in other parts of the tree to accommodate this constraint). These comparisons were especially useful in quantifying the sacrifices in parsimony required to accommodate previously proposed phylogenetic relationships or traditional classifications in terms of the present data set.

Phylogenetic Classification

A Linnean classification, which incorporated inferred phylogenetic information while minimizing disruption of existing taxonomy, was prepared using the methods described by Wiley (1979, 1981) and Wiley et al. (1991). These methods include the use of the "sequencing convention" to avoid daunting numbers of taxonomic ranks, annotation of taxa in unresolved polytomies as *sedis mutabilis,* and identification of possibly paraphyletic or polyphyletic taxa through annotation as *incertae sedis.* Taxa applied to higher taxonomic categories follow standard requirements of availability and seniority (International Commission of Zoological Nomenclature, 1985), based on published synonymies and classifications (Phillips, 1922, 1923, 1925, 1926; Boetticher, 1942, 1952; Wolters, 1976).

Comparative Analyses

General Objectives.—Phylogenetic hypotheses provide an opportunity to examine the history of evolutionary change in selected life-historical parameters (Eldredge and Cracraft, 1980; Felsenstein, 1985*b*; Brooks and McLennan, 1991; Harvey and Pagel, 1991). In this study, a number of ecomorphological attributes not amenable to discrete coding and determination of homology were compiled and mapped *a posteriori* onto phylogenetic trees (Maddison, 1989; Mickevich and Weller, 1990) using MacClade 3.01 (Maddison and Maddison, 1992). Similar phylogenetic mapping was employed in analyses of other anseriform groups (Livezey, 1995*a,* 1995*b,* 1995*c,* in press *a,* in press *b,* in press *c*).

Detailed comparisons of the effects of different optimizations on the traces of attributes—e.g., ACCTRAN (length-neutral favoring of reversals over parallelisms) and DELTRAN (length-neutral favoring of parallelisms over reversals)—were not performed because no justification was evident for favoring one method over another. Moreover, two alternative character optimizations—Dollo optimization, in which it is required that each derived state is uniquely derived (Farris, 1977; Maddison et al., 1984), and the related option of irreversibility of character change (Sanderson, 1993)—were considered inappropriate for this analysis. However, regions of the trees in which ambiguity of traces occurred are shown as "equivocal" (Maddison and Maddison, 1992). Quantitative methods for analysis of characters with respect to a phylogeny (e.g., Coddington, 1988, 1994; Pagel and Harvey, 1988; Grafen, 1989, 1992; Pagel, 1994), including the preliminary methods for tracing continuous characters permitted by MacClade, were not used primarily because of the inclusion of a number of higher taxa (e.g., Cairineae, Anateae) in the analyses that contain species exhibiting a diversity of states for the parameters of interest as well as poor resolution in parts of the phylogeny (see beyond).

Attributes mapped include body mass (unweighted mean of sexes), mean clutch size, mean egg mass, relative clutch mass (mean mass of clutch divided by mean female body mass), preferred nest site (terrestrial or cavity), perching habit, relative frequency of diving, and period of activity (diurnal, crepuscular, or nocturnal). Data for these mapped attributes were taken from unpublished records associated with specimens and from the literature (Niethammer, 1953; Delacour, 1954, 1956, 1959; Scott, 1954; Hallstrom, 1956; Hobbs, 1957; Warham, 1959; Johnsgard, 1960*a,* 1961*a,* 1962, 1965*a,* 1965*b,* 1978; Schönwetter, 1961; Johnson, 1963; Weller, 1964*a,* 1964*b,* 1964*c,* 1976; Frith, 1967; Kear, 1970, 1975; Moffett, 1970; Siegfried, 1979; Clark, 1980; Wilson and Wilson, 1980; Brown et al., 1982; Humphrey and Livezey, 1982, 1985; Livezey and Humphrey, 1984*a,* 1984*b*; Eadie et al., 1988; Livezey, 1988; Madge and Burn, 1988; Rohwer, 1988; Marchant and Higgins, 1990; Triggs et al., 1991, 1992; Williams, 1991; McNeil et al., 1992; Dunning, 1993).

RESULTS

Shortest Trees

Characters Weighted Equally.—Forty most-parsimonious trees were found using equal weighting of characters, each having length 215, consistency index (CI) of 0.670 (0.543 excluding uninformative characters, CI*), homoplasy index (HI) of 0.367 (0.479 excluding uniformative characters, HI*), retention index (RI) of 0.641, and rescaled consistency index (RC) of 0.430. The skewness statistic (g_1) for the unweighted matrix, based on 1000 randomly generated trees, was -0.612; this figure is substantially more negative than that expected for random data.

A strict consensus tree of the 40 topologies revealed only broad inferences shared by the "simplest" interpretations of the equally weighted characters (Fig. 1): (1) monophyly of the taxa analyzed exclusive of *Stictonetta*; (2) a sister relationship between *Plectropterus* and *Sarkidiornis*; (3) monophyly of the typical shelducks and sheldgeese (*Tadorna, Cyanochen, Alopochen, Neochen,* and *Chloephaga*), with intergeneric relationships as inferred by Livezey (1996*a*); (4) monophyly of *Hymenolaimus, Tachyeres,* and *Merganetta,* wherein the last two genera are sister-groups; and (5) a sister relationship between *Salvadorina* and *Malacorhynchus*. The solution set was unchanged if all characters were analyzed as unordered.

A majority of the shortest trees (Fig. 2) indicated the following additional phylogenetic structure: (1) a sister relationship between *Plectropterus* + *Sarkidiornis* and the clade comprising the typical shelducks and sheldgeese (39 of 40 trees); (2) a sister relationship between the preceding two clades and that comprising *Hymenolaimus, Tachyeres,* and *Merganetta* (38 of 40 trees); and (3) monophyly of the six taxa of "typical" anatines (Cairineae, Nettapodeae, Anateae, Aythyini, Mergini, and Oxyurini), within which the three subtribes of Anatini defined by Livezey (1991) are monophyletic and the two subtribes of smaller "perching ducks" are sister-groups.

Comparative Consistencies.—Mean consistency indices for informative characters under equal weighting were: skeletal, 0.63 (n = 27; range, 0.33–1.00); tracheal, 0.75 (n = 2; range, 0.50–1.00); natal, 0.62 (n = 10; range, 0.20–1.00); and definitive integument, 0.64 (n = 27; range, 0.25–1.00). Consistency indices varied among the 40 trees, as a result of differences of single steps, in eight skeletal characters (characters 5, 10, 11, 21, 24, 25, 30, 35), one natal character (46), and ten characters of the definitive integument (55, 56, 91, 93, 95–100).

"Two-Group" Weighting.—A heuristic search employing the "two-group" *a priori* weighting scheme, within which skeletal characters were given a weight of two and all others retained weights of one, discovered four shortest trees sharing the following summary statistics: length = 290, CI = 0.676 (CI* = 0.554), HI = 0.372 (HI* = 0.474), RI = 0.674, and RC = 0.455. The skewness statistic (g_1) for the "two-group" matrix, based on 1000 randomly generated trees, was -0.584. The four topologies differed only in the relationships inferred among the six taxa of "typical" anatines. A strict consensus tree of these four shortest topologies (Fig. 3) confirmed the phylogenetic structure shared by a majority of the trees found under equal weighting (Fig. 2), with the following additional resolutions: (1) the clade comprising *Salvadorina* and *Malacorhynchus* is inferred to be the sister-group of the six taxa of "typical" Anatinae; and (2) within the latter, the Mergini and Oxyurini are inferred to be sister tribes. A majority-rule consensus tree of the topologies under "two-group" weighting revealed that three of the

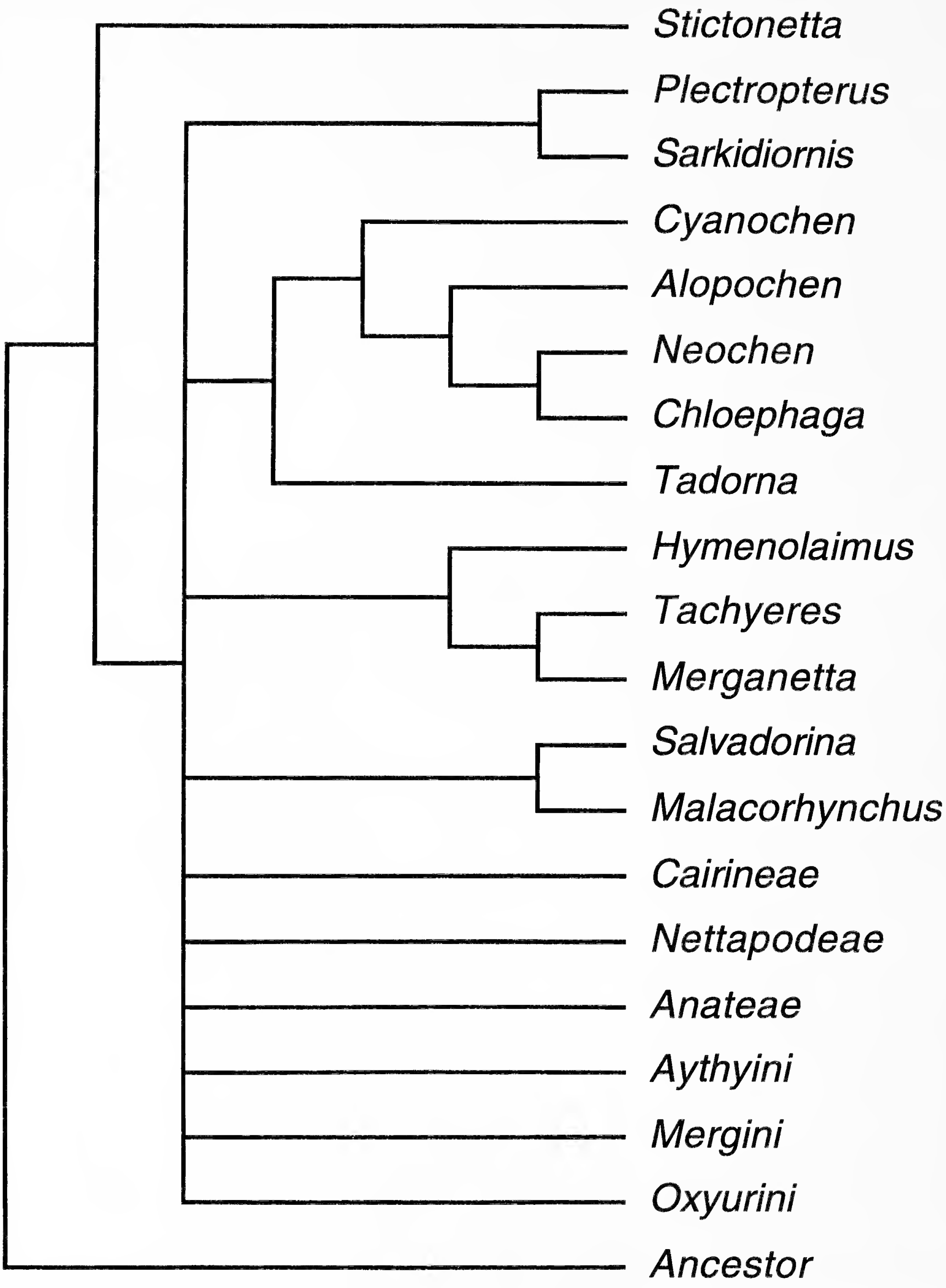


Fig. 1.—Strict consensus tree of 40 equally parsimonious trees for 19 taxa of Anatidae under equal weighting of characters.

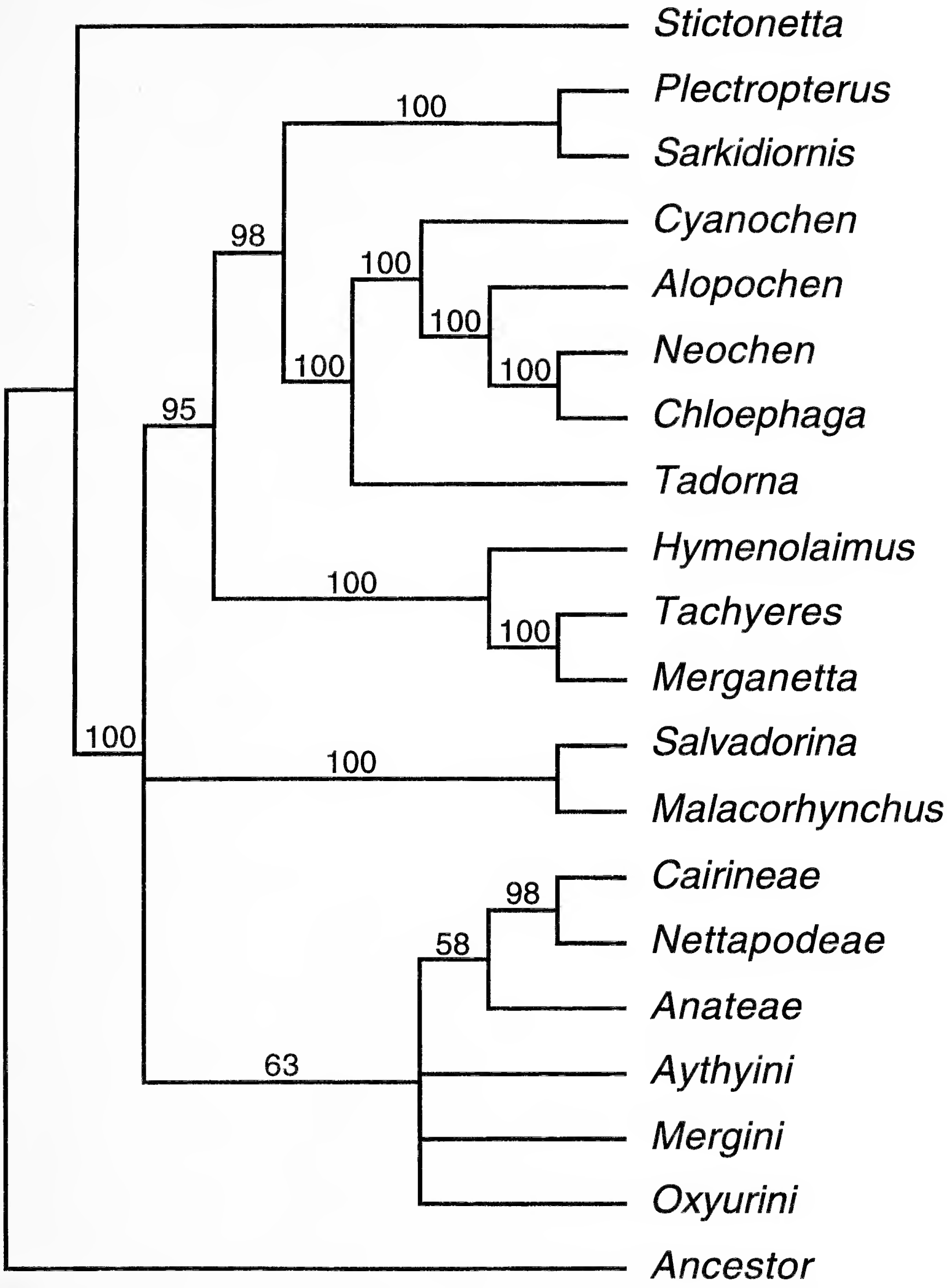


Fig. 2.—Majority-rule consensus tree of 40 equally parsimonious trees for 19 taxa of Anatidae under equal weighting of characters. Percentages of these 40 trees in which each branch was conserved are shown.

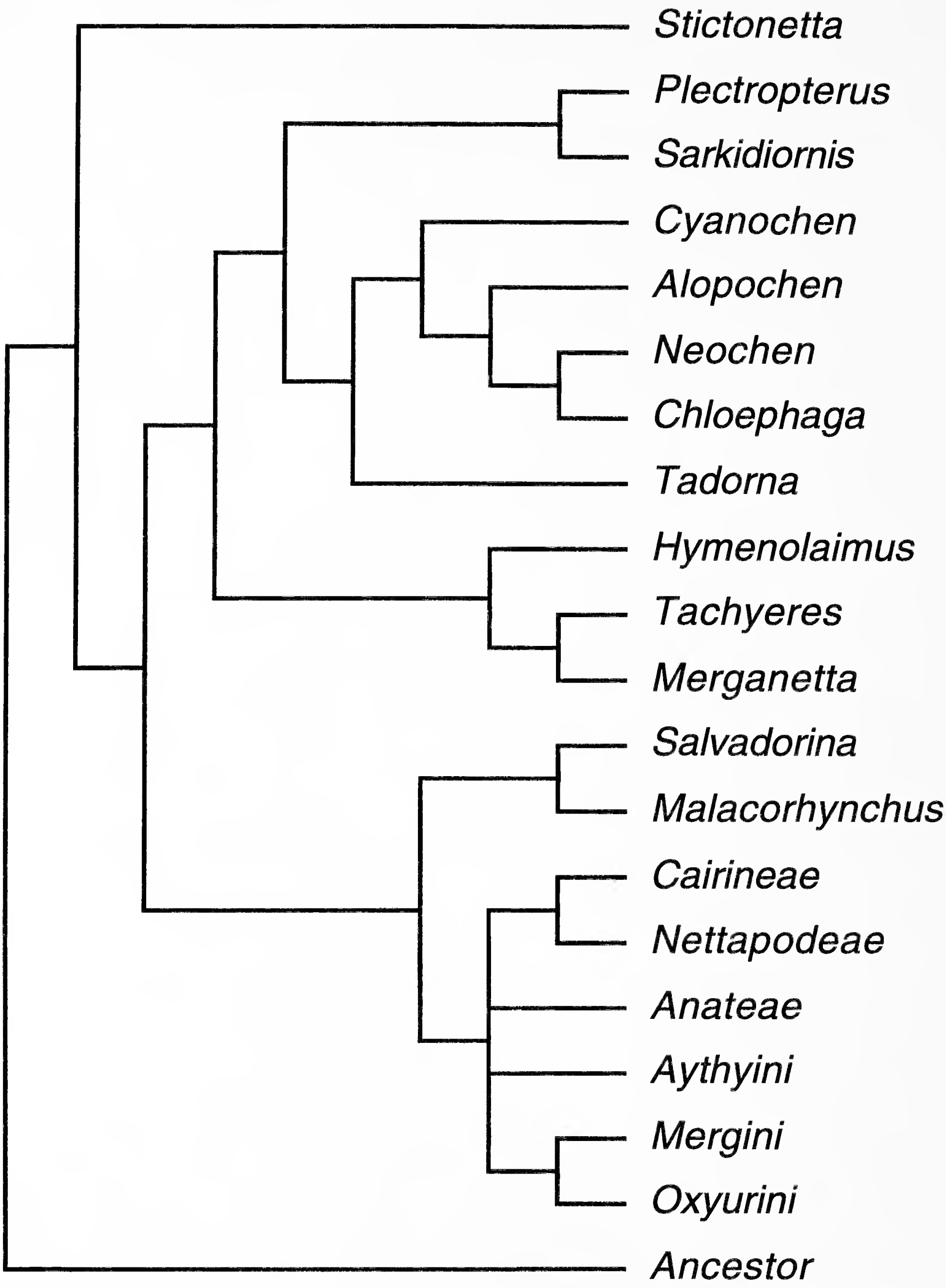


Fig. 3.—Strict consensus tree of four equally parsimonious trees for 19 taxa of Anatidae, wherein skeletal characters were given a weight of two and all other characters a weight of one ("two-group" weighting scheme).

four shortest trees confirmed the sister relationship between the Anateae and the two, generically restricted subtribes of "perching ducks," Cairineae and Nettapodeae (Fig. 4). This solution set is topologically identical to that based on an analysis in which all characters were treated as unordered.

Numbers of unambiguous character changes supporting each branch in the first of the four most-parsimonious trees varied from the single synapomorphy uniting *Salvadorina* and *Malacorhynchus* with the "typical" anatines, to the seven uniting *Hymenolaimus, Tachyeres,* and *Merganetta* (Fig. 5); identities of supporting characters are shown in Figure 6. As in all the weighting schemes for these taxa, the most prominent component of differentiation among taxa was autapomorphy, which does not contribute to resolution of phylogenetic relationships. The topological variants within the Anatinae differed primarily in the transformations inferred for characters 46, 56, and 99 (Appendices 1, 2).

"Four-Group" Weighting.—Under the "four-group" weighting scheme, wherein weights of 4, 3, 2, and 1 were applied to characters of the skeleton, trachea, natal integument, and definitive integument, respectively, a single most-parsimonious tree was found. The skewness statistic (g_1) for the "four-group" matrix, based on 1000 randomly generated trees, was -0.588. The topology of this tree was identical to the first of the four shortest trees recovered under the "two-group" weighting scheme (Fig. 5, 6), and had the following summary statistics: total length = 476, CI = 0.676 (CI* = 0.559), HI = 0.378 (HI* = 0.471), RI = 0.691, and RC = 0.468. Analysis using the same weighting scheme but in which all characters were treated as unordered resulted in a single tree that differed in only two topological features: (1) *Plectropterus* was placed as the sister-group to all included taxa but *Stictonetta* (as in Livezey, 1986*a*); and (2) the Cairineae was placed as the sister-group to other Anatinae, including *Salvadorina* + *Malacorhynchus.*

Successive Weighting.—Using the equally weighted data matrix as a starting point (admitting 40 shortest trees), two successive reweightings of the characters (base weight 2, using RC) recovered, respectively, eight and two trees of equal length; these two trees were resistant to additional reweighting cycles. Both trees had the following summary statistics: length = 230; CI = 0.857 (CI* = 0.703); HI = 0.178 (HI* = 0.315); RI = 0.828; and RC = 0.709. The skewness statistic (g_1) for 1000 randomly generated trees based on the successively weighted matrix was −0.772.

A strict consensus tree of these two solutions differed from those for the shortest trees derived using *a priori* weighting schemes in two important ways (Fig. 7): (1) placement of the Mergini as the sister-group of all taxa exclusive of *Stictonetta* and the clade comprising *Salvadorina, Malacorhynchus,* Nettapodeae, Anateae, Aythyini, and Oxyurini (a placement made on first iteration); and (2) placement of the Cairineae as the sister-group of the clade comprising *Plectropterus* and *Sarkidiornis* (placement made on the second iteration). The interrelated effects of reweighting on the distributions of character changes in the trees are difficult to interpret, but examination of supporting characters indicates that comparatively few characters underlie these two divergent inferences. Topologically identical series of solutions were found using successive weighting of unordered characters.

The position of the Mergini reflects, at least in part, shared changes in characters 95 (lobation of hallux), 98 (ground color of secondary remiges), and 99 (color of wing linings). The position of the Cairineae in the successive weighting analysis evidently stems from a number of characters that members of the subtribe

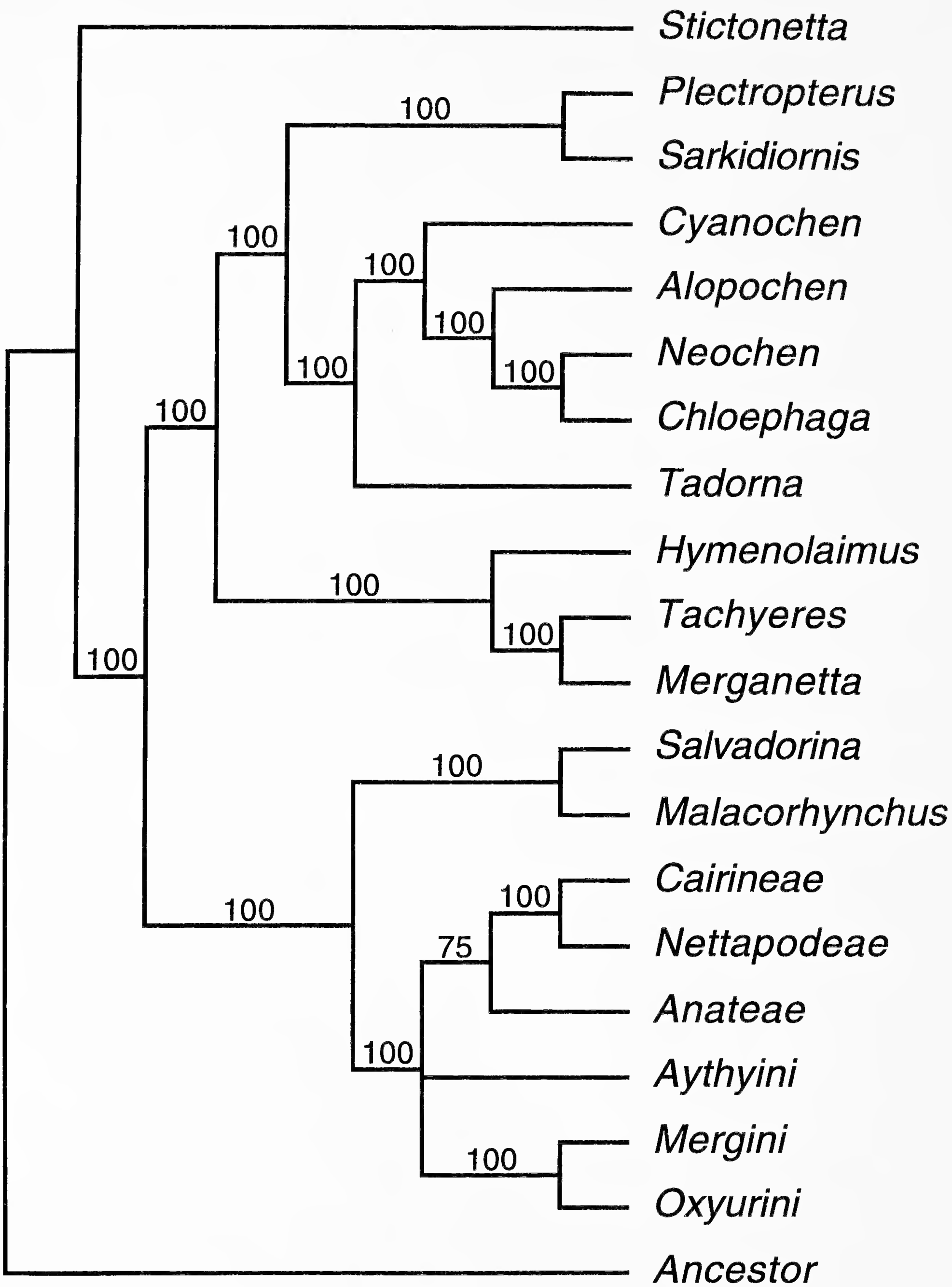


Fig. 4.—Majority-rule consensus tree of four equally parsimonious trees for 19 taxa of Anatidae, wherein skeletal characters were given a weight of two and all other characters a weight of one ("two-group" weighting scheme). Percentages of these four trees in which each branch was conserved are shown.

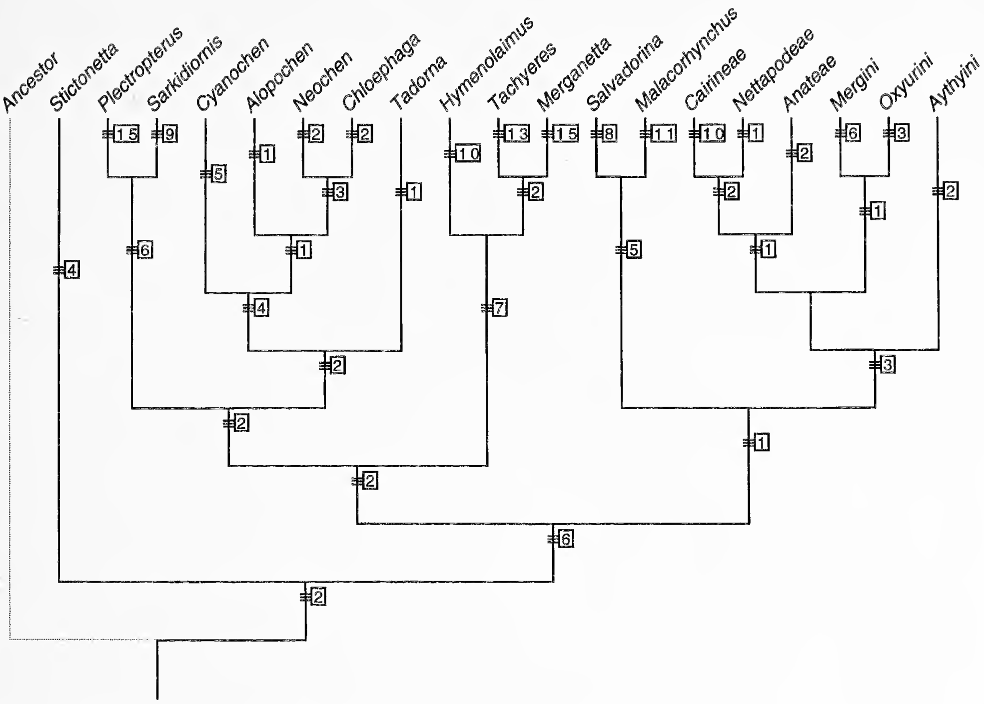
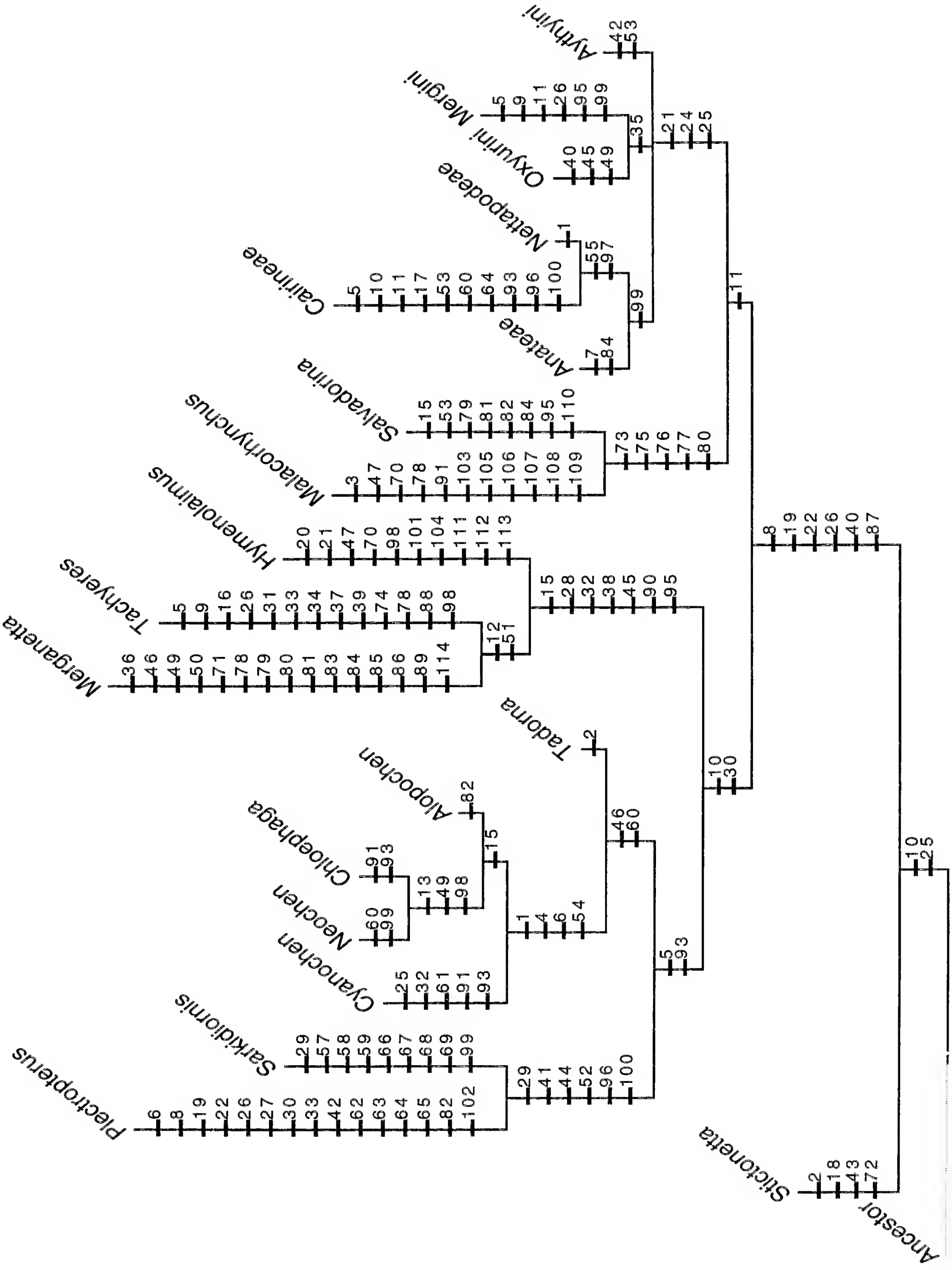


Fig. 5.—One of four equally parsimonious trees for 19 taxa of Anatidae under the "two-group" weighting scheme, showing numbers of unambiguous characters supporting each branch.

shared with *Plectropterus, Sarkidiornis,* or (less commonly) both genera: characters 5 (processus supraorbitalis), 10 (spina externa sterni), 64 (unfeathered facial region), 93 (coloration of tertials), 96 (black dorsal color), and 99 (color of wing linings). Of the characters primarily involved in these two inferences, one posed difficulties in codings for several taxa (character 99) and only three achieved a CI of 1.00 (characters 5, 10, and 96). In addition, most of the foregoing characters suffered declines in consistency with the inclusion of more genera of waterfowl or species-level codings (Livezey, 1991, 1995*b*, in press *a*) of magnitudes in excess of those typically associated with the inclusion of additional taxa (Sanderson and Donoghue, 1989).

Support for Branches

Bootstrapping of Characters.—Under equal weighting of characters, a majority-rule consensus tree of 100 bootstrapped replicates conserved only the nine clades shared by all 40 shortest trees (Fig. 1); support for these branches ranged from 56% for the four genera of sheldgeese to 99% for the ingroup exclusive of *Stictonetta* (Fig. 8). Identical groups were preserved in a majority-rule consensus tree of 100 bootstrapped replicates under the "two-group" weighting scheme, with only minor differences in percentages (Fig. 9). A majority-rule consensus tree of 100 bootstrapped replicates under the "four-group" weighting scheme retained the same groupings with the exception of that uniting *Salvadorina* with *Malacorhynchus* (Fig. 10). Bootstrapping after two iterations of successive


Aythyini
42 53
Mergini
5 9 11 26 95 99
Oxyurini
40 45 49
35
21 24 25
Netapodeae
1
55 97
Cairineae
5 10 11 17 53 60 64 93 96 100
99
Anateae
7 84
11
Salvadorina
15 53 79 81 82 84 95 110
Malacorhynchus
3 47 70 78 91 103 105 106 107 108 109
73 75 76 77 80
8 19 22 26 40 87
Hymenolaimus
20 21 47 70 98 101 104 111 112 113
Tachyeres
5 9 16 26 31 33 34 37 39 74 78 88 98
Merganetta
36 46 49 50 71 78 79 80 81 83 84 85 86 89 114
12 51
15 28 32 38 45 90 95
Tadorna
2
Alopochen
82
Chloephaga
91 93
Neochen
60 99
13 49 98
15
Cyanochen
25 32 61 91 93
1 4 6 54
46 60
Sarkidiornis
29 57 58 59 66 67 68 69 99
Plectropterus
6 8 19 22 26 27 30 33 42 62 63 64 65 82 102
29 41 44 52 96 100
5 93
10 30
10 25
Stictonetta
2 18 43 72
Ancestor

weighting produced a majority-rule consensus tree topologically identical to those derived from bootstrapping under equal weighting or "two-group" weighting (Fig. 8, 9), with the exception of the placement of the Cairineae as sister-group of *Plectropterus* and *Sarkidiornis,* a grouping retained in only 59% of the replicates (Fig. 11).

Near-shortest Trees.—Under equal weighting, numbers of equally parsimonious trees increased precipitously with admission of suboptimal solutions; retention of trees having only two additional steps resulted in the discovery of over 3500 trees (Table 2). Subjecting the matrix to "two-group" weighting lowered the numbers of topologies of near-minimal lengths considerably, and "four-group" weighting further narrowed the solution sets at near-minimal lengths (Table 2). Tallies of near-minimal tree lengths under successive weighting resembled those for the "four-group" weighting scheme (Table 2).

Bremer or "Decay" Indices.—Stability of several clades common to most weighting schemes or consensus techniques with respect to additional homoplasy (i.e., suboptimal tree lengths) was measured using Bremer or "decay" indices. Monophyly of the ingroup exclusive of *Stictonetta* was resistant to increased homoplasy under all weighting schemes, e.g., requiring an additional six steps under equal weighting to disrupt the clade (Table 3). The clade comprising *Hymenolaimus, Tachyeres,* and *Merganetta* showed moderately high resistance to increased homoplasy, an integrity that was magnified under regimes that weighted skeletal characters highly (Table 3). Three other recurrent clades—typical shelducks and sheldgeese, *Plectropterus* + *Sarkidiornis,* and *Malacorhynchus* + *Salvadorina*—required only one to three additional steps before alternative arrangements were admissible under most weighting regimes (Table 3).

Ecomorphological Evolution

Morphological Attributes.—For purposes of *a posteriori* mapping, the first of the four shortest trees derived using "two-group" weighting of characters was used (Fig. 5, 6), a tree sharing most of the well-supported elements common to trees based on other analyses (Fig. 1–4, 7–11). In spite of the generalizations necessary for coding parameters for genera and higher taxa in the ingroup, broad evolutionary patterns in body mass, sexual size dimorphism, and sexual dichromatism were evident. Body mass appears to have undergone a substantial decrease in the common ancestor of the ingroup, although the ancestral state of this attribute is questionable; significant, subsequent increases in body mass characterize three clades: *Sarkidiornis* + *Plectropterus,* the sheldgeese, and *Tachyeres* (Fig. 12A). Uncertainty in the states of associated stems makes the homology of the large body masses of the first two clades indeterminate.

Patterns of sexual size dimorphism within the ingroup shows a similar pattern to that evident in body mass, although increases in the former include *Tadorna* (indicating homology in the increase in a clade comprising seven genera), *Merganetta* (interpretable as homologous to that in *Tachyeres*), and the Cairineae (Fig.

←

Fig. 6.—Detailed phylogenetic tree, one of four equally parsimonious trees for 19 taxa of Anatidae under the "two-group" weighting scheme, showing the characters unambiguously supporting each branch. Character numbers correspond to those used in the character descriptions (Appendix 1) and data matrix (Appendix 2).

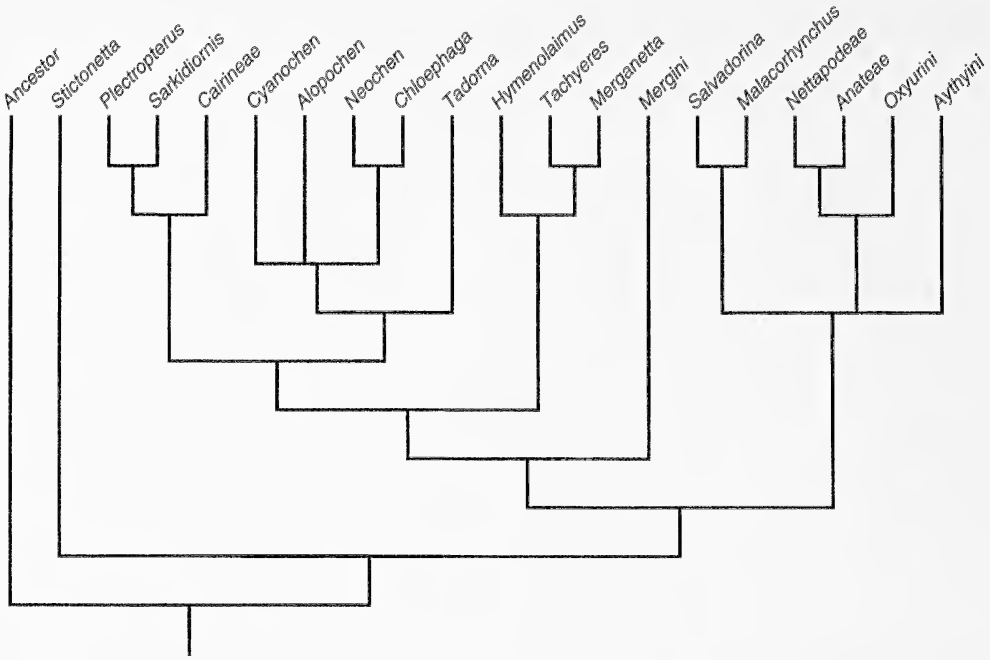


Fig. 7.—Strict consensus tree of the two shortest phylogenetic trees for 19 taxa of Anatidae converged upon after three successive reweightings of characters based on rescaled consistency indices, using equal initial weights and a base for reweighting of two.

12B). The moderately high dimorphism of the Cairineae is more parsimoniously interpreted under the alternative position of this group, as sister-group to *Sarkidiornis* and *Plectropterus,* supported by successive weighting (Fig. 7, 11).

Sexual dichromatism manifested evolutionary patterns completely distinct from those for sexual size dimorphism (Fig. 12C). Comparatively minor, quantitative dichromatism appears to have evolved independently in *Sarkidiornis, Tachyeres,* and basal Anateae; this intermediate state evidently gave rise to pronounced, qualitative dichromatism in a number of more-derived members of the latter subtribe (Livezey, 1991). Distinct, qualitative sexual dichromatism appears to have evolved in four other lineages independently: *Chloephaga, Tadorna, Merganetta,* and the remaining taxa of "typical" Anatinae (Fig. 12C).

Parameters of Reproduction.—Polygyny without establishment of significant pair-bonds, inferred to be derived in this group of Anseriformes, is shared by the clade comprising *Plectropterus* and *Sarkidiornis* and the Cairineae (Fig. 12D). Among Anseriformes, parental investment by males is inversely correlated with sexual size dimorphism (Sigurjónsdóttir, 1981), an attribute that was especially high in these three taxa (Fig. 12B; Livezey and Humphrey, 1984*a*). The association between paternal investment and sexual dichromatism in waterfowl is less clear (Johnsgard, 1962; Scott and Clutton-Brock, 1989). Sexual dichromatism in Anseriformes has traditionally been interpreted in terms of isolating mechanisms among closely related species (e.g., Sibley, 1957; Johnsgard, 1960*b*, 1963), a perspective of questionable utility among these diverse taxa showing little or no

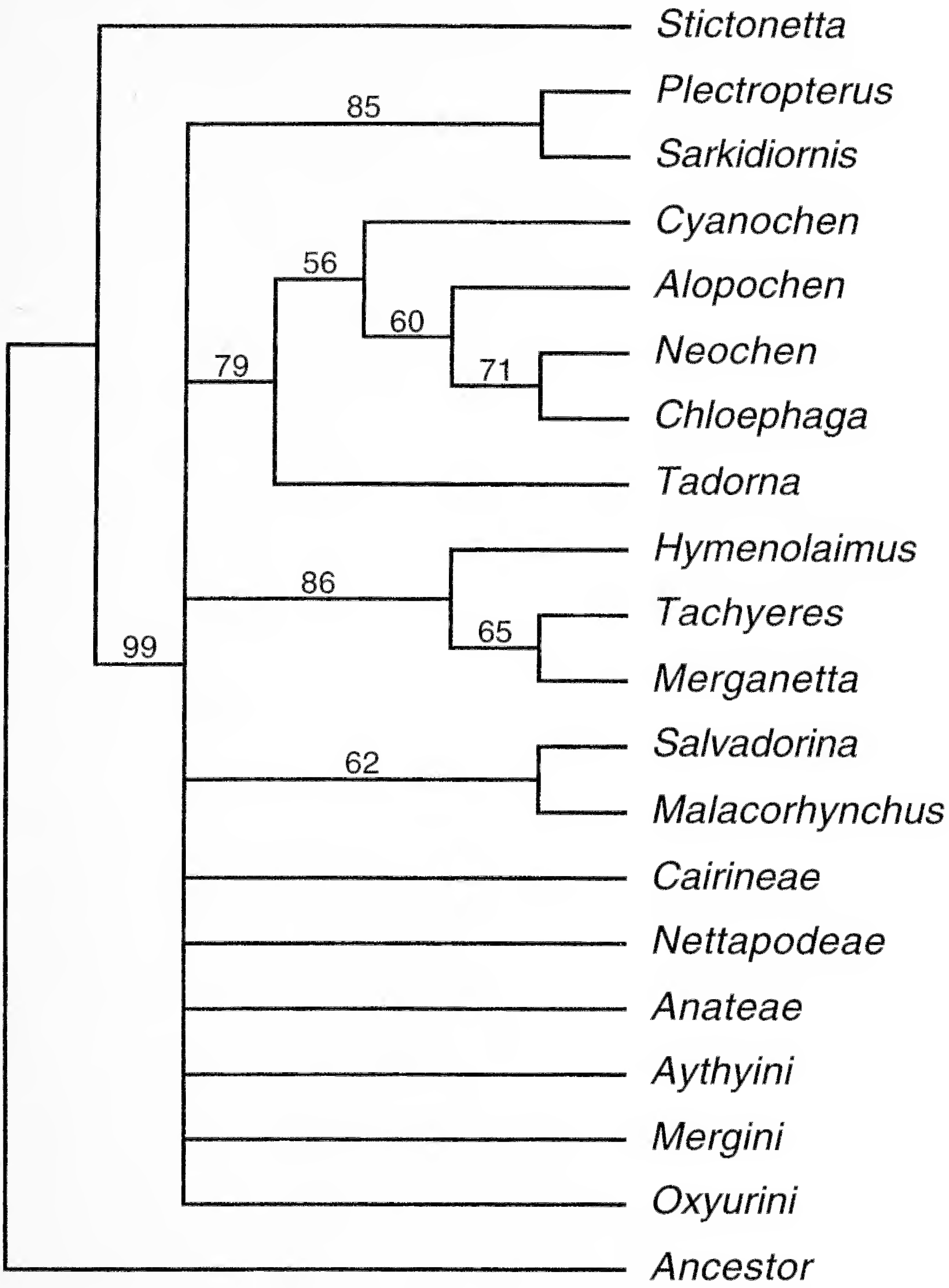


Fig. 8.—Majority-rule consensus trees for 19 taxa of Anatidae of 100 bootstrapped replicates under equal weighting of characters.

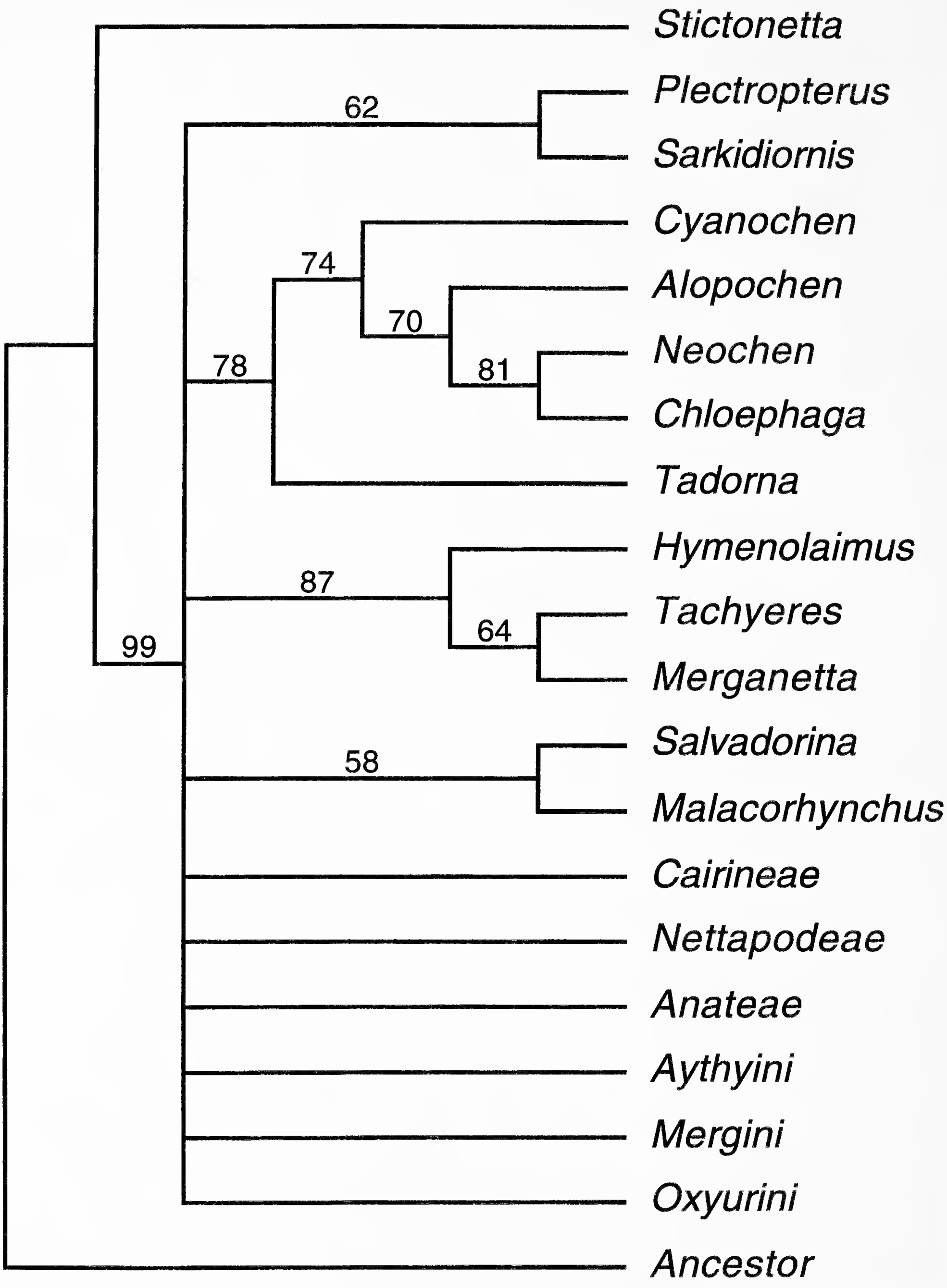


Fig. 9.—Majority-rule consensus trees for 19 taxa of Anatidae of 100 bootstrapped replicates under "two-group" weighting.

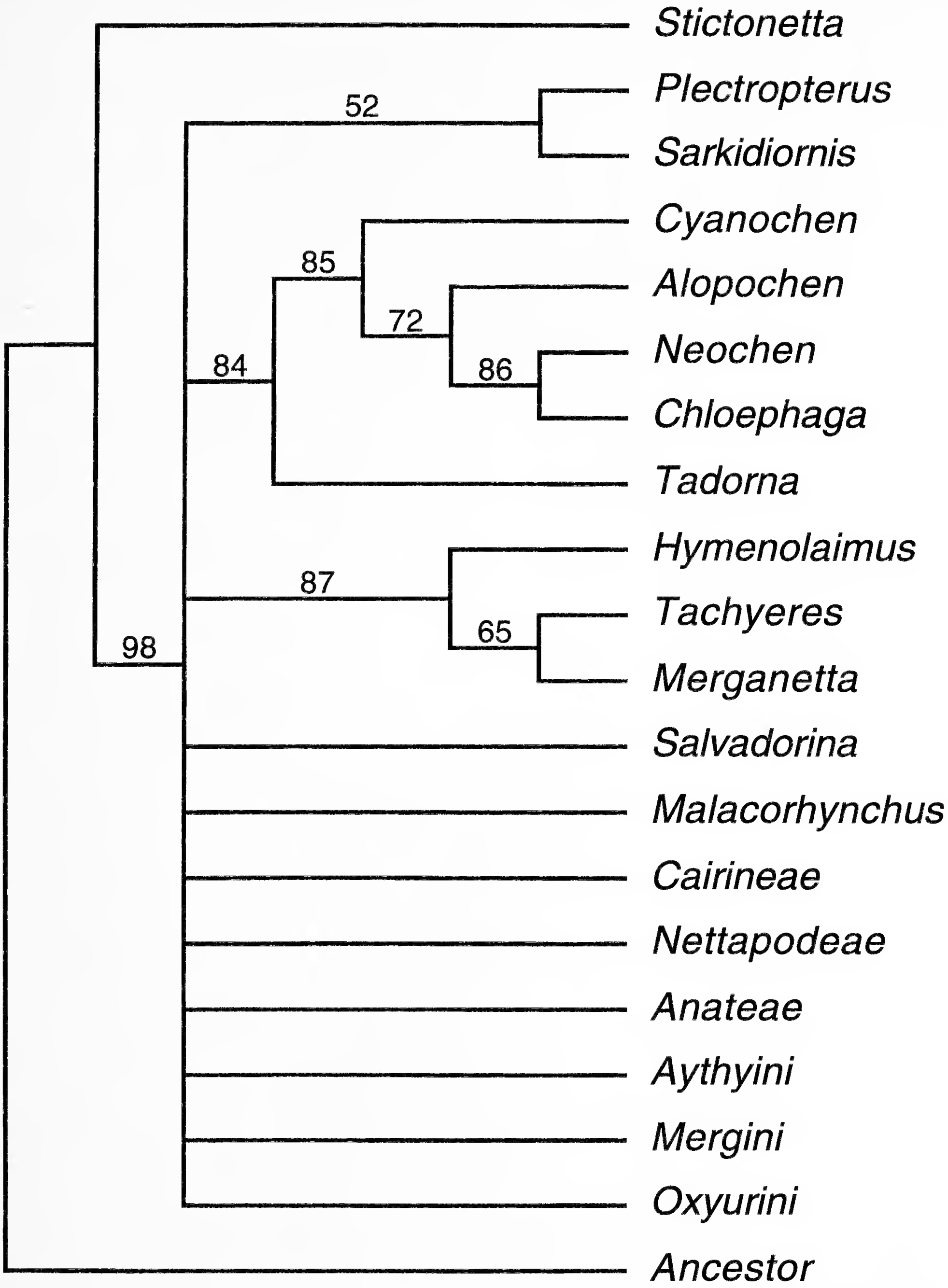


Fig. 10.—Majority-rule consensus trees for 19 taxa of Anatidae of 100 bootstrapped replicates under "four-group" weighting.

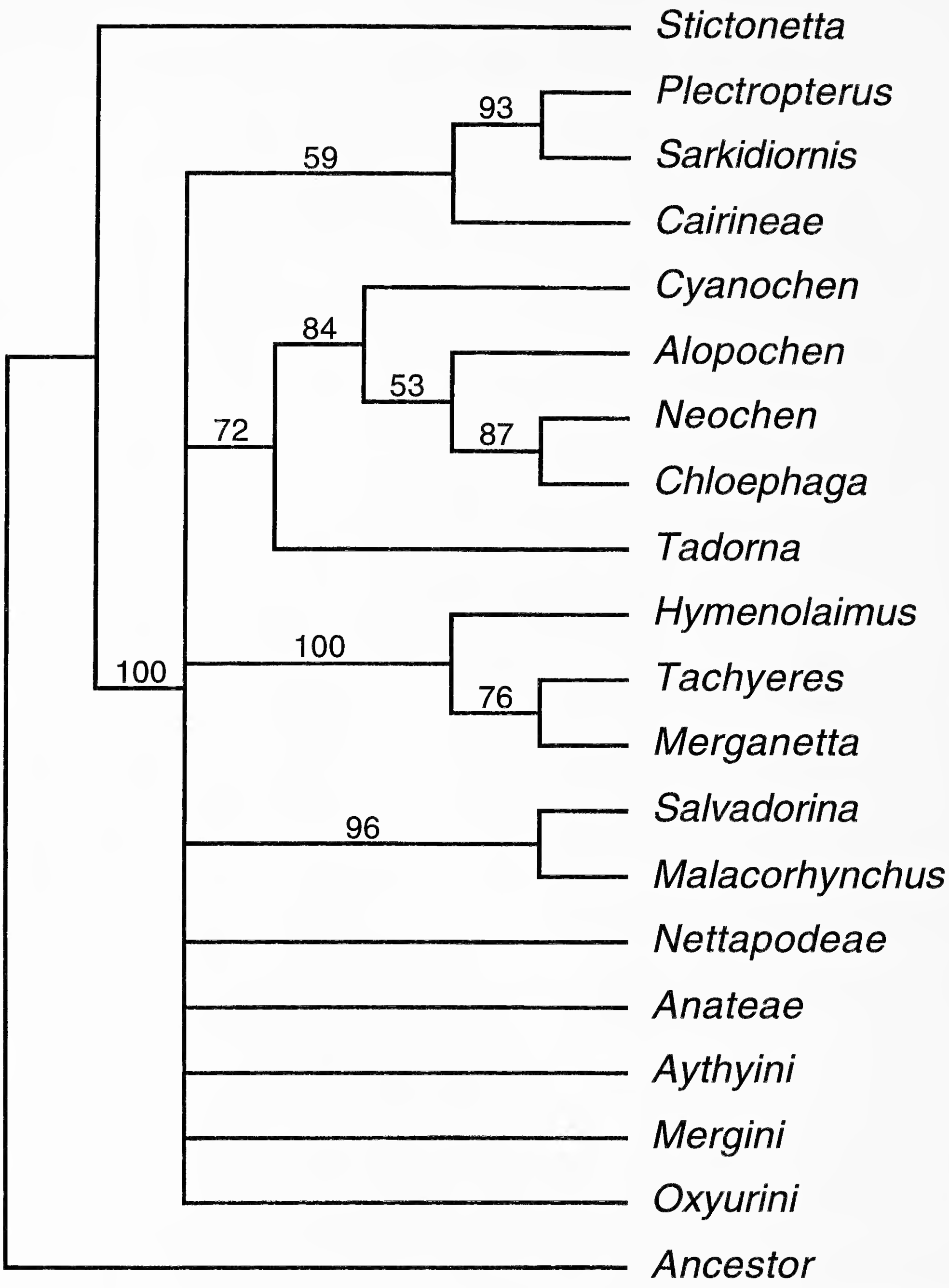


Fig. 11.—Majority-rule consensus trees for 19 taxa of Anatidae of 100 bootstrapped replicates for matrix subjected to successive weighting (see text for details).

Table 2.—*Numbers of trees of minimal and near-minimal lengths under three a priori and one successive weighting schemes for 19 generic, subtribal, and tribal taxa of Anatidae.*

Weighting scheme	Minimal length (m)	Numbers of trees of length				
		m	m + 1	m + 2	m + 3	m + 4
Unit (equal)	215	40	488	3503	—	—
"Two-group"	290	4	34	148	657	—
"Four-group"	476	1	9	28	114	425
Successive	230	2	8	36	188	673

tendency toward hybridization (Scherer and Hilsberg, 1982) and in light of conceptual difficulties with this emphasis (Livezey, 1991, 1995*b*).

Preferred nest site appears to have undergone two independent shifts to cavities, in *Tadorna* and (within the context of this particular tree, homologously) in the Cairineae and Nettapodeae (Fig. 12E). Modal clutch size varied greatly in this group (Fig. 12F), and states of terminal taxa rendered hypotheses of states indeterminate for most stems and characterization of the Anateae, Mergini, Oxyurini, and Aythyini problematic. Suggested evolutionary changes in this parameter are (Fig. 12F): (1) an increase in the ancestor of the ingroup; (2) several increases within the shelducks and sheldgeese; (3) decreases, possibly homologous, in *Hymenolaimus* and *Merganetta*; and (4) increases, interpretable as homologous within the context of this particular tree, in the Cairineae and Nettapodeae.

Mean egg masses (g) for the eight key genera of the ingroup were: *Stictonetta* (66), *Plectropterus* (131), *Sarkidiornis* (65), *Hymenolaimus* (73), *Merganetta* (62), *Tachyeres* (115–167), *Malacorhynchus* (31), and *Salvadorina* (57). Egg mass is generally correlated with body mass in the ingroup, making a mapping of this parameter largely redundant with that presented for body mass (Fig. 12A). Explicit mapping of relative clutch mass also proved intractable for these taxa because of variation in the three parameters composing this ratio (female body mass, egg mass, clutch size), some of which are poorly known for some genera. In addition, generalizing this ratio for the tribal and generic vectors also proved problematic; the range of values within several subtribal and tribal taxa encompassed a greater range than all eight of the genera of primary interest combined. Estimates for relative clutch masses (percentages of female body mass, largely based on Rohwer, 1988) for the key ingroup genera were as follows: *Stictonetta* (55), *Plec-*

Table 3.—*Bremer or "decay" indices for selected clades within 19 generic, subtribal, and tribal taxa of Anatidae under three* a priori *and one successive weighting schemes. Percentage of minimal total tree length represented by each index is given in parentheses to facilitate comparisons across weighting schemes.*

Clade	Weighting scheme			
	Equal	Two-group	Four-group	Successive
Tadorninae + Anatinae[a]	6 (2.8)	7 (2.4)	8 (1.7)	6 (2.6)
Tadornini[b]	1 (0.5)	2 (0.7)	3 (0.6)	1 (0.4)
Plectropterus + *Sarkidiornis*	3 (1.4)	5 (1.7)	5 (1.1)	5 (2.2)
Hymenolaimus + *Tachyeres* + *Merganetta*	3 (1.4)	4 (1.4)	20 (4.2)	9 (3.9)
Malacorhynchus + *Salvadorina*	2 (0.9)	4 (1.4)	1 (0.2)	2 (0.9)

[a] Includes all taxa analyzed herein except hypothetical ancestor and *Stictonetta*.
[b] Includes *Cyanochen, Alopochen, Neochen, Chloephaga,* and *Tadorna.*

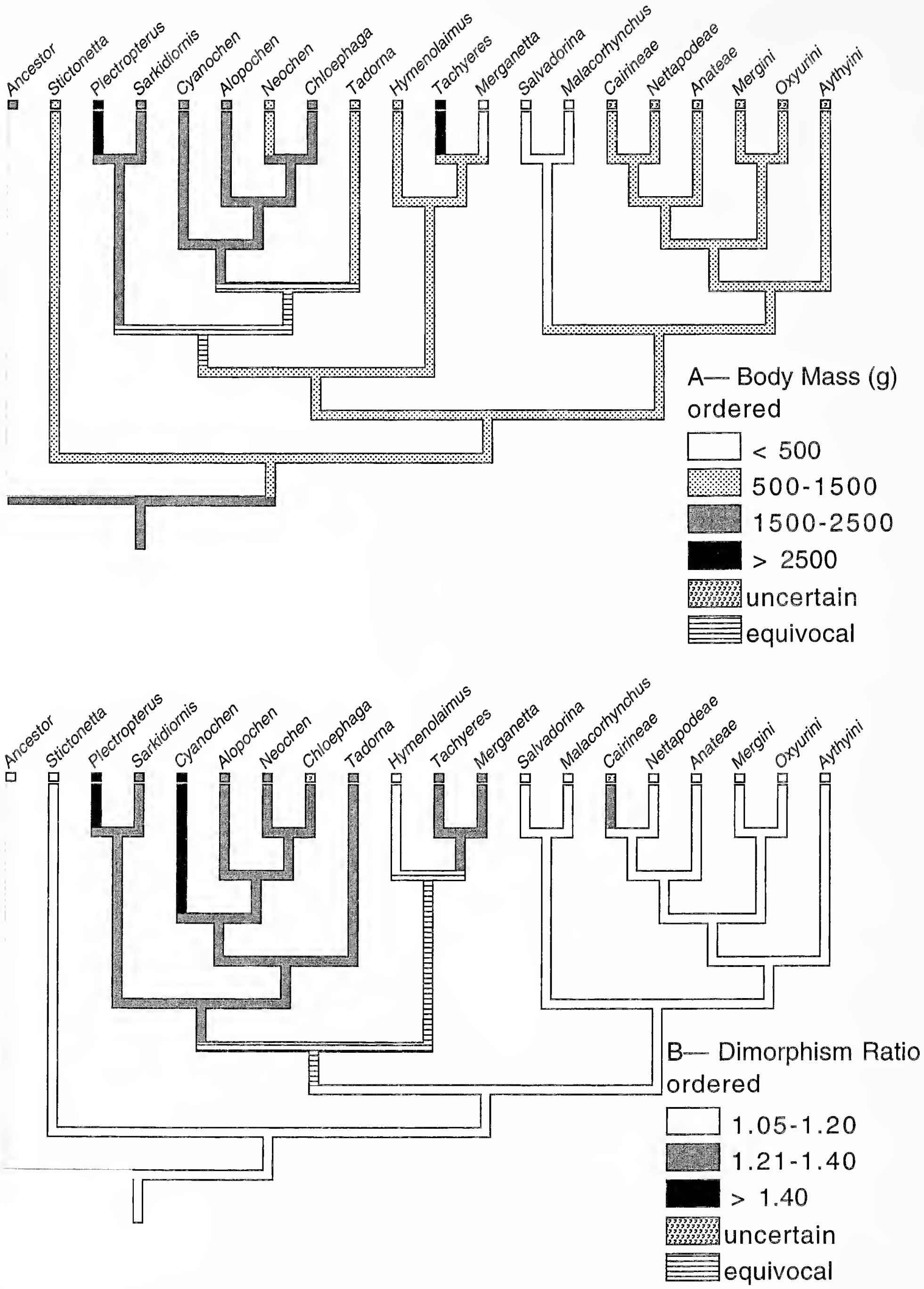


Fig. 12.—Mapping of eight ecomorphological attributes on the first of four minimal-length trees recovered under "two-group" weighting of characters (Appendices 1, 2): A—body mass, B—sexual size dimorphism, C—sexual dichromatism, D—mating system, E—typical nest site, F—clutch size, G—paternal attendance of broods, and H—diving habit. The tree shown is topologically identical to the single shortest tree found under the "four-group" weighting scheme, in which a soft polytomy involving the taxa Aythyini, Oxyurini, Mergini, Cairineae, Nettapodeae, and Anateae is depicted as resolved.

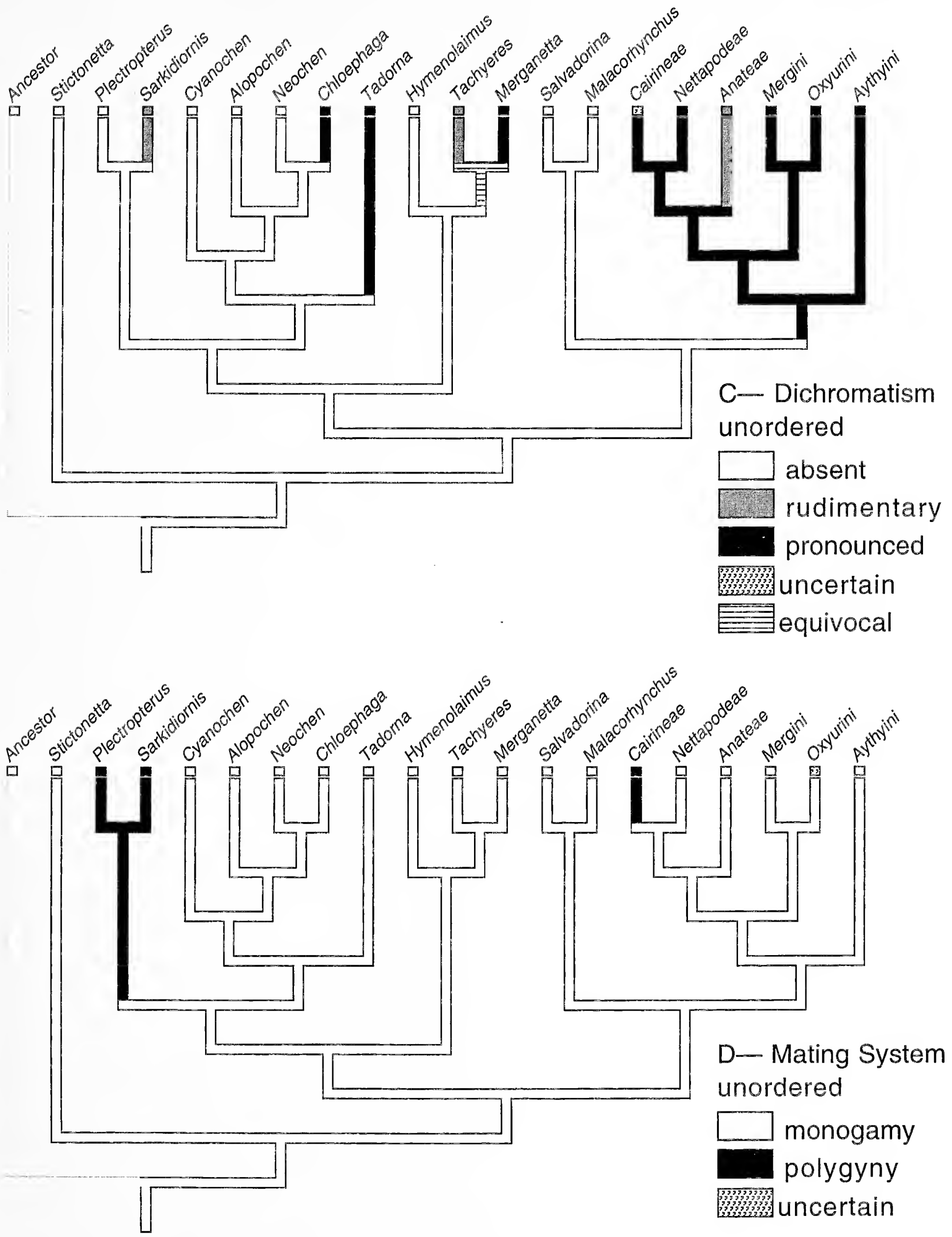


Fig. 12.—Continued.

tropterus (41), *Sarkidiornis* (31), *Hymenolaimus* (49), *Merganetta* (62), *Tachyeres* (30–35), *Malacorhynchus* (63), and *Salvadorina* (37).

In addition to the three taxa in which polygyny is typical (*Plectropterus, Sarkidiornis,* and Cairineae), a derived loss of paternal attendence of broods is characteristic of the Aythyini, Mergini, and Oxyurini; variation within the Anateae in

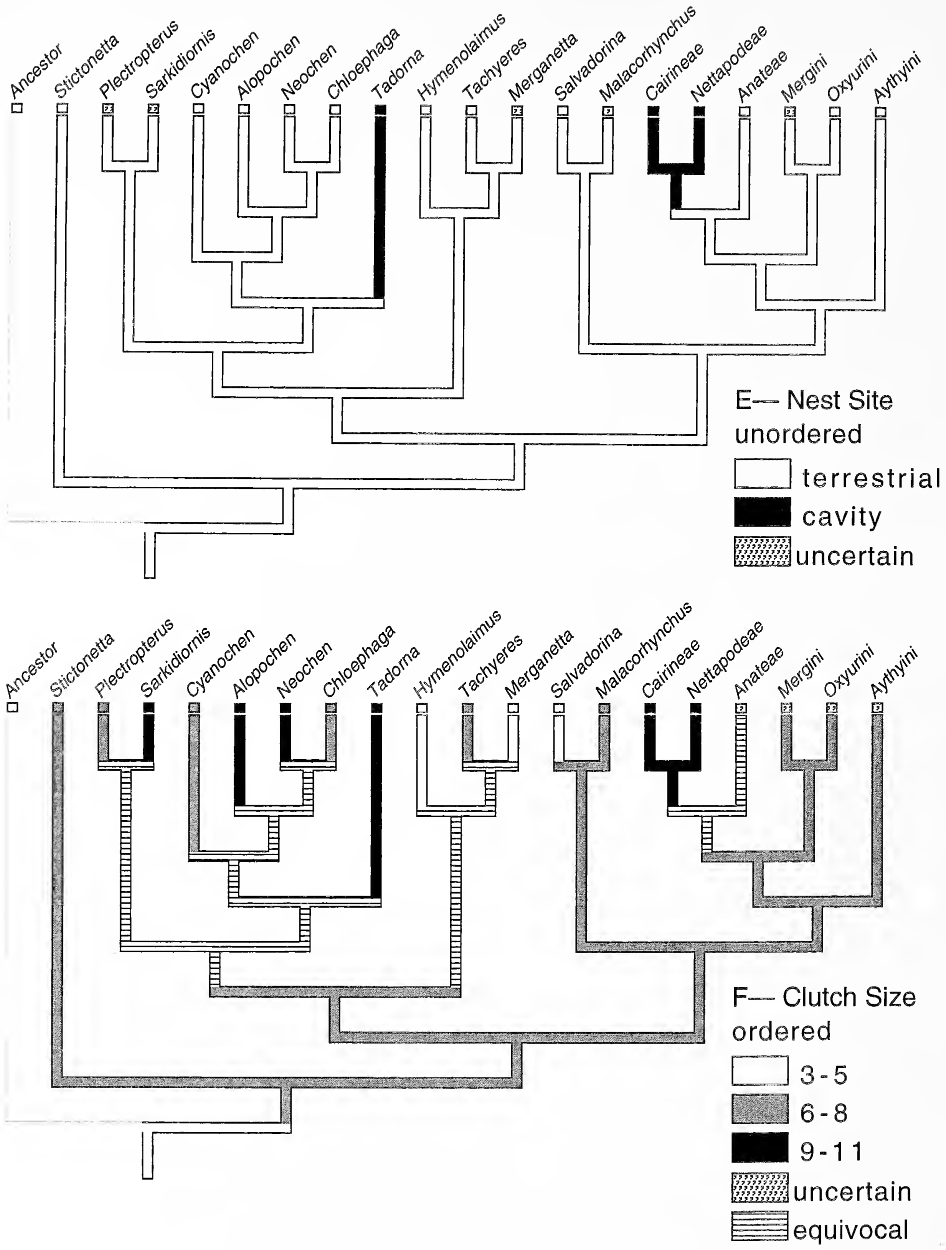


Fig. 12.—Continued.

this attribute necessitated coding the taxon as polymorphic (Fig. 12G). Within the phylogenetic hypothesis used as a basis for mapping, the simplest evolutionary pattern suggested is a loss of paternal attendance in the ancestor of the "typical" Anatinae, with subsequent, independent reversals in the Nettapodeae and some Anateae.

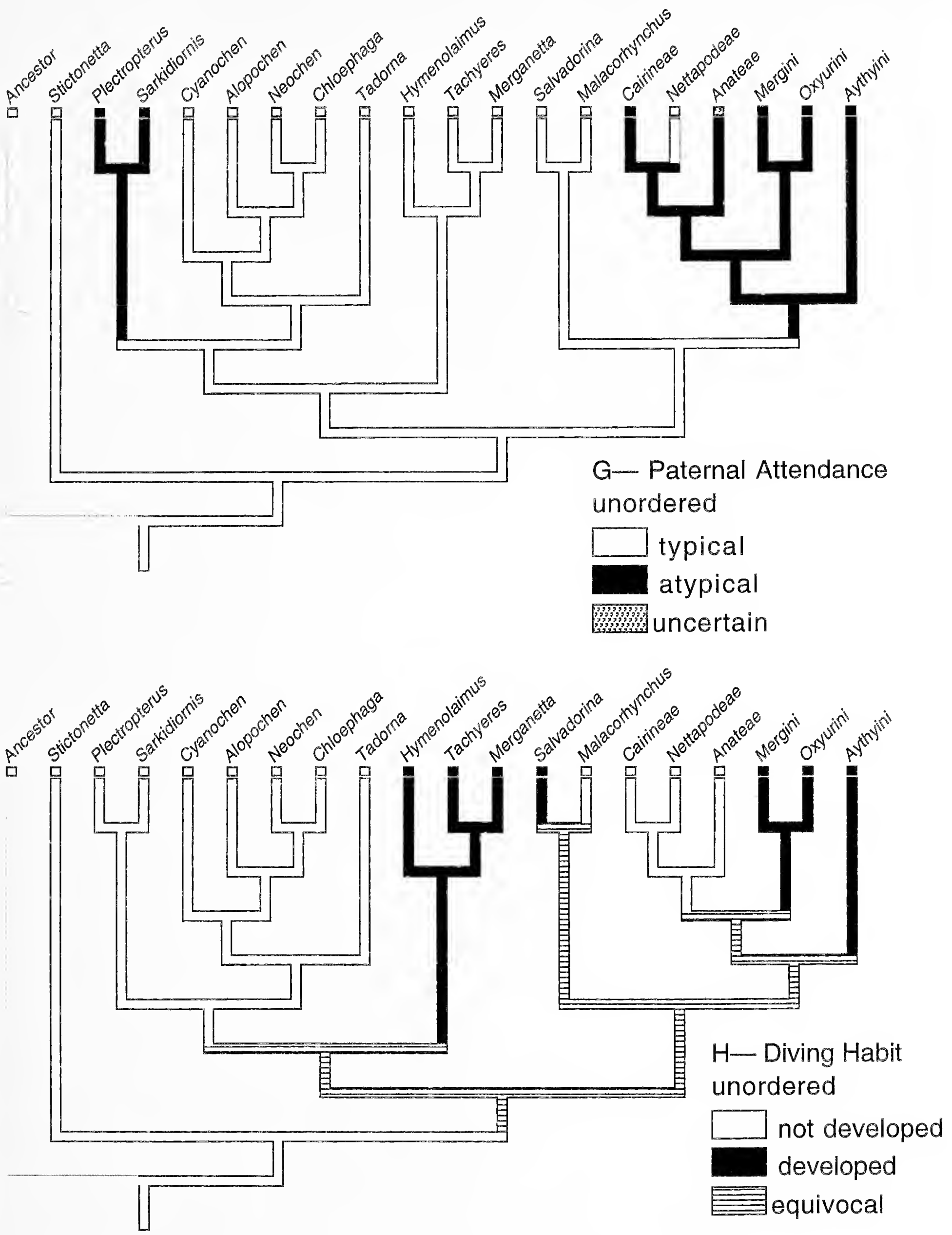


Fig. 12.—Continued.

Ecological Trends.—Most ecological attributes successfully mapped in other anseriform groups (Livezey, 1995*b*, 1995*c*, in press *a*, in press *b*, in press *c*) remain too poorly known for the key genera under study here, and furthermore were variable within the higher taxa included in this analysis. These inadequately documented attributes include: diel pattern, in which most species are probably crepuscular, but some like marine *Tachyeres* are influenced by tides (Livezey, 1988; McNeil et al., 1992); diet, in which most species probably feed on both plants and invertebrates, rarely vertebrates; aquatic habitat, in which all species are primarily freshwater except most *Tachyeres,* some *Tadorna,* some *Chloephaga,* and most Mergini; nest parasitism, which is probably infrequent in most ingroup taxa as in most Anseriformes (Rohwer and Freeman, 1989); formation of crèches (Eadie et al., 1988); parental carrying of young (Johnsgard and Kear, 1968) through the air (reported in *Sarkidiornis, Tadorna, Alopochen, Chloephaga,* and some members of the Cairineae, Anateae, Mergini, and Oxyurini) or on water (reported in *Salvadorina,* and some members of *Chloephaga,* the Mergini and Oxyurini); and migratory habit, wherein most species show variable seasonal movements, with the notable exceptions being sedentary *Hymenolaimus* and Merganetta, and flightless species of *Tachyeres.*

Diving habit is characteristic of four taxa in this analysis, evidently representing either: (1) three or four convergent acquisitions, the interpretation most consistent with most described evolutionary scenarios (Delacour and Mayr, 1945; Johnsgard, 1978; Faith, 1989); or (2) a single derivation in the ancestor of the Tadorninae and Anatinae followed by three independent losses (Fig. 12H). Possible homoplasy in several morphological characters related to diving habit or its loss (e.g., characters 38, 41), both having locally high consistencies but showing global homoplasy (Livezey, 1986*a*; Faith, 1989), might compromise their utility for phylogenetic inference (especially with respect to *Hymenolaimus, Merganetta,* and *Tachyeres*). Several of these diving-related characters are coded for this analysis as lacking for tribes in which a majority of the members possess the trait (Aythyini, Mergini, Oxyurini), because the absence of the character in basal members of each tribe indicates the character was acquired independently in more-derived members of these groups (Livezey, 1995*b,* 1995*c,* in press *b*).

Discussion

Phylogenetic Inferences

Points of Concern.—With the exception of the support for the monophyly of the ingroup exclusive of *Stictonetta* (i.e., Tadorninae + Anatinae), most members of the ingroup are characterized more by unique divergence than nested, unifying characters. For example, *Merganetta* and *Tachyeres* are inferred to be sister-genera on the basis of two unambiguous synapomorphies, whereas the genera are themselves supported by 15 and 13 autapomorphies, respectively (Fig. 6). In part because of concerns regarding possible homoplasy stemming from convergent life histories, I remain somewhat suspicious with respect to the clade comprising *Hymenolaimus, Merganetta,* and *Tachyeres,* in part because of the possible effects of "long-branch attraction" (see below). However, there are seven unambiguous characters that support this clade (Fig. 6), the grouping is comparatively robust with respect to weighting schemes (Table 3; Fig. 1–11), and there is a significant sacrifice of parsimony (Table 4) required to accommodate the positions of these genera proposed by Johnsgard (1965*a,* 1978, 1979).

The position of the Cairineae remains a challenging problem; this group comprises three genera and five species traditionally included among the "perching ducks" (e.g., Delacour and Mayr, 1945; Delacour, 1959; Johnsgard, 1961*a,* 1965*a,* 1978, 1979), but was inferred by Livezey (1991) to be the sister-group of a clade comprising the Nettapodeae and Anateae. In this study, most weighting schemes

Table 4.—*Minimal numbers of additional steps required to preserve previously hypothesized taxonomic grouping among 19 generic, subtribal, and tribal taxa of Anatidae, under three* a priori *and one successive weighting schemes. Percentage of minimal total tree length represented by each index is given in parentheses to facilitate comparisons across weighting schemes.*

Taxonomic group	Weighting scheme			
	Equal	Two-group	Four-group	Successive
Tribe Cairinini[a]	2 (0.9)	6 (2.1)	12 (2.5)	3 (1.3)
Subfamily Anatinae[b]	10 (4.7)	18 (6.2)	31 (6.5)	18 (7.8)
Subfamily Anatinae[b] exclusive of *Hymenolaimus*	2 (0.9)	6 (2.1)	12 (2.5)	5 (2.2)
Tree based on Johnsgard (1961*a*, 1978)[c]	36 (16.7)	62 (21.4)	117 (24.6)	58 (25.2)
Tree depicted by Livezey (1986*a*:fig. 1)[d]	16 (7.4)	19 (6.6)	29 (6.1)	43 (18.7)
Stictonetta + Oxyurini[e]	7 (3.3)	16 (5.5)	31 (6.5)	9 (3.9)

[a] Of the taxa defined herein, includes *Plectropterus, Sarkidiornis,* Cairineae, and Nettapodeae; *Amazonetta* and *Callonetta,* included in this tribe by Johnsgard (1978), are here included as basal members of the Anateae (Livezey, 1991).

[b] Includes *Plectropterus, Sarkidiornis, Hymenolaimus, Merganetta, Malacorhynchus, Salvadorina,* Cairineae, Nettapodeae, Anateae, Aythyini, Mergini, and Oxyurini (Johnsgard, 1965*a,* 1978, 1979).

[c] Conservative reconstruction of phylogenetic diagrams depicted by Johnsgard (1961*a,* 1978) as permitted using the present taxonomic units (Fig. 13).

[d] Constraint follows Livezey (1986*a*:fig. 1), except Anatinae simplified to polytomy involving *Salvadorina* (missing taxon), Cairineae, Nettapodeae, Anateae, Aythyini, and Mergini + Oxyurini.

[e] Grouping followed by Marchant and Higgins (1990).

either: (1) failed to establish the higher-order relationships of this taxon (Fig. 1, 8–10); or (2) placed the Cairineae as the sister-group to the Nettapodeae (*contra* Livezey, 1991) with or without indicating a sister-relationship of the latter to the Anateae (Fig. 2–6). Under "four-group" weighting, the alternative treatment of two ordered characters as unordered alone resulted in the placement of the Cairineae as the sister-group of other Anatinae, along with an associated placement of *Plectropterus* as sister-group of Tadorninae + Anatinae. Under successive weighting, the Cairineae were inferred to be the sister-group of the "tadornine" clade comprising *Plectropterus* and *Sarkidiornis* (Fig. 7, 11); this was the only significant discrepancy between the findings of *a priori* and successive weighting schemes that were robust to bootstrapping. Pending further study, I recommend tentatively retaining the Cairineae, Nettapodeae, and Anateae as subtribes of the Anatini (as in Livezey, 1991), while noting the likely monophyly of the first two subtribes (*contra* Livezey, 1991) and the less well-supported alternative placement of the Cairineae (apart from the Nettapodeae) with *Plectropterus* and *Sarkidiornis* (*contra* Livezey, 1986*a,* 1991).

One analytical artifact of parsimony analysis is "long-branch attraction" or the tendency for branches showing many character changes to be joined under certain analytical circumstances (Felsenstein, 1978; Huelsenbeck and Hillis, 1993; Penny et al., 1994; Hillis, 1995; Huelsenbeck, 1995). Three couplets of taxa united in this analysis might be vulnerable to this artifact (Fig. 6): (1) *Plectropterus* and *Sarkidiornis,* (2) *Merganetta* and *Tachyeres* (perhaps also including *Hymenolaimus*), and (3) *Malacorhynchus* and *Salvadorina.* The extent to which these groupings were fostered by "long-branch attraction" cannot be tested at present, but the possibility should be considered in any assessment of these groupings of problematic genera.

Apparent intertribal relationships within the Anatinae indicated in this analysis are among the weakest aspects of the study. None of the weighting schemes provided well-supported resolution of relationships among the Cairineae, Nettapodeae, Anateae, Aythyini, Mergini, and Oxyurini (Fig. 8–11). A sister-group relationship between the Mergini and Oxyurini was indicated in a number of the shortest topologies recovered (Fig. 3–6), an inference based on a single apomorphy related to the diving-related modification of the pelvic girdle and very possibly convergent (Appendix 1). The agreement between this inference and that indicated in the single tree depicted by Livezey (1986*a*) provides no independent confirmation because both studies shared most osteological characters, and furthermore supplementary analysis of the matrix used by Livezey (1986*a*) revealed that other arrangements were equally parsimonious (J. Harshman, personal communication).

Comparison with Previous Studies.—Congruence among independent studies is an important component of the assessment of phylogenetic reconstruction (Mickevich and Johnson, 1976; Mickevich, 1978; Hillis, 1987, 1995; Miyamoto and Fitch, 1995). Unfortunately, little phylogenetic work has been performed for the taxa of concern here, a deficiency particularly marked for molecular data and which significantly limits the comparisons that are possible. Support in this analysis for a clade comprising *Plectropterus* and *Sarkidiornis* as the sister-group of the four genera of "typical" shelducks and sheldgeese (Fig. 2–6) represents a significant departure from the position inferred for *Plectropterus* by Livezey (1986*a*). This revised inference, however, is consistent with the close relationship between these genera proposed by most recent workers (Delacour and Mayr, 1945; Delacour, 1959; Johnsgard, 1961*a,* 1965*a,* 1978, 1979). However, available evidence confirms the polyphyletic nature of the "Tribe Cairinini" as generally constituted (comprising nine genera and 13 species; e.g., Johnsgard, 1965*a,* 1978).

The close relationships inferred among the genera *Hymenolaimus, Tachyeres,* and *Merganetta* (Fig. 1–11) are consistent with several other anatomical and behavioral characteristics. All three are extremely territorial, even by tadornine standards, and this pugnacity is shown by both sexes (Wright, 1965; Kear and Steel, 1971; Kear, 1972; Weller, 1976; Eldridge, 1985, 1986*a,* 1986*b*; Livezey and Humphrey, 1985; Veltman and Williams, 1990). Also, in all three genera, territorial combat often involves blows using the variably developed metacarpal wing-knobs (Kear and Steel, 1971; Weller, 1968; Livezey and Humphrey, 1985; Eldridge, 1986*b*). In part because of inadequately defined states and a paucity of comparative data, no consistent indications of phylogenetic relationships are indicated by courtship displays and other ritualized behaviors in these three genera (Moynihan, 1958; Johnsgard, 1961*a,* 1965*a,* 1966; Eldridge, 1979, 1985, 1986*a*).

The inferred positions of *Salvadorina* and *Malacorhynchus,* found herein to be sister-genera and together composing the sister-group of "typical" Anatinae under the two *a priori* weighting schemes (Fig. 1–11), represent significant departures from that inferred for *Malacorhynchus* by Livezey (1986*a*) or those assumed for *Salvadorina* by Livezey (1986*a,* 1991). The present hypothesis seems intuitively consistent with the "subfamilial intermediacy" implied by the placements of these genera as tadornine or as basal, "aberrant" anatines (Delacour and Mayr, 1945; Delacour, 1959; Johnsgard, 1965*a,* 1965*b,* 1978) and is consistent with skeletal similarities noted by Mlíkovský (1989). This analysis indicates that the characters shared between *Salvadorina* and the genera *Hymenolaimus* and *Merganetta* cited by Kear (1975) are either plesiomorphous or homoplasious; however, the rec-

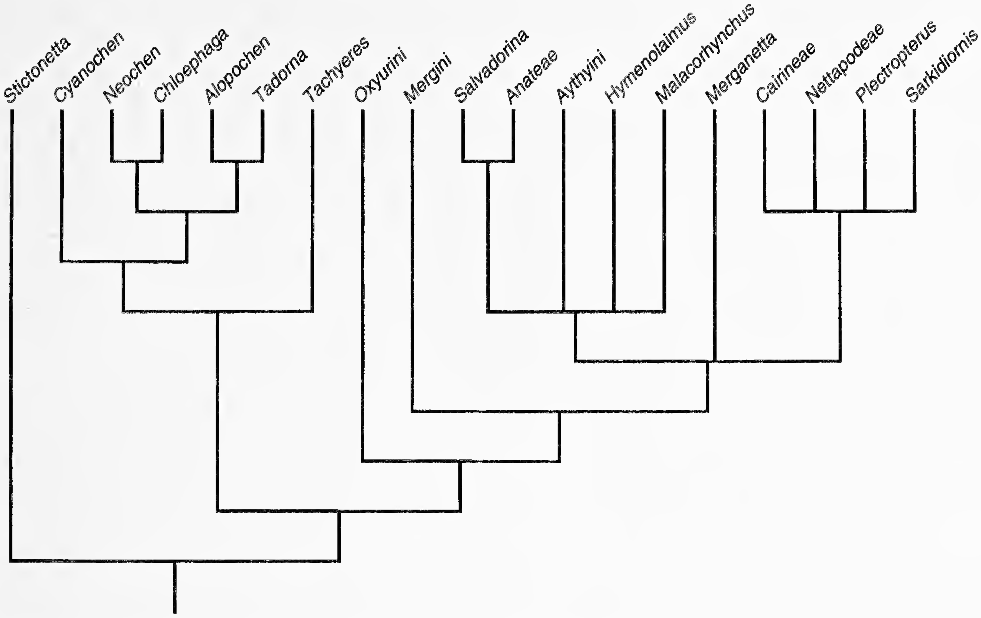


Fig. 13.—Phylogenetic tree summarizing the relationships among 19 taxa of Anatidae as depicted or described by Johnsgard (1961*a*, 1978), the basis for the analytical constraint used to estimate additional steps required to accommodate this hypothesis using the characters defined herein. Regions for which contradictory or inadequately detailed assessments were given are shown as polytomies.

ommendation by Kear (1975) that *Salvadorina* be recognized as a genus distinct from *Anas* is supported. The territorial behavior of *Salvadorina* (Hallstrom, 1956; Kear, 1975)—shared by the two aforementioned genera, most Tadorninae, and some basal Anatini—also appears to be locally plesiomorphous. Although Kear (1975) reported that *Salvadorina* uses wing knobs in combat, the presence of "true" calcar alae (character 30) in this genus is unlikely based on examination of skin specimens (Appendices 1, 2).

Searches under topological constraints (Table 4) were employed to provide quantitative assessments of the "penalties" (minimal increases in total tree length) of preserving groupings suggested by other classifications and hypotheses. To preserve as monophyletic the traditionally constituted "perching ducks" (assuming no specific topology within the group) requires, depending on weighting scheme, an additional 2–12 steps (1–3% increase in total length; Table 4). Constraining the analyses to preserve as monophyletic the Anatinae as traditionally constituted (e.g., Johnsgard, 1965*a*, 1978, 1979), without assuming any constraints regarding topology within the subfamily, requires an additional 10–31 steps or 5–8% increase in tree length (Table 4). Exclusion of *Hymenolaimus* from this group revealed that a majority of the additional steps were attributable to the classification of this genus alone (Table 4). Analyses constrained to preserve all of the intergeneric relationships depicted by Johnsgard (1961*a*, 1978), graphically summarized in Figure 13, indicated that 36–117 additional steps were required using the present data matrix, representing an increase in total tree length of 17–25% (Table 4). A similar constrained analysis determined that the tree depicted by Livezey (1986*a*), to the level of detail permitted by taxa analyzed in both studies, would require 16–43 extra steps (6.1–18.7% increase in total length), depending on weighting scheme (Table 4).

A sister-relationship between *Stictonetta* and the Oxyurini (cf. Fullagar et al., 1990; Marchant and Higgins, 1990), without assuming any specific placement of the composite group within the tree, requires a minimum of 7–31 additional steps, a 3–7% increase in total tree length (Table 4). Movement of *Stictonetta* with the Oxyurini (cf. Marchant and Higgins, 1990) to the position proposed for the latter by Sibley and Monroe (1990)—as sister-group of all Anseriformes exclusive of Anhimidae, *Anseranas, Dendrocygna,* and *Thalassornis*—requires several steps in addition to those required simply to link the Oxyurini with *Stictonetta* (Livezey, in press *c*).

Proposed Classification of Modern Members

Subfamilial Taxa.—Based on the phylogenetic inferences using the weighting schemes considered to favor the most reliable characters (conservatively summarized in Fig. 3, preferred variant shown in Fig. 4), I recognize three subfamilies within the present group of 19 taxa (Appendix 3): Stictonettinae (monotypic, *Stictonetta naevosa*), Tadorninae (three modern tribes, ten modern genera), and Anatinae (five modern tribes, one new, and one *incertae sedis*). This subfamilial taxonomy differs from that proposed by Livezey (1986*a*) in the inclusion of *Plectropterus,* formerly a monotypic subfamily Plectropterinae Gray, 1840, as a tribe (with *Sarkidiornis*) in the Tadorninae (Appendix 3).

Tribes of Tadorninae.—The Tadorninae here reconstructed (Fig. 3–6), comprise three tribes (Appendix 3): Tribe Merganettini, comprising *Hymenolaimus, Tachyeres,* and *Merganetta*; Tribe Plectropterini, comprising *Plectropterus* and *Sarkidiornis*; and Tribe Tadornini, comprising the subtribes Chloephageae (*Cyanochen, Alopochen, Neochen, Chloephaga*) and Tadorneae (*Tadorna*). Differences from the generic classification given by Livezey (1986*a*) include: (1) inclusion of *Plectropterus* (formerly a separate subfamily) with *Sarkidiornis* (formerly a separate tribe) as sister-groups in a single tribe of the Tadorninae; (2) monophyly of the Tadornini, in which the subtribe Tadorneae (comprising *Tadorna*) is the sister-group of the sheldgeese (formerly subtribes Cyanocheneae and Chloephageae; Livezey, in press *a*); and (3) exclusion of *Malacorhynchus* from the subfamily. Furthermore, contrary to the provisional allocation by Livezey (1991), *Salvadorina* is not included in the Tadorninae.

Tribes of Anatinae.—Five modern tribes are recognized in this subfamily (Appendix 3), in which the order of all but the first is unresolved, hence the subfamily is annotated *sedis mutabilis* (Fig. 3, 4): Tribe Malacorhynchini, new taxon, comprising *Malacorhynchus* and *Salvadorina*; Tribe Anatini, *incertae sedis,* tentatively comprising three subtribes Cairineae, Nettapodeae, and Anateae (Livezey, 1991); Tribe Aythini (Livezey, in press *b*); Tribe Mergini (Livezey, 1995*b*); and Tribe Oxyurini (Livezey, 1995*c*). Generic composition of the Aythyini, Mergini, and Oxyurini remains unchanged from that proposed by Livezey (1986*a*), and the provisional generic composition of the Anatini advocated here follows that proposed by Livezey (1991). Provisional retention of the three subtribes of the Anatini recognized by Livezey (1991) is recommended, in part, to avoid the confusion that would stem from applying the tribal taxon "Cairinini," traditionally including nine genera and 13 species, to a restricted group comprising only the Cairineae (three genera, five species) and Nettapodeae (two genera, four species), and excluding *Plectropterus, Sarkidiornis, Amazonetta,* and *Callonetta.*

Biogeographical Patterns

Biogeographical patterns in this region of the phylogeny of Anseriformes are complicated by the broad but different distributional patterns shown by several taxa (e.g., Anateae, Aythyini, and Oxyurini). Furthermore, comparisons with the distributional limits of tribes given by Weller (1964*d*) are problematic because of important differences in the composition of tribes (especially Cairinini, Anatini) defined in this study and those used by Weller (1964*d*). In spite of these difficulties, the frequency of predominantly southern-hemisphere genera in these taxa (*Stictonetta, Plectropterus, Sarkidiornis,* most Tadornini, *Hymenolaimus, Tachyeres, Merganetta, Salvadorina, Malacorhynchus*), as well as the southern distributions of basal members of the Anatini (Livezey, 1991) and Oxyurini (Livezey, 1995*c*), corroborate the hypothesis of southern origins for the Stictonettinae, Tadorninae, and Anatinae. This inference is consistent with a larger hypothesis of a southern-hemispheric origin for the Anseriformes (Livezey, 1986*a,* 1989).

The sister-relationship inferred for *Merganetta* and *Tachyeres* (Fig. 1–11) is at least consistent with the Neotropical distributions of the genera (Delacour, 1954, 1959). Similarly, the distributional limits of another counterintuitive pair of genera inferred to be sister-groups, *Salvadorina* and *Malacorhynchus,* is geographically "parsimonious" given the Australasian distributions of the two genera (Delacour, 1959).

Several fossil taxa assignable to this region of the anseriform phylogeny also indicate the predominantly southern-hemisphere distributions of the member taxa. The peculiar genus *Euryanas finschi* from New Zealand (Van Beneden, 1875, 1876; Oliver, 1930, 1945) was most parsimoniously placed as the sister-group of the present ingroup exclusive of *Stictonetta* in an earlier, more-limited analysis (Livezey, 1989). Another subfossil endemic of New Zealand, *Pachyanas chathamica* (Oliver, 1955), also appears to belong to the Tadornini (unpublished study of material recently collected by P. Millener). Other fossil taxa assignable to the Tadornini include the Madagascan genera *Centrornis* (Andrews, 1897) and *Chenalopex* (Andrews, 1897; Brodkorb, 1964), and the Nearctic genera *Anabernicula* (Ross, 1935; Howard, 1946, 1964*a,* 1964*b*; Short, 1970) and *Brantadorna* (Howard, 1963).

Directions for Future Study

A number of aspects of anseriform phylogeny remain poorly understood, and a majority of these involve the relationships among the taxa analyzed in the present analysis (Fig. 1–11). This state of affairs is ironic, given that the original motivation for the earlier analysis (Livezey, 1986*a*), which formed the basis for this and other species-level studies, was the placement of the genus *Tachyeres* among the Tadorninae and Anatinae. This situation is particularly vexing in that these poorly resolved segments of the phylogeny of waterfowl include those among most tribes of the Anatinae, the largest subfamily in the order and one of particular importance for comparative studies (Sigurjónsdóttir, 1981; Faith, 1989; Scott and Clutton-Brock, 1989). Poor resolution, combined with a great diversity of physical and ecological characters among genera in the vicinity of the "tadornine–anatine divergence," rendered many ecomorphological parameters all but noncomparable in this study (Fig. 12 and associated text).

In order to resolve the phylogenetic relationships that remain resistant to analysis, characters (morphological, molecular, or behavioral) of intermediate evolutionary conservatism are needed. Characters of greatest utility would be those which are less conservative than those uniting the Tadorninae and Anatinae, but more conservative than those accumulating as autapomorphies in the present analysis (some of which are useful, however, as synapomophies for polytypic genera). Morphological systems deserving of particular attention in this regard are accessible only using anatomical (fluid-preserved) specimens, however, and therefore will not be useful for the placement of fossil taxa in this region of the anseriform phylogeny. These systems include the anatomical details of tracheal and syringeal myology and osteology, cranial and pelvic myology, pteryolography, and bucco–lingual integument.

ACKNOWLEDGMENTS

This research was supported by National Science Foundation grants BSR-8515523, BSR-9129545, and BSR-9396249, as well as grants from the National Museum of Natural History and the American Museum of Natural History. The hospitality of G. Mack and R. L. Zusi is much appreciated. In addition to access to specimens in the collections of Carnegie Museum of Natural History, I am grateful for loans and/or access to collections provided by the curatorial personnel of the following institutions: Division of Birds, National Museum of Natural History, Washington, D.C. (USNM); Department of Ornithology, American Museum of Natural History, New York, New York (AMNH); Division of Birds, Museum of Zoology, University of Michigan, Ann Arbor, Michigan (UMMZ); Division of Birds, Field Museum of Natural History, Chicago, Illinois (FMNH); Bird Group, Natural History Museum, Tring, Hertfordshire, United Kingdom (BMNH); Wildfowl and Wetlands Trust, Slimbridge, Gloucester, United Kingdom (WWT); Department of Ornithology, Royal Ontario Museum, Toronto, Ontario, Canada (ROM); Department of Ornithology, Australian Museum, Sydney, Australia (AUM); and Division of Ornithology, Natural History Museum, University of Kansas, Lawrence, Kansas (KUMNH). I thank M. Brown (Wildfowl and Wetlands Trust) for loans of natal and tracheal specimens. I thank P. S. Humphrey, P. C. Chu, and two anonymous referees for helpful criticisms of the manuscript.

LITERATURE CITED

ANDREWS, C. W. 1897. On some fossil remains of carinate birds from central Madagascar. Ibis, 39: 343–359.

ARCHIE, J. W. 1989*a*. A randomization test for phylogenetic information in systematic data. Systematic Zoology, 38:239–252.

———. 1989*b*. Homoplasy excess ratios: New indices for measuring levels of homoplasy in phylogenetic systematics and a critique of the consistency index. Systematic Zoology, 38:253–269.

———. 1990. Homoplasy excess statistics and retention indices: A reply to Farris. Systematic Zoology, 39:169–174.

ARCHIE, J. W., AND J. FELSENSTEIN. 1993. The number of evolutionary steps on random and minimum length trees for random evolutionary data. Theoretical Population Biology, 43:52–79.

BARRETT, M., M. J. DONOGHUE, AND E. SOBER. 1991. Against consensus. Systematic Zoology, 40: 486–493.

BARRIEL, V., AND P. TASSY. 1993. Characters, observations and steps: Comment on Lipscomb's "Parsimony, homology and the analysis of multistate characters." Cladistics, 9:223–232.

BAUMEL, J. J., AND L. M. WITMER. 1993. Osteologia. Pp. 45–132, *in* Handbook of Avian Anatomy: Nomina Anatomica Avium, 2nd edition (J. J. Baumel, A. S. King, J. E. Breazile, H. E. Evans, and J. C. Vanden Berge, eds.), Publication Number 23, Nuttall Ornithological Club, Cambridge, Massachusetts, xxiv + 779 pp.

BLEDSOE, A. H., AND R. J. RAIKOW. 1990. A quantitative assessment of congruence between molecular and nonmolecular estimates of phylogeny. Journal of Molecular Evolution, 30:247–259.

BOETTICHER, H. VON. 1942. Über die Einteilung der Familie der Entenvögel (Anatidae) in Unterfamilien und Sektionen. Zoologischer Anzeiger, 140:37–48.

———. 1952. Gänse- und Entenvögel aus aller Welt. Geest and Portig K.-G., Leipzig, Germany, 95 pp.

BONAPARTE, C. L. 1856. Conspectus Anserum Systematicus. Comptes Rendus des Séances de l'Académie des Sciences, 43:647–652.

BOTTJER, P. D. 1983. Systematic relationships among the Anatidae: An immunological study, with a history of anatid classification, and a system of classification. Unpublished Ph.D. dissert., Yale University, New Haven, Connecticut, ix + 324 pp.

BREMER, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. Evolution, 42:795–803.

———. 1994. Branch support and tree stability. Cladistics, 10:295–304.

BRODKORB, P. 1964. Catalogue of fossil birds: Part 2 (Anseriformes through Galliformes). Bulletin of the Florida State Museum (Biological Science), 8:195–335.

BROOKS, D. R., AND D. A. MCLENNAN. 1991. Phylogeny, Ecology, and Behavior: A Research Program in Comparative Biology. University of Chicago Press, Chicago, Illinois, xii + 434 pp.

BROOKS, D. R., R. T. O'GRADY, AND E. O. WILEY. 1986. A measure of the information content of phylogenetic trees, and its use as an optimality criterion. Systematic Zoology, 35:571–581.

BROWN, L. H., E. K. URBAN, AND K. NEWMAN. 1982. The Birds of Africa, Volume 1. Academic Press, London, United Kingdom, xiii + 521 pp.

BRUSH, A. H. 1976. Waterfowl feather proteins: Analysis of use in taxonomic studies. Journal of Zoology (London), 179:467–498.

CAMPBELL, A. J. 1899. On the trachea of the Freckled Duck of Australia (*Stictonetta nævosa*). Ibis, 41:362–363.

CARPENTER, J. M. 1988. Choosing among multiple equally parsimonious cladograms. Cladistics, 4: 291–296.

———. 1992. Random cladistics. Cladistics, 8:147–153.

CHIPPINDALE, P. T., AND J. J. WEINS. 1994. Weighting, partitioning, and combining characters in phylogenetic analysis. Systematic Biology, 43:278–287.

CLARK, A. 1980. Notes on the breeding biology of the Spur-winged Goose. Ostrich, 51:179–182.

CODDINGTON, J. A. 1988. Cladistic tests of adaptational hypotheses. Cladistics, 4:1–22.

———. 1994. The roles of homology and convergence in studies of adaptation. Pp. 53–78, *in* Phylogenetics and Ecology (P. Eggleton and R. I. Vane-Wright, eds.), Linnean Society Symposium 17, Academic Press, London, United Kingdom, x + 376 pp.

CONOVER, B. 1943. A study of the Torrent Ducks. Field Museum of Natural History Zoological Series, 24:345–356.

CORBIN, K. W., B. C. LIVEZEY, AND P. S. HUMPHREY. 1988. Genetic differentiation among the steamer-ducks (Anatidae: *Tachyeres*): An electrophoretic analysis. Condor, 90:773–781.

CRACRAFT, J. 1968. The lacrimal–ectethmoid bone complex in birds: A single character analysis. American Midland Naturalist, 80:316–359.

———. 1983. Species concepts and speciation analysis. Pp. 159–187, *in* Current Ornithology, Volume 1 (R. F. Johnston, ed.), Plenum Press, New York, New York, xvi + 425 pp.

———. 1987. DNA hybridization and avian phylogenetics. Pp. 47–96, *in* Evolutionary Biology, Volume 21 (M. K. Hecht, B. Wallace, and G. T. Prance, eds.), Plenum Press, New York, New York, xv + 434 pp.

———. 1988. Speciation and its ontology: The empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. Pp. 28–59, *in* Speciation and Its Consequences (D. Otte and J. A. Endler, eds.), Sinauer Associates, Sunderland, Massachusetts, xiii + 679 pp.

DAVIS, J. I. 1993. Character removal as a means for assessing stability of clades. Cladistics, 9:201–210.

DE PINNA, M. C. C. 1991. Concepts and tests of homology in the cladistic paradigm. Cladistics, 7: 367–394.

DE QUEIROZ, A., AND P. H. WIMBERGER. 1993. The usefulness of behavior for phylogeny estimation: Levels of homoplasy in behavioral and morphological characters. Evolution, 47:46–60.

DE QUEIROZ, K. 1985. The ontogenetic method for determining character polarity and its relevance to phylogenetic systematics. Systematic Zoology, 34:280–299.

DELACOUR, J. 1938. La sytématique des Anatidés et leurs mæurs. Pp. 225–242, *in* Proceedings of the Eighth International Ornithological Congress, Oxford, July 1934 (F. C. R. Jourdain, ed.), University Press, Oxford, United Kingdom, x + 761 pp.

———. 1954. The Waterfowl of the World, Volume 1. Country Life, London, United Kingdom, 284 pp.

———. 1956. The Waterfowl of the World, Volume 2. Country Life, London, United Kingdom, 232 pp.

———. 1959. The Waterfowl of the World, Volume 3. Country Life, London, United Kingdom, 270 pp.

———. 1964. Corrections and additions. Pp. 327–354, *in* The Waterfowl of the World, Volume 4 (J. Delacour, ed.), Country Life, London, United Kingdom, 364 pp.

DELACOUR, J., AND E. MAYR. 1945. The family Anatidae. Wilson Bulletin, 57:3–55.

———. 1946. Supplementary notes on the Family Anatidae. Wilson Bulletin, 58:104–110.

DONOGHUE, M. J., R. G. OLMSTEAD, J. F. SMITH, AND J. D. PALMER. 1992. The importance of fossils in phylogeny reconstuction. Annual Review of Ecology and Systematics, 20:431–460.

DUNNING, J. B., JR. 1993. CRC Handbook of avian body masses. CRC Press, Boca Raton, Florida, 371 pp.

EADIE, J. MCA., F. P. KEHOE, AND T. D. NUDDS. 1988. Pre-hatch and post-hatch brood amalgamation in North American Anatidae: A review of hypotheses. Canadian Journal of Zoology, 66:1709–1721.

EDKINS, E., AND I. A. HANSEN. 1972. Wax esters secreted by the uropygial glands of some Australian waterfowl, including the Magpie Goose. Comparative Biochemistry and Physiology (Series B), 41:105–112.

ELDRIDGE, J. L. 1979. Display inventory of the Torrent Duck. Wildfowl, 30:5–15.

———. 1985. Display inventory of the Blue Duck. Wildfowl, 36:109–121.

———. 1986*a*. Observations on a pair of Torrent Ducks. Wildfowl, 37:113–122.

———. 1986*b*. Territoriality in a river specialist: The Blue Duck. Wildfowl, 37:123–135.

ELDREDGE, N., AND J. CRACRAFT. 1980. Phylogenetic Patterns and the Evolutionary Process: Method and Theory in Comparative Biology. Columbia University Press, New York, New York, viii + 349 pp.

EYTON, T. C. 1838. A Monograph on the Anatidae, or Duck Tribe. Longmans, London, United Kingdom, x + 178 pp.

FAITH, D. P. 1989. Homoplasy as pattern: Multivariate analysis of morphological convergence in anseriforms. Cladistics, 5:235–258.

FAITH, D. P., AND P. S. CRANSTON. 1991. Could a cladogram this short have arisen by chance alone?: On permutation tests for cladistic structure. Cladistics, 7:1–28.

FARRIS, J. S. 1969. A successive approximations approach to character weighting. Systematic Zoology, 18:374–385.

———. 1977. Phylogenetic analysis under Dollo's Law. Systematic Zoology, 26:77–88.

———. 1989. The retention index and the rescaled consistency index. Cladistics, 5:417–419.

FELSENSTEIN, J. 1978. Cases in which parsimony or compatibility methods will be positively misleading. Systematic Zoology, 27:401–410.

———. 1985*a*. Confidence limits on phylogenies: An approach using the bootstrap. Evolution, 39: 783–791.

———. 1985*b*. Phylogenies and the comparative method. American Naturalist, 125:1–15.

FRITH, H. J. 1955. The downy ducklings of the Pink-eared and White-eyed ducks. Emu, 55:310–312.

———. 1964*a*. Taxonomic relationship of *Stictonetta naevosa* (Gould). Nature, 202:1352–1353.

———. 1964*b*. The downy young of the Freckled Duck *Stictonetta naevosa*. Emu, 64:42–47.

———. 1965. Ecology of the Freckled Duck, *Stictonetta naevosa* (Gould). Commonwealth Science and Industrial Research Organization, Wildlife Research, 10:125–139.

———. 1967. Waterfowl in Australia. East–West Center Press, Honolulu, Hawaii, xxi + 328 pp.

FROST, D. R., AND D. M. HILLIS. 1990. Species in concept and practice: Herpetological applications. Herpetologica, 46:87–104.

FROST, D. R., AND A. G. KLUGE. 1994. A consideration of epistemology in systematic biology, with special reference to species. Cladistics, 10:259–294.

FULLAGAR, P. J., C. C. DAVEY, AND D. K. RUSHTON. 1990. Social behaviour of the Freckled Duck *Stictonetta naevosa* with particular reference to the Axlegrind. Wildfowl, 41:53–61.

GARROD, A. H. 1875. On the form of the lower larynx in certain species of ducks. Proceedings of the Zoological Society of London, 1875:279–284.

GRAFEN, A. 1989. The phylogenetic regression. Philosophical Transactions of the Royal Society of London (Series B), 326:119–157.

———. 1992. The uniqueness of the phylogenetic regression. Journal of Theoretical Biology, 156: 405–423.

GRAY, G. R. 1841. A List of the Genera of Birds, With Their Synonyms, and an Indication of the Typical Species of Each Genus, 2nd edition. Richard and John E. Taylor, London, United Kingdom, xii + 115 pp.

———. 1871. Hand-list of Genera and Species of Birds, Distinguishing Those Contained in the British Museum. Part III. Struthiones, Grallæ, and Anseres, with Indices of Generic and Specific Names. British Museum (Natural History), London, United Kingdom, xi + 350 pp.

HALL, B. K. (ed.). 1994. Homology: The Hierarchical Basis of Comparative Biology. Academic Press, San Diego, California, xvi + 483 pp.

HALLSTROM, E. 1956. Breeding of Salvadori's Duck (*Anas waigiuensis*) in New Guinea. Avicultural Magazine, 62:89.

HARVEY, P. H., AND M. D. PAGEL. 1991. The Comparative Method in Evolutionary Biology. Oxford University Press, Oxford, United Kingdom, viii + 239 pp.

HAUSER, D. L., AND W. PRESCH. 1991. The effect of ordered characters on phylogenetic reconstruction. Cladistics, 7:243–265.

HENDY, M. D., AND D. PENNY. 1982. Branch and bound algorithms to determine minimal evolutionary trees. Mathematical Bioscience, 59:277–290.

HENNIG, W. 1966. Phylogenetic Systematics. University of Illinois Press, Urbana, Illinois, 263 pp.

HILLIS, D. M. 1987. Molecular versus morphological approaches to systematics. Annual Review of Ecology and Systematics, 18:23–42.

———. 1991. Discriminating between phylogenetic signal and random noise in DNA sequences. Pp. 278–294, *in* Phylogenetic Analysis of DNA Sequences (M. M. Miyamoto and J. Cracraft, eds.), Oxford University Press, Oxford, United Kingdom, x + 358 pp.

———. 1995. Approaches for assessing phylogenetic accuracy. Systematic Biology, 44:3–16.

HILLIS, D. M., AND J. J. BULL. 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. Systematic Biology, 42:182–192.

HILLIS, D. M., AND J. P. HUELSENBECK. 1992. Signal, noise and reliability in molecular phylogenetic analysis. Journal of Heredity, 83:189–195.

HOBBS, J. N. 1957. Notes on the Pink-eared Duck. Emu, 57:265–268.

HOUDE, P. 1987. Critical evaluation of DNA hybridization studies in avian systematics. Auk, 104: 17–32.

HOWARD, H. 1946. A review of the Pleistocene birds of Fossil Lake, Oregon. Carnegie Institute of Washington Contributions to Paleontology, 551:141–195.

———. 1963. Fossil birds from the Anza-Borrego Desert. Los Angeles County Museum Contributions in Science, 73:1–33.

———. 1964*a*. Fossil Anseriformes. Pp. 233–326, *in* The Waterfowl of the World, Volume 4 (J. Delacour, ed.), Country Life, London, United Kingdom, 364 pp.

———. 1964*b*. A new species of the "Pigmy Goose," *Anabernicula,* from the Oregon Pleistocene, with a discussion of the genus. American Museum Novitates, 2200:1–14.

HOYO, J. DEL, A. ELLIOTT, AND J. SARGATAL (eds.). 1992. Handbook of the Birds of the World, Volume 1. Lynx Editions, Barcelona, Spain, 696 pp.

HUELSENBECK, J. P. 1991. Tree-length distribution skewness: An indicator of phylogenetic information. Systematic Zoology, 40:257–270.

———. 1995. Performance of phylogenetic methods in simulation. Systematic Biology, 44:17–48.

HUELSENBECK, J. P., AND D. M. HILLIS. 1993. Success of phylogenetic methods in the four-taxon case. Systematic Biology, 42:247–264.

HUMPHREY, P. S., AND G. A. CLARK, JR. 1964. The anatomy of waterfowl. Pp. 167–232, *in* The Waterfowl of the World, Volume 4 (J. Delacour, ed.), Country Life, London, United Kingdom, 364 pp.

HUMPHREY, P. S., AND B. C. LIVEZEY. 1982. Molts and plumages of Flying Steamer-Ducks (*Tachyeres patachonicus*). University of Kansas, Museum of Natural History Occasional Papers, 103:1–30.

———. 1985. Nest, eggs, and downy young of the White-headed Flightless Steamer-Duck. Pp. 949–954, *in* Neotropical Ornithology (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, eds.), Ornithological Monograph 36, American Ornithologists' Union, Washington, D.C., 1041 pp.

INTERNATIONAL COMMISSION OF ZOOLOGICAL NOMENCLATURE. 1985. International Code of Zoological Nomenclature, 3rd edition. International Trust for Zoological Nomenclature, London, United Kingdom, xx + 338 pp.

JACOB, J. 1982. Integumentlipide—ihre chemische Struktur und ihre Bedeutung als systematisches Merkmal in der Zoologie. Funktionelle Biologie und Medizin, 1:83–90.

JACOB, J., AND A. GLASER. 1975. Chemotaxonomy of Anseriformes. Biochemical Systematics and Ecology, 2:215–220.

JACOB, J., AND H. HOERSCHELMANN. 1993. Ein Beitrag zur Chemotaxonomie der Entenvögel (Aves: Anseriformes). Mitteilungen aus der Hamburgischen Zoologischen Museum und Institut, 90:379–400.

JOHNSGARD, P. A. 1960*a*. Comparative behavior of the Anatidae and its evolutionary implications. Wildfowl, 11:31–45.

———. 1960*b*. Hybridization in the Anatidae and its taxonomic implications. Condor, 62:25–33.

———. 1961*a*. The taxonomy of the Anatidae—a behavioural analysis. Ibis, 103a:71–85.

———. 1961*b*. Tracheal anatomy of the Anatidae and its taxonomic significance. Wildfowl, 12: 58–69.

———. 1962. Evolutionary trends in the behaviour and morphology of the Anatidae. Wildfowl, 13: 130–148.

———. 1963. Behavioral isolating mechanisms in the family Anatidae. Pp. 531–543, *in* Proceedings XIII International Ornithological Congress, Volume 1 (C. G. Sibley, ed.), American Ornithologists' Union, Washington, D.C., xiv + 610 pp.

———. 1965*a*. Handbook of Waterfowl Behavior. Constable, London, United Kingdom, xiv + 378 pp.

———. 1965*b*. Observations on some aberrant Australian Anatidae. Wildfowl, 16:73–83.

———. 1966. The biology and relationships of the Torrent Duck. Wildfowl, 17:66–74.

———. 1971. Observations on sound production in the Anatidae. Wildfowl, 22:46–59.

———. 1978. Ducks, Geese, and Swans of the World. University of Nebraska Press, Lincoln, Nebraska, xxiii + 404 pp.

———. 1979. Order Anseriformes. Pp. 425–506, *in* Checklist of Birds of the World, Volume 1, 2nd edition (E. Mayr and C. W. Cottrell, eds.), Museum of Comparative Zoology, Cambridge, Massachusetts, xvii + 547 pp.

JOHNSGARD, P. A., AND J. KEAR. 1968. A review of parental carrying of young by waterfowl. Living Bird, 7:89–102.

JOHNSON, A. W. 1963. Notes on the distribution, reproduction and display of the Andean Torrent Duck *Merganetta armata*. Ibis, 105:114–116.

KÄLLERSJÖ, M., J. S. FARRIS, A. G. KLUGE, AND C. BOLT. 1992. Skewness and permutation. Cladistics, 8:275–287.

KEAR, J. 1970. The adaptive radiation of parental care in waterfowl. Pp. 357–392, *in* Social Behaviour in Birds and Mammals (J. H. Crook, ed.), Academic Press, New York, New York, xl + 492 pp.

———. 1972. The Blue Duck of New Zealand. Living Bird, 11:175–192.

———. 1975. Salvadori's Duck of New Guinea. Wildfowl, 26:104–111.

KEAR, J., AND P. J. K. BURTON. 1971. The food and feeding apparatus of the Blue Duck *Hymenolaimus*. Ibis, 113:483–493.

KEAR, J., AND R. K. MURTON. 1973. The systematic status of the Cape Barren Goose as judged by its photo-responses. Wildfowl, 24:141–143.

KEAR, J., AND T. H. STEEL. 1971. Aspects of social behaviour in the Blue Duck. Notornis, 18:187–198.

KESSLER, L. G., AND J. C. AVISE. 1984. Systematic relationships among waterfowl (Anatidae) inferred from restriction endonuclease analysis of mitochondrial DNA. Systematic Zoology, 33:370–380.

KING, A. S. 1989. Functional anatomy of the syrinx. Pp. 105–192, *in* Form and Function in Birds, Volume 4 (A. S. King and J. McLelland, eds.), Academic Press, London, United Kingdom, xiii + 591 pp.

———. 1993. Apparatus respiratorius [systema respiratorium]. Pp. 257–299, *in* Handbook of Avian Anatomy: Nomina Anatomica Avium, 2nd edition (J. J. Baumel, A. S. King, A. M. Lucas, J. E. Breazile, and H. E. Evans, eds.), Nuttall Ornithological Club, Cambridge, Massachusetts, xxiv + 779 pp.

KLUGE, A. G., AND J. S. FARRIS. 1969. Quantitative phyletics and the evolution of anurans. Systematic Zoology, 18:1–32.

LIPSCOMB, D. L. 1992. Parsimony, homology and the analysis of multistate characters. Cladistics, 8: 45–65.

LIVEZEY, B. C. 1986*a*. A phylogenetic analysis of Recent anseriform genera using morphological characters. Auk, 103:737–754.

———. 1986*b*. Phylogeny and historical biogeography of steamer-ducks (Anatidae: *Tachyeres*). Systematic Zoology, 35:458–469.

———. 1988. Feeding morphology, foraging behavior, and foods of steamer-ducks (Anatidae: *Tachyeres*). University of Kansas, Museum of Natural History Occasional Papers, 126:1–41.

———. 1989. Phylogenetic relationships of several subfossil Anseriformes of New Zealand. University of Kansas, Museum of Natural History Occasional Papers, 128:1–25.

———. 1991. A phylogenetic analysis and classification of Recent dabbling ducks (Tribe Anatini) based on comparative morphology. Auk, 108:471–507.

———. 1995*a*. A phylogenetic analysis of the whistling and White-backed ducks (Anatidae: Dendrocygninae) using morphological characters. Annals of Carnegie Museum, 64:65–97.

———. 1995*b*. Phylogeny and evolutionary ecology of modern seaducks (Anatidae: Mergini). Condor 97:233–255.

———. 1995*c*. Phylogeny and comparative ecology of stiff-tailed ducks (Anatidae: Oxyurini). Wilson Bulletin, 107:214–234.

———. In press *a*. A phylogenetic analysis of modern sheldgeese and shelducks (Anatidae: Tadornini). Ibis.

———. In press *b*. A phylogenetic analysis of modern pochards (Anatidae: Aythyini). Auk.

———. In press *c*. A phylogenetic analysis of the geese and swans (Anseriformes: Anserinae), including selected fossil species. Systematic Biology.

LIVEZEY, B. C., AND P. S. HUMPHREY. 1984*a*. Sexual dimorphism in continental steamer-ducks. Condor, 86:368–377.

———. 1984*b*. Diving behaviour of steamer ducks *Tachyeres* spp. Ibis, 126:257–260.

———. 1985. Territoriality and interspecific aggression in steamer-ducks. Condor, 87:154–157.

———. 1986. Flightlessness in steamer-ducks (Anatidae: *Tachyeres*): Its morphological bases and probable evolution. Evolution, 40:540–558.

———. 1992. Taxonomy and identification of steamer-ducks (Anatidae: *Tachyeres*). University of Kansas, Museum of Natural History Monographs, 8:1–125.

LIVEZEY, B. C., AND L. D. MARTIN. 1988. The systematic position of the Miocene anatid *Anas*[?] *blanchardi* Milne-Edwards. Journal of Vertebrate Paleontology, 8:196–211.

LIVEZEY, B. C., J. JACOB, AND P. S. HUMPHREY. 1986. Biochemical composition of secretions from uropygial glands of steamer-ducks. Biochemical Systematics and Ecology, 14:445–450.

MABEE, P. M. 1989. An empirical rejection of the ontogenetic polarity criterion. Cladistics, 5:409–416.

MADDISON, D. R. 1991. The discovery and importance of multiple islands of most-parsimonious trees. Systematic Zoology, 40:315–328.

MADDISON, W. P. 1989. Reconstructing character evolution on polytomous cladograms. Cladistics, 5: 365–377.

MADDISON, W. P., AND D. R. MADDISON. 1992. MacClade: Analysis of Phylogeny and Character Evolution, Version 3. Sinauer Associates, Sunderland, Massachusetts, xi + 398 pp.

MADDISON, W. P., M. J. DONOGHUE, AND D. R. MADDISON. 1984. Outgroup analysis and parsimony. Systematic Zoology, 33:83–103.

MADGE, S. C., AND H. BURN. 1988. Waterfowl: An Identification Guide to the Ducks, Geese and Swans of the World. Houghton Mifflin, Boston, Massachusetts, 298 pp.

MADSEN, C. S., K. P. MCHUGH, AND S. R. DE KLOET. 1988. A partial classification of waterfowl (Anatidae) based on single-copy DNA. Auk, 105:452–459.

MARCHANT, S., AND P. J. HIGGINS (COORDS.). 1990. Handbook of Australian, New Zealand and Antarctic Birds, Volume 1, Part B. Oxford University Press, Melbourne, Australia, pp. 737–1400.

MARGUSH, T., AND F. R. MCMORRIS. 1981. Consensus n-trees. Bulletin of Mathematical Biology, 43: 239–244.

MAYR, E. 1931. Anatomie und systematischen Stellung der Salvaldori-Ente (*Salvadorina waigiuensis* Rothsch. & Hartert). Ornithologische Monatsberichte, 39:69–70.

MCKITRICK, M. C., AND R. M. ZINK. 1988. Species concepts in ornithology. Condor, 90:1–14.

MCNEIL, R., P. DRAPEAU, AND J. D. GOSS-CUSTARD. 1992. The occurrence and adaptive significance of nocturnal habits in waterfowl. Biological Review, 67:381–419.

MEIER, R., P. KORES, AND S. DARWIN. 1991. Homoplasy slope ratio: A better measurement of observed homoplasy in cladistic analyses. Systematic Zoology, 40:74–88.

MICKEVICH, M. F. 1978. Taxonomic congruence. Systematic Zoology, 27:35–45.

MICKEVICH, M. F., AND M. S. JOHNSON. 1976. Congruence between morphological and allozyme data in evolutionary inference and character evolution. Systematic Zoology, 30:351–370.

MICKEVICH, M. F., AND D. LIPSCOMB. 1991. Parsimony and the choice between different transformations for the same character set. Cladistics, 7:111–139.

MICKEVICH, M. F., AND S. J. WELLER. 1990. Evolutionary character analysis: Tracing character change on a cladogram. Cladistics, 6:137–170.

MIYAMOTO, M. M., AND W. M. FITCH. 1995. Testing species phylogenies and phylogenetic methods with congruence. Systematic Biology, 44:64–76.

MLÍKOVSKÝ, J. 1989. Note on the osteology and taxonomic position of Salvadori's Duck *Salvadorina waigiuensis* (Aves: Anseridae [Anatidae]). Bulletin of the British Ornithologists' Club, 109:22–25.

MOFFETT, G. M., JR. 1970. A study of nesting Torrent Ducks in the Andes. Living Bird, 9:5–28.

MÖLLER, W. 1969. Vergleichend-morphologische Untersuchungen an Schädeln höckertragender Anatiden mit einem Beitrag zur Mechanik des Anatidenschädels II. Gegenbaurs Morphologisches Jahrbuch, 115:161–200.

MORITZ, C., AND D. M. HILLIS. 1990. Molecular systematics: Context and controversies. Pp. 1–10, *in*

Molecular Systematics (D. M. Hillis and C. Moritz, eds.), Sinauer Associates, Sunderland, Massachusetts, xvi + 588 pp.

MOYNIHAN, M. 1958. Notes on the behavior of the Flying Steamer Duck. Auk, 75:183–202.

NEFF, N. A. 1986. A rational basis for a priori character weighting. Systematic Zoology, 35:110–123.

NIETHAMMER, G. 1952. Zur Anatomie und systematischen Stellung der Sturzback-Ente *Merganetta armata*. Journal für Ornithologie, 93:357–360.

———. 1953. Zur Vogelwelt Boliviens. Bonner Zoologische Beiträge, 4:195–303.

NIXON, K. C., AND J. I. DAVIS. 1991. Polymorphic taxa, missing values and cladistic analysis. Cladistics, 7:233–241.

NUMACHI, K., M. WATADA, R. KAKIZAWA, N. KURODA, AND S. UTIDA. 1983. Evolutionary genetics of the Anatidae. Tori, 32:63–74.

OLIVER, W. R. B. 1930. New Zealand Birds, 1st edition. A. H. & A. W. Reed, Wellington, New Zealand, viii + 541 pp.

———. 1945. Avian evolution in New Zealand and Australia. Emu, 45:119–152.

———. 1955. New Zealand Birds, 2nd edition. A. W. Reed, Wellington, New Zealand, 661 pp.

OLSON, S. L. 1977. Notes on subfossil Anatidae from New Zealand, including a new species of Pink-eared Duck (*Malacorhynchus*). Emu, 77:132–135.

———. 1985. The fossil record of birds. Pp. 79–238, *in* Avian Biology, Volume 8 (D. S. Farner, J. R. King, and K. C. Parkes, eds.),Academic Press, New York, New York, xxiii + 256 pp.

OLSON, S. L., AND A. FEDUCCIA. 1980. *Presbyornis* and the origin of the Anseriformes (Aves: Charadriomorphae). Smithsonian Contributions to Zoology, 323:1–24.

OMLAND, K. E. 1994. Character congruence between a molecular and a morphological phylogeny for dabbling ducks (*Anas*). Systematic Biology, 43:369–386.

PAGE, R. D. M. 1993. On islands of trees and efficacy of different methods of branch swapping in finding most-parsimonious trees. Systematic Biology, 42:200–209.

PAGEL, M. 1994. Detecting correlated evolution on phylogenies: A general method for the comparative analysis of discrete characters. Proceedings of the Royal Society of London, 255:37–45.

PAGEL, M. D., AND P. H. HARVEY. 1988. Recent developments in the analysis of comparative data. Quarterly Review of Biology, 63:413–440.

PARKES, K. C. 1978. A guide to forming and capitalizing compound names of birds in English. Auk, 95:324–326.

PATTON, J. C., AND J. C. AVISE. 1985. Evolutionary genetics of birds IV: Rates of protein divergence in waterfowl (Anatidae). Genetica, 68:129–143.

PENGELLY, W. J., AND J. KEAR. 1970. The hand rearing of a young Blue Duck. Wildfowl, 21:115–121.

PENNY, D., P. J. LOCKHART, M. A. STEEL, AND M. D. HENDY. 1994. The role of models in reconstructing evolutionary trees. Pp. 211–230, *in* Models in Phylogeny Reconstruction (R. W. Scotland, D. J. Siebert, and D. M. Williams, eds.), Clarendon Press, Oxford, United Kingdom, xi + 360 pp.

PETERS, J. L. 1931. Check-list of Birds of the World, Volume 1. Harvard University Press, Cambridge, Massachusetts, xviii + 345 pp.

PHILLIPS, J. C. 1922. A Natural History of the Ducks, Volume 1. Houghton Mifflin, Boston, Massachusetts, x + 264 pp.

———. 1923. A Natural History of the Ducks, Volume 2. Houghton Mifflin, Boston, Massachusetts, xii + 409 pp.

———. 1925. A Natural History of the Ducks, Volume 3. Houghton Mifflin, Boston, Massachusetts, ix + 383 pp.

———. 1926. A Natural History of the Ducks, Volume 4. Houghton Mifflin, Boston, Massachusetts, ix + 489 pp.

PLATNICK, N. I., C. E. GRISWOLD, AND J. A. CODDINGTON. 1991. On missing entries in cladistic analysis. Cladistics, 7:337–343.

POGUE, M. G., AND M. F. MICKEVICH. 1990. Character definitions and character state delineations: The bête noire of phylogenetic inference. Cladistics, 6:319–361.

RAIKOW, R. J. 1970. The function and evolution of the supraorbital process in ducks. Auk, 87:568–572.

RAND, A. L. 1954. On the spurs on birds' wings. Wilson Bulletin, 66:127–134.

ROHWER, F. C. 1988. Inter- and intraspecific relationships between egg size and clutch size in waterfowl. Auk, 105:161–176.

ROHWER, F. C., AND S. FREEMAN. 1989. The distribution of conspecific nest parasitism in birds. Canadian Journal of Zoology, 67:239–253.

ROSS, R. C. 1935. A new genus and species of pigmy goose from the McKittrick Pleistocene. Transactions of San Diego Society of Natural History, 8:107–114.

ROTHSCHILD, W. 1895. On *Salvadorina waigiuensis* Rothsch. & Hartert. Novitates Zoologicae, 2:22.

SALVADORI, T. 1895. Catalogue of the Chenomorphæ (Palamedeæ, Phoenicopteri, Anseres), Crypturi and Ratitæ in the Collection of the British Museum. Longmans, London, United Kingdom, xv + 636 pp.

SANDERSON, M. J. 1989. Confidence limits on phylogenies: The bootstrap revisited. Cladistics, 5:113–129.

———. 1993. Reversibility in evolution: A maximum likelihood approach to character gain/loss bias in phylogenies. Evolution, 47:236–252.

SANDERSON, M. J., AND M. J. DONOGHUE. 1989. Patterns of variation in levels of homoplasy. Evolution, 43:1781–1795.

SARICH, V. M., C. W. SCHMID, AND J. MARKS. 1989. DNA hybridization as a guide to phylogenies: A critical analysis. Cladistics, 5:3–32.

SCHERER, S., AND T. HILSBERG. 1982. Hybridisierung und Verwandtschaftsgrade innerhalb der Anatidae—eine systematische und evolutionstheoretische Betrachtung. Journal für Ornithologie, 123: 357–380.

SCHERER, S., AND C. SONTAG. 1986. Zur molekularen Taxonomie und Evolution der Anatidae. Zeitschrift für Zoologische Systematik und Evolutionforschung, 24:1–19.

SCHÖNWETTER, M. 1961. Handbuch der Oologie, Part 3. Akademie Verlag, Berlin, Germany, pp. 129–192.

SCLATER, P. L. 1880. List of the certainly known species of Anatidæ, with notes on such as have been introduced into the zoological gardens of Europe, and remarks on their distribution. Proceedings of the Zoological Society of London, 1880:496–536.

SCOTT, D. K., AND T. H. CLUTTON-BROCK. 1989. Mating systems, parasites and plumage dimorphism in waterfowl. Behavioral Ecology and Sociobiology, 26:261–273.

SCOTT, P. 1954. Behaviour of the Bolivian Torrent Duck. Wildfowl, 6:69–72.

SHORT, L. L. 1970. Mid-Pleistocene birds from western Nebraska, including a new species of sheldgoose. Condor, 72:147–152.

SHUFELDT, R. W. 1909. Osteology of Birds. New York State Museum Bulletin 130. State University of New York, Albany, New York, 381 pp.

SIBLEY, C. G. 1957. The evolutionary and taxonomic significance of sexual dimorphism and hybridization in birds. Condor, 59:166–191.

SIBLEY, C. G., AND J. E. AHLQUIST. 1972. A comparative study of the egg white proteins of nonpasserine birds. Peabody Museum of Natural History Bulletin, 39:1–276.

———. 1990. Phylogeny and Classification of Birds: A Study in Molecular Evolution. Yale University Press, New Haven, Connecticut, xxiii + 976 pp.

SIBLEY, C. G., AND B. L. MONROE, JR. 1990. Distribution and Taxonomy of Birds of the World. Yale University Press, New Haven, Connecticut, xxiv + 1111 pp.

SIBLEY, C. G., J. E. AHLQUIST, AND B. L. MONROE, JR. 1988. A classification of the living birds of the world based on DNA–DNA hybridization studies. Auk, 105:409–423.

SIEGFRIED, W. R. 1979. Social behaviour of the African Comb Duck. Living Bird, 17:85–104.

SIGURJÓNSDÓTTIR, H. 1981. The evolution of sexual size dimorphism in gamebirds, waterfowl and raptors. Ornis Scandinavica, 12:249–260.

SLOWINSKI, J. B. 1993. "Unordered" versus "ordered" characters. Systematic Biology, 42:155–165.

SOKAL, R. R., AND F. J. ROHLF. 1981. Taxonomic congruence in the Leptopodomorpha re-examined. Systematic Zoology, 30:309–325.

SPRINGER, M., AND C. KRAJEWSKI. 1989. DNA hybridization in animal taxonomy: A critique from first principles. Quarterly Review of Biology, 64:269–318.

SWOFFORD, D. L. 1991. When are phylogeny estimates from molecular and morphological data incongruent? Pp. 295–333, *in* Phylogenetic Analysis of DNA Sequences (M. M. Miyamoto and J. Cracraft, eds.), Oxford University Press, New York, New York, xi + 358 pp.

———. 1993. PAUP: Phylogenetic Analysis Using Parsimony. Version 3.1. Laboratory of Molecular Systematics, Smithsonian Institution, Washington, D.C., vi + 257 pp.

TODD, F. S. 1979. Waterfowl: Ducks, Geese and Swans of the World. Harcourt-Brace Jovanovich, New York, New York, x + 399 pp.

TRIGGS, S., M. WILLIAMS, S. MARSHALL, AND G. CHAMBERS. 1991. Genetic relationships within a population of Blue Duck *Hymenolaimus malacorhynchos.* Wildfowl, 42:87–93.

TRIGGS, S. J., M. J. WILLIAMS, S. J. MARSHALL, AND G. K. CHAMBERS. 1992. Genetic structure of Blue Duck (*Hymenolaimus malacorhynchos*) populations revealed by DNA fingerprinting. Auk, 109: 80–89.

TYLER, C. 1964. A study of the egg shells of the Anatidae. Proceedings of the Zoological Society of London, 142:547–583.

VAN BENEDEN, P. J. 1875. Un oiseau fossile nouveau des cavernes de la Nouvelle Zélande. Annales de la Société Geologie de Belgique, 2:123–130.

———. 1876. A new fossil bird, *Anas finschi,* from the Earnscleaugh Caves, Otago, New Zealand. Transactions of the New Zealand Institute, 9:599–602.

VELTMAN, C. J., AND M. WILLIAMS. 1990. Diurnal use of time and space by breeding Blue Ducks. Wildfowl, 41:62–74.

VERHEYEN, R. 1953. Contribution à l'ostéologie et à la systématique des Anseriformes. Gerfaut, 43 (Supplement):373–497.

———. 1955. La systématique des Ansériformes basée sur l'ostéologie comparée. Institut Royal des Sciences Naturelles de Belgique Bulletin, 31(35–38):1–72.

WARHAM, J. 1959. The nesting of the Pink-eared Duck. Wildfowl, 9:118–127.

WATROUS, L. E., AND Q. D. WHEELER. 1981. The out-group comparison method of character analysis. Systematic Zoology, 30:1–11.

WELLER, M. W. 1964*a*. General habits. Pp. 15–34, *in* The Waterfowl of the World, Volume 4 (J. Delacour, ed.), Country Life, London, United Kingdom, 364 pp.

———. 1964*b*. Ecology. Pp. 80–107, *in* The Waterfowl of the World, Volume 4 (J. Delacour, ed.), Country Life, London, United Kingdom, 364 pp.

———. 1964*c*. The reproductive cycle. Pp. 35–79, *in* The Waterfowl of the World, Volume 4 (J. Delacour, ed.), Country Life, London, United Kingdom, 364 pp.

———. 1964*d*. Distribution and species relationships. Pp. 108–120, *in* The Waterfowl of the World, Volume 4 (J. Delacour, ed.), Country Life, London, United Kingdom, 364 pp.

———. 1968. Plumages and wing spurs of Torrent Ducks *Merganetta armata.* Wildfowl, 19:33–40.

———. 1976. Ecology and behaviour of steamer ducks. Wildfowl, 27:45–53.

WHEELER, Q. D. 1986. Character weighting and cladistic analysis. Systematic Zoology, 35:102–109.

———. 1990. Ontogeny and character phylogeny. Cladistics, 6:225–268.

WILEY, E. O. 1978. The evolutionary species concept reconsidered. Systematic Zoology, 27:17–26.

———. 1979. An annotated Linnaean hierarchy, with comments on natural taxa and competing systems. Systematic Zoology, 28:308–337.

———. 1981. Phylogenetics: The Theory and Practice of Phylogenetic Systematics. J. Wiley & Sons, New York, New York, xv + 439 pp.

WILEY, E. O., D. SIEGEL-CAUSEY, D. R. BROOKS, AND V. A. FUNK. 1991. The compleat cladist. University of Kansas Museum of Natural History Special Publication, 19:1–158.

WILKINSON, M. 1992. Ordered versus unordered characters. Cladistics, 8:375–385.

WILLIAMS, D. M., R. W. SCOTLAND, AND S. BLACKMORE. 1990. Is there a direct ontogenetic criterion in systematics? Biological Journal of the Linnean Society, 39:99–108.

WILLIAMS, M. 1991. Social and demographic characteristics of Blue Duck *Hymenolaimus malacorhynchos.* Wildfowl, 42:65–86.

WILSON, R. T., AND M. P. WILSON. 1980. Notes sur la nidification du Canard casqué (*Sarkidiornis melanotos*) en zone soudano-sahélienne. Oiseau, 50:117–124.

WOLTERS, H. E. 1976. Die Vogelarten der Erde, Part 2. Paul Parey, Hamburg and Berlin, Germany, pp. 81–160.

WOOLFENDEN, G. E. 1961. Postcranial osteology of the waterfowl. Florida State Museum Bulletin (Biological Science), 6:1–129.

WORTHY, T. H. 1995. Descriptions of some post-cranial bones of *Malacorhynchus scarletti,* a large, extinct Pink-eared Duck from New Zealand. Emu, 95:13–22.

WRIGHT, J. K. 1965. Observations of behavior of the Andean Torrent Duck. Condor, 67:535.

YARRELL, W. 1827. Observations on the tracheæ of birds; with descriptions and representations of several not hitherto figured. Transactions of the Linnean Society of London, 15:378–391.

APPENDIX 1

Character Descriptions

Characters are numbered continuously through skeletal, tracheal, natal, and definitive subgroups. Characters for which polarity remains undetermined are indicated by asterisks. Consistency indices (CI) listed are those associated with trees derived under equal weighting of characters; ranges of indices are given for those characters in which CIs varied among equally parsimonious trees.

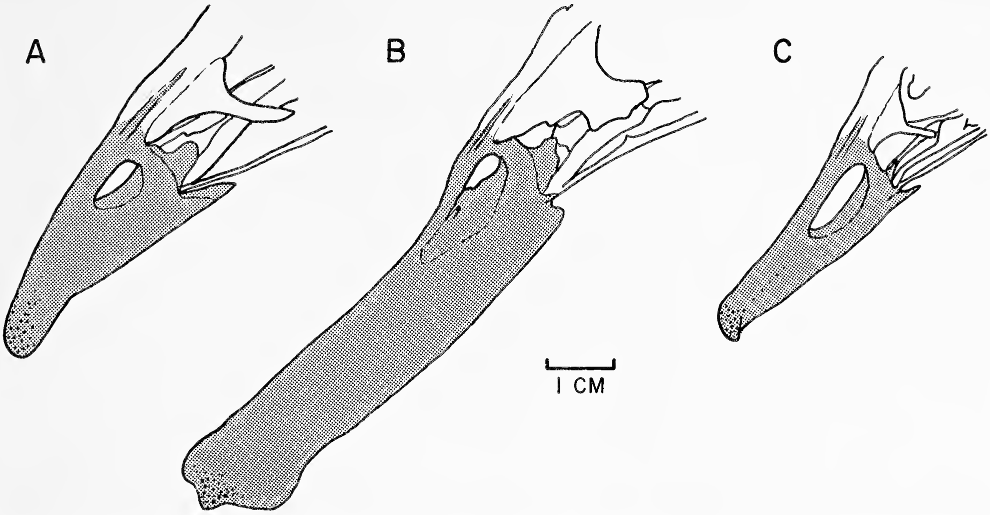


Fig. 14.—Maxillae of selected genera of Anatidae, laterodorsal views: A—*Hymenolaimus malacorhynchos* (KUMNH 55871), B—*Malacorhynchus membranaceus* (UMMZ 204438), C—*Merganetta* (*a.*) *armata* (UMMZ 153796).

Skeleton.—Those adapted from Livezey (1986*a*) are revised to include only relevant states and to assume local polarity. Synapomorphies for genera within subtribes of Anatini from Livezey (1991), as well as tribal synapomorphies for Aythyini (Livezey, in press *b*), Mergini (Livezey, 1995*a*), and Oxyurini (Livezey, 1995*b*), are not included. Characters 15, 33, and 61 from Livezey (1986*a*), and character 156 from Livezey (1991) are excluded as unreliable for these groups. States for *Salvadorina* are unknown except as determined from skin specimens, Mayr (1931), and Mlíkovský (1989). Nomenclature follows Baumel and Witmer (1993).

1. Maxilla, typical shape: (a) not "subconical"; (b) "subconical," with essentially straight culmen (*Alopochen* intermediate, variable, sexually dimorphic). Note—see Fig. 14. CI = 0.50.

2. Maxilla and (to lesser degree) mandibula, distinct recurvature: (a) absent, (b) present (*Stictonetta* extreme, *T. tadorna* most conspicuous of genus). CI = 0.50.

3. Maxilla and mandibula, distally spatulate conformation: (a) absent, (b) present (*Malacorhynchus;* convergent state in subgenus *Spatula* of *Anas*). (Livezey 1991:character 157.) Note—see Fig. 15. CI = 1.00.

4. Cranium, os lacrimale, processus supraorbitalis and os frontale, margo lateralis, prominent enclosed foramen (not to be confused with minute, largely occluded foramina neurovascularia): (a) absent, (b) present (*Alopochen* variable, obscured in adult males), (a/b) polymorphic (derived state in *Cairina*). CI = 1.00.

5. Cranium, os lacrimale, processus supraorbitalis: (a) essentially lacking or small, straight, and coplanar with dorsal surface of skull; (b) comparatively large, flat, often triangular in dorsal aspect, appressed to laterodorsal margin of orbit; (c) large, thick, rugose, dorsolaterally prominent; (d) long, slender, dorsally prominent. (Livezey 1986*a*:character 11.) Note—state "b" affected in appearance by

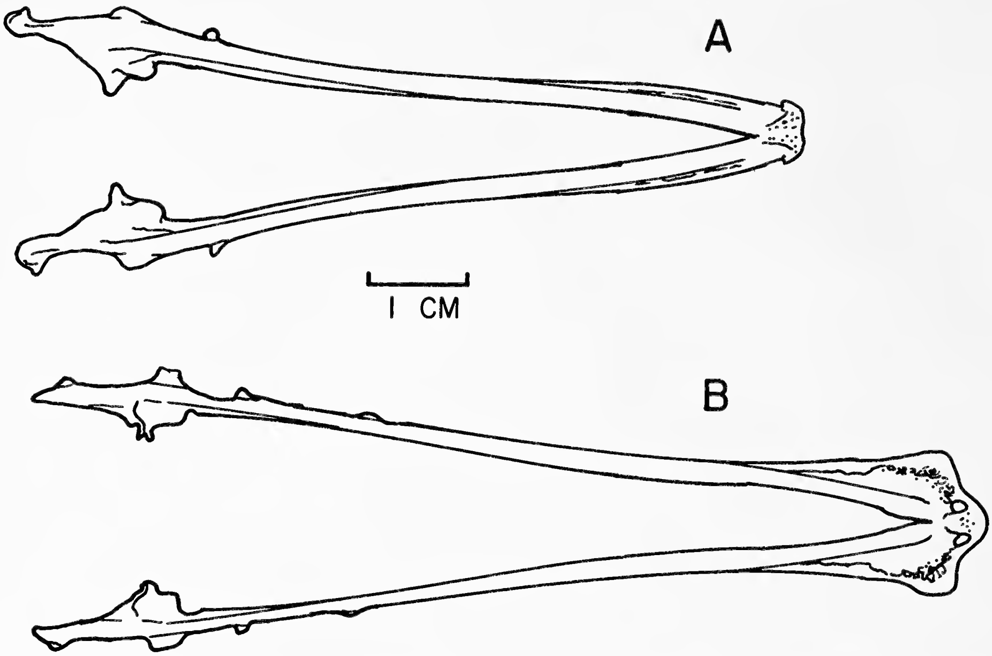


Fig. 15.—Mandibulae of selected genera of Anatidae, ventral views: A—*Hymenolaimus malachorhynchos* (KUMNH 55871), B—*Malacorhynchus membranaceus* (UMMZ 204434).

variably developed sulcus glandulae nasalis in some genera; this and other aspects of os lacrimale in *Stictonetta* confounded by unique synostosis of processus orbitalis with dorsally ossified Membrana jugolacrimale. CI = 0.75–1.00.

6. Cranium, ossa frontales, pneumatic dorsal convexity (males): (a) absent; (b) present, rounded, confined to region immediately caudal to zona flexoria craniofacialis; (c) present, variably produced into two-parted prominence, the more-caudal one bilaterally compressed and interorbital in position. Note—revised state for *Cyanochen* based on examination of skins, few skeletons available inadequate for diagnosis of this variably developed, sexually dimorphic character; see Möller (1969) and Livezey (in press*a,* in press*c*). (Livezey, 1986*a:*character 16, revised, corrected.) CI = 1.00.

7. Cranium, basis cranii, lamina parasphenoidalis: (a) rounded; (b) distinctly convex ventrally, with prominent medial ridge (Anateae). (Livezey, 1991:character 155.) CI = 1.00.

8. Vertebrae cervicales, modal number: (a) 17; (a/b) polymorphic, 16–17; (b) 16. (Livezey, 1986*a:*character 21, revised.) CI = 0.86.

9. Sternum, corpus sterni, foramen pneumaticum: (a) present, (b) absent. (Livezey, 1986*a:*character 78.) CI = 0.50.

10. Sternum, rostrum sterni, spina externa: (a) lateromedially compressed flange (ancestor); (b) elongate, peg-like spine; (c) small or obsolete. (Livezey, 1986*a:*character 79, revised significantly.) CI = 0.50–0.67.

11. Sternum, rostrum sterni, spina interna: (a) absent; (b) present, small. (Livezey, 1986*a:*character 82 [incorrect for *Chenonetta*]; Livezey, 1991:character 151.) CI = 0.33–1.00.

12. Sternum, carina sterni, margo ventralis, profile in lateral view: (a) distinctly convex throughout length, (b) essentially straight for caudal half. (Livezey, 1986*a:* character 80.) CI = 1.00.

13. Sternum, trabecula lateralis: (a) essentially equal in caudal extent to caudal terminus of linea intermusculus, (b) extend well caudad to caudal terminus of linea intermusculus. (Livezey, 1986*a:*character 81, revised.) CI = 1.00.

14. Furcula, extremitas omalis claviculae, processus acrocoracoideus: (a) present, although of variable conspicuousness; (b) obsolete. (Livezey, 1986*a:*character 101.) CI = 0.50.

15. Furcula, extremitas sternalis claviculae, apophysis furculae: (a) present, (b) obsolete. Note—see Woolfenden (1961), Mlíkovsky (1989). CI = 0.33.

16. Scapula, extremitas cranialis scapulae, tuberculum coracoideum: (a) coplanar with corpus scapulae, margo ventralis; (b) protrusive, distinctly ventral to corpus scapulae, margo ventralis. (Livezey, 1986*a:*character 107.) CI = 1.00.

17. Coracoideum, extremitas omalis coracodei, processus acrocoracoideus, subtending pneumatic depression: (a) absent, (b) present. (Livezey, 1986*a:*character 95, Livezey, 1991:character 154.) CI = 1.00.

18. Coracoideum, corpus coracoidei, facies ventralis, impressio m. supracoracoideus: (a) absent, (b) present. (Livezey, 1986*a:*character 96.) CI = 1.00.

19. Coracoideum, extremitas sternalis coracoidei, facies articularis sternalis, crista ventralis: (a) ventrally prominent, forming buttress; (b) inconspicuous. (Livezey, 1986*a:*character 100.) CI = 0.50.

20. Humerus, extremitas proximalis, facies caudalis immediately distal to caput: (a) variably convex; (b) with transverse trench-like depression, distinctly concave. (Livezey, 1986*a:*character 24.) CI = 1.00.

21. Humerus, extremitas proximalis, crista deltopectoralis: (a) margo dorsocranialis prominent, rounded, facies caudalis concave; (b) margo dorsocranialis angular, facies caudalis convex. (Livezey, 1986*a:*character 25.) CI = 0.25–0.50.

22. Humerus, extremitas proximalis humeri, tuberculum ventrale: (a) comparatively proximal, exposing fossa pneumotricipitalis in caudal view; (b) comparatively distal, largely or completely obscuring fossa pneumotricipitalis in caudal view. (Livezey, 1986*a:*character 27.) CI = 0.50.

23. Humerus, extremitas proximalis humeri, fossa pneumotriciptalis, foramen pneumaticum: (a) present, (b) absent. (Livezey, 1986*a:*character 28.) CI = 1.00.

24. Humerus, extremitas proximalis humeri, tuberculum dorsale: (a) prominent, buttressed; (b) not prominent, buttressed. (Livezey, 1986*a:*character 32.) CI = 0.25–0.33.

25. Humerus, corpus humeri, margo caudalis ("capital shaft ridge"): (a) prominent, proximally directed toward caput humeri; (b) prominent, proximally directed toward tuberculum dorsale; (c) obsolete. (Livezey, 1986*a:*character 22, ordering not assumed.) CI = 0.40–0.67.

26. Humerus, extremitas distalis humeri, tuberculum supracondylare ventrale: (a) not elevated, essentially coplanar with corpus humeri; (b) elevated, angled distally; (c) elevated, angled medially. (Livezey, 1986*a:*character 26.) CI = 0.50.

27. Os carpi radiale: (a) not modified into spur, (b) modified into spur. (Livezey, 1986*a:*character 49.) Note—see Rand (1954). CI = 1.00.

28. Carpometacarpus, extremitas proximalis carpometacarpi, trochlea carpalis, labrum dorsalis, distal terminus, prominent swelling: (a) present, (b) absent. (Livezey, 1986*a:*character 37.) CI = 1.00.

29. Carpometacarpus, extremitas proximalis carpometacarpi, processus flexo-

rius, orientation relative to shaft (ordered): (a) perpendicular to or proximally directed, (b) slightly distally directed, (c) distinctly distally directed. (Livezey, 1986*a:*character 41, revised.) CI = 1.00.

30. Carpometacarpus, extremitas proximalis carpometacarpi, os metacarpale alulare, processus extensorius, enlargement into "spur" (calcar alae): (a) absent; (b) present, especially prominent in adult males. (Livezey, 1986*a:*character 42.) CI = 0.33–0.50.

31. Carpometacarpus, extremitas proximalis carpometacarpi, fovea carpalis caudalis: (a) present but comparatively shallow; (b) present, comparatively deep, distinctly ovate. (Livezey, 1986*a:*character 46.) CI = 1.00.

32. Carpometacarpus, extremitas proximalis carpometacarpi, trochlea carpalis, labrum ventralis: (a) of uniform depth, (b) distinctly thickened proximally. (Livezey, 1986*a:*character 47.) CI = 0.50.

33. Carpometacarpus, corpus carpometacarpi, os metacarpale majus, facies dorsalis, impressio m. extensor metacarpi ulnaris, position relative to synostosis metacarpalis proximalis: (a) opposite, at least partly; (b) completely proximal. (Livezey, 1986*a:*character 43, revised.) CI = 0.50.

34. Illium, ala preacetabularis ilii, facies dorsalis, fossa iliaca dorsalis: (a) presenting smooth, only moderately concave surface; (b) containing deep, irregularly shaped depression. (Livezey, 1986*a:*character 113.) CI = 1.00.

35. Pubis, scapus pubis: (a) concave dorsally, (b) convex dorsally. (Livezey, 1986*a:*character 115.) CI = 0.50–1.00.

36. Femur, corpus femoris, craniocaudal curvature (lateral perspective): (a) absent or slight, (b) moderate. (Livezey, 1986*a:*character 55.) CI = 0.50.

37. Femur, corpus femoris, facies caudalis, linea intermuscularis caudalis: (a) present but not prominent; (b) prominent, produced into overhanging ridge proximally. (Livezey, 1986*a:*character 60.) CI = 1.00.

38. Femur, extremitas distalis femoris, fossa poplitea: (a) shallow, (b) deep. (Livezey, 1986*a:*character 56.) CI = 1.00.

39. Tarsometatarsus, corpus tarsometatarsi, facies dorsalis, margo medialis, dorsal prominence relative to margo lateralis: (a) essentially equal, (b) distinctly less prominent. (Livezey, 1986*a:*character 75.) CI = 1.00.

Trachea (Fig. 16).—Pertain to males. Nomenclature follows King (1989, 1993). (Livezey, 1986*a:*character 7 incorrect for *Stictonetta,* excluded.)

40. Asymmetrical bulla syringealis: (a) absent, (b) present (*Malacorhynchus* vestigial). (Livezey, 1986*a:*character 6, revised.) CI = 0.50.

41. Syrinx, narrow constriction between tympanum and bulla: (a) absent, (b) present. Note—see Garrod (1875). CI = 1.00.

42. Bulla syringealis (if present), fenestrae: (a) absent; (b) present, but relatively prominent, widely distributed; (c) present, small, few, confined to craniolateral margin. CI = 1.00.

43. Bilobate bulbus trachealis: (a) absent; (b) present, males. Note—see Campbell (1899). CI = 1.00.

Natal Integument (Fig. 17).

44. Ground color of venter*: (a) yellow, (b) dusky, (c) white, (x) basal state not determinable (Mergini). Note—polarity difficult, see Livezey, 1991:character 121. CI = 0.50.

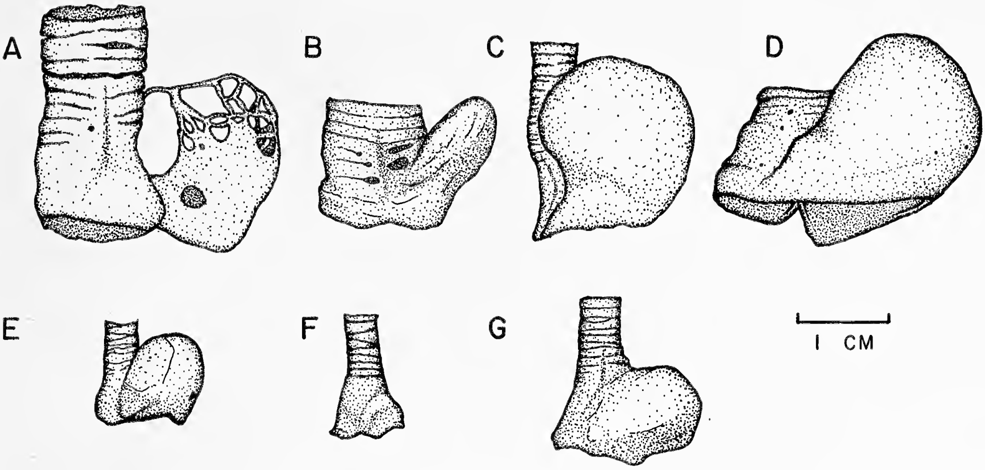


Fig. 16.—Bullae syringeales of selected genera of Anatidae, males, ventral views: A—*Plectropterus gambensis* (USNM 431245), B—*Sarkidiornis melanotus* (AMNH 15667), C—*Hymenolaimus malacorhynchos* (BMNH 1959·14·1), D—*Tachyeres patachonicus* (KUMNH 77972), E—*Merganetta* (*armata*) *colombiana* (ROM 93343), F—*Malacorhynchus membranaceus* (UMMZ 204438), G—*Salvadorina waigiuensis* (WWT 1752).

45. Dark, vertical supraorbital stripe: (a) absent, (b) present. CI = 0.50.

46. Dark auricular spot: (a) absent, (b) present, (x) noncomparable. CI = 0.20–0.250.

47. Pale scapular spots*: (a) absent, (b) present, (x) unknown or basal state not determinable. CI = 0.33.

48. Pale rump spots*: (a) absent, (b) present (*Hymenolaimus* rufous), (x) unknown or basal state not determinable. CI = 1.00.

49. Dorsal scapular and rump spots (if present): (a) separate, (b) confluent. CI = 0.33.

50. Pale, medial mantle stripe: (a) absent, (b) present. CI = 1.00.

51. Foot color: (a) gray(ish), (b) bright yellow or orange. CI = 1.00.

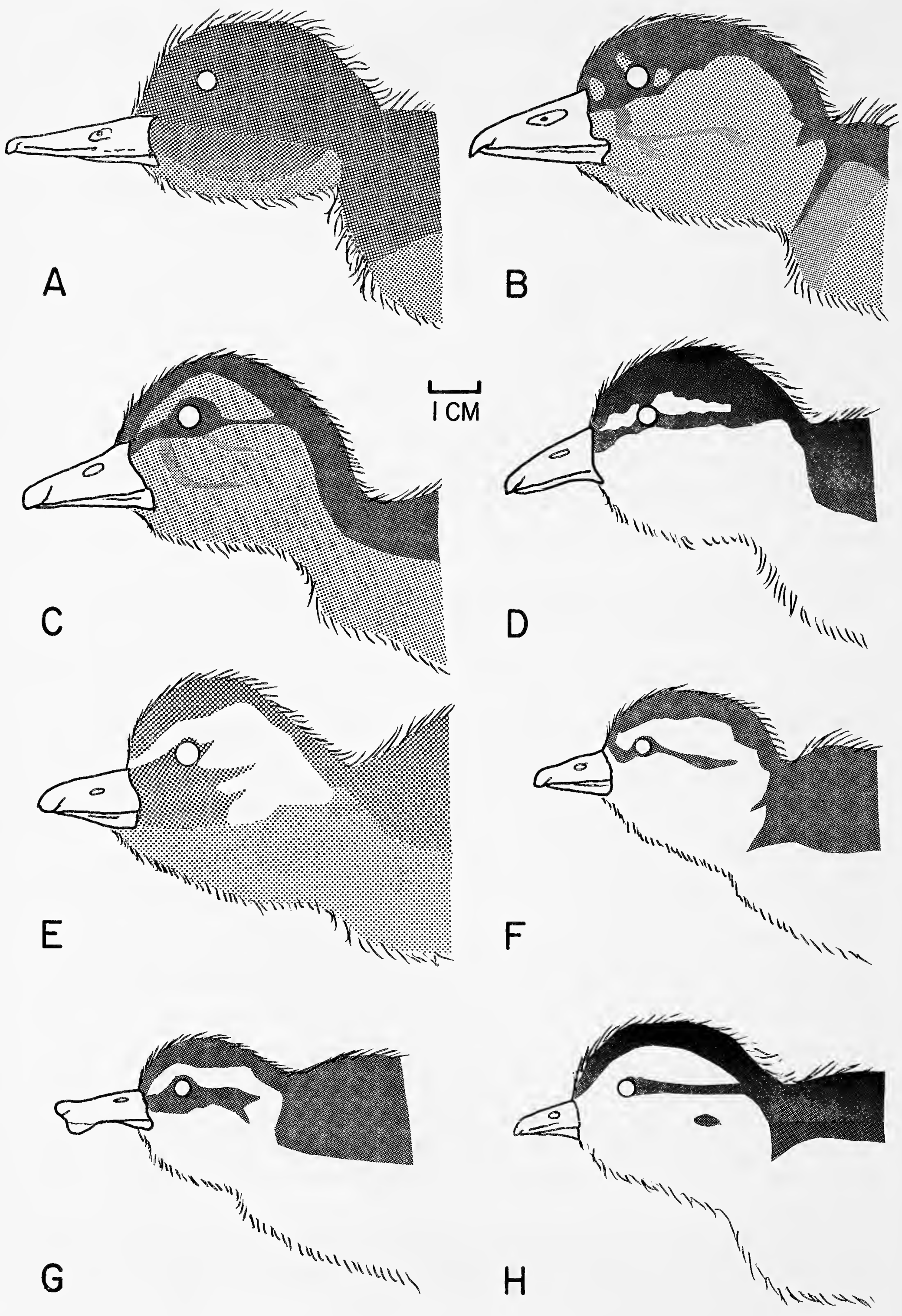
52. Dusky, oblique facial stripes: (a) absent, (b) present. Note—intraspecifically variable. CI = 1.00.

53. Sharp, dark preorbital (loral) stripe: (a) present, (b) absent (Cairineae excluding *Pteronetta*). (Livezey, 1991:character 107.) CI = 0.33.

54. Broad, pale supraorbital stripe, continuing caudoventrally around dark orbital patch along sides of neck: (a) absent, (b) present. CI = 1.00.

Definitive Integument.—Character 101 of Livezey (1991) was deemed not reliably characterized at this scale and excluded. Redundant synapomorphies for anatine tribes (see other works), as well as characters defining clades within genera of Tadornini (Livezey, in press *a*) or clades within *Tachyeres* (Humphrey and Livezey, 1985; Corbin et al., 1986; Livezey, 1986*a;* Livezey and Humphrey, 1992), also were excluded.

55. Rectrices: (a) not as follows (including narrow elongate tails of *Merganetta, Salvadorina*); (b) long and broad, typically extending beyond feet in prepared skin specimens. (Livezey, 1991:character 1.) CI = 0.50–1.00.


A
B
1 CM
C
D
E
F
G
H

56. Dark, variably extensive postorbital stripe (juvenal and definitive basic plumages of both sexes, as well as definitive alternate of females in some): (a) absent, (b) present (possibly excluding micro-teal, *Heteronetta*). (Livezey, 1991: character 128.) CI = 0.50–1.00.

57. Black, lateromedially compressed comb-like crista carnosa on culmen: (a) absent, (b) present. CI = 1.00.

58. Sharp, black speckling of white face: (a) absent (but see *Cairina scutulata*), (b) present. CI = 1.00.

59. Narrow, black shoulder marks at cranial margin of darkened sides: (a) absent, (b) present (obscured in *S. sylvicola*). CI = 1.00.

60. Lesser dorsal wing coverts, contrasting pale (typically white) color: (a) absent (*Plectropterus* nonhomologous, see character d8), (b) present. CI = 0.33.

61. Lesser dorsal wing coverts, contrasting pale color (if present): (a) white, (b) blue. CI = 1.00.

62. Cranialmost lesser dorsal wing coverts, contrastingly white producing narrow white leading edge of wing: (a) absent, (b) present. CI = 1.00.

63. Jagged, black coloration on sides: (a) absent, (b) present. CI = 1.00.

64. Bare, variably colored facial region (from bill to eye to auricular region, including ramal and interramal areas of mandibles) in males: (a) absent, (b) present. CI = 0.50.

65. Single, bare, fleshy-red patches on sides of neck of adult males: (a) absent, (b) present. CI = 1.00.

66. Crista nuchalis pennarum of black-tipped, white feathers from corona to base of neck: (a) absent, (b) present. CI = 1.00.

67. Sides of head and neck, variable suffusion with yellowish buff: (a) absent, (b) present. CI = 1.00.

68. Undertail coverts, variable suffusion with yellowish buff: (a) absent, (b) present. CI = 1.00.

69. Well-defined single black lines from sides of rump extending ventrally and demarcating the belly from the undertail coverts: (a) absent, (b) present. CI = 1.00.

70. Well-developed tomial flaps of maxilla, opposed by lateral extensions of mandibular: (a) absent, (b) present (*Malacorhynchus* extreme). CI = 0.50.

71. Maxilla and mandibula, narrow, submergine conformation: (a) absent, (b) present. CI = 1.00.

72. Mandibular rami, lateral compression defining long, very narrow interramal region: (a) absent, (b) present. CI = 1.00.

73. Black-and-white scalloping on sides and flanks: (a) absent, (b) present (terminal white band narrower in *Salvadorina*). CI = 1.00.

74. Sharply defined gray-and-chestnut breast and sides, contrasting sharply with white venter: (a) absent, (b) present. CI = 1.00.

←

Fig. 17.—Facial patterns of natal plumages of the Freckled Duck and selected genera of Anatidae, lateral views: A—*Stictonetta naevosa* (AUM 0.60097), B—*Plectropterus gambensis* (ROM 91832), C—*Sarkidiornis melanotus* (AMNH 731312), D—*Hymenolaimus malacorhynchos* (WWT 2359), E—*Tachyeres patachonicus* (USNM 48560), F—*Merganetta* (*armata*) *turneri* (FMNH 208125), G—*Malacorhynchus membranaceus* (WWT 3572), H—*Salvadorina waigiuensis* (based on Kear, 1975:fig 2; see also Delacour, 1956:pl. XXIII).

75. Narrow white barring of mantle: (a) absent, (b) present (comparatively extensive, including entire dorsum in *Salvadorina*). CI = 1.00.

76. Narrow white terminal white tips of secondary remiges: (a) absent, (b) present. CI = 1.00.

77. Sharply defined black scalloping on otherwise white wing linings, extending to axillars: (a) absent, (b) present (marks on axillars of *Salvadorina* tending to spotting). CI = 1.00.

78. Modal number of pairs of rectrices (ordered): (a) five, (b) six, (c) seven, (d) nine. CI = 0.75.

79. Rectrices: (a) not elongate, narrow; (b) elongate, narrow. Note—see character 55. CI = 0.50.

80. Black-and-white barring of rump: (a) absent, (b) present. CI = 0.50.

81. Leg color: (a) black or gray, (b) yellow, (c) red. CI = 0.50.

82. Bill color (breeding males): (a) gray; (b) pinkish white; (c) orange or red, including pink and coral; (d) yellow; (a/c) polymorphic (Anateae). CI = 0.67.

83. Wing linings, fine vermiculations: (a) absent, (b) present. CI = 1.00.

84. Major secondary coverts tipped with narrow white(ish) bars, producing cranial border to speculum (if any): (a) absent (*Malacorhynchus,* caudal only; *T. radjah,* broad, not homologous), (b) present (Anateae, excluding microteal). CI = 0.33.

85. Rufous underparts (females): (a) absent, (b) present. CI = 1.00.

86. Bifurcating, black, postorbital stripe: (a) absent, (b) present. CI = 1.00.

87. Tarsus, dorsal surface: (a) reticulate, (b) scutellate. CI = 1.00.

88. Contrastingly white venter: (a) absent, (b) present. CI = 1.00.

89. Wing spurs, prominent claws: (a) absent, (b) present. CI = 1.00.

90. Uniformly gray dorsal wing coverts: (a) absent, (b) present. CI = 1.00.

91. Rump, ground color: (a) brown(ish); (b) black; (c) uniformly gray; (d) white; (a/b) polymorphic, black or brown. CI = 0.57–0.67.

92. Dorsal chestnut wash: (a) absent, (b) present. CI = 0.33.

93. Uniformly black tertials (in some extending to scapulars or entire dorsum): (a) absent, (b) present. CI = 0.25–0.33.

94. Demarcation of color between neck and breast: (a) absent, (b) present. Note—see Livezey (in press *a*). CI = 0.50.

95. Lobation of hallux, and enlargement of subungual lobes in other digits: (a) absent (including basal Aythyini, Oxyurini), (b) present. CI = 0.33–0.50.

96. Dorsum entirely glossy black: (a) absent, (b) present. CI = 0.50–1.00.

97. Dorsum, iridescent greenish (to purplish) color on dark dorsum of wings: (a) absent; (b) present, including all of dorsal surface of wing except distal primaries and (in some) leading edge; (c) present, limited to secondary coverts (Cairineae in part, Nettapodeae variable); (d) present, limited to secondary remiges (Chloephageae variable). CI = 0.75–1.00.

98. Secondary remiges, ground color: (a) brown(ish), (b) iridescent greenish black (including tribes in which border produces speculum), (c) largely white, (d) gray. CI = 0.43–0.60.

99. Wing linings: (a) grayish brown, in some mottled with whitish (*Malacorhynchus* white with brown bars); (b) "pure" white; (c) black; (d) gray. CI = 0.43–0.60.

100. Pedal unguis: (a) not strongly developed, curved; (b) strongly developed, curved, subraptorial. CI = 0.50–1.00.

101. Unguis of pedal digit III: (a) not qualitatively distinct from other digits;

(b) distinctly broadened with marked concavity on plantar surface, medially displaced with enlarged lobate cutaneous pad enclosed in plantar cavity. CI = 1.00.

102. Interdigital webs of pedal digits, deep incisura: (a) absent, (b) present. CI = 1.00.

103. Bill lamellae, extreme ventral elongation and increase in number: (a) absent, (b) present. CI = 1.00.

104. Bill lamellae, confinement to proximal half of maxilla: (a) absent, (b) present. CI = 1.00.

105. Dark crown and nape band: (a) absent, (b) present. Note—possibly related to brown head of *Salvadorina.* CI = 1.00.

106. White terminal tail band formed by narrow pale tips of rectrices: (a) absent, (b) present. CI = 1.00.

107. Dark periorbital patch: (a) absent, (b) present. CI = 1.00.

108. Small pink postorbital spot: (a) absent, (b) present. CI = 1.00.

109. Contrastingly buffy undertail coverts: (a) absent, (b) present. CI = 1.00.

110. Head and neck contrastingly dark grayish black: (a) absent, (b) present. CI = 1.00.

111. Uniformly blue-gray ground color of body plumage: (a) absent, (b) present. CI = 1.00.

112. Reddish brown mottling of breast, mantle, and wing linings: (a) absent, (b) present. CI = 1.00.

113. Scapulars, vexilla externum with contrasting, narrow, black margins: (a) absent, (b) present. CI = 1.00.

114. Venter boldly striped (adult males): (a) absent, (b) present. CI = 1.00.

Attributes For Mapping
(primitive states in boldface)

A. Body mass (g, ordered): (a) <500, (b) 500–1500, **(c) 1500–2500**, (d) >2500.

B. Sexual size dimorphism (ratio, ordered): **(a) 1.05–1.20**, (b) 1.21–1.40, (c) >1.40.

C. Sexual dichromatism: **(a) absent** (others); (b) rudimentary, confined to quantitative differences in coloration of plumage and rhamphotheca (Anateae included here on the basis of states in basal members); (c) pronounced, involving distinct qualitative differences in pattern; (b/c) two states of almost equal frequency among members (*Cairina* and *Pteronetta,* b; *Aix,* c).

D. Mating system: **(a) monogamy**, (b) serial polygyny.

E. Typical nest site: **(a) terrestrial** (including over water), (b) cavity.

F. Clutch size (median, ordered): **(a) 3–5**, (b) 6–8, (c) 9–11.

G. Paternal attendance of broods: **(a) typical** (including poorly known *Nettapus*), (b) atypical.

H. Diving habit: **(a) not developed**, (b) developed (including only moderately specialized *Salvadorina*).

APPENDIX 2

Data Matrix

Matrix of 114 morphological characters (numbered, described in Appendix 1) used in the phylogenetic analysis of *Stictonetta,* genera of "tadornines," clades of "anatines," and a hypothetical ancestor, followed by eight attributes mapped *a posteriori* (lettered A–H). Skeletal characters are labelled "s1" to "s39," tracheal characters "t1" to "t4," natal characters "n1" to "n11," and those of definitive integument "d1" to "d60." States are coded as lower-case letters, and questions marks (coded as "x" in Appendix 1) signify undetermined states.

	Character														
Taxon	1 s1	2 s2	3 s3	4 s4	5 s5	6 s6	7 s7	8 s8	9 s9	10 s10	11 s11	12 s12	13 s13	14 s14	15 s15
1 Ancestor	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
2 *Stictonetta*	a	b	a	a	a	a	a	a	a	b	a	a	a	a	a
3 *Plectropterus*	a	a	a	a	b	c	a	a	a	c	a	a	a	b	a
4 *Sarkidiornis*	a	a	a	a	b	a	a	b	a	c	a	a	a	a	a
5 *Cyanochen*	b	a	a	b	b	b	a	a/b	a	c	a	a	a	b	a
6 *Alopochen*	b	a	a	b	b	b	a	a/b	a	c	a	a	a	b	b
7 *Neochen*	b	a	a	b	b	b	a	a/b	a	c	a	a	b	b	b
8 *Chloephaga*	b	a	a	b	b	b	a	a/b	a	c	a	a	b	b	b
9 *Tadorna*	a	b	a	a	b	a	a	a/b	a	c	a	a	a	b	a
10 *Hymenolaimus*	a	a	a	a	a	a	a	b	a	c	a	a	a	a	b
11 *Tachyeres*	a	a	a	a	c	a	a	b	b	c	a	b	a	a	b
12 *Merganetta*	a	a	a	a	a	a	a	b	a	c	a	b	a	a	b
13 *Salvadorina*	a	a	a	a	?	a	a	?	a	b	?	?	a	a	b
14 *Malacorhynchus*	a	a	b	a	a	a	a	b	a	b	b	a	a	a	a
15 Cairineae	a	a	a	a/b	b	a	a	b	a	c	a	a	a	a	a
16 Nettapodeae	b	a	a	a	a	a	a	b	a	b	b	a	a	a	a
17 Anateae	a	a	a	a	a	a	b	b	a	b	b	a	a	a	a
18 Aythyini	a	a	a	a	a	a	a	b	a	b	b	a	a	a	a
19 Mergini	a	a	a	a	d	a	a	b	b	b	a	a	a	a	a
20 Oxyurini	a	a	a	a	a	a	a	b	a	b	b	a	a	a	a

	Character														
Taxon	16 s16	17 s17	18 s18	19 s19	20 s20	21 s21	22 s22	23 s23	24 s24	25 s25	26 s26	27 s27	28 s28	29 s29	30 s30
1 Ancestor	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
2 *Stictonetta*	a	a	b	a	a	a	a	a	a	b	a	a	a	a	a
3 *Plectropterus*	a	a	a	a	a	a	a	a	a	b	a	b	a	b	a
4 *Sarkidiornis*	a	a	a	b	a	a	b	a	a	b	b	a	a	c	b
5 *Cyanochen*	a	a	a	b	a	a	b	a	a	c	b	a	a	a	b
6 *Alopochen*	a	a	a	b	a	a	b	a	a	b	b	a	a	a	b
7 *Neochen*	a	a	a	b	a	a	b	a	a	b	b	a	a	a	b
8 *Chloephaga*	a	a	a	b	a	a	b	a	a	b	b	a	a	a	b
9 *Tadorna*	a	a	a	b	a	a	b	a	a	b	b	a	a	a	b
10 *Hymenolaimus*	a	a	a	b	b	b	b	a	b	b	b	a	b	a	b
11 *Tachyeres*	b	a	a	b	a	a	b	a	b	b	c	a	b	a	b
12 *Merganetta*	a	a	a	b	a	a	b	a	a	b	b	a	b	a	b
13 *Salvadorina*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
14 *Malacorhynchus*	a	a	a	b	a	a	b	b	a	b	b	a	a	a	a
15 Cairineae	a	b	a	b	a	b	b	a	b	c	b	a	a	a	a
16 Nettapodeae	a	a	a	b	a	b	b	a	b	c	b	a	a	a	a
17 Anateae	a	a	a	b	a	b	b	a	b	c	b	a	a	a	a
18 Aythyini	a	a	a	b	a	b	b	a	b	c	b	a	a	a	a
19 Mergini	a	a	a	b	a	b	b	a	b	c	c	a	a	a	a
20 Oxyurini	a	a	a	b	a	b	b	a	b	c	b	a	a	a	a

APPENDIX 2—*Continued.*

	Character														
	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
Taxon	s31	s32	s33	s34	s35	s36	s37	s38	s39	t1	t2	t3	t4	n1	n2
1 Ancestor	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
2 *Stictonetta*	a	a	a	a	a	a	a	a	a	a	a	a	b	b	a
3 *Plectropterus*	a	a	b	a	a	a	a	a	a	b	b	c	a	a	a
4 *Sarkidiornis*	a	a	a	a	a	a	a	a	a	b	b	a	a	a	a
5 *Cyanochen*	a	b	a	a	a	a	a	a	a	b	a	a	a	c	a
6 *Alopochen*	a	a	a	a	a	a	a	a	a	b	a	a	a	c	a
7 *Neochen*	a	a	a	a	a	a	a	a	a	b	a	a	a	c	a
8 *Chloephaga*	a	a	a	a	a	a	a	a	a	b	a	a	a	c	a
9 *Tadorna*	a	a	a	a	a	a	a	a	a	b	a	a	a	c	a
10 *Hymenolaimus*	a	b	a	a	a	a	a	b	a	b	a	a	a	c	b
11 *Tachyeres*	b	b	b	b	a	a	b	b	b	b	a	a	a	c	b
12 *Merganetta*	a	b	a	a	a	b	a	b	a	b	a	a	a	c	b
13 *Salvadorina*	?	?	?	?	?	?	?	?	?	b	a	a	a	c	a
14 *Malacorhynchus*	a	a	a	a	a	b	a	a	a	b	a	a	a	c	a
15 Cairineae	a	a	a	a	a	a	a	a	a	b	a	a	a	c	a
16 Nettapodeae	a	a	a	a	a	a	a	a	a	b	a	a	a	c	a
17 Anateae	a	a	a	a	a	a	a	a	a	b	a	a	a	c	a
18 Aythyini	a	a	a	a	a	a	a	a	a	b	a	b	a	c	a
19 Mergini	a	a	a	a	b	a	a	a	a	b	a	a	a	?	a
20 Oxyurini	a	a	a	a	b	a	a	a	a	a	a	a	a	a	b

	Character														
	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Taxon	n3	n4	n5	n6	n7	n8	n9	n10	n11	d1	d2	d3	d4	d5	d6
1 Ancestor	a	?	?	a	a	a	a	a	a	a	a	a	a	a	a
2 *Stictonetta*	?	a	a	a	a	a	a	a	a	a	a	a	a	a	a
3 *Plectropterus*	a	b	b	a	a	a	b	a	a	a	a	a	a	a	a
4 *Sarkidiornis*	a	b	b	a	a	a	b	a	a	a	a	b	b	b	a
5 *Cyanochen*	b	b	b	a	a	a	a	a	b	a	a	a	a	a	b
6 *Alopochen*	b	b	b	a	a	a	a	a	b	a	a	a	a	a	b
7 *Neochen*	b	b	b	b	a	a	a	a	b	a	a	a	a	a	a
8 *Chloephaga*	b	b	b	b	a	a	a	a	b	a	a	a	a	a	b
9 *Tadorna*	b	b	b	a	a	a	a	a	a	a	a	a	a	a	b
10 *Hymenolaimus*	a	a	b	a	a	a	a	a	a	a	a	a	a	a	a
11 *Tachyeres*	a	b	b	a	a	b	a	a	a	a	a	a	a	a	a
12 *Merganetta*	b	b	b	b	b	b	a	a	a	a	a	a	a	a	a
13 *Salvadorina*	b	b	b	a	a	a	a	b	a	a	a	a	a	a	a
14 *Malacorhynchus*	?	a	b	a	a	a	a	a	a	a	a	a	a	a	a
15 Cairineae	a	b	b	a	a	a	a	b	a	b	b	a	a	a	b
16 Nettapodeae	a	b	b	a	a	a	a	a	a	b	b	a	a	a	a
17 Anateae	b	b	b	a	a	a	a	a	a	a	b	a	a	a	a
18 Aythyini	a	b	b	a	a	a	a	b	a	a	a	a	a	a	a
19 Mergini	?	?	?	a	a	a	a	a	a	a	a	a	a	a	a
20 Oxyurini	b	b	b	b	a	a	a	a	a	a	b	a	a	a	a

APPENDIX 2—*Continued.*

	Character														
Taxon	61 d7	62 d8	63 d9	64 d10	65 d11	66 d12	67 d13	68 d14	69 d15	70 d16	71 d17	72 d18	73 d19	74 d20	75 d21
1 Ancestor	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
2 *Stictonetta*	a	a	a	a	a	a	a	a	a	a	a	b	a	a	a
3 *Plectropterus*	a	b	b	b	b	a	a	a	a	a	a	a	a	a	a
4 *Sarkidiornis*	a	a	a	a	a	b	b	b	b	a	a	a	a	a	a
5 *Cyanochen*	b	a	a	a	a	a	a	a	a	a	a	a	a	a	a
6 *Alopochen*	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
7 *Neochen*	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
8 *Chloephaga*	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
9 *Tadorna*	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
10 *Hymenolaimus*	a	a	a	a	a	a	a	a	a	b	a	a	a	a	a
11 *Tachyeres*	a	a	a	a	a	a	a	a	a	a	a	a	a	b	a
12 *Merganetta*	a	a	a	a	a	a	a	a	a	a	b	a	a	a	a
13 *Salvadorina*	a	a	a	a	a	a	a	a	a	a	a	a	b	a	b
14 *Malacorhynchus*	a	a	a	a	a	a	a	a	a	b	a	a	b	a	b
15 Cairineae	a	a	a	b	a	a	a	a	a	a	a	a	a	a	a
16 Nettapodeae	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
17 Anateae	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
18 Aythyini	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
19 Mergini	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
20 Oxyurini	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a

	Character														
Taxon	76 d22	77 d23	78 d24	79 d25	80 d26	81 d27	82 d28	83 d29	84 d30	85 d31	86 d32	87 d33	88 d34	89 d35	90 d36
1 Ancestor	a	a	c	a	a	a	a	a	a	a	a	a	a	a	a
2 *Stictonetta*	a	a	c	a	a	a	a	a	a	a	a	a	a	a	a
3 *Plectropterus*	a	a	c	a	a	a	c	a	a	a	a	b	a	a	a
4 *Sarkidiornis*	a	a	c	a	a	a	a	a	a	a	a	b	a	a	a
5 *Cyanochen*	a	a	c	a	a	a	a	a	a	a	a	b	a	a	a
6 *Alopochen*	a	a	c	a	a	c	c	a	a	a	a	b	a	a	a
7 *Neochen*	a	a	c	a	a	c	a	a	a	a	a	b	a	a	a
8 *Chloephaga*	?	a	c	a	a	c	a	a	a	a	a	b	a	a	a
9 *Tadorna*	a	a	c	a	a	c	a	a	a	a	a	b	a	a	a
10 *Hymenolaimus*	a	a	c	a	a	a	b	a	a	a	a	b	a	a	b
11 *Tachyeres*	a	a	d	a	a	a	c	a	a	a	a	b	b	a	b
12 *Merganetta*	a	a	a	b	b	c	c	b	b	b	b	b	a	b	b
13 *Salvadorina*	b	b	c	b	b	b	d	a	b	a	a	b	a	a	a
14 *Malacorhynchus*	b	b	b	a	b	a	a	a	a	a	a	b	a	a	a
15 Cairineae	a	a	c	a	a	a	a	a	a	a	a	b	a	a	a
16 Nettapodeae	a	a	c	a	a	a	a	a	a	a	a	b	a	a	a
17 Anateae	a	a	c	a	a	a	a/c	a	b	a	a	b	a	a	a
18 Aythyini	a	a	c	a	a	a	a	a	a	a	a	b	a	a	a
19 Mergini	a	a	c	a	a	a	a	a	a	a	a	b	a	a	a
20 Oxyurini	a	a	c	a	a	a	a	a	a	a	a	b	a	a	a

APPENDIX 2—*Continued.*

	Character															
Taxon	91 d37	92 d38	93 d39	94 d40	95 d41	96 d42	97 d43	98 d44	99 d45	100 d46	101 d47	102 d48	103 d49	104 d50	105 d51	106 d52
1 Ancestor	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
2 *Stictonetta*	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
3 *Plectropterus*	b	a	b	a	a	b	b	b	b	b	a	b	a	a	a	a
4 *Sarkidiornis*	b	a	b	a	a	b	b	b	c	b	a	a	a	a	a	a
5 *Cyanochen*	c	a	a	a	a	a	d	b	b	a	a	a	a	a	a	a
6 *Alopochen*	b	b	b	b	a	a	d	b	b	a	a	a	a	a	a	a
7 *Neochen*	b	b	b	b	a	a	d	c	c	a	a	a	a	a	a	a
8 *Chloephaga*	d	a	a	b	a	a	d	c	b	a	a	a	a	a	a	a
9 *Tadorna*	b	b	b	b	a	a	d	b	b	a	a	a	a	a	a	a
10 *Hymenolaimus*	c	a	a	a	b	a	a	d	d	a	b	a	a	b	a	a
11 *Tachyeres*	c	a	a	a	b	a	a	c	d	a	a	a	a	a	a	a
12 *Merganetta*	c	a	a	a	b	a	a	b	d	a	a	a	a	a	a	a
13 *Salvadorina*	a	a	a	a	b	a	a	b	a	a	a	a	a	a	a	a
14 *Malacorhynchus*	d	a	a	a	a	a	a	a	a	a	a	a	b	a	b	b
15 Cairineae	b	a	b	a	a	b	c	b	c	b	a	a	a	a	a	a
16 Nettapodeae	a/b	a	a	a	a	a	c	b	c	a	a	a	a	a	a	a
17 Anateae	a	a	a	a	a	a	a	b	c	a	a	a	a	a	a	a
18 Aythyini	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
19 Mergini	a	a	a	a	b	a	a	b	b	a	a	a	a	a	a	a
20 Oxyurini	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a

	Character															
Taxon	107 d53	108 d54	109 d55	110 d56	111 d57	112 d58	113 d59	114 d60	115 A	116 B	117 C	118 D	119 E	120 F	121 G	122 H
1 Ancestor	a	a	a	a	a	a	a	a	c	a	a	a	a	a	a	a
2 *Stictonetta*	a	a	a	a	a	a	a	a	b	a	a	a	a	b	a	a
3 *Plectropterus*	a	a	a	a	a	a	a	a	d	c	a	b	a/b	b	b	a
4 *Sarkidiornis*	a	a	a	a	a	a	a	a	c	b	b	b	a/b	c	b	a
5 *Cyanochen*	a	a	a	a	a	a	a	a	c	c	a	a	a	b	a	a
6 *Alopochen*	a	a	a	a	a	a	a	a	c	b	a	a	a	c	a	a
7 *Neochen*	a	a	a	a	a	a	a	a	b	b	a	a	a	c	a	a
8 *Chloephaga*	a	a	a	a	a	a	a	a	c	a/b	c	a	a	b	a	a
9 *Tadorna*	a	a	a	a	a	a	a	a	b	b	c	a	b	c	a	a
10 *Hymenolaimus*	a	a	a	a	b	b	b	a	b	a	a	a	a	a	a	b
11 *Tachyeres*	a	a	a	a	a	a	a	a	d	b	b	a	a	b	a	b
12 *Merganetta*	a	a	a	a	a	a	a	b	a	b	c	a	a/b	a	a	b
13 *Salvadorina*	a	a	a	b	a	a	a	a	a	a	a	a	a	a	a	b
14 *Malacorhynchus*	b	b	b	a	a	a	a	a	a	a	a	a	a/b	b	a	a
15 Cairineae	a	a	a	a	a	a	a	a	b/c	b/c	b/c	b	b	c	b	a
16 Nettapodeae	a	a	a	a	a	a	a	a	a/b	a	c	a	b	c	a	a
17 Anateae	a	a	a	a	a	a	a	a	a/b	a	b	a	a	b/c	a/b	a
18 Aythyini	a	a	a	a	a	a	a	a	a/b	a	c	a	a	b/c	b	b
19 Mergini	a	a	a	a	a	a	a	a	a/b	a	c	a	a/b	a/b	b	b
20 Oxyurini	a	a	a	a	a	a	a	a	a/b	a	c	a/b	a	a/b	b	b

APPENDIX 3

Classification

Formation and hyphenation of English group names follow conventions of Parkes (1978); capitalization of those for *Sarkidiornis, Tachyeres,* and *Merganetta* indicate currently recognized or tentatively proposed polytypy.

Order Anseriformes (Wagler, 1831).
  Suborder Anseres Wagler, 1831.
    Family Anatidae Vigors, 1825.

Subfamily Stictonettinae Wolters, 1976.
    Genus *Stictonetta* Reichenbach, 1853.—Freckled Duck.
Subfamily Tadorninae Reichenbach, "1850."—Shelducks and allies.
  Tribe Merganettini Delacour and Mayr, 1945.
    Genus *Hymenolaimus* Gray, 1843.—Blue Duck.
    Genus *Tachyeres* Owen, 1875.—Steamer-ducks (see Livezey and Humphrey, 1992).
    Genus *Merganetta* Gould, 1842.—Torrent-ducks.
  Tribe Plectropterini, new taxon.
    Genus *Plectropterus* Stephens, 1824.—Spur-winged Goose.
    Genus *Sarkidiornis* Eyton, 1838.—Comb-ducks.
  Tribe Tadornini Delacour and Mayr, 1945 (see Livezey, in press *a*).
   Subtribe Chloephageae Boetticher, 1942.
    Genus *Cyanochen* Bonaparte, 1856.
    Genus *Alopochen* Stejneger, 1885.
    Genus *Neochen* Oberholser, 1918.
    Genus *Chloephaga* Eyton, 1838.
   Subtribe Tadorneae Boetticher, 1942.
    Genus *Tadorna* Oken, 1817.
Subfamily Anatinae Swainson, 1837, *sedis mutabilis.*—Dabbling ducks and allies.
  Tribe Malacorhynchini, new taxon.
    Genus *Malacorhynchus* Swainson, 1831.—Pink-eared Duck.
    Genus *Salvadorina* Rothschild and Hartert, 1894.—Salvadori's Duck.
  Tribe Anatini Delacour and Mayr, 1945; *incertae sedis* (see Livezey, 1991).
   Subtribe Anateae Boetticher, 1942.
   Subtribe Cairineae Boetticher, 1942.
   Subtribe Nettapodeae Livezey, 1991.
  Tribe Aythyini Delacour and Mayr, 1945 (see Livezey, in press *c*).
  Tribe Mergini Delacour and Mayr, 1945 (see Livezey, 1995*b*).
  Tribe Oxyurini Delacour and Mayr, 1945 (see Livezey, 1995*c*).

INSTRUCTIONS FOR AUTHORS

ANNALS OF CARNEGIE MUSEUM consist of contributions to the earth sciences, life sciences and anthropology, in 30 by 46 picas format (127 by 195 mm or 5 by 7⅝ inches). Submit all manuscripts to the Office of Scientific Publications. Authors should give particular attention to scientific content, format, and general style for the ANNALS. **Manuscripts that do not conform to the style of the ANNALS will be returned to the author immediately.** Every manuscript will be peer reviewed by at least two outside persons. Authors will be asked to subsidize, if funds are available, any or all costs of publication (approximately $100/page printed).

Manuscript style.—Articles should include the following items in this order: title page, abstract, text (with desired headings), acknowledgments, literature cited, tables, figure captions, and copies of illustrations. All manuscripts must be typed ***double-spaced*** on standard 8½ by 11 inch white bond paper, with at least one inch margins all around, and submitted ***in triplicate***—an original for the editors, and two review copies. All pages should be numbered, including tables, literature cited, and the list of figure captions. Only correspondence quality or better dot matrix printouts will be accepted; draft mode is unacceptable. A fixed-space font (e.g., Courier) is preferred.

Title Page. The title, on a separate title page should be brief, include the animal or plant group involved, and appear two to three inches below the top margin. Include the authors name(s) and the affiliations of non-CMNH authors. In the case of multiple authorship indicate the address to which proofs should be sent.

Abstracts. Abstracts should be short, double-spaced and substantive and included at the head of the first page of text.

Text. Do not right justify text or break (hyphenate) a word at the end of a line. ***Footnotes and acknowledgments as footnotes are unacceptable.*** All text is double-spaced.

Tables and figure legends. The list of figure legends and each table should be typed consecutively on individual pages separate from the text. Tables must be double-spaced throughout with **no vertical lines.**

Abbreviations. Refer to the CBE Style Manual for correct abbreviations. Mammalian dentition: use capital letters (I, C, P, M, D, for incisor, canine, premolar, molar, deciduous, respectively) and superscript/subscript numbers (M^2, P_3) to designate upper and lower teeth.

Measurements. Metric units should be used, if possible.

Literature Cited. All references in text must appear in the Literature Cited section. The data (author, date and page) in both citations must agree. ***Do not abbreviate the titles of periodicals or serials.*** The following style, double-spaced, should be used in Literature Cited:

1) Two authors in an institutional series:
    Matthew, W. D., and W. Granger. 1923. The fauna of the Houldjin Gravels. American Museum of Natural History Novitates, no. 97: 1–6.
2) Same authors repeated—use three-em dash:
    ———. 1923. The fauna of the Ardyn Obo Formation. American Museum of Natural History Novitates, no. 98:1–5.
3) Same authors plus a third author—repeat all authors:
    Matthew, W. D., W. Granger, and G. G. Simpson. 1928. Paleocene multituberculates from Mongolia. American Museum of Natural History Novitates, no. 331:1–4.
4) Chapter in an edited volume:
    Rausch, R. L. 1963. A review of the distribution of Holarctic mammals. Pp. 29–43, *in* Pacific Basin Biography (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.
6) Book:
    White, M. J. D. 1961. The Chromosomes. Methuen and Co., Ltd., London.
7) Journal articles with usual volume and issue number:
    Anderson, W. I. 1969. Lower Mississippian conodonts from northern Iowa. Journal of Paleontology, 43(4):916–928.

Illustrations. All illustrations will be called figures, and are to be numbered in Arabic numerals. Three sets of illustrations are required, one (original artwork) for reproduction, two for reviewers. Xerox copies of photographs for reviewers are usually not acceptable but are adequate for line drawing review copies. Illustrations may not be larger than 72 by 102 picas (305 by 432 mm or 12 by 17 inches). All illustrations must be reducible to a maximum of 127 by 195 mm (30 by 46 picas) without loss of clarity. Line copy should be designed for reduction to ⅔ or ½ of actual size. Typewritten illustration copy will not be accepted. Photographic figures should be submitted at **actual reproduction size,** if possible.

Two or more small figures should be combined for reproduction as a unit or plate, but, if feasible, do not combine halftones and line drawings. Rectangular halftone figures should be abutted, without intervening spaces. The printer will insert narrow white spaces during the reproduction process. Halftone figures with solid black backgrounds will not be accepted unless the author agrees to pay for the printing costs. All plates must have ***minimally*** one inch borders all around. Each plate should be given a protective cover and identified on the back side.

Lettering and/or a magnification scale (linear metric scale) for rectangular halftone figures should be placed directly on the photo, not in a blank space between photos. The scale or lettering for closely cropped photos can be placed in blank areas close to the figure.

Proof.—The author should answer all queried proof marks and check the entire proof copy. Return corrected page proof with the edited manuscript ***promptly*** to the editors.

If an author chooses to make extensive alterations to a paper in proof stage the author or appropriate section will bear the cost. Original manuscripts will not be returned unless requested. Illustrations will be returned to the author.

ISSN 0097-4463

ANNALS of CARNEGIE MUSEUM

THE CARNEGIE MUSEUM OF NATURAL HISTORY
4400 FORBES AVENUE • PITTSBURGH, PENNSYLVANIA 15213

VOLUME 65 16 MAY 1996 NUMBER 2

CONTENTS

ARTICLES

REVIEW

Manuscripts, subscriptions, orders for individual numbers, and changes of address should be sent to:

Office of Scientific Publications
Carnegie Museum of Natural History
4400 Forbes Avenue
Pittsburgh, PA 15213-4080
Phone (412) 622-3287
Fax (412) 622-8837
E-mail: schmidtm@clp2.clpgh.org

ANNALS OF CARNEGIE MUSEUM is published quarterly by The Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213-4080, by the authority of the Board of Trustees of Carnegie Institute.

THE CARNEGIE
MUSEUM OF
NATURAL HISTORY

ANNALS OF CARNEGIE MUSEUM
VOL. 65, NUMBER 2, PP. 89–152 16 MAY 1996

OBSERVATIONS ON THE MAMMALS OF TUCUMÁN PROVINCE, ARGENTINA. I. SYSTEMATICS, DISTRIBUTION, AND ECOLOGY OF THE DIDELPHIMORPHIA, XENARTHRA, CHIROPTERA, PRIMATES, CARNIVORA, PERISSODACTYLA, ARTIODACTYLA, AND LAGOMORPHA

Michael A. Mares[1, 3]
Research Associate, Section of Mammals

Rubén M. Bárquez[2]
Visiting Museum Specialist, Section of Mammals

Janet K. Braun[1]

Ricardo A. Ojeda[4]
Visiting Museum Specialist, Section of Mammals

Abstract

The systematics, distribution, and ecology of the Didelphimorphia, Xenarthra, Chiroptera, Primates, Carnivora, Perissodactyla, Artiodactyla, and Lagomorpha of Tucumán Province, Argentina, are summarized. Sixty-eight species belonging to 16 families are considered; two species are of probable occurrence (*Tayassu pecari* and *Myrmecophaga tridactyla*), and another species occurred in the province within the memories of locals living in the area (*Cebus apella*). A checklist also contains information on occurrence and status. Species accounts provide data on taxonomy, specimens examined and additional records, standard external and cranial morphological measurements, reproduction, molting, habitat preferences, general natural history, and other information. Geography, climate, and vegetation of the province are summarized. Mammal extirpations, potential threats to species, and mammalian conservation are discussed.

Resumen

La sistemática, distribución, y ecología de los Didelphimorphia, Xenarthra, Chiroptera, Primates, Carnivora, Perissodactyla, Artiodactyla, y Lagomorpha de la provincia de Tucumán son resumidas. Sesenta y ocho especies perteneciendo a 16 familias son consideradas; también se incluye dos especies que probablemente ocurren en la provincia (*Tayassu pecari* y *Myrmecophaga tridactyla*) y otra que ocurría allí según los relatos de habitantes de la zona. Una lista de especies conteniendo información sobre ocurriencia y estatus está incluida. La historia natural de las especies incluye información sobre taxonomía, reproducción, medidas, muda, y habitat. También se comenta sobre la geografía, clima, y vegetación de la provincia. Aspectos importantes de la conservación de varias especies son mencionadas.

Introduction

The small province of Tucumán is located in northwestern Argentina (Fig. 1). Its small size notwithstanding (22,524 km^2, about the size of New Hampshire),

---

[1] Oklahoma Museum of Natural History, University of Oklahoma, Norman, Oklahoma 73019.
[2] Instituto Miguel Lillo, Universidad Nacional de Tucumán, 4400 Tucumán, Argentina.
[3] Department of Zoology, University of Oklahoma, Norman, Oklahoma 73019.
[4] Instituto Argentino de Investigaciones de las Zonas Aridas (IADIZA), C. C. 507, 5500 Mendoza, Argentina.

Submitted 8 February 1995.

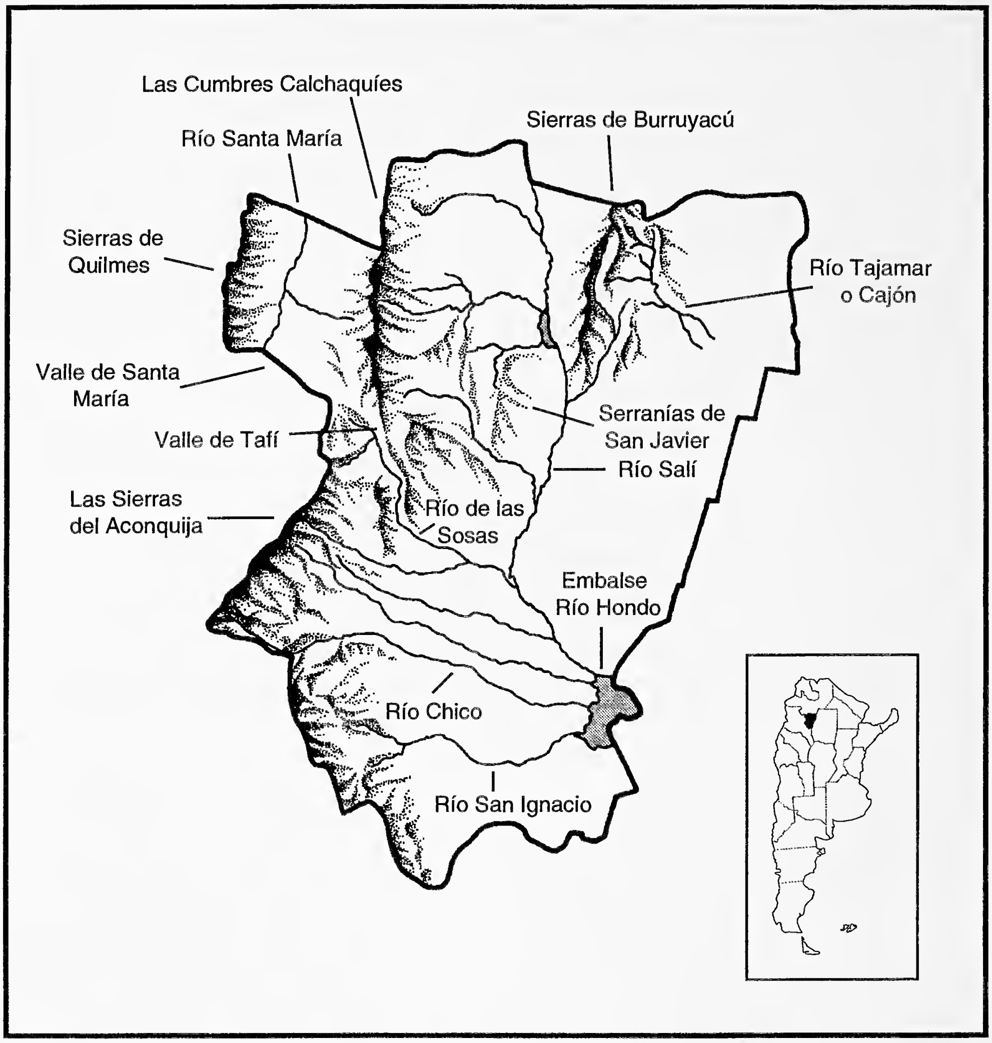


Fig. 1.—Map showing the location of Tucumán Province in Argentina and the major mountain chains and rivers.

Tucumán is both exceptionally rich in the diversity of habitats that it supports, as well as in its vertebrate fauna. Indeed, with more than 100 species of mammals known to occur in the province, and many yet to be found, its richness of mammal species would suggest an area of much greater geographic extent. For example, the state of New Mexico, a large, topographically diverse area, supports 149 species of native mammals (Findley, 1987), a number that is somewhat higher than the number of species that will ultimately be found to occur in Tucumán. Yet New Mexico is 14 times larger than Tucumán.

Clearly, Tucumán's rich floristic diversity, great topographic relief, varied patterns of precipitation, and location at a conjunction of major macrohabitats (Ojeda and Mares, 1989) just slightly south of the Tropic of Capricorn, provide a mixture of factors that has led to the province's high richness of mammal species. Moreover, because one of Argentina's oldest cities is in the province (San Miguel de Tucumán—founded in 1565 and the city where Argentine independence from Spain was established in 1816), and because the city is an important agricultural and educational center, especially in the biological sciences, there have been many investigations of the province's biota. These have included extensive studies on the flora of the province (e.g., Meyer, 1963; Digilio and Legname, 1966; Morello and Adámoli, 1968), as well as a number of reports on Tucumán's mammals (e.g., Olrog, 1958, 1959, 1976; Olrog and Lucero, 1981; Lucero, 1983; Bárquez et al., 1991). Nevertheless, our recent field work surveying the mammals of the province continues to discover species new to the province and taxa (species and genera) new to science, indicating that the province cannot yet be considered to be well studied from the viewpoint of its mammals.

Although a popular guide to the mammals of Tucumán Province was recently published (Bárquez et al., 1991), neither it, nor the earlier works of various authors, provided detailed information on the distribution, systematics, or other technical aspects of the biology of the province's mammals. In this report, we provide data on the nonrodent fauna of Tucumán. (We will deal with the province's complex rodent fauna in a subsequent paper.) We also review the physical setting of the province, its floral richness, its climate, and its history, for all of these have influenced the number of species of mammals that today occurs in the province. Finally, we place our observations in a conservation perspective, so that the status and importance of Tucumán's mammals can be better appreciated and understood.

GEOGRAPHY

Tucumán is the smallest of Argentina's provinces. Within its borders are a diversity of habitats that extend from the Chacoan lowlands in the east to the complex vegetation of the high mountains in the west. Tucumán contains a great deal of topographic diversity, ranging from low hills and small mountains in the east and northeast, to Andean massifs in the west. There are three major orographic systems in Tucumán (Fig. 1). In the western parts of the province, Las Cumbres Calchaquíes and Las Sierras del Aconquija extend from the northern to the southern borders. The Cumbres Calchaquíes, the southernmost extension of the eastern Andean Cordillera, reach elevations of approximately 4500 m; in addition to high, snow-covered peaks, the high mountains form many valleys and lakes. Numerous valleys having economic importance as ranchlands, farmlands, and tourist centers are found in the western highlands. One montane valley that is especially important is the Valle de Tafí, which is a rich bunchgrass prairie that crosses the Abra de Infiernillo at 3042 m and extends northward to the arid Valle de Santa María. The depression formed by these two valleys separates the Cumbres Calchaquíes from the Sierras del Aconquija. The latter are composed of many mountains, among them Cerro Muñoz, the Cerros de las Animas, the Nevados del Aconquija, and the Sierras de Santa Ana. Near the center of the province, just to the west of the capital city of San Miguel de Tucumán, is a series of low mountain formations known as the Serranías de San Javier, mountains covered with a verdant subtropical forest.

The Sierras de Burruyacú are a sub-Andean chain found in northeastern Tucumán. The easternmost mountains of the province include the Sierra de Medina, Cumbre del Nogalito, Sierra de la Ramada, and Sierra del Campo. These ranges

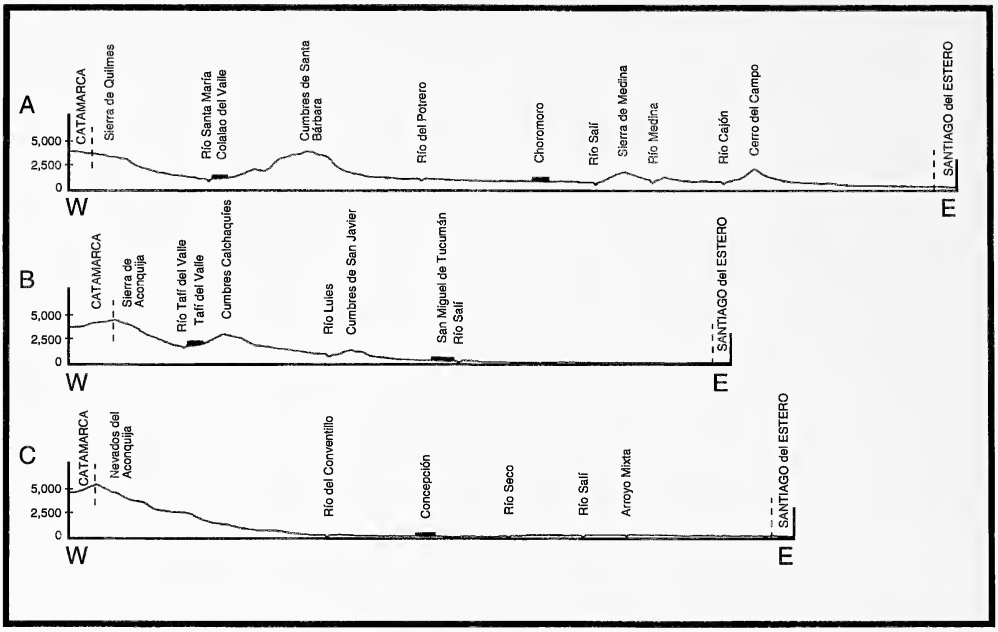


Fig. 2.—Three east–west topographic profiles through the province of Tucumán showing major geographic features taken along: A, latitude 26°25′; B, latitude 26°50′; and C, latitude 27°20′. Height is in meters above sea level. Population centers are designated by black rectangles.

are generally considered the extreme southern limit of the sub-Andean mountains, which are most extensive in Salta and Jujuy provinces to the north (Anonymous, 1981).

West of the Sierras del Aconquija and forming the extreme northwestern boundary of the province is a fourth mountain system, composed of the eastern faces of the Sierras de Quilmes that border the Valle de Santa María on the west, with the Cumbres Calchaquíes bordering the valley on the east. The southern edges of these ranges are located in adjacent Catamarca Province. Indeed, the Cerro del Bolsón in southern Tucumán along the Catamarca border is the highest point in the province at 5550 m.

The great elevational variation in the province is a major factor contributing to its wide array of habitats. An indication of the topographic diversity of the province is given in Figure 2, which illustrates three topographic profiles across Tucumán at approximately 26°30′, 26°52′, and 27°16’ south latitude. The low, flat plain in the eastern part of the province corresponds to the "great Tucumán plain"; the gradual decline in elevation of the mountain ranges as one proceeds southward and eastward is also depicted. Figure 1 shows the major mountain chains and rivers of Tucumán.

CLIMATE

Climatically, the province is at the limits of both the subtropical and the temperate regions. Thus, the area does not experience four distinct seasons, but rather has two well-defined ones. Summer months are hot and humid and winter months are cool and dry. Additionally, its pronounced elevational relief means that major climatic zones will appear at different elevations in the mountains. Three basic climate types are distinguishable within Tucumán: tropical with a dry season in the northern and eastern portions, tropical montane in the central low mountains, and subtropical arid in the high mountains and western lowland valleys.

Temperate climates characterize the higher mountainous regions of the province, but most of the province is influenced by the tropical montane climate. This is due to the north–south orientation of the mountain ranges that interrupt the westward movement of winds carrying moisture from the Atlantic Ocean. The humidity originating from the southern Atlantic air mass is retained by the transverse mountains, where orographic rain falls primarily on the eastern slopes. This produces a thick accumulation of clouds, generally between 2000–2500 m elevation in the mountains of central and west-central Tucumán, which may produce large amounts of rain. As might be expected, this rain results in rich floristic diversity along the eastern slopes and at mid elevations on the mountains.

As the air mass continues to move westward, it becomes progressively more arid, until the drier climates of the western portions of the province develop. The subtropical climatic region, which has a distinct dry season, is restricted to a narrow band located in the eastern part of the province and a second narrow band in the arid mountains and lowland valleys that characterize western Tucumán.

Most rivers in Tucumán descend from the eastern slopes of the mountains and unite in the valleys and ravines. The hydrology of the province is defined by the Río Salí River basin (north-central Tucumán), the Río Santa María (northwestern Tucumán), the Río Tajamar or Cajón (northeastern Tucumán), and several montane rivers in the south (Fig. 1).

Rainfall in the province is greatest along the central mountain chains, reaching 3000 mm annually in the forests on the east-facing montane slopes just west of the capital city of San Miguel in the Serranías de San Javier. Both in far eastern Tucumán and in the far western parts of the province rainfall decreases markedly, with dry thorn scrub resulting in the east and desert scrublands in the west.

VEGETATION

Tucumán supports a complex variety of major phytogeographic areas due to the province's diverse topography, climate, and hydrology. The general pattern of macrohabitats is shown in Figure 3. For a more detailed description of the plants comprising these various vegetational communities, the reader should consult Cabrera (1976), whose findings are summarized here.

Three Neotropical dominions (each containing a number of major macrohabitats) are found in Tucumán. The Amazonian Dominion is represented by the Yungas Phytogeographic Province, the Chaco Dominion is represented by the Chaco, Prepuna, and Monte Phytogeographic provinces, and the Andean–Patagonian Dominion is represented by the High Andean and Puna Phytogeographic provinces. We describe these briefly.

Yungas Phytogeographic Province.—The eastern plain of Tucumán originally supported a transitional forest with dominants that included the trees tipa and pacará (*Tipuana tipu* and *Enterolobium contortisiliquum*). According to Meyer and Weyrauch (1966), the plain also supported native cedars, i.e., cedro (*Cedrela lilloi*), lapachos (*Tabebuia avellanedae*), and cébiles (*Piptadenea macrocarpa*). Since this forest primarily occurred in areas that have been subjected to extensive human habitation over more than four centuries, it has largely disappeared, being

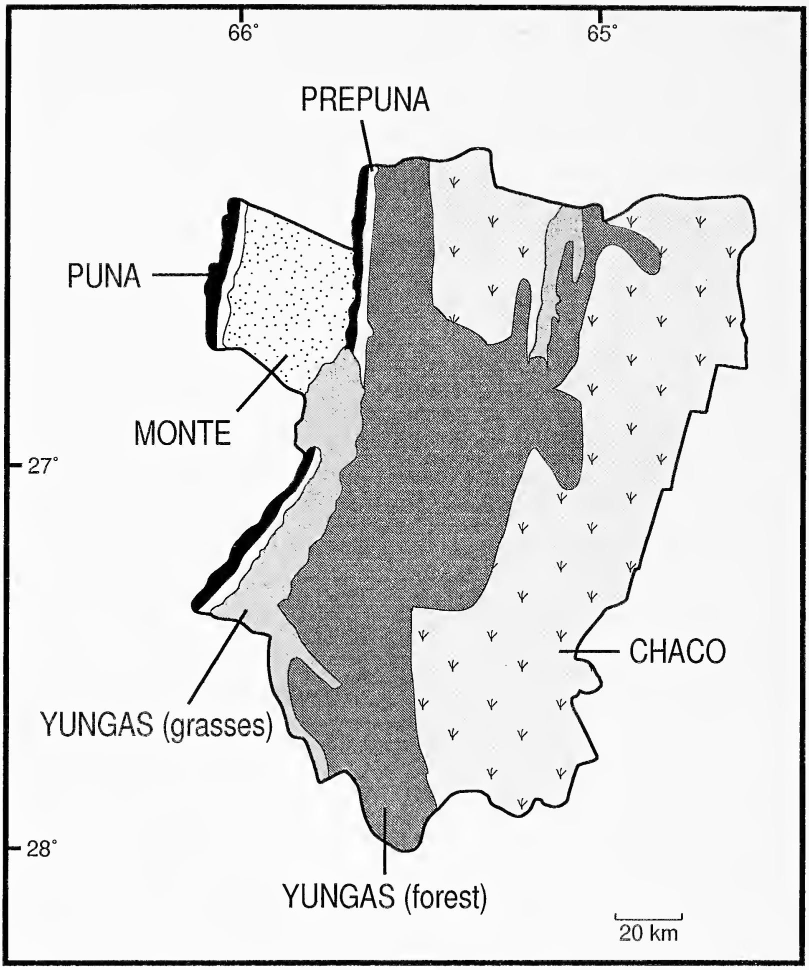


Fig. 3.—Some of the principle macrohabitats of Tucumán Province (after Cabrera, 1976; Vervoorst, 1982).

replaced by orchards and plantations of sugar cane and tobacco (Cabrera, 1976; see also Roig, 1991).

The eastern montane slopes of the central mountains support humid montane forest (Vervoorst, 1982), which is frequently divided into three forest types on the basis of elevation. The basal forest (or laurel forest) is found between 400–800 m elevation and includes laurel (*Phoebe porphyria*), palo amarillo (*Terminalia triflora*), tarco (*Jacaranda mimosifolia*), tabaquillo (*Solanum verbascifolium*), tipa (*Tipuana tipu*), lapacho (*Tabebuia avellanedae*), nogal (*Juglans australis*), cedro (*Cedrela lilloi*), and San Antonio (*Rapanea laetevirens*). A forest of mirtaceous trees lies between 800–1400 m. This forest is dominated by horco molle (*Blepharocalyx gigantea*), and guil (*Eugenia pseudomato*), as well as several dominant trees in other families, roblina (*Ilex argentina*), Tucumán laurel (*Phoebe porphyria*), nogal (*Juglans australis*), cedro (*Cedrela lilloi*), and some elements from the lower-elevation forest. An alder forest (*Alnus jorullensis*) is found at the

Fig. 4.—The montane subtropical forest of central Tucumán. (Photograph by M. A. Mares.)

highest elevations (from 1400–2100 m) and occasionally intermixes with pine (*Podocarpus parlatorei*) forests (Meyer, 1963).

At the higher elevations, in areas where soil conditions or microclimate lead to drier conditions, there is an increase in grasses, especially bunch grasses such as *Festuca, Stipa, Chloris,* and *Calamagrostis.* Queñoales "pines" (*Polylepis australis*) occur in ravines lying between 1900–2300 m, although in some regions they are found up to 3000 m elevation. The two lower levels are characterized by largely Neotropical plant species, but the upper elevation forest exhibits a number of Holarctic elements, including *Alnus, Juglans, Anemone, Ranunculus, Thalictrum,* and *Geranium.* These species extended their distributions southward along the Andean Cordillera during earlier geologic periods.

The montane forest, excluding the monospecific stands of alders and conifers, is normally a dense forest in which various strata are differentiated according to light requirements. Trees of the upper stratum reach approximately 30 m in height and include such species as laurel (*Phoebe porphyria*), horco molle (*Blepharocalyx gigantea*), cedars (*Cedrela*), horco cébil (*Piptadenia excelsa*), and nogal (*Juglans australis*). The second stratum is formed by trees that do not exceed 20 m in height—cochucho (*Fagara coco*), San Antonio (*Rapanea laetevirens*), ramo (*Cupania vernalis*), chalchal (*Allophyllus edulis*), and palo luz (*Prunus tucumanensis*). The shrub stratum is characterized by ramo tucumano (*Boehmeria caudata*), hediondilla (*Solanum lorentzi*), *Celtis triflora, Piper tucumanus, Urera baccifera, Miconia ioneura, Cestrum lorentzianum,* and *Psychotria carthagenensis.* The lowest stratum is dominated by helecho (*Pteris deflexa*) and the herbaceous stratum by *Oplismenus hirtellus, Panicum* cf. *demissum,* and *Axonopus compressus.* Throughout this forest, vines, lianas, and epiphytes are abundant, especially on the laurels and tipas; mosses, lichens, and ferns are abundant on the ground. Forest canopy vegetation is shown in Figure 4.

Chaco Phytogeographic Province.—The Chaco Phytogeographic Province is

Fig. 5.—The montane Chacoan forest of northern Tucumán Province at Las Juntas, 22 km W Choromoro. (Photograph by J. K. Braun.)

found on the large extension of the flat plain of eastern Tucumán where the Chaco proper reaches its western limit. The Chaco, a xerophytic forest with floristic affinities to the monte desert and the high elevation prepuna, is an extensive thorn scrub characterized by *Schinopsis lorentzii* and numerous thorny trees, such as species in the genera *Cercidium, Acacia, Prosopis,* and *Geoffroea.* Chaco serrano, or montane Chaco, characterizes the lower slopes of the drier eastern mountain ranges and the western slopes of the mountain ranges located to the east and northeast of the Sierras de San Javier. In this area, the Chaco is characterized by quebracho montano (*Schinopsis haenkeana*). In general, the Chaco has been heavily exploited throughout the province, resulting in invasions of vinal (*Prosopis ruscifolia*) from the northeast and jarilla (*Larrea* spp.) from the south.

The Chaco of Tucumán, with annual precipitation ranging from 500–800 mm, is much drier than the eastern Chaco of north-central and eastern Argentina (Fig. 5). A major Chacoan plant community in Tucumán is the quebrachal community, composed of trees of quebracho colorado (*Schinopsis lorentzii*) and quebracho blanco (*Aspidosperma quebracho-blanco*). Other important trees include itín (*Prosopis kuntzei*), algarrobo negro (*Prosopis nigricans*), chañar (*Geoffroea decorticans*), mistol (*Zizyphus mistol*), quayacan (*Caesalpinia paraguariensis*), and sombra de toro (*Jodina rombifolia*). Cardones (*Trichocereus* and *Cereus*), quimil (*Opuntia quimilo*), and other cacti and epiphytic bromeliads are also present.

Monte Phytogeographic Province.—In Tucumán, the monte is limited to areas west of the Cumbres de Calchaquíes. Throughout this region rain is scarce (never more than 200 mm annually) and falls primarily between October and March (summer), peaking in January. Average annual rainfall (based on 47 years of records) at Santa María, Catamarca Province, immediately south of the Tucumán border in the monte desert, is 181.7 mm (Morello, 1958). In Tucumán Province proper, average annual rainfall does not exceed 160 mm at Colalao del Valle and

Fig. 6.—The monte desert of northwestern Tucumán Province at the Quilmes ruins. (Photograph by J. K. Braun.)

Amaicha del Valle (based on eight years of data). The monte is characterized by jarilla, or creosotebush (*Larrea divaricata* and *Larrea cuneifolia*), and various trees and shrubs (*Prosopis, Tricomaria, Mimosa, Bulnesia, Cassia*) (Fig. 6). Intermontane forests formed by *Prosopis flexuosa, Geoffroea decorticans, Acacia visco,* and *Atamisquea emarginata* extend along temporary rivers or along the borders of the dry western valleys (Vervoorst, 1982). Columnar cacti (*Trichcereus*) are also common.

Prepuna Phytogeographic Province.—In the provinces of Tucumán, Catamarca, and La Rioja, this phytogeographic province is generally found at elevations between 2000–3000 m and is located either between the Chaco and Puna Phytogeographic provinces, or between the Monte and Puna Phytogeographic provinces (Cabrera, 1976). In general, the presence or absence of the prepuna depends upon the altitude, arrangement, and orientation of the mountain ranges. The climate is dry and rainfall occurs in the summer. It is strongly related to the Monte Province, but differs fundamentally by the absence of *Larrea* and by the abundance of many species of columnar cacti (genus *Trichocereus*) and terrestrial, ring- or cushion-shaped ground bromeliads (*Dyckia, Deuterocohnia, Abromeitiella*). Prepuna plant communities (Fig. 7) are able to grow on rocky mountain slopes with both eastern and western exposures (Vervoorst, 1982).

Puna and High Andean Phytogeographic Provinces.—In Tucumán, the Andean Patagonian Domain is represented by the Puna and High Andean Phytogeographic provinces (Fig. 7). The latter is found in high mountain regions from the peaks down to the tree line. In Tucumán it occurs on the Aconquija range and the Nevados del Cajón. Normally, the soils in the high Andean Phytogeographic Province are rocky, stony, or sandy. Bogs may occur in moist areas. The montane climate is cold and dry, and the winds strong. There are only two endemic families of plants in this province, but there are a number of endemic genera. The dominant

Fig. 7.—The prepuna northwest of El Infiernillo above Tafí del Valle. Puna vegetation can be seen in the background on the higher slopes. (Photograph by J. K. Braun.)

vegetation is grassland steppes or steppes of low-growing plants having large roots (e.g., *Adesmia, Baccharis, Oxalis, Senecio*). The puna occurs on high mountains and plateaus, typically between 3400–4500 m. The soils are poor in organic material and are frequently rocky or sandy. The dominant vegetation is the shrub steppe, although herbaceous steppes and bog areas are not uncommon. The puna is related to the Patagonian region and many dominant plant genera are shared between them, including *Junellia, Fabiana, Chuquiraga, Nardophyllum, Adesmia,* and *Mulinum* (Cabrera, 1976).

METHODS

General.—Specimens were collected using standard Museum Special snap traps, Victor rat traps, Havahart traps (48 × 15 × 15 cm), gopher traps, leg-hold traps, Sherman live traps (7.6 × 7.6 × 25.4 cm and 12.7 × 12.7 × 38.1 cm), home-made live traps, mist nets, and .22 caliber rifles. All specimens were prepared as skins plus skulls or skeletons, or preserved in 10% formalin and alcohol. Beginning in 1990, tissues were collected and frozen in liquid nitrogen and representative specimens were karyotyped. Data collected included standard external measurements, reproductive condition, and molting pattern. Ecological or natural history data were noted when specimens were collected ancillary to ecological or physiological research. Specimens collected by us over the past quarter century are deposited in the following museums: Carnegie Museum of Natural History, Pittsburgh; Colección Miguel Lillo, Instituto Miguel Lillo, Tucumán; IADIZA, Colección de Mamíferos, Mendoza; Oklahoma Museum of Natural History, University of Oklahoma, Norman; Texas Cooperative Wildlife Collection, Texas A & M University, College Station (frozen tissues and chromosomal preparations).

Taxonomy.—We have chosen to follow, with four exceptions, the most recent

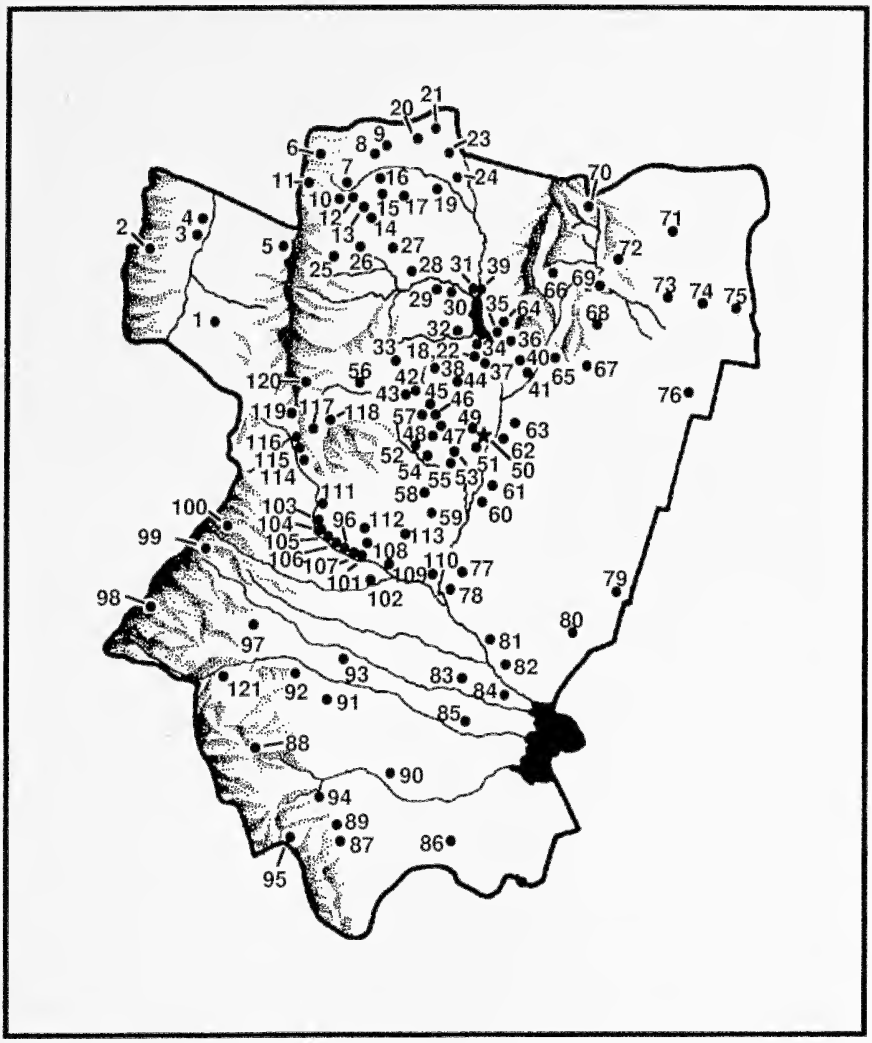


Fig. 8.—Collecting localities for mammals listed in the text. Numbers correspond to those given in the Gazetteer.

edition of "Mammal Species of the World: A Taxonomic and Geographic Reference" (Wilson and Reeder, 1993) for the taxonomic arrangement of families, subfamilies, genera, and species. *Sturnira oporaphilum* is used instead of *S. bogotensis.* Based on studies using allozyme and mitochondrial DNA data (Baker et al., 1988; Morales and Bickham, 1995), we recognize *Lasiurus blossevillii* for the South American red bats. *Eumops patagonicus* is recognized as a distinct species; this species is included in *Eumops bonariensis* in Wilson and Reeder (1993). We follow Garcia-Perea (1994) in the recognition of *Lynchailurus* as a distinct genus containing three species; *L. pajeros* is found in Tucumán Province.

Collecting Localities.—The principal localities for specimens cited in the text in Tucumán Province are shown in Figure 8. The Gazetteer lists the localities and coordinates of south latitude and west longitude in degrees and minutes for all specimens cited in the text that could be located. Localities are listed alphabetically and numerically; departments and numbers corresponding to numbered localities in Figure 8 are given in parentheses. Coordinates were obtained from Gazetteer No. 103 (Argentina) of the United States Board of Geographic Names prepared by the Office of Geography, Department of Interior, Washington, D. C. (Anonymous, 1968), used in conjunction with various maps. Localities have been kept as they appeared on the original labels, except for obvious misspellings. Maps of Tucumán published by the Automóvil Club Argentino (1974, 1977, 1982, 1986), the series of 1:500,000 provincial maps published the Ejército Argentino, Instituto Geográfico Militar in 1966 (number 2966) and 1972 (number 2766), and the 1:250,000 maps of the province published by the Ejército Argentino, Instituto Geográfico Militar in 1986 (number 2766-IV), 1987 (number 2766-III), and 1988 (number 2766-I) were used to plot localities. Aeronautical maps TPC Q-27A (1: 500,000; 1988) and Q-27 (1:1,000,000; 1973), prepared and published by the Defense Mapping Agency Aerospace Center, were also used to plot localities.

CHECKLIST OF THE MAMMALS OF TUCUMÁN PROVINCE

A list of the orders, families, genera, and species of mammals known or expected to occur in Tucumán Province, Argentina, is given in Table 1. The designations of relative abundance are largely subjective and are based on our long experience with the species of the province. We present them only to guide biologists as to which species might be of special concern for conservation and which might be relatively easy to study in the province. In some cases, we have actual mark-recapture data, or collecting data, to estimate commonness or rarity. In other cases, we have formed impressions as to whether or not a species is common or rare based on experiences in capturing or observing the species.

SPECIES ACCOUNTS

In the following sections we present the individual species accounts for those mammal species known to occur in Tucumán Province. Accounts are arranged according to order, family, and subfamily (where appropriate). Genera and species are arranged alphabetically within families or subfamilies. For each scientific name, the authority and literature citation for the first recognized description are given. In the measurements presented for each species, mean and range for adult males and females are listed separately. For two or fewer specimens, only the measurements are listed. Measurements are given in millimeters.

Specimens from the following museum collections (acronyms given in parentheses) were examined: The Natural History Museum, London, England (BMNH); Carnegie Museum of Natural History, Pittsburgh, Pennsylvania (CM); Colección Lillo, Instituto Miguel Lillo, Tucumán, Argentina (CML); Colección de Mamíferos, Centro Regional de Investigaciones Científicas y Técnicas—CRICYT, Mendoza, Argentina (IADIZA); Facultad Ciencias Exactas y Naturales, Mamíferos, Universidad Nacional de Buenos Aires, Buenos Aires, Argentina (FCM); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina (MACN); Oklahoma Museum of Natural History, University of Oklahoma, Norman, Oklahoma (OMNH); personal collection of Rubén Bárquez, Tucumán, Argentina (RMB); The Museum, Texas Tech University, Lubbock, Texas (TTU).

Order Didelphimorphia
Family Didelphidae
Subfamily Didelphinae
Didelphis albiventris Lund

Didelphis albiventris Lund, Konigelige Danske Videnskabernes Selskabs Afhandlinger, Kjöbenhavn, p. 20, 1840.

Specimens Examined.—(26) Aconquija, Concepción, 5 (BMNH); Cerro del Campo, 800 m, 1 (BMNH); El Cadillal Dike, 25 km NW San Miguel de Tucumán, 2 (CM); El Cajón, 1 (CML); 4 km W of junction 338 and road to Horco Molle, on road to San Javier, 2,750 ft., 1 (OMNH); Biological Reserve at Horco Molle, 2,400 ft., 3 (1 CML, 1 IADIZA, 1 OMNH); Los Romanos, 1 (CML); Mala Mala, 1 (BMNH); Escuela Normal, Monteros, 1 (MACN); Piedra Tendida, 12 km WNW Burruyacú along Río Cajón, 2,500 ft., 2 (1 IADIZA, 1 OMNH); San Fernando, 1 (CML); San Pedro de Colalao, 3 (CML); at km marker 42, on highway 364, south of San Pedro de Colalao, 4,700 ft., 3 (1 CML, 1 IADIZA, 1 OMNH); Tucumán, no specific locality, 1 (BMNH).

Additional Records.—Aguas Chiquitas (Cajal, 1976); Pozo Hondo (R. M. Bárquez, personal observation); Dique Escaba (J. K. Braun, personal observation); Santa Rosa de Leales (Massoia and Fornes, 1965); Tafí del Valle (J. K. Braun, personal observation).

Measurements.—External measurements (eight males, ten females, unless noted otherwise): total length, 518.5 (292.0–723.0), 588.2 (370.0–770.0); tail, 237.4 (84.0–337.0), 294.6 (175.0–390.0); hindfoot, 45.0 (32.0–54.0), 46.0 (30.0–60.0); ear, 49.7 (40.0–55.0), 50.2 (39.0–56.0); weight (four males, four females), 331.0 (210.0–508.0), 354.8 (144.0–910.0). Cranial measurements (two males, four females, unless noted otherwise): greatest length of skull, 77.5, 94.0, 77.4 (52.0–93.9); condylobasal length, 76.0, 91.0, 75.1 (45.7–91.8); least interorbital length, 10.0, 10.7, 10.2 (9.8–10.6); zygomatic breadth, 38.7, 53.6, 40.8 (28.0–48.3); breadth of braincase (two males, three females), 21.0, 27.4, 24.6 (23.7–25.8); length of maxillary toothrow, 21.0, 36.1, 27.7 (18.9–35.6); palatal length (one male, four females), 55.1, 45.0 (30.2–54.2); length of mandibular toothrow (one male, two females), 37.5, 32.3, 37.9; greatest length of mandible (one male, two females), 76.6, 60.0, 73.6.

Reproduction.—See Table 2.

Molt.—A subadult female and male were molting in January.

Habitat.—This species is widely distributed throughout Argentina from north of 41°S latitude in Río Negro Province northward. Specimens were collected in transitional forest, areas bordering transitional forest, and in pine forest. Individuals were captured in Havahart traps, Sherman live traps, and in Victor rat traps. Both individuals from Piedra Tendida were captured in Havahart traps baited with either lunchmeat or sardines (M. L. Campbell, personal observation). One juvenile was caught in a trap set in a tree. Lucero (1983) noted that this species inhabits a variety of habitats including cities and urban areas. It is found at altitudes up to 2500 m (Lucero, 1983). The species is seldom found in arid or semiarid areas, preferring mesic agricultural zones, forests, and other moist habitats. The opossum from Tafí del Valle was seen crossing the road (Highway 307) north of Tafí del Valle at night (J. K. Braun, personal observation). Although we did not observe any individuals, locals at Dique Escaba indicated that *D. albiventris* was common in the area (J. K. Braun, personal observation).

Remarks.—There is some question regarding the specimens in the Natural History Museum, London, collected by Shipton from Concepción, Aconquija. The location on the skin tag is listed as Concepción, but the locations on the skull tags have been changed to Aconquija. Cajal (1976) reported on the population ecology of this species in Tucumán Province.

Table 1.—*Checklist of the mammals of Tucumán Province. The occurrence of each species is indicated as being: (*) collected, seen, or museum specimens examined by us; (l) reported in the literature; (p) of probable occurrence due to the presence of the species in adjacent provinces in similar habitats. In addition, we note whether, in the province of Tucumán, the species is common (c), uncommon (u), rare (r), in danger of extirpation (e), or probably extirpated from the province (x).*

Taxon	Occurrence	Status
Order Didelphimorphia		
Family Didelphidae		
Subfamily Didelphinae		
Didelphis albiventris	*, l	c
Lutreolina crassicaudata	*	u
Monodelphis dimidiata	*	r
Thylamys elegans	*, l	c
Thylamys pallidior	*, l	u
Order Xenarthra		
Family Dasypodidae		
Subfamily Dasypodinae		
Cabassous chacoensis		r
Chaetophractus vellerosus	*, l	c
Euphractus sexcinctus	*	u
Priodontes maximus	p	r?, x?
Tolypeutes matacus	*, l	e
Family Myrmecophagidae		
Myrmecophaga tridactyla		x?
Tamandua tetradactyla	*	u
Order Chiroptera		
Family Phyllostomidae		
Subfamily Phyllostominae		
Chrotopterus auritus	*	r
Subfamily Stenodermatinae		
Artibeus planirostris	*	c
Sturnira erythromos	*	u
Sturnira lilium	*	c
Sturnira oporaphilum	*	r
Subfamily Desmodontinae		
Desmodus rotundus	*	c
Family Vespertilionidae		
Subfamily Vespertilioninae		
Eptesicus diminutus	*	u
Eptesicus furinalis	*	u
Histiotus macrotus	*	u
Lasiurus blossevillii	*, l	c
Lasiurus cinereus	*	c
Lasiurus ega	*, l	c
Myotis albescens	*	c
Myotis keaysi	*	c
Myotis levis	*	c
Myotis nigricans	*, l	c
Family Molossidae		
Eumops bonariensis	*	c
Eumops dabbenei	*	u
Eumops glaucinus	*	c
Eumops patagonicus	*	c
Eumops perotis	*, l	c
Molossops temminckii	*, l	c
Molossus molossus	*	c
Nyctinomops macrotis	*	c
Promops nasutus	*	c
Tadarida brasiliensis	*, l	c

Table 1.—*Continued.*

Taxon	Occurrence	Status
Order Primates		
Family Cebidae		
Subfamily Cebinae		
Cebus apella		x?
Order Carnivora		
Family Canidae		
Cerdocyon thous	*	c
Pseudalopex culpaeus	*	u
Pseudalopex griseus	*	u
Pseudalopex gymnocercus	*	c
Family Felidae		
Subfamily Felinae		
Herpailurus yaguarondi	*	u
Leopardus pardalis	*, l	u
Lynchailurus pajeros	*	r
Oncifelis geoffroyi	*, l	c
Oreailurus jacobita	*, l	r
Puma concolor	*, l	c
Subfamily Pantherinae		
Panthera onca		x
Family Mustelidae		
Subfamily Lutrinae		
Lontra longicaudis	*	e
Subfamily Mephitinae		
Conepatus chinga	*	c
Subfamily Mustelinae		
Eira barbara	*	u
Galictis cuja	*	c
Lyncodon patagonicus	*, l	u
Family Procyonidae		
Subfamily Procyoninae		
Nasua nasua	*	u
Procyon cancrivorus	*	u
Order Perissodactyla		
Family Tapiridae		
Tapirus terrestris	*, l	p?, x?
Order Artiodactyla		
Family Tayassuidae		
Catagonus wagneri	*	r
Pecari tajacu	*	c
Tayassu pecari	l, p	?
Family Camelidae		
Lama guanicoe	*, l	u
Vicugna vicugna	l	x
Family Cervidae		
Subfamily Odocoileinae		
Hippocamelus antisensis	*	u
Mazama americana	*	u
Mazama gouazoupira	*	c
Ozotoceros bezoarticus	l	x
Order Lagomorpha		
Family Leporidae		
Sylvilagus brasiliensis	*	u

Table 2.—*Reproductive data for the Didelphidae. Symbols: A = adult; SA = subadult; J = juvenile; TSL = large scrotal testes; lac = lactating; NRA = not reproductively active; length and width of testes, or qualitative evaluation, are given in parentheses; CRL = crown–rump length of embryos or young. May, August, October, and November have no data.*

Taxon	Sex	January	February	March	April	June	July	September	December
Didelphis albiventris	M	1 J/SA	1 A				1 SA (12 × 15)		
		1 J/SA (small)					1 SA (14 × 10)		
		1 J/SA (7 × 4)							
	F	3 J/SA		1 A		1 A	1 A		
		1 A with 7 pouched young, CRL = 59 mm							
Thylamys elegans	M	1 A TSL (12 × 7)	2 A	3 A		3 A	1 A	3 A	
		1 A TSL (9 × 7)				1 A (6 × 4)			
		2 J							
	F	2 A lac	1 A	3 A NRA	1 A		2 A	3 A	2 A lac
		2 A NRA		1 A					1 J
		1 A							
		1 J							

Lutreolina crassicaudata (Desmarest)

Didelphis crassicaudata Desmarest, Nouveau dictionnaire d'histoire naturelle, appliquée aux arts, à l'agriculture, à l'économie rurale et domestique, à la médicine, etc. par une société de naturalistes et d'agriculteurs, nouveau édition, Ch. Deterville, Paris, 24:19, 1804.

Specimens Examined.—(7) Aconquija, 1 (BMNH); Sierras de Medina, Aguas Chiquitas, El Cadillal, 1 (CM); Piedras Coloradas, 3 (MMP); Quebrada de Lules, 11 km SW San Pablo, 1 (CM); Raco, Sierra San Javier, 3 (2 BMNH, 1 CML); 25 km NW San Miguel de Tucumán, 1 (CM); San Pablo, 11 km al NO, 1 (CML).

Additional Record.—El Indio, Ruta 307 (R. M. Bárquez, personal observation).

Measurements.—External measurements (two males, one female): total length, 446.0, 522.0, 370.0; tail, 226.0, 262.0, 180.0; hindfoot, 38.4, 40.5, 28.0; ear (two males), 24.0, 23.5; weight (one male), 217.0. Cranial measurements (two males, one sex unknown, unless noted otherwise): greatest length of skull (one male, one sex unknown), 64.2, 58.0; condylobasal length (one male, one sex unknown), 63.2, 57.1; least interorbital length, 8.1, 8.4, 7.5; zygomatic breadth, 29.2, 32.2, 29.3; breadth of braincase (one male, one sex unknown), 19.2, 17.3; length of maxillary toothrow, 24.1, 29.7, 23.9; palatal length, 32.8, 31.6, 33.1; length of mandibular toothrow, 19.2, 26.7, 22.4; greatest length of mandible, 45.4, 48.4, 44.4.

Habitat.—In northwestern Argentina, this species is found primarily in humid forested areas in lower montane zones (Olrog, 1976), but it may frequent open areas near water, as in the pampas (Cabrera and Yepes, 1960). *Lutreolina* may be found in habitats ranging from 600–2000 m in elevation. This species is found near water courses (Lucero, 1983).

Remarks.—The populations in northwestern Argentina may possibly represent a new subspecies (Olrog, 1976; Lucero, 1983).

Monodelphis dimidiata (Wagner)

Didelphis dimidiata Wagner, Abhandlungen der Mathem.-physikalischen Classe der Königlich Bayerischen Akademie der Wissenschaften (München), 5(1):151, footnote, 1847.

Specimen Examined.—(1) Concepción, 1 (BMNH).

Measurements.—Cranial measurements (one sex unknown): greatest length of skull, 36.1; condylobasal length, 35.6; least interorbital length, 4.9; zygomatic breadth, 20.1; breadth of braincase, 12.8; length of maxillary toothrow, 12.9; palatal length, 18.9; length of mandibular toothrow, 13.5; greatest length of mandible, 26.8.

Habitat.—It is difficult to define the distribution of this species without causing some taxonomic confusion. Wilson and Reeder (1993) reported the distribution as including Uruguay, southeastern Brazil, and northeastern Argentina, but failed to cite records from north-central and northwestern Argentina. In addition to the province of Tucumán, *M. dimidiata* has been reported from Buenos Aires (Reig, 1964; Dalby, 1975; Pine et al., 1985), Cordoba (Crespo, 1964), and Salta (Ojeda and Mares, 1989). It appears to be a widely distributed, but exceedingly rare, species in northern Argentina.

Remarks.—This specimen housed in the BMNH was collected by Shipton. It is represented by a skull; the skin does not exist. This genus is in need of revision. Although little is known about the biology of this species in the western portion of its range, the ecology, development, and morphometrics have been studied in Buenos Aires Province (Dalby, 1975; Pine et al., 1985). Redford and Eisenberg (1992) did not show this species in Tucumán Province.

Thylamys elegans (Waterhouse)

Didelphis elegans Waterhouse, Mammalia, *in* Darwin, C., The Zoology of H. M. S. *Beagle,* Under the Command of Captain Fitzroy, During the Years 1832–1836, with Notes by Charles Darwin, Part II. Smith, Elder and Co., London, 95, 1839.

Specimens Examined.—(95) Aconquija, 3000 m, 9 (MACN); Burruyacú, 1300 m, 4 (BMNH); 45 km S Cafayate along Hwy 40, 1 (CM); Cerro del Campo, 1 (BMNH); Cerro de Tafí Viejo, 2400 m, 1 (BMNH); Cerro San Javier, 6 (1 CML, 5 MACN); Concepción, 21 (5 BMNH, 1 CML, 15 MACN); El Cadillal, 25 km N San Miguel de Tucumán, 1 (CM); Biological Reserve at Horco Molle, near residencia, 2,400 ft., 17 (6 CML, 5 IADIZA, 6 OMNH); 4 km W junction Hwy 338 and road to Horco Molle along 338, on road to San Javier, 2,750 ft., 1 (OMNH); Horco Molle, 25 km NW San Miguel de Tucumán, 2 (CM); La Higuera, 4 (CML); 5 km N Las Higuerillas on Hwy 308, 2,900 ft., 2 (1 IADIZA, 1 OMNH); 3 km W Lules, 1 (CM); Ñorco, Vipos, 2500 m, 5 (BMNH); Piedra Tendida, 12 km WNW Burruyacú along Río Cajón, 2,500 ft., 2 (OMNH); San Pablo, 2 (BMNH); at km marker 42 on highway 364, south of San Pedro de Colalao, 4,700 ft., 2 (OMNH); 11 km S San Pedro de Colalao, 1 (CM); 17 km NW San Miguel de Tucumán, 3 (CM); Tucumán, 450 m, 1 (BMNH); Villa Nougués, 1200 m, 2 (BMNH); Vipos, 2 (1 CML, 1 MACN).

Additional Records.—Cerro de Raco, Trancas (Tate, 1933); El Cadillal (R. A. Ojeda, personal observation); Sierra de Tucumán (Tate, 1933).

Measurements.—External measurements (33 males, 26 females, unless noted otherwise): total length, 234.6 (148.0–284.0), 233.4 (184.0–281.0); tail, 131.7 (75.0–152.0), 128.7 (98.0–152.0); hindfoot, 16.3 (13.0–20.0), 15.6 (13.0–19.0); ear (32 males, 26 females), 24.0 (16.0–29.8), 24.2 (19.0–30.1); weight (17 males, 18 females), 27.8 (9.0–55.0), 20.3 (12.5–44.0). Cranial measurements (17 males, 11 females, unless noted otherwise): greatest length of skull, 28.9 (22.2–33.3), 29.6 (24.6–32.3); condylobasal length, 28.2 (21.8–32.9), 29.0 (23.7–32.3); least interorbital length, 4.8 (4.3–5.5), 4.6 (4.2–5.1); zygomatic breadth (16 males, ten females), 15.3 (11.8–18.1), 16.1 (12.9–17.8); breadth of braincase, 11.0 (9.7–11.9), 11.0 (9.7–11.5); length of maxillary toothrow (14 males, ten females), 11.1 (7.7–12.2), 11.3 (9.3–11.9); palatal length, 15.0 (11.0–17.2), 15.2 (12.4–16.5); length of mandibular toothrow (14 males, ten females), 10.6 (8.6–12.2), 10.5 (7.9–11.4); greatest length of mandible (14 males, ten females), 19.8 (14.7–23.2), 20.9 (16.3–23.8).

Reproduction.—See Table 2.

Molt.—Molting adults were found in January, March, and September; a molting juvenile was found in January.

Habitat.—Cabrera (1957) and Olrog and Lucero (1981) restricted the distribution of this species to the northwestern Argentine provinces of Salta, Jujuy, Tucumán, and northern Catamarca. Individuals of this species prefer transitional and humid forest below 2000 m, and mesic agricultural areas. Most specimens were collected using Sherman live traps; several were collected in Museum Special traps. At least one individual was collected in a trap set in a tree. At Piedra Tendida, one individual was captured in a Sherman trap set in a dense mat of shrubs, vines, and fallen trees 1–2 m above the ground (M. L. Campbell, personal observation). A second individual was captured in a trap on the ground (M. L. Campbell, personal observation). Lucero (1983) noted that *T. e. cinderella* is found in the humid forest up to 1000 m and *T. e. venusta* is found in the semiarid Chacoan region of the eastern part of the province.

Remarks.—Budin (Thomas, 1926:608–609) noted that "They live in the straw-covered fields, and these specimens I captured by setting the traps in the entrance to the holes of cuises [*Microcavia* and *Galea*]. In other places where I have collected Achocayas I have generally found them under stones and tree-trunks and in holes made on the hill-sides. Very damaging to specimens caught, attacking the head of the latter and extracting the brain."

Thylamys pallidior (Thomas)

Marmosa elegans pallidior Thomas, Annals and Magazine of Natural History, series. 7, 10:161, 1902.

Specimens Examined.—(4) El Bracho, 1 (CML); El Cadillal, 1 (CML); Las Mesadas, 1 (CML); San Pedro de Colalao, 1 (BMNH).

Additional Records.—Tafí del Valle (Tate, 1933); Tapia (Tate, 1933); Vipos (Thomas, 1926; Tate, 1933).

Measurements.—External measurements (two males, one sex unknown): total length, 200.0, 150.0, 186.0; tail, 101.0, 75.0, 92.0; hindfoot, 12.0, 10.0, 11.0; ear, 24.0, 15.0, 23.0. Cranial measurements (one male, one sex unknown, unless noted otherwise): greatest length of skull (one male), 22.8; condylobasal length (one sex unknown), 24.2; least interorbital length, 3.7, 3.8; zygomatic breadth, 12.8, 14.7; breadth of braincase, 10.0, 10.6; length of maxillary toothrow, 8.2, 9.3; palatal length, 11.6, 13.2; length of mandibular toothrow, 9.3, 9.9; greatest length of mandible, 15.8, 18.3.

Habitat.—*Thylamys pallidior* is distributed in western Argentina from Neuquén and Río Negro northward. This species is found in the arid and semiarid regions of Tucumán—the Chaco, the monte desert (Mares, 1973, 1976), and occasionally in transitional forest (Cajal, 1981; Ojeda and Mares, 1989). *Thylamys p. bruchi* inhabits the mountains and hills of the lowlands of the province; *T. p. pallidor* inhabits the arid shrubby steppes in the mountainous portion of the province (Lucero, 1983).

Remarks.—Budin (Thomas, 1926:609) noted that a single individual was "Trapped on a stony hill on the banks of the Río Vipos." Tate (1933) discussed the difference between *pusilla* and *pallidior.* He (Tate, 1933:223) stated that "*Pusilla* bears a considerable likeness to *pallidior,* but can be distinguished by its longer tail, much greater size in adulthood, larger feet and ears,—besides the cranial characters pertaining to the section in which the animals belong, as interorbital breadth, etc." Specimens of *T. pallidior* lack the pronounced postorbital constriction that is present in *T. pusilla. Thylamys pallidior* was recently recognized again as a species distinct from *T. pusilla*; the distribution of *T. pusilla* has been restricted to northeastern Argentina, central and southern Brazil, Paraguay, and southeastern Bolivia (Wilson and Reeder, 1993).

Order Xenarthra
Family Dasypodidae
Subfamily Dasypodinae
Cabassous chacoensis Wetzel

Cabassous chacoensis Wetzel, Annals of Carnegie Museum, 49:335, 1980.

Specimens Examined.—(0) None.

Additional Record.—Departamento Burruyacú (C. C. Olrog, personal observation).

Habitat.—Lucero (1983) noted that this armadillo inhabits the subtropical semihumid transitional forest, savannas, and mountains in the northeastern region of the province. In general, the distribution of this species coincides with the distribution of the Gran Chaco of northwestern Argentina, western Paraguay, and southeastern Bolivia and perhaps part of western Brazil (Wetzel, 1980). This species may occur in the dry Chaco found in eastern Tucumán Province.

Remarks.—Although there are no specimen records of this species for the province, specimens have been reported from Santiago del Estero and Formosa (Wetzel, 1980). The individual listed above was observed in early April. Specimens belonging to this species may be listed as *C. loricatus* (Yepes, 1935; Cabrera, 1957), which was synonymized with *C. chacoensis* by Wetzel (1980). There is little information on this species. It seems generally to be rare and known specimen records are scarce. Redford and Eisenberg (1992) did not extend the distribution of this species to Tucumán Province.

Chaetophractus vellerosus (Gray)

Dasypus vellerosus Gray, Proceedings of the Zoological Society of London, 1865:376, 1865.

Specimens Examined.—(12) Agua Rosada, 1 (CML); Concepción, 2 (1 MACN, 1 BMNH); Estancia El Cavao, 1 (CML); La Cocha, 380 m, 1 (BMNH); San Miguel de Tucumán, 4 (2 BMNH, 2 CML); San Pedro de Colalao, 1 (CML); Tapia de Tucumán, 600 m, 1 (BMNH); Vipos, 1 (MACN).

Additional Records.—12 km W La Quebradita, km 81 along Hwy 307, 9,500 ft. (J. K. Braun, personal observation; M. L. Campbell, personal observation); Tucumán (Thomas, 1902; Yepes, 1929).

Measurements.—External measurements (one male, one female): total length, 335.0, 443.0; tail, 102.0, 110.0; hindfoot, 43.0, 50.0; ear, 31.0, 32.0. Cranial measurements (three males, two females, one sex unknown): greatest length of skull, 65.1 (63.7–66.1), 65.3, 62.5, 62.2; condylobasal length, 59.2 (43.7–64.6), 52.3, 61.0, 49.0; least interorbital length, 16.6 (16.2–17.2), 15.5, 17.1, 16.8; zygomatic breadth, 40.1 (37.7–41.8), 37.0, 38.8, 38.4; breadth of braincase, 26.3 (25.8–27.1), 26.9, 25.8, 26.5; length of maxillary toothrow, 29.6 (25.8–27.1), 29.2, 27.3, 27.8; palatal length, 37.4 (33.8–41.0), 41.0, 34.6, 39.5; length of mandibular toothrow, 30.9 (30.4–31.3), 31.5, 29.3, 30.4; greatest length of mandible, 49.8 (49.2–50.5), 49.5, 48.4, 48.1.

Habitat.—This species is common in the monte desert; it is also found in forests and in the Chaco. Burrows of this species were seen at La Quebradita (J. K. Braun, personal observation; M. L. Campbell, personal observation).

Remarks.—Single individuals have been collected in March and July. The ecology of this species in other provinces (Jujuy, La Rioja, and San Luis) has been described (Crespo, 1944; Greegor, 1975, 1980*a*, 1980*b*, 1985). Wetzel (1982, 1985) suggested that this species is in need of systematic study.

Euphractus sexcinctus (Linnaeus)

Dasypus sexcinctus Linnaeus, Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tenth edition. Laurentii Salvii, Stockholm, 1:51, 1758.

Specimens Examined.—(5) Capital, San Miguel de Tucumán, 1 (CML); Monte Bello, Trancas, 1 (CML); San Pedro de Colalao, 2 (CML); Tapia, 1 (BMNH).

Additional Record.—Tapia (Thomas, 1907).

Measurements.—Cranial measurements (three males, unless noted otherwise): greatest length of skull, 110.8 (104.1–120.5); condylobasal length, 103.1 (83.0–121.3); least interorbital length, 26.8 (25.5–28.5); zygomatic breadth (two males), 72.3, 58.0; breadth of braincase, 42.0 (40.2–45.5); length of maxillary toothrow, 50.0 (48.1–53.7); palatal length, 65.0 (59.5–69.6); length of mandibular toothrow (two males), 58.8, 52.6; greatest length of mandible (two males), 92.0, 80.1.

Habitat.—This species is found in transitional forests, savannas, Chacoan thorn scrub, and mountains up to 2000 m (Olrog and Lucero, 1981; Lucero, 1983).

Olrog and Lucero (1981) restricted the distribution of this species to the Chaco region.

Remarks.—Single individuals have been captured in March, April, and September. Redford and Wetzel (1985) described the biology of this species.

Priodontes maximus Kerr 1792

Dasypus maximus Kerr, *in* Linnaeus, The animal kingdom, or zoological system, of the celebrated Sir Charles Linnaeus. J. Murray and R. Faulder, London, p. 112.

Specimens Examined.—(0) None.

Habitat.—In this part of Argentina, the giant armadillo is found in mature Chacoan thorn scrub.

Remarks.—Mares et al. (1989) reported this species across eastern Salta Province, all the way to the Tucumán border. Olrog and Lucero (1981) show the range of the species in Argentina as just abutting the limits of northeastern Tucumán Province. We consider this species to be probable in the Chacoan zone of extreme northeastern Tucumán. *Priodontes maximus* is considered vulnerable by the International Union for the Conservation of Nature (1994).

Tolypeutes matacus (Desmarest)

Loricatus matacus Desmarest, Nouveau dictionnaire d'histoire naturelle, appliquée aux arts, à l'agriculture, à l'économie rurale et domestique, à la médicine, etc. par une société de naturalistes et d'agriculteurs, Nouveau édition., Ch. Deterville, Paris, 24:28, 1804.

Specimens Examined.—(4) Agua Rosada, San Pedro de Colalao, 1 (CML); Chicligasta, 1 (CML); Rearte Norte, 1 (CML); San Pedro de Colalao, 1 (CML).

Additional Records.—Tucumán, 450 m (Sanborn, 1930); Tucumán, no specific locality (Desmarest, 1804).

*Habitat.*This species is found in a variety of habitats, but is most common in savannas, mountains, and shrubby arid regions in the mountains of northwestern Tucumán Province up to 2000 m (Olrog and Lucero, 1981; Lucero, 1983).

Remarks.—According to Cabrera (1957) and Wetzel (1982), this species once inhabited all of northern Argentina southward to Río Negro and Santa Cruz. The distribution was later restricted to no further south than the province of Buenos Aires (Wetzel, 1985). *Tolypeutes* may be absent from Entre Ríos, Corrientes, and Misiones. The type locality was designated as Tucumán by Sanborn (1930). Single individuals have been collected in January, March, and August.

Family Myrmecophagidae

Myrmecophaga tridactyla Linnaeus

Myrmecophaga tridactyla Linnaeus, Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tenth edition. Laurentii Salvii, Stockholm, 1:35, 1758.

Specimens Examined.—(0) None.

Habitat.—If this species occurs in the province, it would inhabit the Chacoan thorn scrub or possibly the transitional forest.

Remarks.—Cabrera (1957) reported this species from the provinces of Salta, Formosa, Chaco, and Misiones. It is also common and widely distributed in the province of Santiago del Estero. Olrog and Lucero (1981) indicated the distribution as also including Corrientes Province, northern Santa Fe Province, and Tucumán. This species inhabits the Chacoan habitat of Tucumán (C. C. Olrog, personal communication), although there is no recent information regarding its presence. This species is considered vulnerable in Argentina (International Union for the Conservation of Nature, 1990, 1994). This anteater is considered an Appendix II species in Argentina and is protected (Fuller and Swift, 1984).

Tamandua tetradactyla (Linnaeus)

Myrmecophaga tetradactyla Linnaeus, Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tenth edition. Laurentii Salvii, Stockholm, 1:35, 1758.

Specimens Examined.—(5) Alderetes, 1 (CML); Chicligasta, 1 (CML); Cuesta del 25, Ruta 9, entrada al Cadillal, 1 (CML); Garmendia, Departamento Burruyacú, 1 (CML); San Javier, Ciudad Universitaria, 1 (CML).

Additional Records.—El Cadillal (R. M. Bárquez and R. A. Ojeda, personal observation); Horco Molle (R. M. Bárquez, personal observation).

Habitat.—Lucero (1983) noted that this species inhabits the Chaco, grasslands, and transitional forests of the province. It is distributed throughout northern Argentina, from the western forests, across the Chaco, to northern Córdoba, Santa Fe, and Entre Ríos.

Remarks.—This is considered an Appendix II species in Argentina and is protected (Fuller and Swift, 1984). Single individuals have been collected in June, July, and December. This species is relatively common in the province especially in transitional forest and in the lower-elevation montane forests. It is less common in the Chacoan thorn scrub. Redford and Eisenberg (1992) did not extend the distribution of this species to Tucumán Province.

Order Chiroptera

Family Phyllostomidae

Subfamily Phyllostominae

Chrotopterus auritus (Peters)

Vampyrus auritus Peters, Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin, 1865:5, 1856.

Specimen Examined.—(1) Dique San Ignacio, 1 (CML).

Habitat.—In Argentina, this species is found in dense forests in Jujuy, Salta, Tucumán, Chaco, Formosa, and Misiones (Bárquez, 1987).

Remarks.—The subspecies found in Argentina is *C. a. australis* (Bárquez, 1987). Bárquez (1987) summarized the biology of this species. Although we have netted extensively for this bat in Tucumán, this remains the only known record of occurrence for the province.

Subfamily Stenodermatinae

Artibeus planirostris (Spix)

Phyllostoma planirostre Spix, Simiarum et Vespertilionum Brasiliensium species novae. Monachii, p. 66, 1823.

Specimens Examined.—(19) Agua Colorada, 8 (MACN); Aguas Chiquitas, El Cadillal, 800 m, 1 (CM); Reserva Provincial "Aguas Chiquitas" El Cadillal, 4 (CM); Las Juntas, 22 km W Choromoro on Hwy 312, 3,500 ft., 2 (1 CML, 1 OMNH); Playa Larga, 1 (CML); Quebrada del Toro, 1 (CML); Río Loro, 1 (CML); Taco Yana, 1 (CML).

Measurements.—External measurements (two males, one female): total length, 90.0, 95.0,—; hindfoot, 16.4, 7.0,—; ear, 21.0, 22.0,—; forearm,—, 69.0,—;

weight, 55.8, 60.0, 45.0. Cranial measurements (two males): greatest length of skull, 30.0, 32.1; condylobasal length, 27.3, 29.0; least interorbital length, 7.5, 7.9; zygomatic breadth, 19.9, 19.7; breadth of braincase, 14.0, 15.0; length of maxillary toothrow, 10.7, 11.9, palatal length, 14.7, 15.6; length of mandibular toothrow, 10.0, 11.6; greatest length of mandible, 21.4, 20.4.

Reproduction.—See Table 3.

Habitat.—In Argentina, this species is restricted to the provinces of the northwest, Jujuy, Salta, Tucumán, and possibly Catamarca. Specimens have been collected in humid and transitional forest, including montane transitional forest (Bárquez and Ojeda, 1992; Mares et al., 1995). Individuals captured at Las Juntas were collected in a net placed over the Río Choromoro (Mares et al., 1995). The Río Loro locality is transitional forest surrounded by Chacoan vegetation (Bárquez and Ojeda, 1992).

Remarks.—In some publications, for example, Olrog and Lucero (1981), this species is listed as *A. jamaicensis.* At Las Juntas, this species was captured with individuals of *Sturnira erythromos, Histiotus macrotus, Lasiurus blossevillii,* and *Tadarida brasiliensis.* Specimens have been collected in January (*n* = 1), July (*n* = 2), and October (*n* = 4). *Artibeus planirostris* is either uncommon in the province or common but not abundant (Bárquez, 1988). Bárquez (1987) reviewed the biology of this species in Argentina.

Sturnira erythromos (Tschudi)

Phyllostoma erythromos Tschudi, Untersuchungen über die Fauna Peruana. Therologie. Scheitlin und Zollikofer, St. Gallen, Switzerland, p. 64, 1844.

Specimens Examined.—(52) Reserva Provincial El Cadillal "Aguas Chiquitas," 1 (CM); El Naranjal, 1 (TTU); Horco Molle, 15 km W San Miguel de Tucumán, 28 (8 CM, 20 CML); Biological Reserve at Horco Molle, near residencia, 2,400 ft., 1 (OMNH); Las Juntas, 22 km W Choromoro, 3,500 ft., 2 (1 CML, 1 OMNH); Piedra Tendida, 12 km WNW Burruyacú, along Río Cajón, 2,500 ft., 3 (1 CML, 1 IADIZA, 1 OMNH); Playa Larga, 1 (CML); Quebrada de Lules, 11 km NW San Pablo, 3 (CM); Río de los Sosa, Ruta 307, km 19.7, camino a Tafí del Valle, 750 m, 1 (OMNH); Río de los Sosa, Ruta 307, km 23.9, camino a Tafí del Valle, 850 m, 5 (OMNH); Río de los Sosa, Ruta 307, km 24.9, camino a Tafí del Valle, 850 m, 3 (OMNH); at km marker 42, on highway 364, south of San Pedro de Colalao, 4,700 ft., 1 (OMNH); entrando por Ticucho, cola del Dique El Cadillal, 1 (OMNH); Ticucho, 1 (CML).

Measurements.—External measurements (17 males, 12 females, unless noted otherwise): total length, 56.5 (50.0–63.0), 54.1 (49.0–60.0); hindfoot, 11.2 (7.0–14.0), 12.1 (9.0–14.0); ear, 16.7 (12.0–18.7), 16.6 (14.0–18.0); forearm, 41.4 (38.8–43.0), 41.0 (39.5–42.4); weight (16 males, 12 females), 16.0 (12.0–23.0), 16.4 (12.0–21.0). Cranial measurements (16 males, 11 females, unless noted otherwise): greatest length of skull, 20.9 (19.6–21.8), 20.4 (19.8–21.4); condylobasal length, 18.9 (18.0–19.8), 18.6 (18.1–19.8); least interorbital length, 6.0 (5.6–6.3), 5.9 (5.6–6.1); zygomatic breadth (15 males, six females), 12.7 (11.2–13.6), 12.5 (11.9–13.0); breadth of braincase, 10.3 (9.8–11.0), 10.1 (9.8–10.5); length of maxillary toothrow (16 males, ten females), 5.9 (5.1–6.3), 5.7 (5.3–6.1); palatal length (16 males, nine females), 8.2 (5.2–9.4), 8.3 (8.0–8.5); length of mandibular toothrow (16 males, ten females), 5.3 (4.9–6.1), 5.4 (5.0–5.6); greatest length of mandible (15 males, nine females), 13.0 (11.8–19.9), 12.5 (11.9–13.2).

Reproduction.—See Table 3.

Molt.—Individuals collected in July showed no sign of molting.

Habitat.—In Argentina, this species is known only from the provinces of Jujuy, Salta, and Tucumán (Bárquez, 1987). In Tucumán, all specimens were collected

Table 3.—*Reproductive data for the Chiroptera. Symbols: A = adult; SA = subadult; J = juvenile; TSL = large scrotal testes; lac = lactating; NRA = not reproductively active; length and width of testes, or qualitative evaluation, are given in parentheses; CRL = crown–rump length of embryos or young. August has no data.*

Taxon	Sex	January	February	March	April	May	June	July	September	October	November	December
Artibeus planirostris	M	1 A						1 A (6 × 4)		Males (TS)		
	F							1 (VO)				
Sturnira erythromos	M	1 A (5 × 4) 5 A				1 (TA)		1 (TA) (5 × 3) 1 A	4 NS (4.1–5.6) 1 (TA) (3.1 × 1.4)	3 (TS)		
	F	1 (VC)					1 A	2 A	5 A	2 (Pg, *n* = 1) 1 (VO) 1 A	1 A	
Sturnira lilium	M	1 (TS)		1 A					1 (TA) 4.1 1 (TA) 4.4 1 (TA) 2.1	1 (TS) 2 A		
	F			2 A		1 A			4 A 1 (Pg, *n* = 1) CRL = 17.1	5 A		
Sturnira oporaphilum	M	1 (TS)										
	F											
Desmodus rotundus	M								1 (TS)	1 A		
	F								1 A			
Eptesicus diminutus	M	1 J										
	F	1 lac 1 A										1 A
Eptesicus furinalis	M											1 A
	F	1 A		1 A								2 A
Histiotus macrotus	M		1 A	1 A				1 A				
	F		4 A						1 A		1 A	
Lasiurus blossevillii	M							1 A				
	F		1 A									
Lasiurus ega	M						1 (TS) (6.0)					
	F											
Myotis albescens	M	1 A			1 (TS)							
	F					2 A 1 (VC)						

Table 3.—*Continued.*

Taxon	Sex	January	February	March	April	May	June	July	September	October	November	December
Myotis	M						1 A					
keaysi	F											
Myotis	M	4 A										2 A
levis	F	12 A										
		1 J										
Myotis	M			1 (TSL)				1 (TA) (1 × 1)				
nigricans	F		1 A									
Eumops	M			1 A								2 A
bonariensis	F	3 A		1 A	1 A					3 A		3 A
												2 lac
Eumops	M											1 J
dabbenei												
	F											
Eumops	M			1 A	1 (TS)							
patagonicus	F			1 A						1 A		
Eumops	M			1 (TA small) (4.1)							J?	
perotis	F										J?	
Molossops	M									1 (TS)		
temminckii	F											
Molossus	M											
molossus	F											1 J
Nyctinomops	M					NRA	NRA					
macrotis	F					NRA	NRA					
Promops	M						1 (TS)					
nasutus	F											
Tadarida	M	(4 × 2)		1 (TA)						2 A		
brasiliensis		(3 × 2)										
		1 A										
	F			d1 (VC)				5 A		1 A		

in transitional forest, primarily in nets near sources of water. Bárquez and Ojeda (1992) noted that all Chacoan localities in the province are near Yungas forest.

Remarks.—Because individuals of this species have been confused with *S. lilium* and *S. oporaphilum,* little is known (with confidence) about the biology of this species (but see Bárquez, 1987). Specimens have been captured in January (*n* = 7), May (*n* = 1), June (*n* = 1), July (*n* = 4), September (*n* = 10), October (*n* = 6), and November (*n* = 1). At Horco Molle, this was the only species captured; individuals of *Tadarida brasiliensis* were captured several days earlier (Mares et al., 1995). Other species captured at Las Juntas include *Artibeus planirostris, Histiotus macrotus, Lasiurus blossevillii,* and *Tadarida brasiliensis. Myotis keaysi* and *Myotis nigricans* also were captured at Piedra Tendida, and at San Pedro de Colalao *Myotis levis* also was captured.

Sturnira lilium (E. Geoffroy)

Phyllostoma lilium E. Geoffroy, Annales Museum d'Histoire Naturelle, Paris, 15:181, 1810.

Specimens Examined.—(57) Agua Colorada, 11 (9 MACN, 2 TTU); Casa de Piedra, Río Los Sosa, 4 (CML); Dique San Ignacio, 1 (CML); El Cadillal, 1 (OMNH); Horco Molle, 15 km W San Miguel de Tucumán, 17 (10 CM, 7 OMNH); Ingenio San Pablo, 1 (MACN); La Cocha, Dique San Ignacio, 1 (OMNH); Los Sarmientos, 1 (CML); Playa Larga, 8 (CML); Río Los Sosa, Ruta 307, km 19.7, 700 m, 1 (OMNH); Ruta 307, km 19.7, camino a Tafí del Valle, 750 m, 5 (OMNH); Ruta 307, km 23.9, 850 m, 1 (OMNH); Ruta 307, km 24.9, camino a Tafí del Valle, 850 m, 2 (OMNH); San Miguel de Tucumán, 2 (BMNH); San Pedro de Colalao, 1 (TTU).

Measurements.—External measurements (eight males, 13 females, unless noted otherwise): total length, 60.5 (57.0–64.5), 61.1 (51.0–70.0); hindfoot, 12.3 (9.2–14.1), 12.2 (9.3–14.8); ear, 17.6 (16.0–19.5), 17.2 (13.0–19.5); forearm (nine males, 13 females), 44.1 (41.7–46.0), 43.1 (38.7–45.9); weight (eight males, 11 females), 22.8 (20.0–28.0), 21.7 (17.0–25.0). Cranial measurements (eight males, 13 females, unless noted otherwise): greatest length of skull (eight males, 12 females), 23.1 (22.1–23.9), 22.2 (20.1–23.3); condylobasal length (eight males, 12 females), 21.1 (20.3–21.8), 20.2 (18.4–21.0); least interorbital length (nine males, 13 females), 6.1 (5.8–6.5), 6.0 (5.5–6.8); zygomatic breadth (seven males, nine females), 13.7 (13.0–14.0), 13.3 (12.1–14.3); breadth of braincase, 10.8 (10.2–11.3), 10.6 (9.5–11.2); length of maxillary toothrow (nine males, 11 females), 6.8 (6.3–7.4), 6.6 (5.5–7.3); palatal length (seven males, 13 females), 9.7 (9.4–10.0), 9.2 (8.4–10.0); length of mandibular toothrow, 6.5 (6.2–6.9), 6.3 (5.0–6.7); greatest length of mandible (eight males, 12 females), 14.6 (13.8–15.5), 14.0 (13.0–15.0).

Reproduction.—See Table 3. Bárquez (1988) reported on the reproductive biology of bats sampled between 12–16 October at Ruta 307, km 23.9. For females sampled, 41% were pregnant, 6% were lactating, 41% had open (perforate) vaginas but without palpable fetuses, and 12% had closed vaginas. Males with abdominal testes comprised 58% of the sample; 42% had scrotal testes. During a later survey (28–30 October), all males (100%) had scrotal testes, 50% of the females had small palpable fetuses, and 50% were near parturition. In mid-January, young were flying and there was a decrease in reproductive activity. Samples at this time showed 4% of males with scrotal testes, 43% were adults with abdominal testes, and 53% were juveniles with abdominal testes. Adult females were lactating, but 77% of all females were juveniles. Individuals captured at a nearby location in May were not reproductivly active and population densities were lower.

Habitat.—In Argentina, *S. lilium* is distributed in the northwestern provinces of Jujuy, Salta, Tucumán, and Catamarca. It is also found in the northeastern provinces of Chaco, Formosa, Misiones, Entre Ríos, and Santa Fe (Bárquez, 1987). Lucero (1983) noted that *S. lilium* is locally common in humid and transitional forests. It apparently prefers the low vegetation forest stratum (Bárquez, 1987). Few specimens document the presence of this species in the Chaco of Tucumán. Two localities, Agua Colorada and El Cadillal, are gallery forests. Bárquez and Ojeda (1992) suggested that these records reflect a shift from forests to the Chaco during periods of limited availability of fruit.

Remarks.—At Río Los Sosa, Rt. 307, km 23.9, this species was captured with *Artibeus planirostris, Histiotus macrotus, Lasiurus cinereus,* and *Tadarida brasiliensis. Sturnira lilium* commonly eats the fruit of the Solanaceae, although at Horco Molle it has been found eating fruit of the introduced moras (mulberry). This species is not common in urban environments, although Bárquez (1987) reported that pellets from Barn Owls (*Tyto alba*) found in buildings in the city of Tucumán contained skulls of young and subadult *S. lilium.* Owls might prey on *S. lilium* as they fly through the city or else are foraging in nearby forests.

Sturnira oporaphilum (Tschudi)

Phyllostoma oporaphilum Tschudi, Untersuchungen über die Fauna Peruana. Therologie. Scheitlin und Zollikofer, St. Gallen, Switzerland, p. 64, 1844.

Specimen Examined.—(1) Casa de Piedra, Ruta 307, km 23.9, 850 m, 1 (OMNH).

Additional Record.—A specimen identified as this species was recently captured and released at Piedra Tendida (P. Capllonch, personal communication).

Measurements.—External measurements (one male): total length, 58.5; hindfoot, 9.5; ear, 18.5; forearm, 44.2; weight, 21.0. Cranial measurements (one male): greatest length of skull, 22.7; condylobasal length, 20.7; least interorbital length, 6.2; zygomatic breadth, 13.6; breadth of braincase, 10.9; palatal length, 9.0; length of mandibular toothrow, 6.5; greatest length of mandible, 13.5.

Reproduction.—See Table 3.

Habitat.—In Argentina, *S. oporaphilum* is distributed in the transitional forest habitats of Jujuy, Salta, and Tucumán.

Remarks.—Bárquez (1987) reviewed the biology of this species, which is little known in Argentina. In Wilson and Reeder (1993), this species is listed as *S. bogotensis.* In the localities where it has been captured, it is sympatric with *S. lilium* and *S. erythromos.*

Subfamily Desmodontinae

Desmodus rotundus (E. Geoffroy)

Phyllostoma rotundus E. Geoffroy, Annales Museum d'Histoire Naturelle, Paris, 15:181, 1810.

Specimens Examined.—(13) El Cadillal, 1 (CML); Horco Molle, 15 km SW San Miguel de Tucumán, 1 (CM); Monte Bello, 3 (CML); Piedra Buena, 1 (TTU); Playa Larga, 1 (CML); Río Los Sosas, Ruta 307, km 23.9, 1 (OMNH); Vipos, Estancia San Pedro, 3 (CML).

Measurements.—External measurements (three males, two females, unless noted otherwise): total length, 82.9 (80.0–88.0), 85.0, 91.0; hindfoot, 16.7 (16.0–17.0), 16.0, 18.6; ear, 17.9 (17.0–19.6), 18.0, 20.7; forearm (four males, two females), 62.1 (60.0–64.0), 62.0, 65.2; weight (one male, one female), 43.0, 48.0. Cranial measurements (four males, two females, unless noted otherwise): greatest length of skull, 24.7 (24.2–25.4), 24.7, 25.6; condylobasal length, 22.4 (22.2–22.6), 22.5, 22.9; least interorbital length, 5.6 (5.2–6.0), 5.7, 5.4; zygomatic breadth, 12.3 (11.9–12.7), 12.5, 11.6; breadth of braincase, 12.1 (11.1–12.6), 12.8, 12.8; length of maxillary toothrow (one female), 3.5; palatal length (three males, one female), 9.0 (8.9–9.2), 8.8; greatest length of mandible (one male, one female), 14.2, 16.1.

Reproduction.–See Table 3.

Habitat.—Vampire bats are widely distributed in Argentina as far south as approximately 32°S latitude. In Tucumán, these bats are found in savannas, grasslands, and open rural areas up to 2000 m (Olrog and Lucero, 1981; Lucero, 1983).

Remarks.—Although groups composed of up to 5000 individuals have been reported in other parts of the range, in Tucumán vampire bats form much smaller aggregations. They commonly are found in wells in the countryside. Bárquez (1987) reviewed the biology of this species in Argentina.

Family Vespertilionidae
Subfamily Vespertilioninae
Eptesicus diminutus Osgood

Eptesicus diminutus Osgood, Field Museum of Natural History, Zoological Series, 10:197, 1915.

Specimens Examined.—(4) Aguas Chiquitas, Sierras de Medina, 800 m, 3 (CM); El Cadillal, Estación de Piscicultura, 1 (CM).

Measurements.—External measurements (one male, two females): total length, 86.0, 89.0, 91.0; tail, 32.0, 35.0, 32.0; hindfoot, 6.2, 6.8, 7.0; ear, 13.3, 13.5, 13.6; forearm, 32.3, 32.7, 34.0; weight, 4.9, 5.7, 6.3. Cranial measurements (one male, two females, unless noted otherwise): greatest length of skull, 13.1, 13.6, 13.3; condylobasal length, 12.4, 12.6, 12.9; least interorbital length, 3.6, 3.8, 3.8; zygomatic breadth, 8.6, 8.9, 8.9; breadth of braincase, 6.5, 6.7, 7.1; length of maxillary toothrow, 4.7, 5.0, 4.9; palatal length, 4.7, 5.3, 5.2; length of mandibular toothrow, 4.2, 4.5, 4.6; greatest length of mandible (two females), 9.9, 9.5.

Reproduction.—See Table 3.

Habitat.—*Eptesicus diminutus* is widely distributed in Argentina, although museum records are scarce. In addition to the localities given above for Tucumán, this species is known from one locality each in the provinces of La Pampa, Buenos Aires, Santa Fe, Corrientes, Misiones, Jujuy, and Salta (Bárquez, 1987; Bárquez and Lougheed, 1990).

Remarks.—The taxonomic history of this taxon was discussed by Bárquez (1987). Specimens were captured in December ($n = 1$) and January ($n = 3$). Little is known of the biology of this species.

Eptesicus furinalis (d'Orbigny)

Vespertilio furinalis d'Orbigny, Voyage dans l'Amérique Méridionale (le Brésil, la République orientale de Uruguay, la République Argentine, la Patagonie, la République du Chile, la République de Bolivia, la République du Perou) executé pendant das années 1826, 1827, 1828, 1829, 1830, 1831, 1832, et 1833. Pitois-Levrault, et cie, Paris, Strasbourg, 4:13, 1847.

Specimens Examined.—(13) Aguas Chiquitas, Sierras de Medina, 800 m, 4 (CM); Concepción, 3 (BMNH); El Cadillal, 1 (CML); Las Mesadas, 1 (CML); Las Talas, 1 (CML); Las Talas, 4 km al N de Bella Vista, 1 (OMNH); San Miguel de Tucumán, 2 (1 BMNH, 1 CML).

Measurements.—External measurements (one male, four females): total length, 102.0, 104.2 (99.5–111.0); tail, 40.0, 41.6 (37.0–45.0); hindfoot, 7.7, 8.6 (7.1–10.1); ear, 15.0, 15.6 (14.7–17.3); forearm, 38.8, 39.7 (37.6–41.2); weight, 8.5, 10.2 (7.4–13.0). Cranial measurements (one male, four females): greatest length of skull, 15.0, 15.5 (14.8–16.0); condylobasal length, 14.5, 15.0 (14.3–15.3); least interorbital length, 3.7, 3.8 (3.7–4.0); zygomatic breadth, 10.4, 10.8 (9.8–11.3); breadth of braincase, 7.0, 7.7 (7.2–8.0); length of maxillary toothrow, 5.6, 5.9 (5.7–6.0); palatal length, 6.1, 6.5 (6.0–7.4); length of mandibular toothrow, 5.3, 5.8 (5.5–6.5); greatest length of mandible), 11.3, 11.9 (11.2–12.2).

Habitat.—*Eptesicus furinalis* is distributed from 36°S latitude northward, excluding the provinces of San Luis and San Juan (Bárquez, 1987; Bárquez and Lougheed, 1990).

Remarks.—*Eptesicus f. findleyi* occurs in the montane regions of northwestern Argentina (Williams, 1978). Myers and Wetzel (1983) synonymized this taxon with *E. f. furinalis*, an arrangement that was followed by Bárquez (1987). Little is known about the biology of this species in Argentina. Myers (1977) and Myers and Wetzel (1983) reported on the biology of this species in Paraguay.

Histiotus macrotus (Poeppig)

Nycticeius macrotus Poeppig, Reise in Chile, Peru und auf dem Amazonenstrome während der Jahre 1827–1832. Friedrich Fleischer, Leipzig, 1:451, 1835.

Specimens Examined.—(29) Anta Mapú, 1 (MACN); El Cadillal, 1 (CML); El Naranjal, 2 (1 MACN, 1 TTU); El Naranjo, 8 (3 MACN, 5 TTU); El Nogalar, km 43, Ruta 307, 1700m, 4 (CML); Horco Molle, 15 km W San Miguel de Tucumán, 1 (CM); Las Juntas, 22 km W Choromoro on Hwy 312, 3,500 ft., 1 (OMNH); Ñorco, 2500 m, 2 (BMNH); San Miguel de Tucumán, 4 (2 BMNH, 1 CM, 1 CML); San Pedro de Colalao, 4 (CML); Tafí, 2000 m, 1 (BMNH).

Measurements.—External measurements (six males, two females, unless noted otherwise): total length (two males, two females), 107.0, 113.0, 110.0, 109.0; tail (four males, two females), 55.0 (50.0-59.0), 46.0, 49.0; hindfoot (five males, two females), 9.2 (7.0–10.0), 9.8, 8.5; ear, 34.1 (27.0–38.0), 37.1, 34.5; forearm, 46.7 (44.0–48.9), 45.2, 47.7; weight (two males, one female), 9.0, 10.5, 11.0. Cranial measurements (four males, two females, unless noted otherwise): greatest length of skull, 17.5 (16.7–18.1), 17.7, 16.5; condylobasal length, 16.3 (15.7–17.0), 17.0, 17.1; least interorbital length (six males, two females), 4.1 (3.8–4.6), 4.0, 4.2; zygomatic breadth, 10.6 (10.1–11.2), 10.1, 10.6; breadth of braincase, 8.4 (8.3–8.4), 7.7, 8.0; length of maxillary toothrow (five males, two females), 6.0 (5.0–6.4), 6.0, 6.0; palatal length (four males, one female), 7.3 (6.8–7.9), 7.2; length of mandibular toothrow, 6.2 (5.6–6.7), 5.5, 6.4; greatest length of mandible, 12.2 (11.8–12.5), 11.8, 12.1.

Reproduction.—Bárquez (1987) reported that specimens captured in May and June were not reproductively active.

Habitat.—*Histiotus macrotus* is found in the forests of the northwestern part of the province and ranges into the arid Monte Phytogeographic Province (Bárquez, 1987). This species is found from Jujuy and Salta south to Río Negro (Bárquez, 1987; Bárquez and Lougheed, 1990). In transitional forest at Las Juntas, a single individual of this species was captured in a net placed over the Río Choromoro (Mares et al., 1995).

Remarks.—At Las Juntas, this species was captured with *Artibeus planirostris, Sturnira erythromos, Lasiurus blossevillii,* and *Tadarida brasiliensis.* Adults were collected in February (n = 5), March (n = 1), July (n = 1), September (n = 1), and November (n = 1). At San Pedro de Colalao, individuals were captured inside a dwelling and were flying over the city (Bárquez, 1987). Little is known about the biology of this species in Argentina.

Lasiurus blossevillii (Lesson and Garnot)

Vespertilio blossevillii Lesson and Garnot, Bulletin des Sciences Naturelles et de Géologie, 8:95, 1826.

Specimens Examined.—(23) Acheral, 1 (CML); Agua Rosada, 1 (CML); Concepción, 3 (BMNH); Horco Molle, 1 (TTU); Ingenio Amalia, 1 (CML); Ingenio Santa Lucía, 1 (CML); Instituto Lillo, 1 (CML); Las Juntas, 22 km W Choromoro on Hwy 312, 3,500 ft., 1 (OMNH); Los Vázquez, 445 m, 3 (BMNH); San Miguel de Tucumán, 6 (3 BMNH, 3 CML); San Pedro de Colalao, 2 (CML); Timbó Nuevo, 1 (CML); Tucumán, 1500 m (no specific locality), 1 (BMNH).

Additional Record.—El Colmenar (Romaña and Abalos, 1950).

Measurements.—External measurements (five males, three females, unless noted otherwise): total length, 97.4 (92.5–104.0), 103.3 (100.0–105.0); tail, 48.5 (45.0–53.0), 49.7 (47.0–52.0); hindfoot, 8.2 (6.5–11.0), 7.8 (7.5–8.0); ear, 9.4 (4.0–13.0), 9.3 (6.0–11.0); forearm (eight males, three females), 38.7 (36.9–40.0), 40.2 (39.0–40.9); weight (one male), 9.0. Cranial measurements (seven males, three females, unless noted otherwise): greatest length of skull, 11.8 (11.2–12.8), 11.8 (11.5–12.1); condylobasal length, 10.5 (9.5–11.3), 11.7 (11.5–11.8); least interorbital length, 4.3 (4.2–4.5), 4.4 (4.3–4.5); zygomatic breadth (five males), 8.5 (8.2–8.9), 9.3 (9.2–9.4); breadth of braincase (six males, three females), 7.0 (6.8–7.2), 7.5 (7.4–7.7); length of maxillary toothrow (five males, three females), 3.8 (3.7–4.0), 4.2 (4.1–4.3); palatal length (six males), 3.7 (2.8–4.2); length of mandibular toothrow (four males, three females), 4.3 (4.2–4.4), 4.8 (4.8–4.9); greatest length of mandible (four males, three females), 8.3 (8.0–8.7), 9.2 (9.1–9.3).

Habitat.—*Lasiurus blossevillii* is distributed throughout northern Argentina. It has not been reported, however, from the provinces of Santa Fe and Santiago del Estero (Bárquez, 1987). It appears to be rare in the Chaco. In Tucumán, this bat has been captured in many different habitats. Open areas appear to be preferred, although individuals have been captured flying over rivers in forests. At Las Juntas, the habitat was montane transitional forest. The single red bat collected at this site was taken in a net placed over the Río Choromoro (Mares et al., 1995).

Remarks.—At Las Juntas, this species was captured with *Artibeus planirostris, Sturnira erythromos, Histiotus macrotus,* and *Tadarida brasiliensis.* Wilson and Reeder (1993) listed this species under *L. borealis.* We have chosen to follow Baker et al. (1988) and Morales and Bickham (1995) in recognizing the distinctness of red bats in the western and southern portions of their range.

Lasiurus cinereus (Beauvois)

Vespertilio cinereus Beauvois, A scientific catalogue of Peale's Museum. S. H. Smith, Philadelphia, p. 18, 1796.

Specimens Examined.—(7) Las Mesadas, 1 (CML); Los Vázquez, 1 (BMNH); Marcos Paz, 1 (CML); Playa Larga, 1 (OMNH); San Miguel de Tucumán, 2 (1 BMNH, 1 CML); Tafí Viejo, 1 (CML).

Measurements,—External measurements (one male, two sex unknown): forearm, 52.6, 49.0, 52.7. Cranial measurements (one male, one sex unknown, unless noted otherwise): greatest length of skull, 15.7, 15.0; condylobasal length, 15.6, 14.9; least interorbital length, 5.4, 5.0; zygomatic breadth (one sex unknown), 11.6; breadth of braincase, 8.7, 8.7; palatal length (one sex unknown), 4.7.

Habitat.—In Argentina, *L. cinereus* is distributed in most provinces from 40°S latitude northward, although no records are known from the provinces of San Juan, Chaco, Formosa, and Misiones (Bárquez, 1987). In Tucumán, *L. cinereus* roosts in trees in gardens and along the streets.

Remarks.—*Lasiurus cinereus* is solitary. There is some evidence from North America that indicates that *L. cinereus* may migrate, although there are no data to support this in Tucumán Province or in Argentina.

Lasiurus ega (Gervais)

Nycticeus ega Gervais, *in* F. Compte de Castelnau, Expèdition dans les parties centrales de l'Amérique du Sud de Rio de Janeiro à Lima, et de Lima au Para; exécutée par ordre du gouvernement français pendant les années 1843 à 1847, sous la direction de Grancis de Castelnau. P. Bertrand, Paris, (Sec. 7), Vol. 1, Pt. 2 (Mammifères):73, 1856.

Specimens Examined.—(9) Acheral, 1 (CML); Ciudad Capital, 1 (OMNH); Los Vázquez, 445 m, 2 (BMNH); San Miguel de Tucumán, 450 m, 4 (1 BMNH, 3 CML); Tafí Viejo, 1 (CML).

Additional Record.—Muñecas (Romaña and Abalos, 1950).

Measurements.—External measurements (two males, three females, unless noted otherwise): total length, 120.0, 106.0, 119.2 (115.0–124.0); tail, 52.0, 46.0, 55.8 (50.0–60.5); hindfoot, 9.0, 6.5, 8.3 (5.0–10.0); ear, 20.0, 15.0, 15.3 (14.0–16.0); forearm (two males, four females), 47.0, 42.7, 46.8 (42.0–49.1); weight (one male), 13.0. Cranial measurements (one male, two females, unless noted otherwise): greatest length of skull, 16.4, 16.5, 17.0; condylobasal length, 15.4, 14.9, 16.0; least interorbital length, 4.5, 4.5, 4.5; zygomatic breadth (one male, one female), 11.2, 11.4; breadth of braincase, 8.2, 8.2, 8.7; length of maxillary toothrow (one male), 5.8; palatal length (one male), 5.5; length of mandibular toothrow (one male), 5.5; greatest length of mandible (one male), 12.1.

Reproduction.—See Table 3.

Habitat.—*Lasiurus ega* is known from northwestern, central, and eastern Argentina, excluding the provinces of Chaco, Santiago del Estero, and Entre Ríos, and northern Santa Fe (Bárquez, 1987). In Tucumán, this bat is common in the humid and transitional forests. *Lasiurus ega* often uses plants, especially palms, in city gardens as refuges; they have also been reported to roost in the roofs of dwellings.

Remarks.—Little is known about the biology of this species in Argentina. Myers (1977) discussed the reproductive biology of this species in Paraguay. Geographic variation in *L. ega* in the Chaco of Paraguay and Bolivia was discussed by Myers and Wetzel (1983). It is thought to be migratory.

Myotis albescens (E. Geoffroy)

Vespertilio albescens E. Geoffroy, Annales Museum d'Histoire Naturelle, Paris, 8:204, 1806.

Specimens Examined.—(15) Aguas Chiquitas, Sierras de Medina, 800 m, 1 (CM); Concepción, 1 (MACN); El Cadillal, Usina, 3 (CML); La Cocha, Dique San Ignacio, 1 (OMNH); Las Talas, 1 (CML); Las Talas, 4 km al N de Bella Vista, 1 (OMNH); Monteagudo, 4 (2 FCM, 1 MACN, 1 TTU); 3 km E Ticucho, cola de Cadillal Dique, 1 (OMNH); Ticucho, cola de embalse El Cadillal, 1 (OMNH); Tranquitas, 1 (MACN).

Measurements.—External measurements (two males, four females, unless noted otherwise): total length, 83.0, 90.0, 88.6 (84.0–94.0); tail, 25.0, 31.0, 34.6 (31.0–40.0); hindfoot, 7.5, 8.0, 7.4 (5.0–8.9); ear, 15.5, 14.0, 14.6 (14.0–15.7); forearm, 35.2, 34.1, 36.6 (35.9–37.3); weight (two males, three females), 7.0, 6.4, 7.8 (7.5–8.0). Cranial measurements (two males, three females, unless noted otherwise): greatest length of skull, 14.4, 13.6, 14.6 (14.2–15.0); condylobasal length, 13.4, 13.0, 13.7 (13.4–14.0); least interorbital length, 4.4, 4.0, 4.1 (4.1–4.1); zygomatic breadth (two males, two females), 8.6, 8.6, 8.6, 8.7; breadth of braincase, 7.4, 6.9, 7.2 (7.1–7.3); length of maxillary toothrow, 5.3, 5.2, 5.3 (5.2–5.5); palatal length (two males, two females), 5.5, 5.4, 5.2, 5.8; length of mandibular toothrow (one male, two females), 4.9, 5.2, 5.3; greatest length of mandible, 9.2, 10.2, 9.5 (9.3–9.6).

Reproduction.—See Table 3.

Habitat.—Myotis albescens is known from the provinces of the northwest and the northeast to south of Buenos Aires Province (Olrog and Lucero, 1981; Bárquez, 1987). In Tucumán, this species is found in grasslands and savannas (Lucero, 1983), in forests, along rivers, and in open Chacoan thorn scrub (Bárquez, 1987).

Remarks.—At Las Talas, individuals of *M. albescens, Eptesicus furinalis,* and *Tadarida brasiliensis* were found in the roof of a rural dwelling (Bárquez, 1988).

Myotis keaysi J. A. Allen

Myotis ruber keaysi J. A. Allen, Bulletin of the American Museum of Natural History, 33:383, 1914.

Specimens Examined.—(7) Agua Colorada, 3 (MACN); El Nogalar, km 43, Ruta 307, 1700 m, 1 (CML); Piedra Tendida, 12 km WNW Burruyacú, along Río Cajón, 2,500 ft., 1 (OMNH); Tranquitas, 2 (1 MACN, 1 TTU).

Measurements.—External measurements (one male): total length, 90.0; tail, 37.0; hindfoot, 8.0; ear, 14.0; forearm, 40.0; weight, 6.0. Cranial measurements (one male): greatest length of skull, 13.9; condylobasal length, 13.3; least interorbital length, 3.7; zygomatic breadth, 8.8; breadth of braincase, 7.1; length of maxillary toothrow, 5.1; palatal length, 5.8; length of mandibular toothrow, 5.2; greatest length of mandible, 9.2.

Habitat.—In Argentina, this species is known only from Salta and Tucumán (Bárquez, 1987). In other parts of its range, *M. keaysi* is commonly found at localities above 2000 m (Bárquez and Ojeda, 1992). In Tucumán, however, it has been captured at much lower elevations in transitional forest and montane forests. These localities are situated primarily in the northeastern part of the province, near Chacoan vegetation, and isolated from the principal mountain chains to the west (Bárquez, 1987; Bárquez and Ojeda, 1992).

Remarks.—This species, in addition to *Sturnira erythromos* and *Myotis nigricans,* was captured in nets placed along a river at Piedra Tendida (Mares et al., 1995). An adult male was captured in June at Piedra Tendida. Redford and Eisenberg (1992) do not show this bat as occurring in the southern cone.

Myotis levis (I. Geoffroy)

Vespertilio levis I. Geoffroy, Annales des Sciences Naturelles, Zoologie, ser. 1, 3:444–445, 1824.

Specimens Examined.—(55) Agua Rosada, 2 (CML); Aguas Chiquitas, 25 km NE San Miguel de Tucumán, 800 m, 5 (CM); Amaicha del Valle, 2000 m, 1 (OMNH); Colalao del Valle, 1 (BMNH); Concepción, 4 (3 BMNH, 1 MACN); Dique San Ignacio, 1 (CML); El Cadillal, 1 (CML); Horco Molle, 1 (CM); La Ciénaga, 2500 m, 1 (BMNH); La Higuera, 1 (CML); Las Pavas, Aconquija, 1 (MACN); Las Talas, 3 (CML); Leocadio Paz, 1 (MACN); Ñorco, Vipos, 2500 m, 2 (BMNH); San Miguel de Tucumán 7 (5 BMNH, 2 MACN); San Pedro de Colalao, 1 (CML); at km marker 42, on highway 364, south of San Pedro de Colalao, 4,700 ft., 13 (3 CML, 3 IADIZA, 7 OMNH); Tacanas 1 (CML); Tafí del Valle, 1 (CML); Tucumán, no specific locality, 2 (BMNH); Vipos, 5 (CML).

Measurements.—External measurements (five males, 16 females, unless noted otherwise): total length, 86.6 (75.0–91.0), 89.3 (77.0–100.0); tail, 39.0 (36.0–40.0), 40.2 (35.5–42.0); hindfoot (five males, 15 females), 7.8 (5.0–9.0), 8.7 (7.3–9.3); ear, 14.3 (14.0–15.5), 14.0 (13.0–16.0); forearm (four males, 15 females), 38.0 (36.8–40.0), 38.0 (36.7–40.0); weight (four males, 14 females), 5.2 (4.3–

5.5), 6.1 (4.4–8.0). Cranial measurements (two males, seven females, unless noted otherwise): greatest length of skull, 14.0, 14.4, 14.3 (14.1–14.8); condylobasal length, 13.3, 13.5, 13.5 (13.0–14.0); least interorbital length, 3.5, 3.6, 3.5 (3.4–3.7); zygomatic breadth (two males, six females), 8.6, 8.2, 8.6 (8.2–9.0); breadth of braincase, 7.1, 6.8, 6.9 (6.6–7.2); length of maxillary toothrow (two males, six females), 5.4, 5.6, 5.6 (5.4–5.8); palatal length (two males, six females), 6.4, 7.0, 6.6 (5.9–7.4); length of mandibular toothrow (two males, two females),—, 5.7, 5.8, 6.0; greatest length of mandible (two males, six females), 10.1, 10.2, 10.6 (10.4–10.8).

Reproduction.—See Table 3. Bárquez (1987) reported capturing lactating females from the end of December to the end of January in transitional forest at Aguas Chiquitas.

Molt.—Three adults, captured in January at San Pedro de Colalao, were molting on the dorsum.

Habitat.—This species is widely distributed throughout northern, central, and eastern Argentina as far south as Neuquén Province (Bárquez, 1987). Although preferring open, natural habitats, it is found also in urban areas; elevation ranges up to 3500 m (Bárquez, 1987). Many of the specimens were captured in transitional forest. Individuals from San Pedro de Colalao were collected in a rural dwelling; the surrounding habitat was transitional forest with a lot of secondary growth.

Remarks.—*Myotis levis* is one of the most common vespertilionid bats in the province, although little is known about its biology. This species is easily confused with other *Myotis*. At San Pedro de Colalao this species was captured with *Sturnira erythromos*.

Myotis nigricans (Schinz)

Vespertilio nigricans Schinz, Das Thierreich, 1:179, 1821.

Specimens Examined.—(8) Acheral, 1 (CML); Agua Colorada, 1 (TTU); Cerro del Campo, 1 (CML); El Cadillal, 25 km N San Miguel de Tucumán, 1 (CM); El Naranjo, 1 (TTU); Piedra Tendida, 12 km WNW Burruyacú, along Río Cajón, 2,500 ft., 1 (OMNH); Tafí Viejo, 2 (CML).

Additional Records.—Monte Bello, Río Chico (Romaña and Abalos, 1950).

Measurements.—External measurements (two males): total length, 78.0, 78.0; tail, 38.0, 31.0; hindfoot, 6.9, 7.0; ear, 15.7, 14.0; forearm, 33.0, 33.0; weight, 4.5, 3.5. Cranial measurements (one male): greatest length of skull, 13.1; condylobasal length, 12.8; least interorbital length, 3.4; zygomatic breadth, 8.3; breadth of braincase, 6.4; length of maxillary toothrow, 5.1; palatal length, 5.7; length of mandibular toothrow, 5.3; greatest length of mandible, 9.7.

Reproduction.—See Table 3. Little is known about the reproductive biology of this species in Argentina.

Molt.—The individual from Piedra Tendida was not molting.

Habitat.—In Argentina, this species is restricted to the northern provinces, Jujuy, Salta, Tucumán, Santiago del Estero, Chaco, Formosa, Corrientes, and Misiones (Bárquez, 1987). Based on capture records, *M. nigricans* prefers humid and transitional forests. Bárquez (1987) noted that this species has been captured in a variety of habitats, from Yungas forest to urban areas, in cities and in rural areas, under roofs and under tree bark.

Remarks.—Other bats collected at Piedra Tendida were *Sturnira erythromos* and *Myotis keaysi* (Mares et al., 1995). Individuals have been captured in February (*n* = 1), March (*n* = 1), and July (*n* = 1).

Family Molossidae

Eumops bonariensis (Peters)

Promops bonariensis Peters, Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin, 1874:232, 1874.

Specimens Examined.—(17) Aguas Chiquitas, 3 (CML); Aguas Chiquitas, Sierras de Medina, 800 m, 4 (CM); Reserva Provincial "Aguas Chiquitas" El Cadillal, 3 (CM); Las Talas, 4 km al N de Bella Vista, 3 (OMNH); 29 km NE San Miguel de Tucumán, 1 (CM); 28 km NE San Miguel de Tucumán, 3 (CM).

Measurements.—External measurements (three males, eight females): total length, 121.0 (117.0–128.0), 115.1 (105.0–129.0); tail, 40.5 (38.0–43.0), 37.8 (33.0–41.0); hindfoot, 9.6 (8.3–10.3), 8.4 (7.0–10.2); ear, 22.0 (21.4–23.0), 22.7 (21.9–24.0); forearm, 47.9 (47.3–48.7), 48.0 (44.8–49.0); weight, 18.2 (17.5–19.0), 17.4 (15.5–20.0). Cranial measurements (three males, eight females, unless noted otherwise): greatest length of skull, 19.3 (19.1–19.5), 18.9 (18.3–19.2); condylobasal length, 18.3 (18.1–18.6), 18.0 (17.2–18.4); least interorbital length, 4.3 (4.2–4.3), 4.2 (4.0–4.3); zygomatic breadth, 11.8 (11.5–12.0), 11.5 (11.1–11.7); breadth of braincase, 9.6 (9.5–9.7), 9.3 (8.8–9.7); length of maxillary toothrow, 7.5 (7.3–7.6), 7.3 (7.1–7.5); palatal length (three males, seven females), 7.3 (7.1–7.4), 7.6 (7.2–7.9); length of mandibular toothrow, 6.7 (6.6–6.9), 6.7 (6.5–7.3); greatest length of mandible, 14.0 (13.8–14.1), 13.8 (13.6–14.0).

Reproduction.—See Table 3. Bárquez (1987) reported that individuals captured at Las Talas at the end of March and the end of April were not reproductively active.

Habitat.—In Argentina, *E. bonariensis* has been recorded from the provinces of Buenos Aires, Santa Fe, Entre Ríos, Córdoba, and Tucumán (Bárquez, 1987). In Tucumán, this species prefers dense transitional forests, but may also be found in rural and open areas, even in roofs and tree holes. At Aguas Chiquitas, a locality surrounded by Chaco serrano, individuals were collected in nets placed across areas of calm water in the forest.

Remarks.—Bárquez (1987) discussed the relationship of *E. bonariensis* and *E. patagonicus,* revalidating the distinction of *E. patagonicus.* Both species are found in sympatry in Tucumán Province. At Las Talas *E. bonariensis* were collected with *E. patagonicus* (reproductively active), *E. furinalis, M. albescens, M. levis dinellii,* and *T. brasiliensis* (Bárquez, 1987). The biology of this species in Argentina is poorly known.

Eumops dabbenei Thomas

Eumops dabbenei Thomas, Annals and Magazine of Natural History, ser. 8, 13:481, 1914.

Specimens Examined.—(2) San Miguel de Tucumán, 2 (CML).

Reproduction.—A juvenile (with cartilaginous phalanges and deciduous upper incisors) was captured in a house in mid-December in the city of Tucumán (Bárquez and Lougheed, 1990; Bárquez and Ojeda, 1992).

Habitat.—In Argentina, *E. dabbenei* is known only from the provinces of Chaco, Santa Fe, and Tucumán (Bárquez, 1987; Bárquez and Lougheed, 1990; Bárquez and Ojeda, 1992).

Remarks.—Little is known about the biology of this species in Argentina.

Eumops glaucinus (Wagner)

Dysopes glaucinus Wagner, Archiv für Naturgeschichte, 9 (1):368, 1843.

Specimens Examined.—(2) San Miguel de Tucumán, 2 (CML).

Habitat.—In Argentina, *E. glaucinus* is known only from the provinces of Jujuy, Salta, and Tucumán (Bárquez, 1987; Bárquez and Lougheed, 1990). The inclusion of the provinces of Catamarca and La Rioja by Olrog and Lucero (1981) is not documented by specimens. In the city of Tucumán it roosts in trees and in cracks in buildings.

Eumops patagonicus Thomas

Eumops patagonicus Thomas, Annals and Magazine of Natural History, ser. 9, 13:234, 1924.

Specimens Examined.—(22) Burruyacú, 1 (MACN); Gobernador Piedrabuena, 20 (17 MACN, 3 TTU); Las Talas, 4 km al N de Bella Vista, 1 (OMNH).

Measurements.—External measurements (one male): total length, 92.4; tail, 35.8; hindfoot, 7.4; ear, 19.7; forearm, 45.4; weight, 15.0. Cranial measurements (one male): greatest length of skull, 18.4; condylobasal length, 16.5; least interorbital length, 4.0; zygomatic breadth, 10.4; breadth of braincase, 9.0; length of maxillary toothrow, 6.6; palatal length, 6.6; greatest length of mandible, 13.1.

Reproduction.—See Table 3.

Habitat.—In Argentina, this species is known from an isolated record in Chubut (type locality), Buenos Aires, Santa Fe, and all of the northern provinces except Jujuy and Catamarca. In Tucumán, *E. patagonicus* is found in open suburban and urban areas, especially in the Chaco.

Remarks.—Bárquez (1987) discussed the relationship of this species with *E. bonariensis* and synonymized *E. b. beckeri* with *E. patagonicus.*

Eumops perotis (Schinz)

Molossus perotis Schinz, *in* Cuvier, Das Thierreich, 1:870, 1821.

Specimens Examined.—(40) Concepción, 27 (7 BMNH, 20 MACN); Las Talitas, 1 (CML); Plaza Independencia, San Miguel de Tucumán, 1 (CM); San Miguel de Tucumán, 10 (2 BMNH, 8 CML); San Pedro de Colalao, 1 (CML).

Additional Record.—Caspichango (Massoia, 1976).

Measurements.—External measurements (three males, seven females, unless noted otherwise): total length, 172.7 (170.0–178.0), 167.5 (155.0–180.0); tail, 60.3 (60.0–61.0), 61.8 (55.0–70.0); hindfoot (four males, six females), 16.1 (15.0–18.4), 15.0 (14.0–16.0); ear, 42.3 (35.0–49.0), 34.7 (33.0–35.0); forearm (six males, five females), 78.2 (75.8–82.5), 78.3 (77.3–80.0); weight (two males), 52.0, 65.0. Cranial measurements (four males, one female, unless noted otherwise): greatest length of skull, 31.0 (30.2–31.7), 29.3; condylobasal length, 30.4 (29.0–30.8), 27.2; least interorbital length (five males, three females), 5.3 (5.1–5.6), 5.8 (5.6–5.9); zygomatic breadth, 18.4 (17.5–18.8), 19.5; breadth of braincase, 13.4 (12.6–14.9), 12.6; length of maxillary toothrow (three males, four females), 12.4 (11.9–12.7), 12.9 (12.5–13.2); palatal length (four males, three females), 12.7 (9.0–14.2), 13.9 (13.2–15.0); length of mandibular toothrow (three males, four females), 13.4 (12.2–14.1), 13.8 (13.3–14.0); greatest length of mandible (three males, four females), 24.4 (24.1–24.7), 23.3 (23.0–23.6).

Reproduction.—See Table 3. Bárquez (1987) reported catching a juvenile in the city of Tucumán in mid-December that had deciduous dentition and cartilaginous phalanges.

Habitat.—This species ranges throughout all of northern Argentina, except the Chaco; it is distributed southward to central Córdoba (Bárquez, 1987). In the city of Tucumán these bats live in palm trees and under roofs. In natural areas, they have been known to roost in rock crevices.

Molossops temminckii (Burmeister)

Dysopes temminckii Burmeister, Systematische übersicht der Thiere Brasiliens. Georg Reimer, Berlin, p. 72, 1854.

Specimens Examined.—(9) Cerro del Campo, 2 (CML); El Cadillal, 1 (CML); La Higuera, 1 (CML); Las Mesadas, 3 (CML); Puesto Portadera, 2 (1 MACN, 1 TTU).

Additional Record.—San Miguel de Tucumán (Fornes and Massoia, 1968).

Measurements.—External measurements: forearm (two males, four females), 31.4, 31.7, 31.1 (30.0–31.5). Cranial measurements (two males, two females, unless noted otherwise): greatest length of skull (one male, one female), 13.8, 13.9; condylobasal length (one female), 14.8; least interorbital length (two males, three females), 3.7, 3.6, 3.7 (3.7–3.7); breadth of braincase, 7.0, 7.0, 7.0, 7.2; length of maxillary toothrow (one male, two females), 5.3, 4.9, 5.2; palatal length (one female), 6.1; length of mandibular toothrow (one male, two females), 5.5, 5.6, 5.8.

Reproduction.—See Table 3. A male with scrotal testes was collected at El Cadillal in mid-October (Bárquez, 1987).

Habitat.—In northwestern Argentina (Jujuy, Salta, Santiago del Estero, and Tucumán), the preferred habitat is Chaco. This species is also known from the Chaco of Formosa, Santa Fe, Corrientes, and Chaco provinces; isolated records have also been reported from Buenos Aires and Chubut provinces (Bárquez, 1987).

Remarks.—Myers and Wetzel (1983) reported dramatic geographic variation in this species in the Chaco of Paraguay, Bolivia, Brazil, and northern Argentina. Individuals are small and light in color in the northwestern Chaco, and large and dark in the eastern Chaco. Specimens from the base of the Andes are as large as, or larger than, those from the eastern Chaco. It appears that specimens from Tucumán Province follow this trend.

Molossus molossus (Pallas)

Vespertilio molossus Pallas, Miscellanea Zoologica. Hagae Comitum, pp. 49–50, 1766.

Specimens Examined.—(7) Ciudad Tucumán, casa céntrica, 1 (OMNH); El Manantial, 1 (CML); San Miguel de Tucumán, 3 (CML); San Pedro de Colalao, 1 (CML); Trancas, 1 (CML).

Measurements.—External measurements (one female): total length, 98.0; tail, 40.0; hindfoot, 12.0; ear, 7.0; forearm, 38.0; weight, 10.0.

Reproduction.—See Table 3.

Habitat.—In Argentina, *M. molossus* is found in the northwestern provinces of Jujuy, Tucumán, Salta, and Santiago del Estero. In eastern Argentina, it ranges from Formosa, Corrientes, Chaco, and Misiones south to Entre Ríos and northern Buenos Aires (Bárquez, 1987). In Tucumán, this species roosts in tree holes and crevices, roofs, and tunnels. It is common in both urban and suburban areas.

Remarks.—This bat may form large colonial groups. Redford and Eisenberg (1992) do not show this species as occurring in Tucumán Province.

Nyctinomops macrotis (Gray)

Nyctinomus macrotis Gray, Annals of Natural History, 4:5, 1840.

Specimens Examined.—(6) San Miguel de Tucumán, 6 (CML).

Reproduction.—See Table 3.

Habitat.—In Argentina, *N. macrotis* has been reported only from the provinces of Jujuy, Salta, Tucumán, Catamarca, and La Rioja (Bárquez, 1987).

Remarks.—This species is common in the city of Tucumán where it uses buildings for shelter (Bárquez, 1987; Bárquez and Ojeda, 1992). Little is known about the biology of this species in Argentina.

Promops nasutus (Spix)

Molossus nasutus Spix, Simiarum et Vespertilionum Brasiliensium species novae. Monachii, p. 58, 1823.

Specimens Examined.—(3) Río Loro, 2 (OMNH); San Miguel de Tucumán, 1 (BMNH).

Reproduction.—See Table 3.

Habitat.—*Promops nasutus* is distributed in the Argentine provinces of Salta, Jujuy, Tucumán, Catamarca, Santiago del Estero, and Misiones (Bárquez, 1987).

Remarks.—The individuals from Río Loro were captured as they left a roost located in a crevice in a river bank (Bárquez, 1987).

Tadarida brasiliensis (I. Geoffroy)

Nyctinomus brasiliensis I. Geoffroy, Annales des Sciences Naturelles, Zoologie, 1:343, 1824.

Specimens Examined.—(113) Burruyacú, 6 (5 MACN, 1 TTU); Cerro San Javier, 1 (CML); Concepción, 10 (5 BMNH, 5 MACN); Dique San Ignacio, 20 (CML); El Cadillal, 1 (CML); Estancia El Cavao, 1 (CML); Estancia San Pedro, Vipos, 2 (CML); Gobernador Piedrabuena, 5 (2 MACN, 3 TTU); Horco Molle, 12 (CM); Biological Reserve at Horco Molle, at residencia, 3 (1 IADIZA, 2 OMNH); Iglesia, 3 (TTU); Instituto Lillo, San Miguel de Tucumán, 1 (CML); Las Juntas, 22 km W Choromoro on Hwy 312, 3,500 ft., 5 (3 IADIZA, 2 OMNH); Las Mesadas, 1 (CML); Las Pavas, 5 (MACN); Las Talas, 2 (CML); Las Talas, 4 km al N de Bella Vista, 2 (OMNH); Marcos Paz, 1 (CML); Playa Larga, 4 (CML); San Miguel de Tucumán, 14 (3 BMNH, 4 USNM, 7 CML); San Pedro de Colalao, 2 (CML); Ruta 307, km 19.7, camino a Tafí del Valle, 750 m, 3 (OMNH); Tacanas, 2 (CML); Tapia, 1 (CML); Timbó Nuevo, 4 (1 MACN, 3 TTU); Vipos, 2 (CML).

Additional Records.—Ingenio Lules (Romaña and Abalos, 1950); Monteagudo (Fornes and Massoia, 1967).

Measurements.—External measurements (nine males, eight females, unless noted otherwise): total length, 96.8 (91.0–102.0), 98.6 (87.7–105.0); tail, 35.9 (33.0–40.0), 37.2 (30.0–41.0); hindfoot, 7.9 (7.2–9.0), 8.6 (7.2–10.0); ear, 17.2 (13.0–21.5), 18.5 (12.0–21.0); forearm (seven males, ten females), 43.3 (41.3–45.0), 43.8 (42.0–45.0); weight (six males, six females), 12.2 (10.0–14.0), 11.5 (10.0–12.0). Cranial measurements (ten males, five females, unless noted otherwise): greatest length of skull, 16.7 (15.4–17.2), 16.5 (16.1–16.9); condylobasal length, 15.7 (14.5–16.2), 15.5 (15.5–15.7); least interorbital length (ten males, six females), 4.0 (3.8–4.2), 4.0 (3.9–4.0); zygomatic breadth (seven males, four females), 9.9 (9.3–10.4), 9.6 (9.2–9.9); breadth of braincase (ten males, six females), 8.4 (7.9–8.6), 8.3 (8.0–8.6); length of maxillary toothrow (ten males, six females), 5.7 (4.7–6.4), 6.0 (4.8–6.7); palatal length (seven males, five females), 6.8 (6.1–7.1), 6.2 (3.6–7.5); length of mandibular toothrow (six males, five females), 6.2 (5.9–6.6), 7.6 (6.2–12.0); greatest length of mandible (five males, four females), 12.1 (11.7–12.6), 11.9 (11.7–12.1).

Reproduction.—See Table 3.

Molt.—An adult male captured at Horco Molle in January was molting on both the dorsum and venter.

Habitat.—This is one of the most widely distributed species in Argentina, found in all provinces north of 43°S latitude, except La Rioja, Chaco, and Corrientes (Bárquez, 1987). It is most common in transitional forest, Chaco, and montane forest. The specimens collected at Horco Molle were roosting behind a rain gutter.

Remarks.—In the province, this species is colonial and forms large groups that roost in caves, holes, crevices, tunnels, and roofs. In the city of Tucumán, *T. brasiliensis* is one of the most common species and is found roosting in building crevices and roofs. At Las Juntas, *Artibeus planirostris, Sturnira erythromos, Histiotus macrotus,* and *Lasiurus blossevillii* also were captured. *Sturnira erythromos* also was captured at Horco Molle.

Order Primates
Family Cebidae
Subfamily Cebinae
Cebus apella (Linnaeus)

Simia apella Linnaeus, Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tenth edition. Laurentii Salvii, Stockholm, 1:28, 1758.

Specimens Examined.—(0) None.

Additional Record.—Dique Escaba (M. L. Campbell, personal observation).

Remarks.—Local inhabitants in the area surrounding the Embalse Escaba in southwestern Tucumán indicated that monkeys had been present in the area as late as the early 1980s (M. L. Campbell and J. K. Braun, personal observation), but we have been unable to confirm this. Redford and Eisenberg (1992) do not show this species as occurring in the province.

Order Carnivora
Family Canidae
Cerdocyon thous (Linnaeus)

Canis thous Linnaeus, Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Volume 1. Regnum Animale. 12th edition. Laurentii Salvii, Stockholm, 1:60, 1766.

Specimens Examined.—(4) Monteros, 1 (MACN); Taficillo, 1 (CML); Tapia, 500 m, 1 (BMNH); Vipos, 1 (BMNH).

Measurements.—External measurements (one female): total length, 932.0; tail, 322.0; hindfoot, 140.0; ear, 67.0. Cranial measurements (one female): greatest length of skull, 127.6; condylobasal length, 133.0; least interorbital length, 26.2; zygomatic breadth, 74.4; breadth of braincase, 46.1; length of maxillary toothrow, 59.0; palatal length, 59.3; length of mandibular toothrow, 62.9; greatest length of mandible, 106.4.

Habitat.—*Cerdocyon thous* is distributed in northern Argentina east of the Andes, including the provinces of Salta, Jujuy, Tucumán, Formosa, Misiones, Corrientes, Santa Fe, Chaco, and Santiago del Estero (Olrog and Lucero, 1981). Lucero (1983) and Olrog and Lucero (1981) noted that this species prefers transitional and humid forests, and mountains, where it occurs up to 2500 m.

Remarks.—One individual each was captured in May, July, and October. The biology of this species was summarized by Berta (1982). Ginsberg and Macdonald (1990) noted that it is considered out of danger by the Argentine Wildlife Board

(Dirección Nacional de Fauna Silvestre). Nothing is known of the biology of this species in the province.

Pseudalopex culpaeus (Molina)

Canis culpaeus Molina, Saggio sulla storia naturale del Chili. S. Tommaso d'Aquino, Bologna, p. 293, 1782.

Specimens Examined.—(4) Aconquija, 1 (BMNH); Agua Rosada, 1 (CML); El Duraznito, 1 (CML); San Javier, 1 (CML).

Measurements.—External measurements (one female): hindfoot, 130.0; ear, 90.0. Cranial measurements (one female, two sex unknown): greatest length of skull, 130.6, 129.8, 129.2; condylobasal length, 129.4, 124.3, 129.0; least interorbital length, 23.1, 23.8, 24.0; zygomatic breadth, 67.9, 66.5, 67.5; breadth of braincase, 44.7, 44.5, 45.3; length of maxillary toothrow, 59.5, 58.2, 58.2; length of mandibular toothrow, 66.2, 64.9, 65.8; greatest length of mandible, 95.3,—,—.

Habitat.—In Argentina, the distribution of *P. culpaeus* extends as a narrow band from the northwest, widening southward to include all of the southern provinces south of Buenos Aires Province (Olrog and Lucero, 1981). This species prefers arid areas and steppes in the mountains at altitudes up to 4500 m (Olrog and Lucero, 1981; Lucero, 1983).

Remarks.—*Pseudalopex culpaeus* has an Appendix II ranking in Argentina (Fuller and Swift, 1984). The biology of this species was summarized by Ginsberg and Macdonald (1990), who also noted that it has endangered status in Argentina. The effects of hunting on populations of this species in Neuquén Province was examined by Novaro (1995).

Pseudalopex griseus (Gray)

Vulpes griseus Gray, Magazine of Natural History (Charlesworth's), 1:578, 1837.

Specimens Examined.—(4) Cerro del Campo, 800 m, 2 (BMNH); Tapia, 500 m, 1 (BMNH); Vipos, 500 m, 1 (BMNH).

Measurements.—External measurements (two males, two females): total length, 887.0, 829.0, 884.0, 887.0; tail, 347.0, 328.0, 322.0, 317.0; hindfoot, 131.0, 125.0, 120.0, 124.0; ear, 81.0, 70.0, 80.5, 82.5. Cranial measurements (two males): greatest length of skull, 124.4, 121.7; condylobasal length, 128.8, 125.4; least interorbital length, 24.8, 23.4; zygomatic breadth, 70.8, 70.7; breadth of braincase, 45.6, 45.9; length of maxillary toothrow, 59.3, 59.3; palatal length, 56.4, 56.8; length of mandibular toothrow, 66.0, 66.0; greatest length of mandible, 97.6, 97.6.

Habitat.—In Argentina, the geographic distribution of this species is similar to that of *P. culpaeus,* although it is not found in Jujuy and eastern Salta (Olrog and Lucero, 1981). Moreover, *P. culpaeus* is a fox of the high mountains, whereas *P. griseus* is primarily a lowland animal. This fox frequents steppes and arid shrubby regions in western, southern, and northeastern Tucumán Province (Lucero, 1983).

Remarks.—Two specimens were captured in August and two were captured in October. The Cerro del Campo specimens were listed as *P. gracilis* by Thomas (1926). In Argentina, this species is considered vulnerable (International Union for the Conservation of Nature, 1990, 1994). The biology of this species was summarized by Ginsberg and Macdonald (1990), who noted its endangered status. Hunting of this species has been banned in Tucumán Province, where little is known about its biology.

Pseudalopex gymnocercus (Fischer)

Procyon gymnocercus Fischer, Zoognosia, 3:xi, 178, 1814.

Specimens Examined.—(11) Agua Rosada, 1 (CML); Burruyacú, 1 (MACN); Chicligasta, 1 (CML); El Simbolar, 1 (CML); El Timbó, 4 (CML); Monteros, 1 (MACN); Nueva España, 1 (CML); Tafí Viejo, 1 (CML).

Measurements.—External measurements (one male, one female): total length, 1010.0, 835.0; tail, 330.0, 305.0; hindfoot, 110.0, 120.0; ear, 80.5, 75.0. Cranial measurements (one male, three females, one sex unknown, unless noted otherwise): greatest length of skull (one male, one female, one sex unknown), 129.3, 123.6, 123.5; condylobasal length, 125.4, 123.5 (120.0–127.7), 117.5; least interorbital length (one male, two females, one sex unknown), 20.5, 22.5, 20.9, 23.1; zygomatic breadth (one male, three females), 63.6, 67.5 (64.0–71.4); breadth of braincase, 45.9, 45.2 (43.9–45.9), 43.1; length of maxillary toothrow (one male, one female, one sex unknown), 56.8, 55.0, 50.9; palatal length (three females, one sex unknown), 63.5 (61.5–64.6), 60.9; length of mandibular toothrow (one male, one sex unknown), 64.6, 60.0; greatest length of mandible (one male, one sex unknown), 93.2, 89.5.

Habitat.—According to Olrog and Lucero (1981), *P. gymnocercus* inhabits all of northern and central Argentina except Misiones Province. The southern distributional limits are northern Río Negro and Neuquén provinces. This fox is found in savannas, mountains, and forests up to 2000 m in elevation (Lucero, 1983).

Remarks.—Specimens have been collected in nearly every month: February ($n = 1$), March ($n = 1$), April ($n = 1$), May ($n = 2$), June ($n = 1$), July ($n = 2$), September ($n = 1$), and November ($n = 1$). Ginsberg and Macdonald (1990) summarized the biology of this species. Crespo (1971) studied the ecology of *P. gymnocercus* in La Pampa Province.

Family Felidae

Subfamily Felinae

Herpailurus yaguarondi (Lacépède)

Felis yaguarondi Lacépède, *in* Azara, Voyage dans l'Amérique Méridionale. Imprimieur-Libraire, Paris, Atlas, 1809, pl. 10, 1809.

Specimens Examined.—(3) Concepción, 1 (CML); El Bracho, 1 (CML); Villa Nougués, 1 (CML).
Additional Record.—Dique Escaba (M. L. Campbell, personal observation).

Measurements.—Cranial measurements (one male): greatest length of skull, 96.5; condylobasal length, 91.9; least interorbital length, 17.3; zygomatic breadth, 62.0; breadth of braincase, 42.1; length of mandibular toothrow, 20.7; greatest length of mandible, 58.1.

Habitat.—This species is distributed throughout northern and central Argentina south to northern Neuquén and Río Negro (Olrog and Lucero, 1981). *Herpailurus yaguarondi* prefers savannas, mountains, and forests to the southern limits of the province (Olrog and Lucero, 1981; Lucero, 1983).

Remarks.—The record of this species at Dique Escaba is based on information obtained from local residents who indicated that a darkly colored cat was present in the area (M. L. Campbell, personal observation). The status of this cat in Argentina is considered indeterminate (i.e., it is known to be either endangered, vulnerable, or rare, but there is too little information to denote a category). In Argentina, this species has an Appendix II ranking (Fuller and Swift, 1984).

Leopardus pardalis (Linnaeus)

Felis pardalis Linnaeus, Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tenth edition. Laurentii Salvii, Stockholm, 1:42, 1758.

Specimens Examined.—(2) Cerro del Campo, 1 (CML); La Fronterita, 1 (MACN).
Additional Records.—Burruyacú; La Cocha (Olrog, 1976).

Measurements.—Cranial measurements (one male): greatest length of skull, 101.1; condylobasal length, 94.8; least interorbital length, 18.6; zygomatic breadth, 65.8; breadth of braincase, 51.3; greatest length of mandible, 64.6.

Habitat.—Ocelots are found only in the northernmost Argentine provinces and Tucumán. Olrog and Lucero (1981) and Lucero (1983) noted that this species is found in transitional forests, mountains, and savannas to southern Tucumán Province.

Remarks.—Cabrera (1961:177) listed a specimen of *Leopardus wiedii* from Burruyacú, Tucumán. *Leopardus wiedii* does not exist in the province. The specimen described is a young individual corresponding to the *Leopardus pardalis* from Cerro de Campo listed above (Olrog, 1976). This cat was listed as vulnerable in Argentina in 1990 (International Union for the Conservation of Nature, 1990), however it now is unlisted (International Union for the Conservation of Nature, 1994). In Argentina, this subspecies is listed in the Appendix I category and is protected (Fuller and Swift, 1984). This species is apparently still relatively common in the province, although it is not easily observed. The specimen from Cerro del Campo was collected in May. Specimens from Burruyacú were collected in 1971 and 1972, and from La Cocha in 1973 (Olrog, 1976).

Lynchailurus pajeros (Desmarest)

Felis pajeros Desmarest, Chat, *Felis*, Linn., Briss. Schreb., Cuv., *in* Nouveau dictionnaire d'Histoire Naturelle, appliquée aux art, à l'agriculture, à l'économie rurale et domestique, à la médecine, etc. Par une société de naturalistes et d'agriculteurs (nouvelle edition), 6:114, 1816.

Specimen Examined.—(1) Concepción, 1 (MACN).
Additional Records.—San Pedro de Colalao (M. A. Mares, personal observation); La Florida Reserva Provincial; Santa Ana Reserva Provincial (Anonymous, in press).

Habitat.—This species is distributed throughout most of Argentina, although its presence in the Chaco is questionable (Olrog and Lucero, 1981; Garcia-Perea, 1994). *Lynchailurus pajeros* is found in mountains, grasslands, and savannas in the western part of the province (Lucero, 1983).

Remarks.—Lucero (1983) mentioned that no recent data indicate its presence in the province, but Mares photographed a specimen taken above San Pedro de Colalao in 1976. In Argentina, this species has an Appendix II ranking (Fuller and Swift, 1984). The status of *L. pajeros* is given as indeterminate by the International Union for the Conservation of Nature (1994). Records of this species are rare. The animal photographed by Mares (Mares and Ojeda, 1984:583) was taken in the high-elevation grasslands in the area near San Pedro de Colalao. Garcia-Perea (1994) reviewed the systematics and biogeography of the members of this genus.

Oncifelis geoffroyi (d'Orbigny and Gervais)

Felis geoffroyi d'Orbigny and Gervais, Nouveau bulletin des sciences par la Société Philomatique, Paris, 1844:40, 1844.

Specimens Examined.—(11) Atahona, 1 (CML); Concepción, 1 (MACN); Departamento Burruyacú, 1 (CML); La Ramada, 1 (CML); Leales, 1 (CML); Quebrada de la Angostura, 1 (CML); Quebrada de los Matos, 1 (CML); San Pedro de Colalao, Junta de los Ríos, 2 (CML); Trancas, 1 (CML); Vipos, 500 m, 1 (BMNH).

Additional Records.—El Manantial (Burmeister, 1943); Piedra Tendida, 12 km WNW Burruyacú, along Río Cajón, 2,500 ft. (M. L. Campbell, in litt.); Pozo Hondo (R. M. Bárquez, personal observation); San Pedro de Colalao (M. A. Mares, personal observation).

Measurements.—External measurements (one young female): total length, 679.0; tail, 255.0; hindfoot, 94.0; ear, 44.0; weight, 81.2. Cranial measurements (one male, three females, unless noted otherwise): greatest length of skull, 91.6, 78.6 (65.7–88.6); condylobasal length (one male, two females), 88.1, 61.2, 76.1; least interorbital length, 16.2, 14.3 (11.2–17.2); zygomatic breadth, 61.4, 53.9 (43.4–64.9); breadth of braincase, 44.6, 40.6 (39.1–43.0); length of maxillary toothrow (one male, two females), 22.1, 19.1, 21.1; length of mandibular toothrow (one male, two females), 21.5, 19.3, 19.2; greatest length of mandible, 58.5, 48.8 (39.2–57.8).

Habitat.—*Oncifelis geoffroyi* is distributed throughout all of Argentina except Tierra del Fuego (Olrog and Lucero, 1981). In 1990, locals stated that this species of cat occurred in the transitional forest around Piedra Tendida (M. L. Campbell, personal observation).

Remarks.—In Argentina, this species has an Appendix II ranking (Fuller and Swift, 1984). One specimen was captured in September and one in October. Ximenez (1975) summarized the biology of this species. *Oncifelis geoffroyi* is common in the province, especially in the Chaco and monte habitats; it is less common in forested habitats.

Oreailurus jacobita (Cornalia)

Felis jacobita Cornalia, Memorie Societa Italiana di Scienze Naturali e Museo Civico di Storia Naturale di Milano, 1:3, 1865.

Specimen Examined.—(1) Morro del Zarzo, 5000 m, 1 (MACN).

Additional Records.—Laguna Huaca Huasi, Cumbres Calchaquíes, approximately 4250 m; Campo de la Gallina, Serranía de Quilmes o El Cajón (Scrocchi and Halloy, 1986); Cumbres Calchaquíes (Lucero, 1983).

Measurements.—External measurements (one sex unknown): total length, 1120.0; tail, 480.0; hindfoot, 115.0.

Habitat.—*Oreailurus jacobita* inhabits the high altitude arid and semiarid mountains found in the western part of the province. The Andean cat has a distribution restricted to high elevations in Jujuy, Salta, Tucumán, and Catamarca provinces (Cabrera, 1961; Olrog and Lucero, 1981).

Remarks.—The locality of the specimen examined was given as Sarzo, Aconquija, Tucumán, by Cabrera (1961:205); the locality given above is that which appears on the specimen tag. In the Argentine Andes, *O. jacobita* was considered rare (International Union for the Conservation of Nature, 1990); currently its status is indeterminate (International Union for the Conservation of Nature, 1994). This species has an Appendix I listing in Argentina and is protected (Fuller and Swift, 1984). S. Halloy photographed this species at Laguna Huaca Huasi on a morning in 1980. Scrocchi and Halloy (1986) suggest that this species may be confused with *Lynchailurus pajeros garleppi,* which is similar in appearance, but which occurs along the eastern slopes of the Peruvian Andes. Little is known about the biology of *O. jacobita.*

Puma concolor (Linnaeus)

Felis concolor Linnaeus, Mantissa Plantarum, 2:522, 1771.

Specimens Examined.—(15) Burruyacú, 1 (CML); Cajón de la Ovejeria, Chorrillos, 5 (CML); Chicligasta, 1 (CML); Gobernador Garmendia, 1 (CML); Graneros, 1 (CML); Leales, 1 (CML); Los Puestos, 1 (CML); Río Nío, 1 (CML); San Miguel de Tucumán, 2 (CML); Trancas, 1 (CML).

Additional Records.—Dique Escaba (M. L. Campbell, personal observation); El Manantial (Burmeister, 1943); Laguna Huaca Huasi (N. Ovrusky, personal communication).

Measurements.—Cranial measurements (one male, three sex unknown, two immature females): greatest length of skull, 156.0, 163.3 (154.0–181.0), 145.4, 121.9; condylobasal length, 148.0, 155.0 (143.0–174.0), 133.2, 108.3; least interorbital length, 29.6, 31.4 (28.2–35.0), 27.4, 21.9; zygomatic breadth, 109.3, 112.5 (102.4–126.6), 96.2, 79.3; breadth of braincase, 64.6, 66.9 (66.0–67.5), 64.9, 61.8; length of maxillary toothrow, 52.6, 54.5 (52.0–58.8),—,—; palatal length, 69.5, 69.9 (64.9–76.8),—,—; length of mandibular toothrow, 62.7, 60.6 (57.3–66.3),—,—; greatest length of mandible, 113.0, 121.3 (110.0–135.0), 103.5, 81.1.

Habitat.—Mountain lions are common in the Chacoan thorn scrub, the monte, and in the mountains of Tucumán Province.

Remarks.—In Argentina, this species has an Appendix II ranking (Fuller and Swift, 1984). Currier (1983) summarized the biology of this species. Individuals have been collected in January ($n = 1$), February ($n = 1$), April ($n = 1$), June ($n = 1$), July ($n = 5$), September ($n = 1$), and November ($n = 1$). Specimens from Leales and Cajón de la Ovejería are young individuals. Local residents of Dique Escaba indicated that this species occurred in the area (M. L. Campbell, personal observation). Pumas are as common in the Chaco as in the more mountainous regions of the province. Little is known about the biology of the species in Argentina. Cajal and Lopez (1987) found that in the San Guillermo Reserve, San Juan Province, guanacos and vicuñas were an important component of the diet of pumas.

Subfamily Pantherinae

Panthera onca (Linnaeus)

Felis onca Linnaeus, Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tenth edition. Laurentii Salvii, Stockholm, 1:42, 1758.

Specimens Examined.—(0) None.

Additional Record.—Tucumán, no specific locality given (De Moussy, 1864).

Remarks.—This species is probably extinct in the province. Originally widespread in distribution, the range of this species has constricted due to hunting and deforestation (Roig, 1991). It still occurs in the neighboring provinces of Salta and Jujuy. Redford and Eisenberg (1992) did not extend the distribution of this species to Tucumán Province.

Family Mustelidae

Subfamily Lutrinae

Lontra longicaudis (Olfers)

Lutra longicaudis Olfers, *in* Eschwege, Journal von Brasilien, oder Vermischte nachrichten aus Brasilien, auf wissenschaftlichen reisen gesammett von W. C. von Echwege . . . Weimer, Im verlage des Gr. H. S. pr. Londes-industries-comptoirs, 15(2):233, 1818.

Specimens Examined.—(1) Río Colorado, Famaillá, 1 (CML).

Measurements.—External measurements (one female): total length, 1030.0; tail, 410.0; hindfoot, 60.6. Cranial measurements (one female): greatest length of skull, 106.7; condylobasal length, 106.2; least interorbital length, 20.8; zygomatic breadth, 67.9; breadth of braincase, 52.6; length of maxillary toothrow, 28.5; palatal length, 48.0; length of mandibular toothrow, 33.9; greatest length of mandible, 68.4.

Habitat.—This otter prefers lagunas, estuaries, and rivers (Olrog and Lucero, 1981; Lucero, 1983).

Remarks.—Otters are rare in the province. Cabrera (1957) and Olrog and Lucero (1981) listed this species as *L. platensis.* Although found widely in central and northern Argentina, the distribution is becoming fragmented. The high value placed on the fur encourages illegal hunting. This species is considered in the Appendix I category by Argentina and is protected (Fuller and Swift, 1984). A conservation action plan and status report is available for the otter (Foster-Turley et al., 1990).

Subfamily Mephitinae

Conepatus chinga (Molina)

Viverra chinga Molina, Saggio sulla storia naturale del Chili. S. Tommaso d'Aquino, Bologna, p. 288, 1782.

Specimens Examined.—(5) Estancia El Cavao, 1 (CML); La Angostura, 1 (CML); La Cuesta, 1 (CML); Quebrada de las Burras, 1 (CML); Río Las Tacanas, 1 (CML).

Additional Record.—El Infiernillo (R. M. Bárquez, personal observation); El Infiernillo, about 3500 m (R. A. Ojeda, personal observation).

Measurements.—External measurements (one female): total length, 660.0; tail, 250.0; hindfoot, 60.0. Cranial measurements (three females, two sex unknown, unless noted otherwise): greatest length of skull, 64.0 (59.1–67.0), 62.8, 64.3; condylobasal length, 61.6 (56.1–64.5), 61.1, 63.5; least interorbital length, 17.1 (16.4–17.7), 16.8, 15.3; zygomatic breadth (one female, one sex unknown), 40.2, 37.6; breadth of braincase, 31.7 (31.0–32.1), 29.6, 27.0; length of maxillary toothrow, 20.0 (19.0–20.5), 19.9, 19.1; palatal length (one female), 28.2; length of mandibular toothrow, 22.4 (19.5–23.9), 22.4, 21.9; greatest length of mandible, 40.6 (37.1–43.6), 40.1, 39.8.

Habitat.—*Conepatus chinga* prefers savannas, mountains, and forests as well as the arid, shrubby areas of western Tucumán Province up to 3500 m (Cabrera, 1957; Lucero, 1983).

Remarks.—The extreme variation in coloration and size and stripe morphology shown by *Conepatus* has led to the description of numerous species. A systematic revision is needed. The few records that exist for the province do not permit us to make a detailed assessment of the color variation. In most systematic works, *C. rex,* which was described by Thomas (1898), is included in *chinga.* The individual observed at El Infiernillo was completely white dorsally and had a white tail, a description that corresponds to that of *C. rex* (Olrog and Lucero, 1981). The distribution of *C. rex* would include the mountainous areas of the province.

Subfamily Mustelinae

Eira barbara (Linnaeus)

Mustela barbara Linnaeus, Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tenth edition. Laurentii Salvii, Stockholm, 1:46, 1758.

Specimens Examined.—(5) Chicligasta, 1 (CML); Cumbres de San Pablo, 1 (BMNH); Monteros, 1 (MACN); Tucumán, no specific locality, 1 (MACN); Yerba Buena, 1 (CML).

Measurements.—External measurements (one male): total length, 1030.0; tail, 420.0; hindfoot, 78.0; ear, 35.0. Cranial measurements (one male): greatest length of skull, 118.0; condylobasal length, 104.0; least interorbital length, 25.6; zygomatic breadth, 71.6; breadth of braincase, 46.5; length of maxillary toothrow, 30.4; palatal length, 59.3; length of mandibular toothrow, 40.3; greatest length of mandible, 77.2.

Habitat.—Eiras are found in northern Argentina east of the Andes and as far south as southern Santiago del Estero Province (Olrog and Lucero, 1981). Lucero (1983) notes that this species is found in savannas, forests, and woodlands.

Remarks.—Individual specimens have been collected in July ($n = 1$) and August ($n = 1$). Eiras are quite common in the province, although records of them are scarce. An individual was seen in dense forest above 1800 m along Highway 65 in Catamarca Province near the Catamarca–Tucumán provincial border (M. A. Mares, personal observation).

Galictis cuja (Molina)

Mustela cuja Molina, Sagio sulla storia naturale del Chili, S. Tommaso d'Aquino, Bologna, p. 291, 1782.

Specimens Examined.—(22) Concepción, 15 (1 CML, 2 MACN, 12 BMNH); El Infiernillo, 1 (CML); El Portezuelo, 1 (CML); El Timbó, 2 (CML); La Higuera, 1 (CML); La Reducción, 1 (CML); Tafí Viejo, 1 (CML).

Additional Record.—Cumbres Calchaquíes (E. Dominguez, S. Halloy, and E. Terán, personal communication).

Measurements.—External measurements (five males, six females, unless noted otherwise): total length (four males, six females), 512.5 (470.0–550.0), 480.3 (360.0–560.0); tail, 144.0 (120.0–170.0), 139.3 (100.0–160.0); hindfoot, 57.1 (50.0–70.0), 50.0 (45.0–55.0); ear, 23.5 (20.5–25.0), 20.5 (16.0–29.0). Cranial measurements (six males, unless noted otherwise): greatest length of skull, 70.0 (58.8–74.4); condylobasal length, 69.9 (58.5–74.9); least interorbital length, 16.6 (14.6–17.9); zygomatic breadth, 42.3 (36.1–44.5); breadth of braincase, 34.3 (25.3–37.8); length of maxillary toothrow, 19.3 (11.8–22.0); palatal length (five males), 32.2 (27.4–34.7); length of mandibular toothrow, 23.9 (19.8–25.4); greatest length of mandible, 42.8 (36.5–45.6).

Habitat.—*Galictis* is found in nearly all of Argentina except Santa Cruz Province and Tierra del Fuego (Olrog and Lucero, 1981). This mustelid prefers mountains, savannas, and arid scrubby regions; it is found up to 3500 m (Olrog and Lucero, 1981; Lucero, 1983).

Remarks.—Individuals have been captured in May ($n = 1$), June ($n = 2$), July ($n = 1$), August ($n = 2$), September ($n = 1$), and October ($n = 3$).

Lyncodon patagonicus (de Blainville)

Mustela patagonica de Blainville, Ostéographie, on description iconographique comparée du squelette et du système dentaire des mammifères récents et fossiles . . . par H.-M. Ducrotay de Blainville, . . . précédé d'une étude sur la vie et les travaux de M. de Blainville, par M. P. Nicard. J.-B. Baillière et fils, 1839–1864, 4 volumes. Mammalia, partie 10 (Viverra):1, 1842.

Specimen Examined.—(1) Banda del Río Salí, 1 (CML).

Additional Records.—Amaicha del Valle; Colalao del Valle (Olrog, 1976); El Timbó (Olrog, 1958).

Measurements.—External measurements (one female): total length, 330.0; tail, 190.0; hindfoot, 29.5; ear, 15.0. Cranial measurements (one female): greatest length of skull, 45.7; condylobasal length, 46.0; least interorbital length, 10.9; zygomatic breadth, 24.3; breadth of braincase, 21.3; length of mandibular toothrow, 15.8; greatest length of mandible, 27.1.

Habitat.—*Lyncodon* is widely distributed in Argentina from Tucumán Province in the north to Córdoba Province in the east and southward to Santa Cruz Province. This species is found in arid, shrubby terrain in the lowlands, and in the mountains up to 2000 m (Olrog and Lucero, 1981; Lucero, 1983).

Remarks.—Olrog (1958) noted that this species was not rare in the province and that it was common in the Valle Calchaquíes up to 2000 m. We have not been able to verify the existence of the specimens listed in the additional records. Olrog (1958, 1976) noted that these specimens from Amaicha del Valle and Colalao del Valle were collected in November; those from El Timbó were collected in May. The specimen from Banda del Río Salí was collected in June.

Family Procyonidae
Subfamily Procyoninae
Nasua nasua (Linnaeus)

Viverra nasua Linnaeus, Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Volume 1. Regnum Animale. 12th edition. Laurentii Salvii, Stockholm, 1:64, 1766.

Specimens Examined.—(3) Cerro San Javier, 1 (CML); Tafí Viejo, 1 (CML); Trancas, 1 (CML).

Measurements.—Cranial measurements (one subadult sex unknown): greatest length of skull, 104.0; least interorbital length, 23.2; zygomatic breadth, 53.9; breadth of braincase, 44.3; length of maxillary toothrow, 34.6; palatal length, 61.6; length of mandibular toothrow, 36.8; greatest length of mandible, 71.0.

Remarks.—The specimen from Cerro San Javier is a young animal. This species is not commonly observed in the province, which constitutes its southern distributional limits. Two populations are found in Argentina. The first occurs in the provinces of Chaco, Corrientes, Formosa, Misiones, and Santa Fe. The second, found in northwestern Argentina, occurs in Jujuy, Salta, and Tucumán. The Gran Chaco appears to separate the two. Mares et al. (1981, 1989) comment on the biology of this species in the neighboring province of Salta. Redford and Eisenberg (1992) did not extend the distribution of this species to Tucumán Province.

Procyon cancrivorus (G. Cuvier)

Ursus cancrivorus G. Cuvier, Tableau elementaire de l'histoire naturelle des Animaux, Paris, p. 113, 1798.

Specimens Examined.—(5) Chicligasta, 1 (CML); Concepción, 3 (1 BMNH, 1 MACN, 1 CML); Los Vázquez, 1 (BMNH).

Additional Records.—Dique Escaba (M. L. Campbell, personal observation); 2 km below La Heladera along Hwy 307, 3,500 ft. (J. K. Braun, personal observation; M. L. Campbell, personal observation); Piedra Tendida (R. M. Bárquez, personal observation).

Measurements.—External measurements (one male, one female): total length, 950.0, 880.0; tail, 330.0, 330.0; hindfoot, 135.0,—; ear, 60.0,—. Cranial measurements (one male, one female): greatest length of skull, 118.4, 115.0; condylobasal length, 125.5, 121.0; least interorbital length, 28.8, 26.9; zygomatic breadth, 92.2, 83.0; breadth of braincase, 61.2, 57.1; length of maxillary toothrow, 49.7, 48.7; palatal length, 62.5, 63.0; length of mandibular toothrow, 55.7, 54.3; greatest length of mandible, 96.9, 93.1.

Habitat.—Crab-eating raccoons are, in general, found in savannas, forests, and woodlands, usually along water courses (Lucero, 1983). *Procyon cancrivorus* is found in all of northern Argentina east of the Andes as far south as San Luis Province (Olrog and Lucero, 1981); Cabrera (1957) had earlier placed the southern distributional limits in northern Catamarca Province. The vegetation at La Heladera was Yungas forest dominated by laurel and Mirtaceae (M. L. Campbell, personal observation). The scat, found in the cavity of a very large tree, contained freshwater crabs and large land snails (J. K. Braun, personal observation; M. L. Campbell, personal observation).

Remarks.—Single specimens have been captured in September, October, and December. The record of this species at Dique Escaba is based on information obtained from local residents (M. L. Campbell, personal observation).

Order Perissodactyla

Family Tapiridae

Tapirus terrestris (Linnaeus)

Hippopotamus terrestris Linnaeus, Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tenth edition. Laurentii Salvii, Stockholm, 1:74, 1759.

Specimens Examined.—(3) Las Pavas, 3 (CML).
Additional Record.—Departamento Famaillá (Lucero, 1983).

Remarks.—Lucero (1983) noted that the tapir has been extinct in the province since 1940, although an isolated population may still exist is some of the heavily forested areas. This species is listed as an Appendix II species in Argentina and is protected (Fuller and Swift, 1984). Historically, tapirs were found in the Yungas forest and gallery forests of the Chacoan thorn scrub, always near water. The distribution has contracted due to hunting pressure and habitat modification (Roig, 1991). Tapirs are found in the provinces of Misiones, Corrientes, Formosa, Chaco, Salta, and Jujuy (Olrog and Lucero, 1981).

Order Artiodactyla

Family Tayassuidae

Catagonus wagneri (Rusconi)

Platygonus carlesi wagneri, Rusconi, Anales del Museo Nacional de Historia Natural "Bernardino Rivadavia," 36:231.1930.

Specimens Examined.—(0) None.
Additional Records.—No specimens of this species have been collected in the province but Olrog, Ojeda, and Bárquez (personal observation) have seen signs of its presence in the northeastern part of the province near the specimen locality (in Santiago del Estero) cited by Olrog et al. (1976). Lucero (1983) also suggested that this peccary may occur in the province. This species was found by Mares in neighboring Santiago del Estero, just a few kilometers from the Tucumán border.

Remarks.—The Chacoan peccary is listed as vulnerable in Argentina (International Union for the Conservation of Nature, 1990). It is endemic to the Gran Chaco of Argentina, Bolivia, and Paraguay. The biology of this species is summarized by Mayer and Wetzel (1986).

Pecari tajacu (Linnaeus)

Sus tajacu Linnaeus, Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tenth edition. Laurentii Salvii, Stockholm, 1: 50, 1758.

Specimens Examined.—(4) Cerro del Campo, 1800 m, 3 (CML); Departamento Chicligasta, 1 (CML).

Additional Records.—Aguas Chiquitas (P. Capllonch, personal communication); Dique Escaba (M. L. Campbell, personal observation); El Nogalar, = Río los Sosa, km 43.0, Ruta 307 (S. Ojeda, personal communication); Piedra Tendida, 12 km WNW Burruyacú, along Río Cajón, 2,500 ft. (M. L. Campbell, personal observation).

Measurements.—Cranial measurements (one female, one subadult sex unknown): greatest length of skull, 450.0, 203.0; condylobasal length, 215.0, 172.0; least interorbital length, 54.0, 44.5; zygomatic breadth, 117.8, 85.5; breadth of braincase, 53.9, 52.9; length of maxillary toothrow,—, 46.2; palatal length, 142.0, 115.0; length of mandibular toothrow,—, 53.0; greatest length of mandible,—, 131.0.

Habitat.—The distribution of the collared peccary includes north-central Argentina east of the Andes and the Yungas forest (Olrog and Lucero, 1981). The southernmost distributional limits are San Luis and northeastern Mendoza provinces. This species is found in savannas, woodlands, and forests of thick vegetation (Olrog and Lucero, 1981; Lucero, 1983). Meyer and Weyrauch (1966) reported that this peccary occurred in subtropical humid forest. Locals interviewed at the Piedra Tendida locality indicated that this peccary is found in the area, but is heavily hunted; it has retreated into the surrounding hills (M. L. Campbell, personal communication). The record of this species is based on information obtained from locals at Dique Escaba who indicated that this species is present in the area (M. L. Campbell, personal communication).

Remarks.—The peccary captured at Cerro del Campo is a young individual. Specimens were collected in April (n = 1) and September (n = 1). Although this species is common in the province, its populations have been reduced by hunting and habitat conversion.

Tayassu pecari (Link)

Sus pecari Link, Beiträge zur Naturgeschichte, 2:104, 1795.

Specimens Examined.—(0) None.

Remarks.—Information on the biology of this species was presented by Mayer and Wetzel (1987). This species tends to inhabit the forested regions of northern Argentina (Olrog and Lucero, 1981). Its presence in the province is unknown, although Meyer and Weyrauch (1966) reported it as a component of the fauna of the subtropical humid forest.

Family Camelidae

Lama guanicoe (Müller)

Camelus guanicoe Müller, Mit einer ausführlichen erklärung ausgefertiget. Des ritters Carl von Linne . . . Vollständigen natursystems supplements und register-ban über aler sechs theile oder classen des thierreichs. G. N. Raspe, Nurnberg, p. 50, 1776.

Specimen Examined.—(1) Nevados del Aconquija, Glacial del Cochuna, 4550 m, 1 (CML).

Additional Records.—Sierras del Cajón; Cumbres Calchaquíes; Cumbres de Santa Barbara; Sierra del Aconquija (Cajal, 1983); Sierras del Aconquija (De Moussy, 1864); Cumbres Calchaquies, Alto de Muñoz (E. Dominguez, S. Halloy, and E. Terán, personal communication).

Measurements.—Cranial measurements (one sex unknown): greatest length of skull, 280.0; condylobasal length, 267.0; least interorbital length, 101.3; zygomatic breadth, 123.7; breadth of braincase, 69.7; length of maxillary toothrow, 62.6; palatal length, 143.5.

Habitat.—This species is distributed from southern Argentina (Santa Cruz Province), where they are relatively abundant, northward to Jujuy Province. In the northern parts of the distribution, guanacos are much less abundant. In Tucumán, guanacos inhabit mountains up to 4000 m (Olrog and Lucero, 1981; Lucero, 1983).

Remarks.—Guanacos are listed as an Appendix II species in Argentina (Fuller and Swift, 1984). The biology of the guanaco has been summarized in Cajal (1991) and Torres (1992). Guanacos are present in La Florida Natural Park, but there are no density estimates. Cajal (1983) estimated 1000 guanacos were present in the Cumbres de Santa Barbara. Aconquija has been proposed as a protected area. This species was originally distributed throughout most of the country, including Chaco, Santa Fe, and Buenos Aires provinces. The range has constricted due to habitat modification and hunting pressure. Cajal (1983) and Cajal and Amaya (1985) reviewed diverse aspects of the biology and history of the guanaco.

Vicugna vicugna (Molina)

Camellus (sic) *vicugna* Molina, Saggio sulla storia naturale del Chili. S. Tommaso d'Aquino, Bologna, 1782:313.

Specimens Examined.—(0) None.

Additional Records.—Sierras del Aconquija, Departamento Tafí del Valle (De Moussy, 1864).

Remarks.—We are unable to verify the precision of the information given by De Moussy (1864). Vicuñas are distributed in the high Andean regions from Jujuy to northern Mendoza (Olrog and Lucero, 1981), although Cajal and Puig (1992) noted that the distribution extended only to northern San Juan Province. Redford and Eisenberg (1992) did not extend the distribution of this species to Tucumán Province.

Family Cervidae

Subfamily Odocoileinae

Hippocamelus antisensis (d'Orbigny)

Cervus antisensis d'Orbigny, Annales Museum d'Histoire Naturelle, Paris, 3:91, 1834.

Specimen Examined.—(1) Cumbres del Aconquija, 1 (CML).

Additional Record.—Laguna Huaca Huasi (S. Halloy, personal communication).

Measurements.—Cranial measurements (one male): greatest length of skull, 255.0; least interorbital length, 73.5; breadth of braincase, 71.0; length of maxillary toothrow, 67.1; palatal length, 116.2; length of mandibular toothrow, 74.7; greatest length of mandible, 227.0.

Habitat.—The huemul is found in the Andes of Salta, Jujuy, Tucumán, Catamarca, and La Rioja (Olrog and Lucero, 1981). This species inhabits the rocky steppes between 3000–4000 m (Olrog and Lucero, 1981; Lucero, 1983).

Remarks.—This deer is considered vulnerable in Argentina (International Union for the Conservation of Nature, 1990, 1994) and is ranked as an Appendix I species (Fuller and Swift, 1984) by Argentina and is protected. The biology was summarized by Moreno (1993). Huemuls were intensively hunted; this species is in danger of being extirpated from the province, although several populations still occur in the central highlands.

Mazama americana (Erxleben)

Moschus americanus Erxleben, Systema regni animalis per classes, ordines, genera, species, varietates, cum synonymia et historia animalium. Classis. I. Mammalia. Weygandianis, Lipsiae, 1:324, 1777.

Specimens Examined.—(0) None.

Additional Records.—On two separate occasions Mares observed these deer standing on the road to Tafí del Valle at the approximate altitude of Piedras Coloradas; Dique Escaba (M. L. Campbell, personal communication); 0.5 km N of Las Higuerillas on Hwy 308, 3,000 ft. (M. L. Campbell, personal communication); Tucumán, no specific locality (Meyer and Weyrauch, 1966).

Habitat.—The distribution of *M. americana* includes the forested regions of Jujuy, Salta, Tucumán, Formosa, Chaco, Santa Fe, Corrientes, and Misiones (Olrog and Lucero, 1981). In Tucumán, this species is found in transitional and humid forests; the southernmost limits of its distribution are along the border with Catamarca Province (Olrog and Lucero, 1981; Lucero, 1983).

Remarks.—The biology of this species has been summarized by Moreno (1993). It is either rare or difficult to observe in its preferred habitat of dense, humid forest. Meyer and Weyrauch (1966) report this deer in the subtropical humid forest of Tucumán. At Dique Escaba, locals indicated that *M. americana* occurred in the area; four piles of scat were found at the Las Higuerillas locality (M. L. Campbell, personal communication).

Mazama gouazoupira (G. Fischer)

Cervus gouazoupira G. Fischer, Zoognosia, 3:465, 1814.

Specimens Examined.—(4) Chicligasta, 3 (CML); Leales, 1 (CML).

Additional Records.—Near the campground near Cochuna (R. A. Ojeda, personal observation); El Cadillal (personal observation); Piedra Tendida, 12 km WNW Burruyacú, along Río Cajón, 2,500 ft. (M. L. Campbell, personal communication).

Measurements.—Cranial measurements (two females): greatest length of skull, 159.5, 169.0; condylobasal length, 147.8, 164.0; least interorbital length, 39.8, 39.9; zygomatic breadth, 72.0, 74.0; breadth of braincase, 55.6, 54.1; length of maxillary toothrow, 40.6, 52.6; palatal length, 92.6, 106.5; length of mandibular toothrow, 45.4, 61.5; greatest length of mandible, 132.9, 143.0.

Habitat.—*Mazama gouazoupira* is more widely distributed than *M. americana,* occurring from east of the Andes to the northeastern provinces, southward to San Luis Province (Olrog and Lucero, 1981). Lucero (1983) notes that this species is abundant in the open savannas, woodlands, thickets, and mountains up to 2000 m along the border with the province of Catamarca. This deer seems to prefer the Chacoan habitat found in the eastern parts of the province.

Remarks.—Moreno (1993) summarized the biology of this species. Scat of this species was found at Piedra Tendida (transitional forest) and hunters indicated that it was a common species in the area (M. L. Campbell, personal communication). Although there are few records and little is known of its biology, this species is more abundant than *M. americana.*

Ozotoceros bezoarticus (Linnaeus)

Cervus bezoarticus Linnaeus, Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tenth edition. Laurentii Salvii, Stockholm, 1:67, 1758.

Remarks.—An expedition report dated 1825–1826 stated that this species once occurred in large numbers in the region between Vipos and Trancas (Roig, 1991).

Jackson (1987) and Moreno (1993) have summarized the biology of this species. It is no longer found in the province. Redford and Eisenberg (1992) did not extend the distribution of this species to Tucumán Province.

Order Lagomorpha
Family Leporidae
Sylvilagus brasiliensis (Linnaeus)

Lepus brasiliensis Linnaeus, Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tenth edition. Laurentii Salvii, Stockholm, 1:58, 1758.

Specimens Examined.—(8) Campo de las Chuñas, San Pedro de Colalao, 1 (CML); Cerro del Campo, 800 m, 1 (BMNH); El Portezuelo, San Pedro de Colalao, 2 (CML); El Tañcillo, 3 (CML); Las Mesadas, 1 (CML).

Additional Records.—El Cadillal (R. M. Bárquez, personal observation); Playa Larga (R. M. Bárquez, personal observation).

Measurements.—External measurements (two males): total length, 390.0, 348.0; tail,—, 19.0; hindfoot, 80.0, 74.0; ear, 75.0, 60.5. Cranial measurements (two males): greatest length of skull, 67.4, 70.8; condylobasal length, 60.5, 58.0; least interorbital length, 14.2, 17.2; zygomatic breadth, 32.7, 33.5; breadth of braincase, 25.3, 24.6; length of maxillary toothrow, 14.0, 12.6; palatal length, 27.8, 31.0; length of mandibular toothrow, 14.0, 12.7; greatest length of mandible, 46.8, 62.5.

Habitat.—Lucero (1983) gives the habitat as transitional forest, open woodlands, and savannas, in mountains up to 2000 m.

Remarks.—This herbivorous species is generally nocturnal and solitary.

DISCUSSION

Our data provide a great deal of information on a rich fauna of mammals that has not been well studied to date. Certainly the many specimens will prove to be useful to systematists in the years to come, as will the tissues and chromosomes. Moreover, to date there has been little quantitative data on habitat selection, distribution, and reproduction. Regarding the latter, there have been few studies to offer comparative data on patterns of reproduction for most groups of mammals in South America (Hamlett, 1992; Harder, 1992; Lacher, 1992). South American bats have also received little attention from the standpoint of their reproductive patterns; however, Myers (1977) and Myers and Wetzel (1983) provided a great deal of information on bats of the Chaco of Paraguay, located not far from Tucuman Province. Pearson and Pearson (1989) studied reproduction in three species of vespertilionid bats in southern Argentina, located much farther away from Tucumán Province than Paraguay, geographically speaking, although still within Argentina.

In the Chaco, it was shown that reproductive activity for four species of vespertilionid bats began as early as the winter month of May, when spermatozoa were found in the reproductive tracts of females (Myers, 1977). Reproductively active Chacoan bats from a wide variety of taxa were found mainly from August through October (Myers and Wetzel, 1983). In southernmost Argentina, the bats that were studied were pregnant in the late spring and summer months of October through December (Pearson and Pearson, 1989). We did not do histological or other microscopic examinations of specimens, although fluid-preserved specimens are available for laboratory analyses. In examining the data for all the bats collected, we found that almost all gross reproductive activity (as determined by embryos, enlarged testes, and lactation) occurred during the late spring and summer months of September through January. Only a few individuals of any species showed any evidence of reproductive activity during the winter (May–July) (e.g., *Sturnira erythromos, Artibeus planirostris, Lasiurus ega*), and none was pregnant or lactating. These results are in accord with the studies conducted in Paraguay and in southern Argentina. Where winters are harsh in Tucumán (e.g., the high mountains), we would expect that bats will show the strict limitations on month of parturition described by Pearson and Pearson (1989). Where conditions are somewhat less stringent in winter (e.g., the Chaco or moist subtropical forest), we would expect bats to show occasionally some activity in colder months. The bats of Tucumán Province are clearly responding to the area in a manner that suggests that parturition is keyed to the warmer months of the year, a pattern that may obtain until truly tropical conditions are encountered, when much more complex patterns of reproduction are possible (Wilson, 1979). Only a larger data base will clarify these patterns over a broad geographic and climatologic scale, as well as under different conditions of allopatry, sympatry, and seasonality of food resources.

Our work documents that 68 nonrodent species of mammals occur, or have recently occurred, in Tucumán Province. Additionally, we have suggested that *Priodontes maximus,* the giant armadillo, may still be found in the Chacoan scrublands of extreme northeastern Tucumán. The species is known to occur in the neighboring provinces of Salta and Santiago del Estero. Although there are likely several provinces in Argentina that support a similar number of mammal species as Tucumán, these provinces are much larger (e.g., Salta, which is seven times larger than Tucumán) and have a portion of their territory located within the tropics.

Because of its small size, long history of extensive human habitation, economic and agricultural development, and limited size of macrohabitats, Tucumán can be considered to be a model system for studying the effects of human population density, economic development, and modern agricultural techniques on the natural environment. With its moist subtropical forest, rich montane woodlands, extensive lowland Chacoan thorn scrub, high-elevation and low-elevation deserts, and glacial watersheds, the province has experienced, and is experiencing, the challenges of rapid development, while attempting to control in some manner the effects of such development on the natural environment. Certainly the history of economic development in Tucumán has had a pronounced influence on the natural habitats of the province and on its mammal fauna.

From the conservation standpoint, some of the most important species are nonrodents. Indeed, Argentina has only one threatened or endangered rodent (the chinchilla, *Chinchilla lanigera*), although some additional potential candidates for protection exist. Still, all other protected, threatened, and endangered mammals are nonrodents and nonbats. Although Tucumán has supported European human populations for almost four-and-a-half centuries, and native populations for millennia, and even though it is presently Argentina's most densely settled province, there have been relatively few extirpations of mammals.

Six species have likely been extirpated from the province during historic times: the jaguar (*P. onca*), tapir (*Tapirus*), pampas deer (*Ozotoceros*), vicuña (*Vicugna*), black-capped capuchin monkey (*Cebus*), and giant anteater (*Myrmecophaga*). The first four were eliminated due to hunting, whereas the giant anteater and the monkey may have occurred in low numbers in the dry Chaco (anteater) or low montane forests (monkey) and been eliminated due both to hunting pressures and habitat modification. Two other species, the three-banded armadillo (*Tolypeutes*) and the otter (*Lontra*) are in very low numbers in Tucumán, their populations reduced by hunting and habitat modification. Both were likely common in the past.

There are four other species in Tucumán that are rare, and hunting pressures almost certainly have had an adverse affect on their numbers, but most of these were probably rare in any case (e.g., *Cabassous, L. pajeros, O. jacobita, Catagonus*). Thus, when viewed as a fauna of more than 100 species, the mammals of Tucumán would seem to have been reduced by "only" six species. But this reduction in the number of species supported in the province has not occurred in a haphazard manner, with species disappearance occurring across taxonomic categories. Rather it is the larger mammals that have been most strongly affected. We will deal with the rodents in a subsequent paper, but few rodents appear to have disappeared from the province due to human activities. Larger mammals are more susceptible to human depredation, serving as food for humans in some cases, competitors in others, and dangerous predators in at least one case.

Among Tucumán's 68 nonrodent species, fully 12 species, or 19% of the nonrodent fauna, have either been eliminated, or are in danger of being extirpated from the province. Among these are the largest-bodied species of mammals found in the province, as well as several important carnivores. If we also exclude bats from consideration, we find that of the 39 nonbat and nonrodent species that occurred in Tucumán Province within the last 200 years, 12 of 39, or 31%, have been extirpated or are at very low population levels, thus almost a third of the larger mammals are no longer found in the province. This is a significant loss of economically and ecologically important species, as well as a loss of species that were spectacular inhabitants of the rich habitats of Tucumán Province.

We suggest that it is not too late to act to recover a significant proportion of the species that have been lost. There is little hope of bringing back a controversial species such as the jaguar, but vicuñas could be reintroduced to the high mountains of the province and tapirs to the forests. Monkeys could also be brought back to the forest they inhabited only a relatively short time ago. Similarly, *Ozotoceros* would not appear to present special difficulties for reintroduction. By setting aside Chacoan thorn scrub reserves, the giant armadillo, giant anteater, *Cabassous,* and *Tolypeutes* could also be either protected or reintroduced.

The recent history of the province involves failed efforts (fortunately) to introduce exotic species such as red deer (*Cervus elephas*) to the alder forests and montane grasslands. It would take much less effort, and be more logical, to recover the fauna of large mammals that has disappeared from Tucumán, thereby impoverishing the fauna of the province and the lives of the people who live there. The ecological situation of Tucumán, while serious, is far from hopeless. If provincial leaders can find the will to act, and if the citizenry can be educated to appreciate its own rich mammal fauna rather than the fauna of Europe, it is highly likely that the large-mammal fauna of Tucumán can be returned to a good approximation of the fauna that occurred in the province at the time of the colonization of South America. In this way, Tucumán could serve not as an indicator of how important species disappear as a result of human activities, but rather how major faunal elements can be preserved in managed reserves and, with protection, in the natural habitats where they once roamed.

ACKNOWLEDGMENTS

Many individuals have participated in field research. Most recently, the following have assisted in collecting and preparing specimens: S. Adams, M. L. Campbell, P. Capllonch, R. L. Humphrey, M. Guevarra, E. Pescetti, and S. Peurach. Funding for field research was provided by a grant to M. A. Mares from the National Science Foundation (BSR-8906665), among other sources. Additional support was provided by the Oklahoma Museum of Natural History and the Department of Zoology, University of Oklahoma. C. Kacmarcik produced the figures. We appreciate the many helpful suggestions of P. Myers, B. Patterson, and an anonymous reviewer, that resulted in a much improved manuscript.

LITERATURE CITED

ANONYMOUS. 1968. Gazetteer No. 103 (Argentina) of the United States Board of Geographic Names. Office of Geography, Department of Interior, Washington, D.C.

———. 1981. Atlas Físico de la República Argentina. Volume 1. Centro Editor de América Latina, Buenos Aires, Argentina, 192 pp.

———. In press. Cats. An Action Plan for Their Conservation. International Union for the Conservation of Nature, Gland, Switzerland.

BAKER, R. J., J. C. PATTON, H. H. GENOWAYS, AND J. W. BICKHAM. 1988. Genic studies of *Lasiurus* (Chiroptera: Vespertilionidae). Occasional Papers, The Museum, Texas Tech University, 117:1–15.

BÁRQUEZ, R. M. 1987. Los Murciélagos de Argentina. Unpublished Ph.D. dissert., Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán, Argentina, 525 pp.

———. 1988. Notes on identity, distribution, and ecology of some Argentine bats. Journal of Mammalogy, 69:873–876.

BÁRQUEZ, R. M., AND S. C. LOUGHEED. 1990. New distributional records of some Argentine bat species. Journal of Mammalogy, 71:261–263.

BÁRQUEZ, R. M., AND R. A. OJEDA. 1992. The bats (Mammalia: Chiroptera) of the Argentine Chaco. Annals of Carnegie Museum, 61:239–261.

BÁRQUEZ, R. M., M. A. MARES, AND R. A. OJEDA. 1991. The Mammals of Tucumán (Mamíferos de Tucumán). Special Publication, Oklahoma Museum of Natural History, Norman, Oklahoma, 282 pp.

BERTA, A. 1982. Cerdocyon thous. Mammalian Species, 186:1–4.

BURMEISTER, H. 1943. Viaje por los estados del Plata (1857–1860). Unión Germánica en la Argentina, Buenos Aires, 2:1–567.

CABRERA, A. 1957. Catálogo de los mamíferos de América del Sur. I. Metatheria, Unguiculata, Carnivora. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," 4:1–307.

———. 1961. Los félidos vivientes de la República Argentina. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," 6:161–247.

CABRERA, A., AND J. YEPES. 1960. Mamíferos Sudamericanos. Second edition. Ediar, Buenos Aires, 1:1–187, 2:1–160.

CABRERA, A. L. 1976. Regiones fitogeográficas Argentinas. Enciclopedia Argentina de Agricultura y Jardinería. ACME, Buenos Aires, 85 pp.

CAJAL, J. L. 1976. Una población de *Didelphis albiventris* Lund según el método de Boguslavsky. Physis, 35:243–249.

———. 1981. Estudios preliminares sobre el área de acción en marsupiales (Mammalia, Marsupialia). Physis, 40:27–37.

———. 1983. Situación del guanaco en la República Argentina. Pp. 3–21, *in* Situación del Guanaco y Estrategia de la Conservación de los Camélidos en la Argentina. Secretaria de Ciencia y Técnica, Buenos Aires, 31 pp.

———. 1991. An integrated approach to the management of wild camelids in Argentina. Pp. 305–321, *in* Latin American Mammalogy: History, Biodiversity, and Conservation (M. A. Mares and D. J. Schmidly, eds.). University of Oklahoma Press, Norman, Oklahoma, 468 pp.

CAJAL, J. L., AND J. N. AMAYA. 1985. Estado actual de las investigaciones sobre camélidos en la República Argentina. Ministerio de Educación y Justicia, Secretaria de Ciencia y Técnica, Programa Nacional de Recursos Naturales Renovables, Buenos Aires, 388 pp.

CAJAL, J. L., AND N. E. LOPEZ. 1987. El puma como depredador de camélidos silvestres en la Reserva San Guillermo, San Juan, Argentina. Revista Chilena de Historia Natural, 60:87–91.

CAJAL, J. L., AND S. PUIG. 1992. 2. Argentina. Pp. 5–9, *in* South American Camelids: An Action Plan for Their Conservation (H. Torres, ed.). International Union for the Conservation of Nature and Natural Resources, Gland, Switzerland, 58 pp.

CRESPO, J. A. 1944. Contribución al conocimiento de la ecología de algunos dasipódidos (Edentata) Argentinos. Revista Argentina Zoogeografía, 4:7–39.

———. 1964. Dos mamíferos nuevos para la provincia de Córdoba. Neotrópica, 10:62.

———. 1971. Ecología del zorro gris *Dusicyon gymnocercus antiquus* (Ameghino) en la Provincia de La Pampa. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," 1: 147–205.

CURRIER, M. J. P. 1983. Felis concolor. Mammalian Species, 200:1–7.

DALBY, P. L. 1975. Biology of pampa rodents, Balcarce area, Argentina. Publications of the Museum, Michigan State University Biological Series, 5:149–272.

DE MOUSSY, M. 1860–1864. Description geographique et statistique de la Confederation Argentine. 3 volumes. Libraire de Fermin Didot Freres, Fils et Cie, Paris.

DESMAREST, A. 1804. Mammifères. *In* Nouveau dictionnaire d'histoire naturelle. Volume 4. Chez Deterville, Paris.

DIGILIO, A. P. L., AND P. R. LEGNAME. 1966. Los árboles indígenas de la Provincia de Tucumán. Opera Lilloana XV, Instituto Miguel Lillo, Tucumán, Argentina.

FINDLEY, J. S. 1987. The Natural History of New Mexican Mammals. University of New Mexico Press, Albuquerque, 164 pp.

FORNES, A., AND E. MASSOIA. 1967. Procedencias nuevas o poco conocidas para murciélagos (Noctilionidae, Phyllostomidae, Vespertilionidae, y Molossidae). Segundas Jornadas Entomoepidemiológicas Argentinas, 1:133–145.

———. 1968. Nuevas procedencias Argentinas para *Noctilio labialis, Sturnira lilium, Molossops temminckii* y *Eumops abrasus* (Mammalia, Chiroptera). Physis, 28:37–38.

FOSTER-TURLEY, P., S. MACDONALD, AND C. MASON, EDS. 1990. Otters. An Action Plan for Their Conservation. International Union for the Conservation of Nature, Gland, Switzerland, 126 pp.

FULLER, K. S., AND B. SWIFT. 1984. Latin American Wildlife Trade Laws. World Wildlife Fund–U.S., 354 pp.

GARCIA-PEREA, R. 1994. The pampas cat group (genus *Lynchailurus* Severtzov, 1858) (Carnivora: Felidae), a systematic and biogeographic review. American Museum Novitates, 3096:1–36.

GINSBERG, J. R., AND D. W. MACDONALD, EDS. 1990. Foxes, Wolves, Jackals, and Dogs. An Action Plan for the Conservation of Canids. International Union for the Conservation of Nature, Gland, Switzerland, 116 pp.

GREEGOR, D. H. 1975. Renal capabilities of an Argentine desert armadillo. Journal of Mammalogy, 56:626–632.

———. 1980*a*. Diet of the little hairy armadillo, *Chaetophractus vellerosus,* of northwestern Argentina. Journal of Mammalogy, 61:331–334.

———. 1980*b*. Preliminary study of movements and home range of the armadillo, *Chaetophractus vellerosus.* Journal of Mammalogy, 61:334–335.

———. 1985. Ecology of the little hairy armadillo *Chaetophractus vellerosus.* Pp. 397–405, *in* The Evolution and Ecology of Armadillos, Sloths, and Vermilinguas (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C., 451 pp.

HAMLETT, W. C., ED. 1992. Reproductive Biology of South American Vertebrates. Springer-Verlag, New York, 328 pp.

HARDER, J. D. 1992. Reproductive biology of South American marsupials. Pp. 211–228, *in* Reproductive Biology of South American Vertebrates (W. C. Hamlett, ed.). Springer-Verlag, New York, 328 pp.

INTERNATIONAL UNION FOR THE CONSERVATION OF NATURE. 1990. 1990 IUCN Red List of Threatened Animals. International Union for the Conservation of Nature, Gland, Switzerland, and Cambridge, United Kingdom, 228 pp.

———. 1994. 1994 IUCN Red List of Threatened Animals. International Union for the Conservation of Nature, Gland, Switzerland, and Cambridge, United Kingdom, 341 pp.

JACKSON, J. E. 1987. Ozotoceros bezoarticus. Mammalian Species, 295:1–5.

LACHER, T. E., JR. 1992. Ecological aspects of reproductive patterns in South American small rodents. Pp. 283–294, *in* Reproductive Biology of South American Vertebrates (W. C. Hamlett, ed.). Springer-Verlag, New York, 328 pp.

LUCERO, M. M. 1983. Lista y distribución de aves y mamíferos de la provincia de Tucumán. Ministerio de Cultura y Educación, Fundación Miguel Lillo, Miscelanea, 75:1–61.

MARES, M. A. 1973. Climates, mammalian communities, and desert rodent adaptations: An investigation into evolutionary convergence. Unpublished Ph.D. dissert., University of Texas, Austin, 345 pp.

———. 1976. Convergent evolution of desert rodents: Multivariate analysis and zoogeographic implications. Paleobiology, 2:39–64.

MARES, M. A., AND R. A. OJEDA. 1984. Faunal commercialization and conservation in South America. BioScience, 34:580–584.

MARES, M. A., R. A. OJEDA, AND M. P. KOSCO. 1981. Observations on the distribution and ecology of the mammals of Salta Province, Argentina. Annals of Carnegie Museum, 50:151–206.

MARES, M. A., R. A. OJEDA, AND R. M. BÁRQUEZ. 1989. Guide to the Mammals of Salta Province, Argentina (Guía de los Mamíferos de la Provincia de Salta, Argentina). University of Oklahoma Press, Norman, Oklahoma, 303 pp.

MARES, M. A., R. M. BÁRQUEZ, AND J. K. BRAUN. 1995. Notes on Argentine mammals: Distribution and ecology of some Argentine bats. Annals of Carnegie Museum, 64:219–237.

MASSOIA, E. 1976. Cuatro notas sobre murciélagos de la República Argentina (Molossidae y Vespertilionidae). Physis, 35:257–265.

MASSOIA, E., AND A. FORNES. 1965. Nuevos datos sobre la morfología, distribución geográfica y etoecología de *Calomys callosus callosus* (Rengger) (Rodentia–Cricetidae). Physis, 25:325–331.

MAYER, J. J., AND R. M. WETZEL. 1986. Catagonus wagneri. Mammalian Species, 259:1–5.

———. 1987. Tayassu pecari. Mammalian Species, 293:1–7.

MEYER, T. 1963. Estudios sobre la selva tucumana. La selva de mirtáceas de "Las Pavas." Opera Lilloana, 10:1–144.

MEYER, T., AND W. K. WEYRAUCH. 1966. Guía para dos excursiones biológicas en la provincia de Tucumán. Miscelanea, Universidad Nacional de Tucumán e Instituto Miguel Lillo, 23:1–127.

MORALES, J. C., AND J. W. BICKHAM. 1995. Molecular systematics of the genus *Lasiurus* (Chiroptera: Vespertilionidae) based on restriction-site maps of the mitochondrial ribosomal genes. Journal of Mammalogy, 76:730–749.

MORELLO, J. 1958. La provincia fitogeográfica del Monte. Opera Lilloana, 2:1–155.

MORELLO, J., AND J. ADÁMOLI. 1968. Las grandes unidades de vegetación y ambiente del Chaco Argentino. Primera parte: Objetivos y metodología. Instituto Nacional de Tecnología Agropecuaria (INTA). La Vegetación de la República Argentina, 10:1–125.

MORENO, D. I. 1993. Ciervos autóctonos de la República Argentina. Fundación Vida Silvestre Argentina, Buenos Aires, 40 pp.

MYERS, P. 1977. Patterns of reproduction of four species of vespertilionid bats in Paraguay. University of California Publications in Zoology, 107:1–41.

MYERS, P., AND R. M. WETZEL. 1983. Systematics and zoogeography of the bats of the Chaco Boreal. Miscellaneous Publications of the Museum of Zoology, University of Michigan, 165:1–59.

NOVARO, A. J. 1995. Sustainability of harvest of culpeo foxes in Patagonia. Oryx, 29:18–22.

OJEDA, R. A., AND M. A. MARES. 1989. A biogeographic analysis of the mammals of Salta Province, Argentina: Patterns of species assemblage in the Neotropics. Special Publications, The Museum, Texas Tech University, 27:1–66.

OLROG, C. C. 1958. Notas mastozoológicas sobre la colección del Instituto Miguel Lillo (Tucumán). Acta Zoologica Lilloana, 16:91–95.

———. 1959. Notas mastozoológicas. II. Sobre la colección del Instituto Miguel Lillo. Acta Zoologica Lilloana, 17:403–419.

———. 1976. Sobre mamíferos del noroeste Argentino. Acta Zoologica Lilloana, 32:5–14.

OLROG, C. C., AND M. M. LUCERO. 1981. Guía de los mamíferos Argentinos. Ministerio de Cultura y Educación, Fundación Miguel Lillo, Tucumán, Argentina, 151 pp.

OLROG, C. C., R. A. OJEDA, AND R. M. BÁRQUEZ. 1976. *Catagonus wagneri* (Rusconi) en el noroeste Argentina. Neotropica, 22:53–56.

PEARSON, O. P., AND A. K. PEARSON. 1989. Reproduction of bats in southern Argentina. Pp. 549–566, *in* Advances in Neotropical Mammalogy (K. H. Redford and J. F. Eisenberg, eds.). The Sandhill Crane Press, Inc., Gainesville, Florida, 614 pp.

PINE, R. H., P. L. DALBY, AND J. O. MATSON. 1985. Ecology, postnatal development, morphometrics, and taxonomic status of the short-tailed opossum, *Monodelphis dimidiata,* an apparently semelparous annual marsupial. Annals of Carnegie Museum, 54:195–231.

REDFORD, K. H., AND J. F. EISENBERG. 1992. Mammals of the Neotropics: The Southern Cone. Volume 2. Chile, Argentina, Uruguay, Paraguay. University of Chicago Press, Chicago, Illinois, 430 pp.

REDFORD, K. H., AND R. M. WETZEL. 1985. Euphractus sexcinctus. Mammalian Species, 252:1–4.

REIG, O. A. 1964. Roedores y marsupiales del partido de General Pueyrredón y regiones adyacentes (Provincia de Buenos Aires, Argentina). Publicaciones del Museo Municipal de Ciencias Naturales de Mar del Plata, 1:203–224.

ROIG, V. G. 1991. Desertification and distribution of mammals in the southern cone of South America. Pp. 239–279, *in* Latin American Mammalogy: History, Biodiversity, and Conservation (M. A. Mares and D. J. Schmidly, eds.). University of Oklahoma Press, Norman, Oklahoma, 468 pp.

ROMAÑA, C., AND J. W. ABALOS. 1950. Lista de quirópteros de la colección del Instituto de Medicina Regional, y sus parásitos. Anales del Instituto de Medicina Regional, 3:111–117.

Sanborn, C. C. 1930. Distribution and habits of the three-banded armadillo (*Tolypeutes*). Journal of Mammalogy, 11:61–68.

Scrocchi, G. J., and S. P. Halloy. 1986. Notas sistemáticas, ecológicas, etológicas, y biogeográficas sobre el gato andino *Felis jacobita* Cornalia (Felidae, Carnivora). Acta Zoologica Lilloana, 38: 157–170.

Tate, G. H. H. 1933. A systematic revision of the marsupial genus *Marmosa*. Bulletin of the American Museum of Natural History, 66:1–250.

Thomas, O. 1898. On some new mammals from the neighborhood of Mount Sahama, Bolivia. Annals and Magazine of Natural History, series 1, 7:277–283.

———. 1902. On mammals collected at Cruz del Eje, central Cordoba, by Mr. P. O. Simon. Annals and Magazine of Natural History, series 7, 9:237–245.

———. 1907. On Neotropical mammals of the genera *Callicebus, Reithrodontomys, Ctenomys, Dasypus,* and *Marmosa.* Annals and Magazine of Natural History, series 7, 20:161–168.

———. 1926. The Spedan Lewis South American exploration. III. On mammals collected by Sr. Budin in the province of Tucumán. Annals and Magazine of Natural History, series 9, 17:602–609.

Torres, H., ed. 1992. South American Camelids. An Action Plan for Their Conservation. International Union for the Conservation of Nature, Gland, Switzerland, 58 pp.

Vervoorst, F. 1982. Noroeste. Pp. 9–24, *in* Conservación de la Vegetación Natural en la República Argentina. Simposio XVIII Jornadas de Botánica, Fundación Miguel Lillo, Tucumán, Argentina.

Wetzel, R. M. 1980. A revision of the naked-tailed armadillos, genus *Cabassous* McMurtrie. Annals of Carnegie Museum, 49:323–357.

———. 1982. Systematics, distribution, ecology, and conservation of South American edentates. Pp. 345–376, *in* Mammalian Biology in South America (M. A. Mares and H. H. Genoways, eds.). Special Publications Series, Pymatuning Laboratory of Ecology, University of Pittsburgh, 6:1–539.

———. 1985. Taxonomy and distribution of armadillos, Dasypodidae. Pp. 23–46, *in* The Evolution and Ecology of Armadillos, Sloths, and Vermilinguas (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C., 451 pp.

Williams, D. F. 1978. Taxonomic and karyologic comments on small brown bats, genus *Eptesicus,* from South America. Annals of Carnegie Museum, 47:361–383.

Wilson, D. E. 1979. Reproductive patterns. Pp. 317–378, *in* Biology of Bats of the New World Family Phyllostomatidae. Part III (R. J. Baker, J. K. Jones, Jr., and D. C. Carter, eds.). Special Publications, The Museum, Texas Tech University, 16:1–441.

Wilson, D. E., and D. M. Reeder. 1993. Mammal Species of the World: A Taxonomic and Geographic Reference. Smithsonian Institution Press, Washington, D.C., 1206 pp.

Ximenez, A. 1975. Felis geoffroyi. Mammalian Species, 54:1–4.

Yepes, J. 1929. Notas sobre la distribución geográfica del pichi ciego menor (*Chlamyphorus truncatus*) y pichi llorón (*Chaetophractus vellerosus*). Physis, 9:439–446.

———. 1935. Las especies Argentinas del género *Cabassous* (Dasypodidae). Physis, 11:438–444.

Gazetteer

Localities are listed in both alphabetical and numerical order. Departments are given in parentheses. Numbers in parentheses correspond to numbered localities in Figure 8.

Acheral (Monteros)—27°07′ 65°27′ (109).
Aconquija (Chicligasta)—27°13′ 66°08′ (99).
Aconquija, 3000 m (Chicligasta)—27°13′ 66°08′ (99).
Agua Colorada (Burruyacú)—26°26′ 64°53′ (72).
Agua Rosada (Trancas)—26°22′ 65°26′ (15).
Agua Rosada, San Pedro de Colalao (Trancas)—26°22′ 65°26′ (15).
Aguas Chiquitas (Burruyacú)—26°37′ 65°12′ (35).
Aguas Chiquitas, El Cadillal, 800m (Burruyacú)—26°37′ 65°12′ (35).
Aguas Chiquitas, Sierras de Medina, 800m (Burruyacú)—26°37′ 65°12′ (35).
Aguas Chiquitas, 25 km NE San Miguel de Tucumán, 800 m (Burruyacú)—26°37′ 65°12′ (35).
Alderetes (Cruz Alta)—26°49′ 65°08′ (63).
Amaicha del Valle (Tafí del Valle)—26°36′ 65°55′ (1).
Amaicha del Valle, 2000 m (Tafí del Valle)—26°36′ 65°55′ (1).
Anta Mapú (Burruyacú)—26°31′ 64°43′ (74).
Atahona (Simoca)—27°25′ 65°17′ (83).

Banda del Río Salí (Cruz Alta)—26°50′ 65°10′ (62).
Biological Reserve at Horco Molle, 2,400 ft. (Yerba Buena)—26°45′ 65°21′ (45).
Biological Reserve at Horco Molle, near residencia, 2,400 ft. (Yerba Buena)—26°45′ 65°21′ (45).
Burruyacú (Burruyacú)—26°30′ 64°45′ (73).
Burruyacú, 1300 m (Burruyacú)—26°30′ 64°45′ (73).
Cafayate, 45 km S, along Hwy 40 (Tafí del Valle)—26°20′ 65°58′ (4).
Cajón de la Ovejeria, Chorrillos (Burruyacú)—26°21′ 64°55′ (70).
Campo de la Gallina, Serranía de Quilmes o El Cajón (Tafí del Valle)—(not located).
Capital, San Miguel de Tucumán (Capital)—26°50′ 65°13′ (50).
Casa de Piedra, Río Los Sosa (Monteros)—27°03′ 65°37′ (106).
Casa de Piedra, Ruta 307, km 23.9, 850m (Monteros)—27°03′ 65°37′ (106).
Caspichango (Monteros)—27°04′ 65°30′ (112).
Cerro de Raco, Trancas (Tafí Viejo)—26°43′ 65°30′ (56).
Cerro de Tafí Viejo, 2400 m (Tafí Viejo)—26°42′ 65°17′ and 26°44′ 65°16′ (between 38 and 44).
Cerro del Campo (Burruyacú)—26°35′ 64°57′ (68).
Cerro del Campo, 800 m (Burruyacú)—26°35′ 64°57′ (68).
Cerro del Campo, 1800 m (Burruyacú)—26°35′ 64°57′ (68).
Cerro San Javier (Yerba Buena)—26°47′ 65°24′ (42).
Chicligasta (Simoca)—27°28′ 65°07′ (84).
Ciudad Capital (Capital)—26°50′ 65°13′ (50).
Ciudad Tucumán, casa céntrica (Capital)—26°50′ 65°13′ (50).
Colalao del Valle (Tafí del Valle)—26°22′ 65°57′ (3).
Concepción (Chicligasta)—27°20′ 65°35′ (93).
Cuesta del 25, Ruta 9, entrada al Cadillal (Tafí Viejo)—26°37′ 65°12′ (34).
Cumbres Calchaquíes—(no specific locality) 26°27′ 65°43′ (5).
Cumbres de San Pablo—(probably 52).
Cumbres de Santa Barbara (Trancas)—26°00′–26°15′ 65°43′ (11).
Cumbres del Aconquija—(no specific locality) 27°13 66°08 (98, 99) to 27°00′ 65°55′ (100).
Departamento Burruyacú—(no specific locality) 26°30′ 64°55′.
Departamento Chicligasta—(no specific locality) 27°20′ 65°35′.
Departamento Famaillá—(no specific locality) 26°55′ 65°30′.
Dique Escaba (J. B. Alberdi)—27°40′ 65°46′ (94).
Dique San Ignacio (La Cocha)—27°44′ 65°40′ (89).
El Bracho (Cruz Alta)—26°59′ 65°11′ (61).
El Cadillal (Tafí Viejo)—26°37′ 65°12′ (34).
El Cadillal Dike, 25 km NW San Miguel de Tucumán (Tafí Viejo)—26°37′ 65°12′ (34).
El Cadillal, Estación de Piscicultura (Tafí Viejo)—26°37′ 65°12′ (34).
El Cadillal, Usina (Tafí Viejo)—26°37′ 65°12′ (34).
El Cadillal, 25 km N San Miguel de Tucumán (Tafí Viejo)—26°37′ 65°12′ (34).
El Cajón (Burruyacú)—26°32′ 64°52′ (69).
El Duraznito (Tafí Viejo)—26°40′ 65°11′ (37).
El Indio, Ruta 307 (Monteros)—27°02′ 65°40′ (104).
El Infiernillo (Tafí del Valle)—26°44′ 65°47′ (119).
El Manantial (Lules)—26°51′ 65°17′ (53).
El Naranjal (Monteros)—27°02′ 65°41′ (105).
El Naranjo (Burruyacú)—26°40′ 65°03′ (65).
El Nogalar, km 43, Ruta 307, 1700m (Monteros)—27°01′ 65°40′ (111).
El Nogalar, = Río los Sosa, km 43.0, Ruta 307 (Monteros)—27°01′ 65°40′ (111).
El Portezuelo (Trancas)—26°08′ 65 °27′ (21).
El Simbolar (Trancas)—26°14′ 65°23′ (19).
El Timbó (Burruyacú)—26°42′ 65°08′ (41).
Embalse Escaba (J. B. Alberdi)—27°40′ 65°46′ (94).
Escuela Normal, Monteros (Monteros)—27°10′ 65°30′ (102).
Estancia El Cavao (Burruyacú)—26°30′ 64°45′ (71).
Estancia San Pedro, Vipos (Trancas)—26°29′ 65°22′ (30).
Garmendia, Departamento Burruyacú (Burruyacú)—26°34′ 64°33′ (75).
Gobernador Garmendia (Burruyacú)—26°34′ 64°33′ (75).
Gobernador Piedrabuena (Burruyacú)—26°45′ 64°40′ (76).
Graneros (Graneros)—27°39′ 65°27′ (90).
Horco Molle (Yerba Buena)—26°45′ 65°21′ (45).
Horco Molle, 15 km SW San Miguel de Tucumán (Yerba Buena)—26°45′ 65°21′ (45).

Horco Molle, 15 km W San Miguel de Tucumán (Yerba Buena)—26°45′ 65°21′ (45).
Horco Molle, 25 km NW San Miguel de Tucumán (Yerba Buena)—26°45′ 65°21′ (45).
4 km W of junction 338 and road to Horco Molle, on road to San Javier, 2,750 ft. (Yerba Buena)—26°49′ 65°21′ (57).
Iglesia (not located).
Ingenio Amalia (Capital)—26°52′ 65°13′ (51).
Ingenio Lules (Lules)—26°55′ 65°20′ (55).
Ingenio San Pablo (Famaillá)—26°54′ 65°19′ (54).
Ingenio Santa Lucía (Monteros)—27°06′ 65°31′ (108).
Instituto Lillo (Capital)—26°49′ 65°13′ (50).
Instituto Lillo, San Miguel de Tucumán (Capital)—26°49′ 65°13′ (50).
La Angostura (Tafí del Valle)—26°55′ 65°41′ (114).
La Ciénaga, 2500 m (Tafí del Valle)—26°46′ 65°39′ (117).
La Cocha (La Cocha)—27°47′ 65°34′ (87).
La Cocha, Dique San Ignacio (La Cocha)—27°44′ 65°40′ (89).
La Cocha, 380m (La Cocha)—27°47′ 65°34′ (87).
La Cuesta (Trancas)—(not located).
La Florida Reserva Provincial—(no specific locality).
La Fronterita (Famaillá)—27°02′ 65°28′ (113).
La Heladera, 2 km below, along Hwy 307, 3,500 ft. (Monteros)—27°01′ 65°40′ (103).
La Higuera (Trancas)—26°23′ 65°26′ (27).
La Quebradita, 12 km W, km 81 along Hwy 307, 9,500 ft. (Tafí del Valle)—26°44′ 65°45′ (116).
La Ramada (Burruyacú)—26°42′ 64°57′ (67).
La Reducción (Lules)—27°57′ 65°22′ (59).
Laguna Huaca Huasi (Tafí Viejo)—26°41′ 65°44′ (120).
Laguna Huaca Huasi, Cumbres Calchaquíes, approximately 4250 m (Tafí Viejo)—26°41′ 65°44′ (120).
Las Higuerillas, 0.5 km N on Hwy 308, 3,000 ft. (J. B. Alberdi)—27°47′ 65°50′ (95).
Las Higuerillas, 5 km N on Hwy 308, 2,900 ft. (J. B. Alberdi)—27°44′ 65°50′ (95).
Las Juntas, 22 km W Choromoro on Hwy 312, 3,500 ft. (Trancas)—26°24′ 65°31′ (26).
Las Mesadas (Trancas)—26°27′ 65°30′ (14).
Las Pavas (Chicligasta)—27°15′ 65°52′ (97).
Las Pavas, Aconquija (Chicligasta)—27°15′ 65°52′ (97).
Las Talas (Leales)—27°00′ 65°17′ (60).
Las Talas, 4 km al N de Bella Vista (Leales)—27°00′ 65°17′ (60).
Las Talitas (Monteros)—(not located).
Leales (Leales)—27°12′ 65°18′ (78).
Leocadio Paz (Trancas)—26°09′ 65°18′ (23).
Los Puestos (Leales)—27°17′ 65°00′ (80).
Los Romanos (Leales)—27°24′ 65°08′ (82).
Los Sarmientos (Río Chico)—27°24′ 65°41′ (91).
Los Vázquez (Capital)—26°50′ 65°13′ (50).
Los Vázquez, 445m (Capital)—26°50′ 65°13′ (50).
Lules, 3 km W (Lules)—26°56′ 65°23′ (58).
Mala Mala (Lules)—26°47′ 65°33′ (118).
Marcos Paz (Yerba Buena)—26°49′ 65°17′ (47).
Monte Bello (Río Chico)—27°22′ 65°45′ (92).
Monte Bello (Trancas)—26°14′ 65°33′ (7).
Monteagudo (Simoca)—27°31′ 65°17′ (85).
Monteros (Monteros)—27°10′ 65°30′ (102).
Morro del Zarzo, 5000 m (Tafí del Valle)—27°00′ 65°54′ (100).
Muñecas (Capital)—26°47′ 65°15′ (52).
Near the campground near Cochuna (Concepcíon)—27°18′ 65°55′ (121).
Nevados del Aconquija, Glacial del Cochuna, 4550 m (Chicligasta)—27°13′ 66°08′ (98).
Ñorco, 2500 m (Trancas)—26°29′ 65°22′ (28).
Ñorco, Vipos, 2500 m (Trancas)—26°29′ 65°22′ (28).
Nueva España (Leales)—27°16′ 65°12′ (81).
Piedra Buena (Burruyacú)—26°44′ 64°40′ (76).
Piedra Tendida (Burruyacú)—26°30′ 64°52′ (69).
Piedra Tendida, 12 km WNW Burruyacú, along Río Cajón, 2,500 ft. (Burruyacú)—26°30′ 64°52′ (69).
Piedras Coloradas (Monteros)—27°04′ 65°40′ (101).
Playa Larga (Monteros)—27°03′ 65°40′ (107).

Plaza Independencia, San Miguel de Tucumán (Capital)—26°50′ 65°13′ (50).
Pozo Hondo (Graneros)—27°49′ 65°20′ (86).
Puesto Portadera (Burruyacú)—(not located).
Quebrada de la Angostura (Trancas)—26°12′ 65°31′ (8).
Quebrada de las Burras (Trancas)—26°19′ 66°04′ (6).
Quebrada de los Matos (Trancas)—26°20’ 65°22′ (13).
Quebrada de Lules, 11 km NW San Pablo (Lules)—26°52′ 65°25′ (48).
Quebrada del Toro (Trancas)—26°18′ 65°21′ (20).
Raco, Sierra San Javier (Tafí Viejo)—26°38′ 65°26′ (33).
Rearte Norte (Trancas)—26°06′ 65°28′ (25).
Reserva Provincial "Aguas Chiquitas" El Cadillal (Burruyacú)—26°37′ 65°12′ (35).
Reserva Provincial El Cadillal "Aguas Chiquitas" (Burruyacú)—26°37′ 65°12′ (35).
Río Colorado (Famaillá)—27°09′ 65°21′ (110).
Río de Los Sosa, km 19.7, Ruta 307, camino a Tafí del Valle, 700 m (Monteros)—27°05′ 65°40′ (96).
Río de Los Sosa, km 19.7, Ruta 307, camino a Tafí del Valle, 750 m (Monteros)—27°05′ 65°40′ (96).
Río de Los Sosa, km 23.9, Ruta 307, camino a Tafí del Valle, 850 m (Monteros)—27°04′ 65°40′ (106).
Río de Los Sosa, km 24.9, Ruta 307, camino a Tafí del Valle, 850 m (Monteros)—27°04′ 65°40′ (106).
Río Las Tacanas (Trancas)—26°12′ 65°27′ (10).
Río Loro (Burruyacú)—26°37′ 65°12′ (34).
Río Los Sosas, Ruta 307, km 23.9 (Monteros)—27°04′ 65°40′ (106).
Río Nío (Burruyacú)—26°26′ 64°56′ (66).
Ruta 307, km 19.7, camino a Tafí del Valle, 750 m (Monteros)—27°05′ 65°40′ (96).
Ruta 307, km 23.9, 850 m (Monteros)—27°04′ 65°40′ (106).
San Fernando (Trancas)—26°22′ 65°27′ (17).
San Javier (Yerba Buena)—26°47′ 65°23′ (42).
San Javier, Ciudad Universitaria (Tafí Viejo)—26°48′ 65°23′ (43).
San Miguel de Tucumán (Capital)—26°50′ 65°13′ (50).
San Miguel de Tucumán, 450m (Capital)—26°50′ 65°13′ (50).
San Miguel de Tucumán, 28 km NE (Burruyacú)—26°37′ 65°07′ (64).
San Miguel de Tucumán, 29 km NE (Burruyacú)—26°37′ 65°07′ (64).
San Miguel de Tucumán, 17 km NW (Tafí Viejo)—26°41′ 65°18′ (18).
San Miguel de Tucumán, 25 km NW (Tafí Viejo)—26°38′ 65°20′ (22).
San Pablo (Lules)—26°52′ 65°19′ (54).
San Pablo, 11 km al NO (Lules)—26°52′ 65°25′ (48).
San Pedro de Colalao (Trancas)—26°14′ 65°29′ (16).
San Pedro de Colalao, Junta de los Ríos (Trancas)—26°14′ 65°29′ (16).
San Pedro de Colalao, 11 km S (Trancas)—26°20′ 65°33′ (12).
San Pedro de Colalao, south of, at km marker 42, on highway 364, 4,700 ft. (Trancas)—26°20′ 65°33′ (12).
Santa Ana Reserva Provincial (Río Chico and J. B. Alberdi)—27°30′ 65°55′ (88).
Santa Rosa de Leales (Leales)—27°09′ 65°15′ (77).
Serranía de Quilmes-Cajón (Tafí del Valle)—26°35′ 66°10′ (2).
Sierra de Tucumán—(no specific locality).
Sierra del Aconquija (Monteros and Tafí del Valle)—27°00′ 65°55′ (100).
Sierras de Medina, Aguas Chiquitas, "El Cadillal" (Burruyacú)—26°37′ 65°12′ (35).
Sierras del Cajón (Tafí del Valle)—26°35′ 66°10′ (2).
Tacanas (Leales)—27°08′ 64°49′ (79).
Taco Yana (Trancas)—26°11′ 65°30′ (9).
Tafí, 2000 m—(no specific locality).
Tafí del Valle (Tafí del Valle)—26°52′ 65°41′ (115).
Tafí Viejo (Tafí Viejo)—26°44′ 65°16′ (44).
Taficillo (Tafí Viejo)—26°42′ 65°17′ (38).
Tapia (Trancas)—26°36′ 65°18′ (32).
Tapia, 500 m (Trancas)—26°36′ 65°18′ (32).
Tapia de Tucumán, 600 m (Trancas)—26°36′ 65°18′ (32).
Ticucho (Trancas)—26°31′ 65°15′ (31).
Ticucho, cola de embalse El Cadillal (Trancas)—26°31′ 65°14′ (39).
Ticucho, entrando por cola del Dique el Cadillal (Trancas)—26°31′ 65°14′ (39).
Ticucho, 3 km E, cola de Cadillal Dique (Trancas)—26°31′ 65°14′ (39).

Timbó Nuevo (Burruyacú)—26°42′ 65°07′ (40).
Trancas (Trancas)—26°13′ 65°17′ (24).
Tranquitas (Burruyacú)—26°37′ 65°02′ (36).
Tucumán—(no specific locality).
Tucumán, 450 m (Capital)—26°50′ 65°13′ (50).
Tucumán, 1500m—(no specific locality).
Villa Nougués (Lules)—26°51′ 65°23′ (52).
Vipos (Trancas)—26°29′ 65°22′ (29).
Vipos, Estancia San Pedro (Trancas)—26°29′ 65°22′ (30).
Vipos, 500 m (Trancas)—26°29′ 65°22′ (29).
Yerba Buena (Yerba Buena)—26°49′ 65°19′ (46).

1. Amaicha del Valle (Tafí del Valle)—26°36′ 65°55′.
   Amaicha del Valle, 2000 m (Tafí del Valle)—26°36′ 65°55′.
2. Serranía de Quilmes-Cajón (Tafí del Valle)—26°35′ 66°10′.
   Sierras del Cajón (Tafí del Valle)—26°35′ 66°10′.
3. Colalao del Valle (Tafí del Valle)—26°22′ 65°57′.
4. Cafayate, 45 km S, along Hwy 40 (Tafí del Valle)—26°20′ 65°58′.
5. Cumbres Calchaquíes-(Trancas and Tafí del Valle)—26°27′ 65°43′.
6. Quebrada de las Burras (Trancas)—26°19′ 66°04′.
7. Monte Bello (Trancas)—26°14′ 65°33′.
8. Quebrada de la Angostura (Trancas)—26°12′ 65°31′.
9. Taco Yana (Trancas)—26°11′ 65°30′.
10. Río Las Tacanas (Trancas)—26°12′ 65°27′.
11. Cumbres de Santa Barbara (Trancas)—26°00′-26°15′ 65°43′.
12. San Pedro de Colalao, 11 km S (Trancas)—26°20′ 65°33′.
    San Pedro de Colalao, south of, at km marker 42, on highway 364, 4,700 ft. (Trancas)—26°20′65°33′.
13. Quebrada de los Matos (Trancas)—26°20′ 65°22′.
14. Las Mesadas (Trancas)—26°27′ 65°30′.
15. Agua Rosada (Trancas)—26°22′ 65°26′.
    Agua Rosada, San Pedro de Colalao (Trancas)—26°22′ 65°26′.
16. San Pedro de Colalao (Trancas)—26°14′ 65°29′.
    San Pedro de Colalao, Junta de los Ríos (Trancas)—26°14′ 65°29′.
17. San Fernando (Trancas)—26°22′ 65°27′.
18. San Miguel de Tucumán, 17 km NW (Tafí Viejo)—26°41′ 65°18′.
19. El Simbolar (Trancas)—26°14′ 65°23′.
20. Quebrada del Toro (Trancas)—26°18′ 65°21′.
21. El Portezuelo (Trancas)—26°08′ 65°27′.
22. San Miguel de Tucumán, 25 km NW (Tafí Viejo)—26°38′ 20°12′.
23. Leocadio Paz (Trancas)—26°09′ 65°18′.
24. Trancas (Trancas)—26°13′ 65°17′.
25. Rearte Norte (Trancas)—26°06′ 65°28′.
26. Las Juntas, 22 km W Choromoro on Hwy 312, 3,500 ft. (Trancas)—26°24′ 65°31′.
27. La Higuera (Trancas)—26°23′ 65°26′.
28. Ñorco, 2500 m (Trancas)—26°29′ 65°22′.
    Ñatnorco, Vipos, 2500 m (Trancas)—26°29′ 65°22′.
29. Vipos (Trancas)—26°29′ 65°22′.
    Vipos, 500 m (Trancas)—26°29′ 65°22′.
30. Estancia San Pedro, Vipos (Trancas)—26°29′ 65°22′.
    Vipos, Estancia San Pedro (Trancas)—26°29′ 65°22′.
31. Ticucho (Trancas)—26°31′ 65°15′.
32. Tapia (Trancas)—26°36′ 65°18′.
    Tapia, 500 m (Trancas)—26°36′ 65°18′.
    Tapia de Tucumán, 600 m (Trancas)—26°36′ 65°18′.
33. Raco, Sierra San Javier (Tafí Viejo)—26°38′ 65°26′.
34. Cuesta del 25, Ruta 9, entrada al Cadillal (Tafí Viejo)—26°37′ 65°12′.
    El Cadillal (Tafí Viejo)—26°37′ 65°12′.
    El Cadillal Dike, 25 km NW San Miguel de Tucumán (Tafí Viejo)—26°37′ 65°12′.
    El Cadillal, Estación de Piscicultura (Tafí Viejo)—26°37′ 65°12′.
    El Cadillal, 25 km N San Miguel de Tucumán (Tafí Viejo)—26°37′ 65°12′.

El Cadillal, Usina (Tafí Viejo)—26°37′ 65°12′.
Río Loro (Burruyacú)—26°37′ 65°12′.
35. Aguas Chiquitas (Burruyacú)—26°37′ 65°12′.
Aguas Chiquitas, El Cadillal, 800m (Burruyacú)—26°37′ 65°12′.
Aguas Chiquitas, Sierras de Medina, 800m (Burruyacú)—26°37′ 65°12′.
Aguas Chiquitas, 25 km NE San Miguel de Tucumán, 800 m (Burruyacú)—26°37′ 65°12′.
Reserva Provincial El Cadillal "Aguas Chiquitas" (Burruyacú)—26°37′ 65°12′.
Reserva Provincial "Aguas Chiquitas" El Cadillal (Burruyacú)—26°37′ 65°12′.
Sierras de Medina, Aguas Chiquitas, "El Cadillal" (Burruyacú)—26°37′ 65°12′.
36. Tranquitas (Burruyacú)—26°37′ 65°02′.
37. El Duraznito (Tafí Viejo)—26°40′ 65°11′.
38. Taficillo (Tafí Viejo)—26°42′ 65°17′.
39. Ticucho, entrando por cola del Dique el Cadillal (Trancas)—26°31′ 65°14′.
Ticucho, cola de embalse El Cadillal (Trancas)—26°31′ 65°14′.
Ticucho, 3 km E, cola de Cadillal Dique (Trancas)—26°31′ 65°14′.
40. Timbó Nuevo (Burruyacú)—26°42′ 65°07′.
41. El Timbó (Burruyacú)—26°42′ 65°08′.
42. Cerro San Javier (Yerba Buena)—26°47′ 65°24′.
San Javier (Yerba Buena)—26°47′ 65°23′.
43. San Javier, Ciudad Universitaria (Tafí Viejo)—26°48′ 65°23′.
44. Tafí Viejo (Tafí Viejo)—26°44′ 65°16′.
45. Horco Molle (Yerba Buena)—26°45′ 65°21′.
Horco Molle, 15 km W San Miguel de Tucumán (Yerba Buena)—26°45′ 65°21′.
Horco Molle, 15 km SW San Miguel de Tucumán (Yerba Buena)—26°45′ 65°21′.
Horco Molle, 25 km NW San Miguel de Tucumán (Yerba Buena)—26°45′ 65°21′.
Biological Reserve at Horco Molle, 2,400 ft. (Yerba Buena)—26°45′ 65°21′.
Biological Reserve at Horco Molle, near residencia, 2,400 ft. (Yerba Buena)—26°45′ 65°21′.
46. Yerba Buena (Yerba Buena)—26°49′ 65°19′.
47. Marcos Paz (Yerba Buena)—26°49′ 65°17′.
48. San Pablo, 11 km al NO (Lules)—26°52′ 65°25′.
Quebrada de Lules, 11 km NW San Pablo (Lules)—26°52′ 65°25′.
49. Muñecas (Capital)—26°47′ 65°15′.
50. Los Vázquez (Capital)—26°50′ 65°13′.
Los Vázquez, 445m (Capital)—26°50′ 65°13′.
San Miguel de Tucumán (Capital)—26°50′ 65°13′.
Tucumán, 450 m (Capital)—26°50′ 65°13′.
San Miguel de Tucumán, 450m (Capital)—26°50′ 65°13′.
Capital, San Miguel de Tucumán (Capital)—26°50′ 65°13′.
Ciudad Capital (Capital)—26°50′ 65°13′.
Ciudad Tucumán, casa céntrica (Capital)—26°50′ 65°13′.
Instituto Lillo (Capital)—26°49′ 65°13′.
Instituto Lillo, San Miguel de Tucumán (Capital)—26°49′ 65°13′.
Plaza Independencia, San Miguel de Tucumán (Capital)—26°50′ 65°13′.
51. Ingenio Amalia (Capital)—26°52′ 65°13′.
52. Villa Nougués (Lules)—26°51′ 65°23′.
Cumbres de San Pablo—(probably 55).
53. El Manantial (Lules)—26°51′ 65°17′.
54. Ingenio San Pablo (Famaillá)—26°54′ 65°19′.
San Pablo (Lules)—26°52′ 65°19′.
55. Ingenio Lules (Lules)—26°55′ 65°20′.
56. Cerro de Raco, Trancas (Tafí Viejo)—26°43′ 65°30′.
57. 4 km W of junction 338 and road to Horco Molle, on road to San Javier, 2,750 ft. (Yerba Buena)—26°49′ 65°21′.
58. Lules, 3 km W (Lules)—26°56′ 65°23′.
59. La Reducción (Lules)—27°57′ 65°22′.
60. Las Talas (Leales)—27°00′ 65°17′.
Las Talas, 4 km al N de Bella Vista (Leales)—27°00′ 65°17′.
61. El Bracho (Cruz Alta)—26°59′ 65°11′.
62. Banda del Río Salí (Cruz Alta)—26°50′ 65°10′.
63. Alderetes (Cruz Alta)—26°49′ 65°08′.

64. San Miguel de Tucumán, 28 km NE (Burruyacú)—26°37′ 65°07′.
San Miguel de Tucumán, 29 km NE (Burruyacú)—26°37′ 65°07′.
65. El Naranjo (Burruyacú)—26°40′ 65°03′.
66. Río Nío (Burruyacú)—26°26′ 64°56′.
67. La Ramada (Burruyacú)—26°42′ 64°57′.
68. Cerro del Campo (Burruyacú)—26°35′ 64°57′.
Cerro del Campo, 800 m (Burruyacú)—26°35′ 64°57′.
Cerro del Campo, 1800 m (Burruyacú)—26°35′ 64°57′.
69. El Cajón (Burruyacú)—26°32′ 64°52′.
Piedra Tendida (Burruyacú)—26°30′ 64°52′.
Piedra Tendida, 12 km WNW Burruyacú, along Río Cajón, 2,500 ft. (Burruyacú)—26°30′ 64°52′.
70. Cajón de la Ovejeria, Chorrillos (Burruyacú)—26°21′ 64°55′.
71. Estancia El Cavao (Burruyacú)—26°30′ 64°45′.
72. Agua Colorada (Burruyacú)—26°26′ 64°53′.
73. Burruyacú (Burruyacú)—26°30′ 64°45′.
Burruyacú, 1300 m (Burruyacú)—26°30′ 64°45′.
74. Anta Mapú (Burruyacú)—26°31′ 64°43′.
75. Garmendia, Departamento Burruyacú (Burruyacú)—26°34′ 64°33′.
Gobernador Garmendia (Burruyacú)—26°34′ 64°33′.
76. Gobernador Piedrabuena (Burruyacú)—26°40′ 64°40′.
Piedra Buena (Burruyacú)—26°44′ 64°40′.
77. Santa Rosa de Leales (Leales)—27°09′ 65°15′.
78. Leales (Leales)—27°12′ 65°18′.
79. Tacanas (Leales)—27°08′ 64°49′.
80. Los Puestos (Leales)—27°17′ 65°00′.
81. Nueva España (Leales)—27°16′ 65°12′.
82. Los Romanos (Leales)—27°24′ 65°08′.
83. Atahona (Simoca)—27°25′ 65°17′.
84. Chicligasta (Simoca)—27°28′ 65°07′.
85. Monteagudo (Simoca)—27°31′ 65°17′.
86. Pozo Hondo (Graneros)—27°49′ 65°20′.
87. La Cocha (La Cocha)—27°47′ 65°34′.
La Cocha, 380m (La Cocha)—27°47′ 65°34′.
88. Santa Ana Reserva Provincial (Río Chico and J. B. Alberdi)—27°30′ 65°55′.
89. Dique San Ignacio (La Cocha)—27°44′ 65°40′.
La Cocha, Dique San Ignacio (La Cocha)—27°44′ 65°40′.
90. Graneros (Graneros)—27°39′ 65°27′.
91. Los Sarmientos (Río Chico)—27°24′ 65°41′.
92. Monte Bello (Río Chico)—27°22′ 65°45′.
93. Concepción (Chicligasta)—27°20′ 65°35′.
94. Dique Escaba (J. B. Alberdi)—27°40′ 65°46′.
Embalse Escaba (J. B. Alberdi)—27°40′ 65°46′.
95. Las Higuerillas, 0.5 km N on Hwy 308, 3,000 ft. (J. B. Alberdi)—27°47′ 65°50′.
Las Higuerillas, 5 km N on Hwy 308, 2,900 ft. (J. B. Alberdi)—27°44′ 65°50′.
96. Río de Los Sosa, km 19.7, Ruta 307, camino a Tafí del Valle, 700 m (Monteros)—27°05′ 65°40′.
Río de Los Sosa, km 19.7, Ruta 307, camino a Tafí del Valle, 750 m (Monteros)—27°05′ 65°40′.
Ruta 307, km 19.7, camino a Tafí del Valle, 750 m (Monteros)—27°05′ 65°40′.
97. Las Pavas (Chicligasta)—27°15′ 65°52′.
Las Pavas, Aconquija (Chicligasta)—27°15′ 65°52′.
98. Nevados del Aconquija, Glacial del Cochuna, 4550 m (Chicligasta)—27°13′ 66°08′.
99. Aconquija (Chicligasta)—27°13′ 66°08′.
Aconquija, 3000 m (Chicligasta)—27°13′ 66°08′.
100. Morro del Zarzo, 5000 m (Tafí del Valle)—27°00′ 65°54′.
Sierra del Aconquija (Monteros and Tafí del Valle)—27°00′ 65°55′.
101. Piedras Coloradas (Monteros)—27°04′ 65°40′.
102. Monteros (Monteros)—27°10′ 65°30′.
Escuela Normal, Monteros (Monteros)—27°10′ 65°30′.
103. La Heladera, 2 km below, along Hwy 307, 3,500 ft. (Monteros)—27°01′ 65°40′.
104. El Indio, Ruta 307 (Monteros)—27°02′ 65°40′.
105. El Naranjal (Monteros)—27°02′ 65°41′.
106. Casa de Piedra, Río Los Sosa (Monteros)—27°03′ 65°37′.

Casa de Piedra, Ruta 307, km 23.9, 850m (Monteros)—27°03′ 65°37′.
Río Los Sosas, Ruta 307, km 23.9 (Monteros)—27°04′ 65°40′.
Río de Los Sosa, km 23.9, Ruta 307, camino a Tafí del Valle, 850 m (Monteros)—27°04′ 65°40′.
Río de Los Sosa, km 24.9, Ruta 307, camino a Tafí del Valle, 850 m (Monteros)—27°04′ 65°40′.
Ruta 307, km 23.9, 850 m (Monteros)—27°04′ 65°40′.
107. Playa Larga (Monteros)—27°03′ 65°40′.
108. Ingenio Santa Lucía (Monteros)—27°06′ 65°31′.
109. Acheral (Monteros)—27°07′ 65°27′.
110. Río Colorado (Famaillá)—27°09′ 65°21′.
111. El Nogalar, km 43, Ruta 307, 1700m (Monteros)—27°01′ 65°40′.
El Nogalar, = Río los Sosa, km 43.0, Ruta 307 (Monteros)—27°01′ 65°40′.
112. Caspichango (Monteros)—27°04′ 65°30′.
113. La Fronterita (Famaillá)—27°02′ 65°28′.
114. La Angostura (Tafí del Valle)—26°55′ 65°41′.
115. Tafí del Valle (Tafí del Valle)—26°52′ 65°41′.
116. La Quebradita, 12 km W, km 81 along Hwy 307, 9,500 ft. (Tafí del Valle)—26°44′ 65°45′.
117. La Ciénaga, 2500 m (Tafí del Valle)—26°46′ 65°39′.
118. Mala Mala (Lules)—26°47′ 65°33′.
119. El Infiernillo (Tafí del Valle)—26°44′ 65°47′.
120. Laguna Huaca Huasi (Tafí Viejo)—26°41′ 65°44′.
Laguna Huaca Huasi, Cumbres Calchaquíes, approximately 4250 m (Tafí Viejo)—26°41′ 65°44′.
121. Near the campground near Cochuna (Concepcíon)—27°18′ 65°55′ (135).
Campo de la Gallina, Serranía de Quilmes o El Cajón (Tafí del Valle)—(not located).
Cerro de Tafí Viejo, 2400 m (Tafí Viejo)—26°42′ 65°17′ and 26°44′ 65°16 (between 38 and 44).
Cumbres del Aconquija—(no specific locality) 27°13′ 66°08′ (98, 99) to 27°00′ 65°55′ (100).
Departamento Burruyacú—(no specific locality) 26°30′ 64°55′.
Departamento Chicligasta—(no specific locality) 27°20′ 65°35′.
Departamento Famaillá—(no specific locality) 26°55′ 65°30′.
Iglesia—(not located).
La Cuesta (Trancas)—(not located).
La Florida Reserva Provincia—(no specific locality).
Las Talitas (Monteros)—(not located).
Puesto Portadera (Burruyacú)—(not located).
Sierra de Tucumán—(no specific locality).
Tafí, 2000 m—(no specific locality).
Tucumán—(no specific locality).
Tucumán, 1500 m—(no specific locality).

ANNALS OF CARNEGIE MUSEUM

VOL. 65, NUMBER 2, PP. 153–166 16 MAY 1996

BIOLOGY AND IMMATURE STAGES OF SNAIL-KILLING FLIES BELONGING TO THE GENUS *TETANOCERA* (INSECTA: DIPTERA: SCIOMYZIDAE). II. LIFE HISTORIES OF PREDATORS OF SNAILS OF THE FAMILY SUCCINEIDAE

B. A. FOOTE[1]

Research Associate, Section of Invertebrate Zoology

ABSTRACT

Information on the life histories and larval feeding habits of four Nearctic species of *Tetanocera* that prey on snails belonging to the pulmonate snail family Succineidae are presented. The four species are quite prey-specific, as larvae of *Tetanocera melanostigma* Steyskal prey on species of *Succinea,* those of *T. oxia* Steyskal and *T. spirifera* Melander attack snails of the genus *Catinella,* and larvae of *T. rotundicornis* Loew are associated with the genus *Oxyloma.* All four species are multivoltine and occur in marshy or swampy habitats containing large populations of succineid snails.

INTRODUCTION

This is the second of a series of papers covering the life histories and larval feeding habits of the North American species of *Tetanocera.* The first paper (Foote, 1996) reviewed literature, gave information on rearing techniques, and discussed the biology of two species whose larvae attack shoreline-inhabiting pulmonate snails.

In this paper I present information on the life histories of four species of *Tetanocera, T. melanostigma* Steyskal, *T. oxia* Steyskal, *T. rotundicornis* Loew, and *T. spirifera* Melander, whose larvae prey on species of succineid snails. The larval feeding habits are described, and information on trophic and spatial resource partitioning in this guild of snail-killing *Tetanocera* is presented.

Species of the three North American genera of pulmonate snails belonging to the family Succineidae are commonly called "amphibious" because of their occurrence in wetland habitats, even though they are not able to survive prolonged submersion. They are frequently encountered in shoreline habitats, although *Succinea ovalis* Say is more common in swampy and mesic forests. Species of *Oxyloma* seemingly prefer open herbaceous marshes, whereas *Catinella* species more commonly occur in shaded habitats beneath shrubs and along the wooded banks of streams.

LIFE HISTORIES

Tetanocera melanostigma Steyskal

Steyskal, 1959. Papers of the Michigan Academy of Science, Arts, and Letters, 44:60.

Tetanocera melanostigma is restricted to the Nearctic region (Knutson et al., 1986), where it is known to range from New Hampshire to Ontario and south to New York and Ohio (Fig. 1).

This species was taken in central New York and northeastern Ohio in moist to

---

[1] Department of Biological Sciences, Kent State University, Kent, Ohio 44242.
Submitted 28 April 1995.

Fig. 1.—Distribution of *T. melanostigma.*

wet floodplain forests and around shaded hillside seepages at the foot of forested slopes. Two sites were especially productive of flies. The first site was the floodplain bordering the outlet stream of Cayuta Lake in Schuyler County, New York, where a swamp forest is broken into a mosaic of habitats. The forest canopy, composed mostly of American elm (*Ulmus americana* L.), is irregularly broken and allows considerable illumination to reach the forest floor. As a result there is a luxuriant, if discontinuous, herbaceous layer. Colonies of cattail (*Typha latifolia* L.) are found in the wetter, more open sites, and there is a thick layer of decaying leaf litter in the more forested areas. The soil is permanently moist, and during the spring months the whole area commonly is covered by 3 cm or more of water. When the area was visited during early September, *Succinea* snails, the preferred food of the larvae, were most abundant on the leaves of cattail, although adults of *T. melanostigma* were more widely distributed over the floodplain. Unfortunately, no larvae were found in the snails collected at this site. The second locality visited was a seepage located at the foot of a forested, northwest-facing slope lying along the Ringwood Branch of Cascadilla Creek about 11 km east of Ithaca, New York. The area is well shaded by deciduous trees and covered by a luxuriant layer of herbs, mostly pale touch-me-not (*Impatiens pallida* Nuttall) and joe-pye-weed (*Eupatorium maculatum* L.). The highly organic soil is always wet and may be submerged during the spring and early summer months. *Succinea* snails were abundant on the leaves of the joe-pye-weed, less common in the stands of *Impatiens,* and quite rare on a narrow-leaved species of *Carex.* All snails were inactive and attached to the leaves by a mucous secretion when collected on July 14 and 30. Four (11%) of the 35 *Succinea* collected on July 14 contained one or more larvae of *T. melanostigma,* but a larva was found in only one (4%) of 23 snails taken on July 30.

Throughout the summer, many viable eggs were obtained from both feral and laboratory-reared females. Most eggs were placed on peat moss in the jars, but a few were scattered over the glass walls. Although eggs were not found in nature, it is probable that they are deposited on vegetation near the snail prey. The incubation period lasted five to seven days under laboratory conditions (n = 35).

Observations were made on the activities of 20 first instars that hatched during the summer months. Groups of five to eight larvae were placed in each of several large Stender dishes containing moist sand and one or two living *S. ovalis.* The larvae moved slowly over the sand, stopping frequently and lifting the anterior parts of their bodies off the substrate and waving them to and fro. When they brushed against a *Succinea,* larvae became highly excited and attempted to crawl up onto the shell. Many then crawled onto the lateral surfaces of the expanded foot and attempted to insert themselves between the foot and the collar forming the edge of the mantle. However, only 14 (70%) of the 20 larvae actually managed to invade seven snails. Other larvae either failed to contact their potential prey or became entangled in the mucous secretion produced by the snails. These latter larvae invariably succumbed and were later found imbedded in small pellets of mucus along the sides and bottoms of the rearing dishes. Examination of three infested snails three or four days after larval attack revealed that each had one to three larvae embedded between the foot and mantle collar. One had three larvae along one side of the foot, and the other two each had a larva present on one side of the foot. No larvae had invaded the breathing orifice of the snails, although three were lying on either side of the opening. The snail containing three larvae remained alive for five days, apparently succumbing when the larvae molted to the second instar. This snail decayed rapidly after its death, but the larvae continued to feed for another day on the decomposing flesh. The following day, all three larvae had left the shell and were crawling about on the moist sand. A living, uninfested *Succinea* was added to the dish, and by the next day, two of the larvae were embedded between the foot and the mantle collar. The third larva had died. The two living larvae continued to feed on the snail and molted to the third instar, but only one larva managed to complete development and form a puparium. The second larva was found dead on the moist sand. In all, only two puparia were obtained from the 14 larvae that initially had infested the *Succinea* snails. Both puparia were formed in the moist sand.

The four *Succinea* containing five larvae collected on July 14 were placed in individual Stender dishes containing moist, coarse sand. One snail was alive, but very feeble, and retracted into its shell when collected from a sedge leaf. Its breathing orifice opened and closed spasmodically, and waves of faint tremors passed over its foot. Two second-instar larvae were imbedded between its foot and mantle collar. Each larva had most of its body buried in the snail, and only the posterior spiracles were visible at the surface of the prey. On the morning of July 16, the snail was dead, but both larvae were still in place laterad of the foot. Two second-instar cephalopharyngeal skeletons and one posterior spiracular disc were recovered from the decaying foot of the snail, indicating that both sciomyzid larvae had molted to the third instar. By July 17 the snail had been reduced to a few shreds of tissue, and only one larva was still within the shell. The second larva was lying quietly on the sand. Another *Succinea* was placed in the Stender dish, and by the following day it was invaded by the larva that last left the original snail. A third *Succinea* was added to the dish on July 18. On July 19 both larvae had vacated the snails and lay on the moist sand. The *Succinea* added the previous day was alive, although inactive, and unattacked. On July 20, one larva burrowed into the sand, while the other invaded the *Succinea.* The snail soon showed distress by producing frothy bubbles around its breathing orifice and a dark yellow mucous secretion on its foot. The snail was quickly killed and largely consumed, and by July 21 both larvae had formed puparia below the surface of the sand.

Another snail was not observed to contain a larva until July 17 when its retracted condition, waves of faint tremors passing over its foot, and an abundance of frothy bubbles around the breathing orifice indicated that it was in distress. At first, no larva could be seen, but within a minute, a small second instar thrust its posterior spiracles to the surface of the flesh laterad of the foot. The snail finally died on July 23, nine days after being collected, presumably harboring a developing larva all that time. By the ninth day the larva had moved to a position outside the mantle against the parietal wall of the shell. By the following day the snail was badly decomposed and partly covered by fungal hyphae, but the larva, now a third instar, was still within the host's shell, although not in a feeding position, as its head was directed away from the decaying flesh. On July 26 the larva left the snail and partly buried itself in the moist sand, where it underwent pupariation during the night of July 27.

None of the five larvae found in the four field-collected *Succinea* attacked a second snail, except for the two in the first described snail whose food supply had been restricted by intraspecific competition. All larvae killed their prey and all partly or completely buried themselves in the moist sand before undergoing pupariation. The various rearings indicated that larvae of *T. melanostigma* tend toward parasitoidism, as they remain within the food snail for extended periods of time before killing it and probably are capable of completing development within one large snail not containing other larvae. However, they may leave decaying and largely consumed snails to attack another living prey.

Under laboratory conditions the first larval stadium lasted six to eight days; the second, three to five days; and the third, from five to 11 days (n = 10).

Usually a few hours intervened between the time a larva left its snail food and pupariated. Some larvae pupariated within four hours after leaving their hosts, but others waited nearly three days before forming puparia. All puparia were oriented parallel to the bottom of the dish or at a slight angle from the horizontal. Under laboratory conditions the pupal stage lasted 14 to 17 days (n = 8).

The period between emergence of a female and her first oviposition lasted from two to five days. Two females that emerged on August 11 began laying eggs on August 13, although neither fly had mated. All their eggs failed to hatch. A wild-caught female produced a total of 213 eggs over a period of 46 days (May 31 to July 15). Her daily egg production was quite variable, ranging from three to 22.

Evidently, *T. melanostigma* larvae can also develop on other species of succineid snails. Of 100 living *Oxyloma effusa* (Pfeiffer) collected at the Inlet Valley marsh on August 13, 1956, two contained a single third instar of *T. melanostigma*. The larvae pupariated in moist sand on August 30 and 31, and adults emerged on September 13 and 14.

In central New York, the earliest seasonal record for adults was May 25, 1957; the latest date was September 5, 1956. Adults were taken in each of the summer months. In northeastern Ohio, adults were collected between early June and late August. Because the life cycle requires about 45 days and females taken at various times during the summer laid viable eggs, *T. melanostigma* probably has at least two annual generations. Winter is probably passed as a pupa, although no overwintering puparia were found.

Tetanocera oxia Steyskal, 1959

Steyskal, 1959. Papers of the Michigan Academy of Science, Arts and Letters, 44:80.

Tetanocera oxia is known only from the Nearctic region (Knutson et al., 1986), where it ranges from Alberta to Newfoundland and south to Colorado and New York (Fig. 2).

Adults were collected near Kent in northeastern Ohio, in hydrophilic vegetation in an alder (*Alnus* sp.) grove separating an open marsh and an adjacent lowland forest. *Tetanocera rotundicornis* was more common in the more open areas of the marsh. At Butternut, Minnesota, *T. oxia* was found in a completely unshaded, grass–sedge meadow (L. V. Knutson, personal communication). In Montana, adults were collected from a mixture of herbaceous and woody vegetation, mostly shrubby willows (*Salix* spp.), bordering an open marsh. Other species of Sciomyzidae commonly collected with *T. oxia* included *Atrichomelina pubera* (Loew), *Pherbellia griseola* (Falle'n), *P. nana* (Falle'n), *P. vitalis* (Cresson), *Antichaeta borealis* Foote, *Renocera brevis* (Cresson), *Tetanocera annae* Steyskal, *T. fuscinervis* (Zetterstedt), *T. plebeja* Loew, and *T. rotundicornis*. Gastropods that were particularly abundant in habitats supporting good populations of *T. oxia* were species of *Catinella* and *Oxyloma* and slugs of the genus *Deroceras*. Aquatic snails were also common and became stranded as water levels dropped during the summer months.

Rearings were initiated from two females and three males collected June 1–4 around the margins of a sedge marsh near Kent, Ohio.

Adults collected on June 1 mated on June 2, and a female began ovipositing on June 15. Only one male and one female survived more than 30 days in the

Fig. 2.—Distribution of *T. oxia.*

laboratory. The male lived until September 5, and the female lived until September 15. This female deposited 99 eggs between June 15 and September 2. Most eggs were scattered over the peat moss substrate in the breeding jar, but 22 were attached to the cheesecloth covers and eight were affixed to the glass walls. Seven eggs were placed along the edges of a blade of grass. In nature, eggs probably are scattered on low-growing herbaceous vegetation or possibly scattered on the moist surface litter. The incubation period lasted five to seven days, and nearly all eggs were viable.

Because *T. oxia* is closely related to *T. rotundicornis,* a predator of *Oxyloma,* and because snails of the family Succineidae were abundant in the adult habitat, the newly hatched larvae were exposed to individuals of the three genera of this snail family as well as to species of more aquatic and terrestrial snails. The larvae of *T. oxia* ignored species of *Gyraulus, Aplexa, Physa, Helisoma, Planorbula, Lymnaea,* and polygryid land snails, but did respond positively to the three succineid genera.

Newly hatched larvae were quite active and constantly wandered about the rearing dish. They showed a distinct tendency to crawl up the sides of the dish, and many desiccated on the lid. Although they crawled over all species of gastropods introduced to the dish, they were particularly attracted to *C. avara* (Say). In contrast, they displayed little or no interest in the other two succineid genera, *Oxyloma* and *Succinea.* Larvae first moved up onto the shell of *Catinella* and wandered about for a few minutes until they made contact with the fleshy mantle exposed in the aperture of the shell. Larvae then moved onto the mantle and attempted to implant themselves between the collar of the mantle and the side of the foot like newly-hatched larvae of *T. rotundicornis.* Up to four larvae were found in any one snail, but usually only one or two larvae were found in place. Most larvae came to rest near the breathing pore of the snail but several embedded themselves at the anterior end of the foot. Larvae remained in place for at least three days while they molted into the second instar, although only 12 managed to reach this stage. Only three molted into the third instar. One of these eventually formed a puparium. Many larvae apparently were rubbed off the surface of the snail's flesh as it moved across the substrate. Other larvae became trapped in accumulations of mucus. Infested snails remained alive for four to ten days and most remained active. However, a few snails affixed themselves to the wall or lid of the rearing dish and remained inactive while being consumed by the fly larvae. Snails infested by two or more larvae generally died two to four days earlier than individuals with only one larva. Most snails died shortly after the larvae molted into the third instar. Larvae generally remained between the foot and mantle collar until they approached the final instar. Late in the second stadium or early in the third, larvae typically moved to a position between the mantle and shell. Larvae abandoned their snails and became free-roaming predators shortly after the prey expired. The single larva that eventually formed a puparium remained within its original snail host until shortly after its second molt, but it killed an additional five snails in the third stadium. Although newly hatched larvae refused to attack *Oxyloma* and *Succinea,* the third instars were more catholic in their diet and attacked snails belonging to all three genera of Succineidae. When an older larva contacted a snail, it quickly moved up onto the mantle and implanted itself between the mantle and the shell. The snail was killed within a few hours, and the larva rarely remained with the snail for more than ten hours. During the one- to three-day intervals between feedings, larvae remained inactive in the peat moss.

The first stadium lasted two to four days ($n = 4$); the second, two to six days ($n = 4$); and the third, about 17 days ($n = 1$). The larva that matured did not feed for four days prior to pupariating and remained buried in the peat moss. The pupal period was 20 days.

With an incubation period of five to seven days, a larval period of 21 to 27 days, and a pupal period of 20 days, the total developmental period was 46 to 54 days. No evidence of a diapause stage was obtained. At least two generations a year are produced at the latitude of northeastern Ohio. The discovery of two floating puparia in a marsh near Ithaca, New York, on April 22 suggested that overwintering occurs as a pupa. Adults emerged from these overwintering puparia on April 29, seven days after the puparia were placed under room temperatures. The earliest (May 6) and latest (August 13) collection dates for adults were both obtained near Butternut, Minnesota. In central New York, the earliest seasonal record for adults was June 10; the latest date was September 4. In northeastern Ohio, adults were collected between mid-May and mid-July, but were most common in mid-June. As a result of severe droughts in Ohio during the summers of 1987 and 1991, succineid populations were greatly reduced. As would be expected, populations of succineid predators have suffered, and no adults of *T. oxia* have been collected by me despite repeated effort in northeastern Ohio since 1992.

The larva is very light gray, similar to that of *T. rotundicornis*. The body wall appears velvety when dry, far more transparent when wet, with heart, intestine, tracheae, and Malpighian tubules very evident. Larvae of *T. oxia* lack the conspicuous body tubercles and float hairs that characterize aquatic larvae in this genus, and the lobes of the posterior spiracular dics are reduced.

Available evidence indicates that the larval feeding habits of *T. oxia* are very similar to those of *T. rotundicornis*, *T. melanostigma*, and *T. spirifera*. As with the larvae of these other species, those of *T. oxia* feed as parasitoids on Succineidae, living within the snails for prolonged periods before killing them. Like all other tetanocerine parasitoids (Berg, 1961; Berg and Knutson, 1978), these larvae evidently leave the host snail shells to pupariate in or on the soil or in ground litter.

Tetanocera rotundicornis Loew

1861. Berlin Entomologische Zeitschrift, 5:344.

Restricted to the Nearctic region (Knutson et al., 1986), *T. rotundicornis* is recorded from Ontario west to Alaska, south to North Carolina, Tennessee, and Oregon (Fig. 3).

In northeastern Ohio, central New York, and Idaho, adults were found most commonly in open vernal and permanent marshes containing large populations of *Oxyloma* snails. However, they do not occur in all habitats containing large *Oxyloma* populations. They tended to be more common in unshaded sites. Adults were not taken in wooded swamps, around shaded hillside seepages, or along sluggish woodland streams, although *Oxyloma* snails frequently were abundant in such habitats.

Rearings were initiated from larvae, puparia, and adults taken at the Inlet Valley, Floral Avenue, and White Church marshes in Tompkins County, New York, and from a large marsh located 9.6 km east of Kent, Portage County, Ohio.

Eggs were deposited repeatedly by laboratory-reared females and by wild-type adults collected in June, July, and August. Over two-thirds of the eggs were placed on projecting sprigs of peat moss used as a substrate in the breeding jars, but several were placed on short lengths of *Typha* and on the glass walls. Less than ten were laid on the shells of living *Oxyloma* and other snails. Eggs were mostly scattered over the substrate, and no clusters of more than four eggs were observed.

Fig. 3.—Distribution of *T. rotundicornis.*

Under laboratory conditions, hatching occurred in seven to ten days (n = 28, Inlet Valley marsh).

The newly hatched larvae were quite active and moved rapidly, if erratically, over the substrate. They stopped frequently and waved the anterior fifth of the body back and forth in the air. Once contact was made with the flesh of an *Oxyloma* snail, the larva attempted to move up onto the expanded foot, where it crawled about slowly. After these exploratory movements, larvae usually attempted to insert themselves between the foot and the collar of the mantle, but a few came to rest outside of the mantle against the shell. Many larvae became trapped and died in the mucus of the snail, and others were rubbed off the foot as snails glided over the rough substrate. As many as five larvae were found embedded up to their posterior spiracular discs in one snail, but usually only one or two larvae were found in each snail. Larvae infested only succineid snails belonging to the genus *Oxyloma,* and attempts to rear them on snails of other families were unsuccessful. In central New York and northeastern Ohio, the snail species utilized as larval food is *O. effusa,* but elsewhere in North America other species are used. In Alaska, Berg (1953) found larvae attacking *O. decampi gouldi* Pilsbry.

On July 2, 20 larvae that hatched from eggs obtained on June 25 were placed in four rearing dishes, each containing two living *O. effusa.* Only one snail was infested by July 10, and it contained two second instars. The remaining 18 larvae were found dead in balls of mucus or desiccated on the sides and tops of the rearing dishes. By July 12 the moribund infested snail had secreted an epiphragm across the shell aperture and had attached itself to the wall of the dish. Its breathing orifice opened and closed sporadically and faint tremors passed over its retracted foot. One larva was located laterad of the foot, but the second larva had temporarily disappeared. On July 16 both larvae were in the third instar. One was lying on the moist sphagnum and when placed on a living snail did not attack and quickly returned to the moss, where it died the next day. The other larva had also left the original snail and had embedded itself up to its spiracular disc in a second *Oxyloma.* This snail was inactive, retracted, and attached to the wall of the dish. By July 18, the larva had left the second snail and was lying on the glass lid of the dish with its gut filled with food. Other living *Oxyloma* were added, and the larva consumed two more individuals before forming a puparium in the peat moss on July 24. It had remained a larva for 22 days (July 2 to 24).

On July 5, 11 larvae were obtained from eggs laid on June 28. The larvae behaved similarly to those of the first rearing, and the one larva that completed development consumed three snails before pupariating on July 24. No other larvae reached the third instar. Perhaps they were unable to develop in the rearing dishes as the dead snails began to decay. Other rearings initiated from eggs were unsuccessful, for although many larvae began feeding on the *Oxyloma* snails, all died while still within the decaying bodies of the snails.

Oxyloma collected in nature frequently contained larvae of *T. rotundicornis.* Collections of 100 snails made weekly at the Inlet Valley marsh between May and September produced 12 larvae. The first larva was found on June 13; the last, on September 26. Infestations remained at low levels (zero to three infested snails per week) throughout the summer. Although a few snails contained two larvae, only one larva was able to complete development on the original snail. The other larva either died or attacked a second *Oxyloma.*

My rearing records indicate that *T. rotundicornis* larvae are predaceous but show parasitoid tendencies. They developed only on succineid snails, fed on a snail for several days before killing it, and killed only a few individuals during larval life. The larvae lack float hairs, are light colored, and have greatly reduced lobes around the posterior spriacular disc, all characters found in larvae adapted to feeding on terrestrial snails.

Puparia obtained from laboratory-reared larvae always were formed away from their prey, usually on or slightly buried in the shredded peat moss. The 65 puparia collected in nature between February and May were also found apart from shells; nearly all were floating at the water surface among emergent vegetation. Because the puparia lack float hairs and do not have the posterior end upturned, they are not well adapted for floating compared to the truly aquatic species (Berg and Knutson, 1978). They probably are formed on moist soil during the late summer and are carried into open water when the marshes refill with water during the following spring. The five puparia obtained in the laboratory rearings produced adults in 12 to 15 days. Of the 65 puparia collected in nature, 38 (59%) produced adults in 12 to 18 days when brought into the heated laboratory.

Reared females were seen to copulate two days after emerging, and copulation was repeated frequently during succeeding days. Mating lasted from less than ten minutes to more than two hours. Fertilized females began ovipositing within five days after emerging. An unfertilized virgin female laid 26 eggs in 18 days. Records were not obtained of the number of eggs laid by laboratory-reared females, but two individuals field-collected on June 20 subsequently deposited 108 and 248 eggs each in 32 days (June 25 to July 27). Adults lived in the breeding jars up to 38 days.

In central New York, the earliest seasonal record for adults was obtained on May 23; the latest record was on September 4. Adults commonly were taken throughout the summer. Probably there are at least two generations per year, as the life cycle can be completed in 56 days. No cessation of development other than that due to cold weather was observed. A puparium formed on October 5 by a larva collected on September 26 at the Inlet Valley marsh produced an adult in 14 days. That overwintering takes place in the pupal stage is indicated by the discovery of puparia containing viable pupae as early as February 9 at the Inlet Valley marsh in New York. Puparia were collected commonly during March, April, and early May.

Seventeen puparia collected in the field during March and April produced ichneumonid wasps. Six (29%) of 21 puparia collected between March 27 and April 2 at the Floral Avenue marsh gave rise to ichneumonids, and records acquired over several years indicate that the rate of parasitization varies from three to 40%. Apparently at least two species of Ichneumonidae are involved.

Tetanocera spirifera Melander

1920. Annals of the Entomological Society of America, 13:330.

Tetanocera spirifera is restricted to the Nearctic region, (Knutson et al., 1986), where it ranges from Manitoba west to Alaska, and south to Colorado and Idaho (Fig. 4).

Adults were taken in open freshwater marshes in which water levels fluctuated greatly, although specimens were not taken in marshy habitats which became dry in summer. In southwestern Montana, adults were taken by sweeping sedges and grasses along a small, mostly unshaded stream. In Colorado, Alberta, and Alaska, adults were taken in open marshes dominated by sedges (*Carex* spp.). Succineid snails were abundant in all habitats examined.

Rearings were initiated on June 28, 1968, from adults collected near East Creek Campground in Beaverhead National Forest in southwestern Montana. Mating was observed in the breeding jars on June 30, and the first eggs were deposited

Fig. 4.—Distribution of *T. spirifera.*

on July 1. Two females deposited a total of 106 eggs in 25 days either onto projecting sprigs of peat moss or affixed to the glass walls of the breeding jars. Five eggs were placed on the shells of dead *Oxyloma.* No clustering was noted, and eggs were scattered widely over the substrate.

The incubation period lasted five to six days ($n = 25$) under laboratory conditions. Because the newly hatched larvae lacked interspiracular processes (float hairs) and had reduced lobing around the posterior spiracular disk, it was assumed that they were more terrestrial and probably fed on shoreline or land gastropods. Small individuals of genera of fingernail clams (*Sphaerium*), aquatic snails (*Aplexa, Helisoma, Lymnaea, Physella*), succineid snails (*Oxyloma, Catinella, Succinea*), land snails (*Discus, Gyraulus, Zonitoides*), and slugs (*Deroceras*) were added to the rearing dishes. After 24 hours of exposure to these molluscs, no attacks on any of the genera of fingernail clams, aquatic or land snails, or slugs had occurred. However, larvae did display interest in the genera of Succineidae and were particularly attracted to a species of *Catinella.* After another 24 hours, first instars were found in several specimens of that genus, but no snails of the genera *Oxyloma* and *Succinea* were invaded. Most of the larvae were embedded up to their posterior spiracles in the slit that runs between the breathing pore and foot. A few larvae were embedded in the side of the foot in front of the breathing pore, and one was embedded in the anterior end of the foot. Up to three larvae were found in each snail, although most snails were invaded by only one larva. Larvae remained in place for at least two days while the snail continued to move about the rearing dishes and even feed. However, by the third day, most of the snails had retracted into their shells and several had affixed their shells to the sides of rearing dishes. Snail death usually occurred on the third day, although one snail remained alive for four days. The larvae continued to feed for another day or so after death as scavengers on the decaying snail flesh. They then abandoned the original snail host and attacked a second individual. Placement of the older larva differed from that of the newly hatched first instar in that the second instar placed itself on the flesh of the snail between the mantle and the shell. Death of the second infested snail occurred within one day, and larvae commonly then attacked a third or even a fourth individual. Older larvae were somewhat more catholic in their choice of prey in that a few individuals consumed snails belonging to the genus *Oxyloma,* however, none attacked species of nonsuccineid snails, slugs, or fingernail clams. After abandoning the final host, larvae usually buried themselves in the peat moss lining the rearing dish and remained inactive for 18 to 24 hours. The one larva that survived formed its puparium in the peat moss.

The first larval stadium lasted one to two days ($n = 8$); the second, two to four days ($n = 4$); and the third, seven days ($n = 1$). No adult emerged from the single puparium that was formed, so the length of the pupal period remains undetermined.

The earliest seasonal record for adults was June 10 (Pitkin, Colorado); the latest record was August 11 (Banff, Alberta). Adults have been captured during all of the summer months. No information was obtained on overwintering habits or on voltinism.

DISCUSSION

How are resources, including space, food, and time, partitioned among these four species of *Tetanocera*? Obviously, there are differences in geographic distribution of the four species. *Tetanocera melanostigma, T. oxia,* and *T. rotundocornis* share similar geographic ranges, although the last species is somewhat more broadly distributed. In contrast, *T. spirifera* is strictly western and seemingly overlaps only *T. rotundicornis* in geographic occurrence. Also, the resource dimension involving habitat is partitioned. *Tetanocera melanostigma* was found most commonly in wet to mesic woodlands, whereas the other three species were found in more open marshes.

Food is definitely partitioned among the four species. Newly hatched larvae of *T. melanostigma* attack *Succinea,* those of *T. rotundicornis* prey on *Oxyloma,* and larvae of *T. oxia* and *T. spirifera* apparently are restricted to *Catinella.* Interestingly, the last two species that utilize a common prey occurring in open marshes have somewhat different geographic distributions (Fig. 2, 4), thus they rarely occur together. All four species seemingly have very similar phenologies and thus do not avoid competing temporally.

The biology of the four Nearctic species is very similar to that reported for *T. arrogans* Meigen in Europe. Knutson (1963) reported that the newly hatched larvae of that species are largely restricted to *Oxyloma* and *Succinea* snails, although older larvae successfully fed on two other genera of land snails.

An unexplored question deals with the possible competition for succineid snails that may occur, as at least 12 sciomyzid species (*Sciomyza aristalis* [Coquillett], *S. dryomyzina* Zetterstedt, *S. simplex* Falle'n, *Pherbellia punctata maculata* [Cresson], *Pteromicra anopla* Steyskal, *Antichaeta borealis* Foote, *A. testacea* Melander, *Hoplodictya spinicornis* [Loew], and the four species of *Tetanocera*) and two species of Calliphoridae (*Melanomyia obscura* (Townsend) and *M. ordinaria* [West]) are known to prey on snails of that family.

ACKNOWLEDGMENTS

Research was supported by grants from the National Science Foundation, National Institute of Allergy and Infectious Diseases, and the National Geographic Society. Appreciation is expressed to G. C. Steyskal of Gainesville, Florida, for his expert help in determining species of *Tetanocera.*

This paper is dedicated to the fond memory of Dr. C. O. Berg, Department of Entomology at Cornell University, who inspired students around the world to pay attention to the details of fly biology and immature stages.

LITERATURE CITED

BERG, C. O. 1953. Sciomyzid larva (Diptera) that feed on snails. Parasitology, 39:630–636.

———. 1961. Biology of snail-killing Sciomyzidae (Diptera) of North America and Europe. Verhandlung der XI International Kongress de Entomologie, 1:197–202.

BERG, C. O., AND L. V. KNUTSON. 1978. Biology and systematics of the Sciomyzidae. Annual Review of Entomology, 23:239–258.

FOOTE, B. A. 1996. Biology and immature stages of snail-killing flies belonging to the genus *Tetanocera* (Insecta: Diptera: Sciomyzidae). I. Introduction and life histories of predators of shoreline snails. Annals of Carnegie Museum, 65:1–12.

KNUTSON, L. V. 1963. Biology and immature stages of snail-killing flies of Europe (Diptera: Sciomyzidae). Unpublished Ph.D. dissert., Cornell University, Ithaca, New York, 390 pp. Order No. Mic 63-4822, University Microfilms, Ann Arbor, Michigan (Dissertation Abstracts, 24:445–446).

KNUTSON, L. V., R. E. ORTH, AND W. L. MURPHY. 1986. Catalog of Sciomyzidae (Diptera) of America north of Mexico. Entomography, 4:1–53.

ANNALS OF CARNEGIE MUSEUM

VOL. 65, NUMBER 2, PP. 167–179 16 MAY 1996

A NEW GENUS OF BEAVER (MAMMALIA: CASTORIDAE: RODENTIA) FROM THE ARIKAREEAN (OLIGOCENE) OF MONTANA AND ITS BEARING ON CASTORID PHYLOGENY

WILLIAM W. KORTH[1]
Research Associate, Section of Vertebrate Paleontology

ABSTRACT

The holotypes of two Arikareean castorids from Montana, *Steneofiber complexus* Douglass and *S. hesperus* Douglass were reexamined in light of recent synonymies of these species with other European and Asian species. The two Montana species are synonyms but are not synonymous with any previously described species of castorid from either Europe or Asia. A new genus, *Neatocastor,* is named for the Montana beaver, *N. hesperus.*

The new genus is most closely related to the otherwise Chadronian to Whitneyan-aged castorid *Agnotocastor* Stirton and the Hemingfordian to Barstovian *Amblycastor* Matthew. A combination of retained primitive characters and derived characters of the skull and dentitions of these genera unite them systematically. This group of genera represents an early offshoot of the Castoridae that is not ancestral to any other group of castorids.

INTRODUCTION

Douglass (1901) described two beavers from the Miocene of Montana, *Steneofiber hesperus* and *S. complexus,* but was uncertain of their age of occurrence. Matthew (1902:301) listed these species as "White River" in age (= Oligocene). Stirton (1935) transferred both of these species to his new genus *Monosaulax* and placed them questionably in the late Miocene (= Barstovian). Most recently, Xu (1994) synonymized these two species (along with four other Eurasian species) under *Steneofiber hesperus* and recognized them as occurring in the late Arikareean. A detailed examination of the holotypes of *S. hesperus* and *S. complexus* has allowed for the recognition of a new genus of castorid and a detailed discussion of the relationships of these species.

Dental nomenclature used follows that of Stirton (1935). Abbreviations for institutions are: AMNH, American Museum of Natural History; CM, Carnegie Museum of Natural History; KU, University of Kansas, Museum of Natural History; USNM, National Museum of Natural History, Smithsonian Institution; YPM-PU, Princeton Collection, Yale-Peabody Museum.

SYSTEMATIC PALEONTOLOGY

Order Rodentia Bowdich, 1821
Superfamily Castoroidea Gray, 1821
Family Castoridae Gray, 1821
Neatocastor, new genus

Type and Only Species.—*Steneofiber hesperus* Douglass, 1901.

Range.—Arikareean (late Oligocene) of Montana.

---

[1] Rochester Institute of Vertebrate Paleontology, 928 Whalen Road, Penfield, New York 14526.
Submitted 28 September 1995.

Diagnosis.—Castorids with elongate rostra; posterior palatine foramina within palatine bone; dorsally, nasals extend more posteriorly than premaxillaries; complex occlusal pattern cheek teeth (multiple fossettes preserved on worn teeth, irregularities of enamel preserved on lophs); cheek teeth subhypsodont and rooted; dP^3 present; anterior face of upper and lower incisors broadly convex anteriorly; upper cheek tooth rows parallel, widely spaced; premolars subequal in size to molars in early stages of wear.

Etymology.—Greek, *neatos,* last or utmost; Latin, *castor,* beaver.

Discussion.—The cheek tooth patterns of *Neatocastor* are more complex than in most other castorids which have a simplified series of reentrant valleys. The rostrum of *Neatocastor* is more elongated than in other castorids, similar to the elongation seen in eutypomyids. The skull and dentition of *Neatocastor* most closely resemble those of the Chadronian to Whitneyan castorid *Agnotocastor.* The latter, however, possesses a P^3, unlike any other castorid. The skull of *Neatocastor* is not flattened and broad as in palaeocastorines. Wahlert (1977) noted two primitive features of the skull that separated *Agnotocastor* from all other castorids: the stapedial foramen was retained in the bulla and the posterior palatine foramina were entirely within the palatine bone. In all other castorids, the stapedial foramen is lost and the posterior palatine passes through the palatine–maxillary suture more anteriorly than in *Agnotocastor.* The bulla of *Neatocastor* is not preserved but it is evident that the posterior palatine foramen is entirely within the palatine bone as in *Agnotocastor.* The posterior extent of the nasals dorsally on the skull of *Neatocastor* (more posterior than premaxillaries) is unlike any castorines, palaeocastorines, or castoroidines in which the nasals are level with or shorter than the premaxillaries. The incisors of palaeocastorines are anteriorly flattened unlike those of *Neatocastor* and all other castorids. The upper cheek tooth rows are parallel and widely spaced in *Neatocastor* unlike those of other castorids except *Agnotocastor.* The premolars in castorines, castoroidines, and most palaeocastorines are the largest of the cheek teeth. The premolars in *Neatocastor* are subequal in size to the molars in early stages of wear. Because the crowns of the molars taper toward their bases, in latest stages of wear the molars become shorter (anteroposteriorly) than the premolars in *Neatocastor* and all other castorids.

Neatocastor differs from species of *Agnotocastor* in being larger with higher-crowned cheek teeth. Cranially, there is little difference between these two genera. Both are characterized by elongate rostra, premolars subequal in size to the molars (not enlarged), and having the maxillary tooth rows parallel rather than divergent. The complexity of the occlusal pattern of the cheek teeth of *Neatocastor* is quite similar to that of *Agnotocastor*: the upper molars retain the elongate J-shaped mesoflexus with multiple fossettes, and the lower cheek teeth preserve the irregularities of the enamel along the borders of the various fossettids even in worn specimens. *Agnotocastor* retains a P^3 (primitive for castorids) whereas in *Neatocastor* a dP^3 is present in juvenile individuals but is not replaced by the permanent tooth.

Neatocastor hesperus (Douglass, 1901)
(Fig. 1, 2; Table 1)

Steneofiber complexus Douglass, 1901:249.
Steneofiber hesperus Douglass, 1901:243.

Monosaulax complexus (Douglass) Stirton, 1935:421.
Monosaulax hesperus (Douglass) Stirton, 1935:422.
"*Monosaulax*" *complexus* (Douglass) Wilson, 1960:72.
"*Monosaulax*" *hesperus* (Douglass) Wilson, 1960:72.
Steneofiber hesperus (= *complexus*) Douglass: Xu, 1994:85.

Type Specimen.—CM 711, left mandible with complete dentition.

Referred Specimen.—CM 712 (holotype of *Steneofiber complexus*), partial skull with incisors, dP^4–M^3 and unerupted P^4 on the right side, and associated mandibles with incisors and dP_4–M_3; right P_4 preserved in crypt.

Horizon and Locality.—Holotype from Blacktail Deer Creek, Beaverhead County, Montana. Referred specimen from gray sandy layer that cuts through White River-age rocks on the west side of the Madison River nine or ten miles south of Three Forks, Gallatin County, Montana.

Age.—CM 711 is from the Arikareean (late Oligocene) Black Tail Deer Creek fauna (see Hibbard and Keenmon, 1950). CM 712 was described from a horizon of unknown age by Douglass (1901). An age determination was not made by Douglass because of the lack of associated mammal fossils. Later, Wood (1933) described specimens of the Arikareean rhinocerotid *Diceratherium armatum* from the same beds but a different locality, establishing the age as Arikareean. Stirton (1935) mistakenly listed both *S. hesperus* and *S. complexus* as being questionably late Miocene (= Barstovian) in age. The age of both CM 712 and CM 711 is clearly Arikareean as noted by Xu (1994).

Description.—The skull of *N. hesperus* (CM 712) is badly damaged and little more than the size and shape of the rostrum is preserved. The rostrum is long (upper diastema 22.7 mm in length), laterally narrow, and not very deep (dorsoventral measurement 11.9 mm) compared to contemporaneous palaeocastorine beavers. The only recognizable foramina on the rostrum are the incisive foramina and the infraorbital foramen on the left side. The incisive foramina are long (3.9 mm) and narrow slits positioned in the center of the anterior part of the palate (diastema). The premaxillary–maxillary suture intersects the center line of the rostrum at the posterior end of the incisive foramina. The infraorbital foramen is low on the rostrum and dorsal to the posterior ends of the incisive foramina. Laterally, the infraorbital foramen is shielded by a flange of bone.

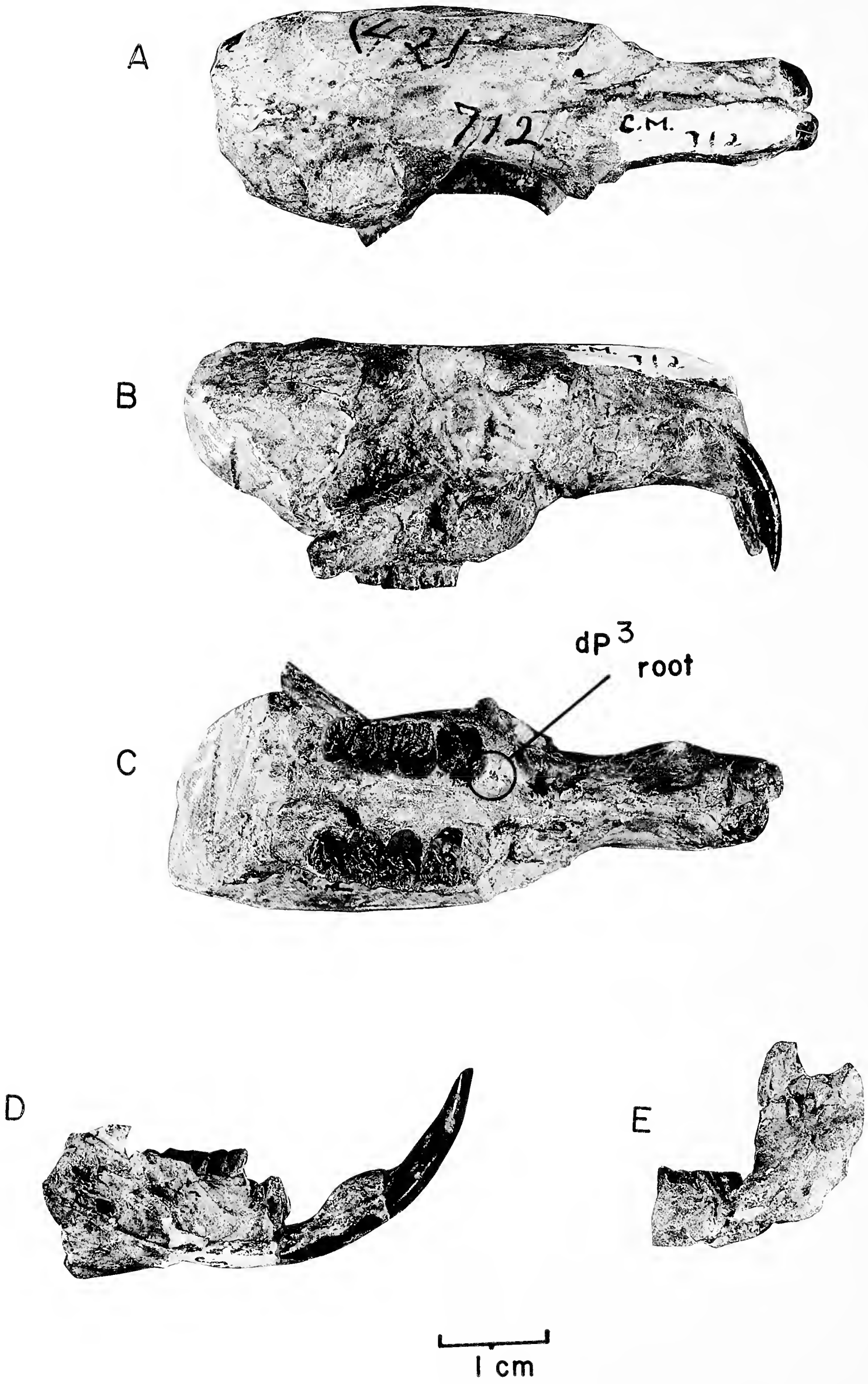
Dorsally, the nasals and premaxillary bones extend posteriorly, level with the anterior margin of the orbits. The nasals extend about 1.8 mm farther posterior than the premaxillaries. A parasagittal crest arises from the posterior margin of the orbit and is directed posteriorly and slightly medially. Only the anterior part of the right parietal is preserved, so it cannot be determined whether there is a sagittal crest at the back of the skull. In *Agnotocastor* there is a single sagittal crest that runs the length of the cranium from a point even with the center of the orbits.

The zygomatic plate is broken away on both sides of the skull and the medial orbital wall is badly crushed, eliminating any evidence of foramina or sutures. However, most of the anterior portion of the palate is preserved. The palatine–maxillary suture extends anteriorly to the level of the anterior margin of the first molars. The posterior palatine foramina are even with the center of M^1 within the palatine bone. The palatal surface is smooth with no indication of any grooves or furrows.

The tooth rows are parallel. The ventral surface of the upper diastema is nearly flat with only a slight dorsal inclination.

The upper incisors are broad with gently convex enamel faces. They appear somewhat procumbant, similar to the condition in *Palaeocastor* (Stirton, 1935:fig. 31). The cheek teeth are subhypsodont. P^4 and the first two molars are subequal in size, M^3 is slightly smaller. On the right side of the skull there is a small peg anterior to the tooth row which appears to be the root of dP^3. In a maxillary specimen listed by Rasmussen (1977) as "*Monosaulax*" *complexus* there is no P^3 associated with the adult dentition, and since dP^4 is still present in CM 712, it is most likely that the root belongs to a deciduous premolar rather than a permanent P^3. DP^4 is lower crowned and slightly smaller than the molars; its occlusal pattern is complex and reminiscent of the molars. There is a long paraflexus that extends lingually, and the sides of the paraflexus are irregular, not straight. A shallow hypoflexus extends from the lingual margin of the tooth anterobuccally and nearly meets the lingual end of the paraflexus. The anterior arm of the hypocone and posterior arm of the protocone fuse near the center of the tooth and extend to the buccal margin of the tooth as a thin loph (= ?mesoloph) which bisects the occlusal surface of the tooth. Anterior to the buccal end of this loph is a minute, circular fossette between the ?mesoloph and the paraflexus. Posterior to the ?mesoloph are three separate fossettes. The largest one is crescentic and forms most of the posterior border of the ?mesoloph. A smaller, ovate fossette is on the posterobuccal corner of the tooth. The last fossette is minute and is near the center line of the tooth along the posterior margin.

P^4 is preserved in CM 712 on the left side but still remains in the crypt. The surface consists of a


A
712
C.M. 712
B
C
dP^3 root
D
E
1 cm

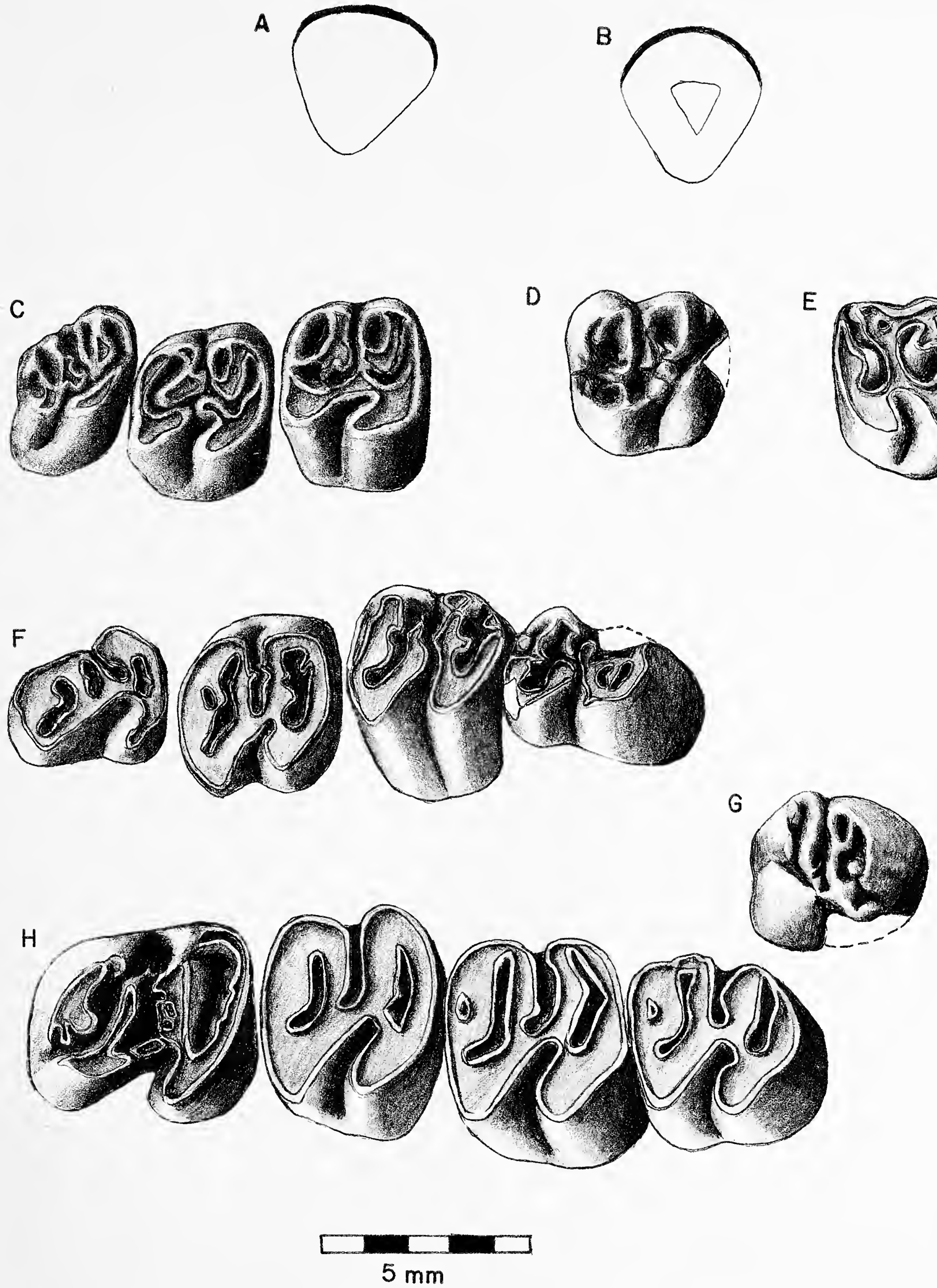


Fig. 2.—Dentitions of *Neatocastor hesperus*. A, C–G, CM 712. B, H, CM 711 (holotype). A, cross section of right I_1. B, cross section of left I_1. C, right M^1–M^3. D, right P^4 (in crypt). E, left dP4. F, left dP_4–M_3. G, partial right P_4 (in crypt). H, left P_4–M_3.

←

Fig. 1.—Skull and mandible of *Neatocastor hesperus*, CM 712 (holotype of "*Steneofiber complexus*"). A, right lateral view of skull. B, ventral view of skull. C, dorsal view of skull. D, lateral view of left mandible. E, lateral view of right mandible.

series of lophs that are covered with enamel that is crenulated and irregular. As in dP^4 there is a deep parafossette and shallow hypofossette that nearly meet. There is a central mesoflexus that extends lingually for nearly the entire width of the tooth. Between the mesoflexus and paraflexus is a smaller, ovate fossette along the buccal margin of the tooth. Posteriorly there is a wide (buccolingually) metafossette that runs the entire width of the tooth. The metafossette opens posteriorly through a shallow valley that may close in early stages of wear. All of the lophs that separate the flexi and fossettes of P^4 are covered with irregular enamel that may produce any number of minute fossettes once the tooth is in occlusion and the lophs begin to wear.

M^1 and M^2 are equal in size. As in P^4 the flexi and fossettes have irregular walls reflecting the enamel irregularities along these lophs. On M^1, there is a long parafossette that may have opened buccally when unworn. The parafossette curves posteriorly at its lingual end, forming a "J" in shape. Similarly, the mesoflexus curves posteriorly at its lingual end, extending posteriorly to the posterior margin of the tooth. The hypoflexus is shallow and directed anterobuccally. Two other small fossettes are present along the buccal edge of the tooth. The first is the smallest and is situated between the paracone and the mesoflexus. The posterior one (metafossette) is larger and located in the posterobuccal corner of the tooth posterior to the metacone. The hypostria extends nearly to the base of the tooth on the lingual side. The mesostria is short, extending less than half the buccal height of the crown. All of the upper molars taper dorsally. In late wear this tapering is manifest in the anteroposterior shortening of the molars.

M^2 is nearly identical to M^1 except in a few features which may be due to a lesser amount of wear. On M^2 the hypoflexus is continuous with the paraflexus on the left side but not on the right. Also on the right, the mesoflexus is continuous with the metafossette at the lingual end. On the left side a posteriorly directed portion of the mesoflexus is closed anterior to the metafossette. A distinct mesocone is present on both M^2s.

M^3 is the smallest of the cheek teeth and is in a very early stage of wear. The paraflexus and hypoflexus are confluent and the paraflexus has a shallow anterior opening at its buccal end. A distinct mesocone is present. There are four buccolingually elongate fossettes along the buccal margin of the tooth.

The mandible is dorsoventrally deep, as is typical of castorids. The masseteric fossa ends anteriorly below the anterior margin of M_1. The diastema is shallow, concave dorsally, and nearly as long as the length of the tooth row. The mental foramen, preserved only on CM 711, is at middepth of the mandible just anterior to the anterior margin of P_4. The ascending ramus rises steeply dorsally, beginning at the level of M_2, and a broad, shallow valley separates the tooth row from the medial border of the ascending ramus. The coronoid process is short and extends vertically, well dorsal to the occlusal surface of the cheek teeth. The articular condyle is directly posterior to the coronoid and just slightly ventral to it. The angle of the mandible is medially deflected, not in line with the ascending ramus.

The lower incisor, like the upper incisor, is broad and gently convex anteriorly. As in the upper cheek teeth, the lophs of the lower cheek teeth are covered with enamel that has numerous irregularities. The dP_4 is smaller than the molars and much lower crowned. In occlusal shape, it is narrow anteriorly and wider posteriorly. The hypoflexid is short and posteriorly directed. There is a small buccolingually elongated fossettid along the posterior edge of the tooth. The mesofossettid is split into two by a short loph (= ?mesolophid). On the right side, this fossettid is completely divided into two separate fossettids, whereas on the left side these two smaller fossettids are still joined at their lingual ends. Anteriorly, there is a crescentic parafossettid.

The lower permanent premolar is preserved not only in the holotype (CM 711) but also in the crypt below dP_4 on the right side of CM 712. The premolar is subequal in size to the anterior molars. Anteriorly there is a long parafossettid that extends the entire width of the tooth. It curves anteriorly at its buccal end and opens anteriorly through a shallow valley in the anterior wall of the tooth. The posterolingual end of the parafossettid appears to close off from the remainder of the fossettid in late stages of wear, isolating an additional fossettid. The mesoflexid is very shallow, and a small triangular fossettid (mesofossettid) is isolated near the center of the tooth. The hypoflexid is also shallow and split buccally by a distinct mesoconid. The metafossettid is buccolingually elongated and runs nearly the entire width of the tooth. Between the metafossettid and the mesofossettid are numerous minute fossettids that may disappear in later wear. Both the mesostriid and hypostriid extend to the base of the crown.

The unworn molars of CM 712 preserve more complexity of the occlusal surface than do the more worn teeth of the holotype. The first two molars of the holotype consist of a deep mesoflexid and hypoflexid that extend at least to the centerline of the tooth, and two transversely elongate fossettids, parafossettid and metafossettid. Both the parafossettid and mesoflexid curve anteriorly at their buccal ends. Irregularities along the edges of the fossettids are remnants of the kind of enamel irregularities seen on the more unworn molars. The hypostriid extends to the base of the crown, whereas the mesostriid is very shallow on the lingual side and would be eliminated after only moderate wear. The last molar of the holotype is similar to the anterior molars but is smaller and slightly reduced posteriorly. The less worn molars of CM 712 have the same basic pattern as those of the holotype but retain numerous minute lophules and reentrants in the fossettids.

Discussion.—Stirton (1935) referred both *Steneofiber complexus* and *S. hesperus* to the generally Barstovian-aged genus *Monosaulax.* Wilson (1960) noted that this was an incorrect allocation that was based only on the shape of the incisors but he did not allocate these species to any other genus, citing them only as "*Monosaulax.*" Xu (1994) listed *S. complexus* as a junior synonym of *S. hesperus* with no discussion of the comparative morphology of their respective type specimens. It does appear, however, that these two species are synonyms. The holotype of *S. complexus* is a young individual that retains the deciduous dentition. However, both the right permanent upper and lower premolars are preserved in their crypts, which allows for direct comparison with the holotype of *N. hesperus* (CM 711). The lower premolars are essentially identical on CM 712 and CM 711, differing only in the greater complexity of the unerupted tooth in CM 712. Similarly, the lower molars of CM 712 are more complex than those of CM 711, in which the reduction in complexity is clearly due to its more advanced stage of wear.

Douglass (1901), in describing both these species, cited four differences: 1) the lower incisor of *S. complexus* was less convex than that of *S. hesperus,* 2) the angle of the mandible was broadly rounded in *S. complexus* and acute in *S. hesperus,* 3) the buccal cusps of the lower cheek teeth were rounded externally in *S. complexus* and angular in *S. hesperus,* and 4) the lingual border of the lower cheek teeth of *S. complexus* was concave (not straight). These features do not appear to be consistent with the holotypes of these species. The anterior surface of the lower incisor is nearly identical in CM 711 and CM 712. The angle of the mandible in both specimens is broken, so the complete shape is not discernible. As for the shape of the lower cheek teeth, the differences cited by Douglass (1901) are clearly due to the greater degree of wear on CM 711. In crown height and complexity of the occlusal surface of the cheek teeth, and cross-sectional shape of the lower incisor, *S. complexus* is identical to *S. hesperus.* In size, the lower cheek teeth of the holotype of *N. hesperus* are only slightly larger than CM 712 (Table 1).

The greatest difference between *N. hesperus* and species referred to *Monosaulax* is the lack of complexity of the lophs of the cheek teeth and the relatively enlarged premolars of the latter. The lophs separating the fossettes (-ids) or flexi on the cheek teeth of *Monosaulax* species are simple, smooth, and generally straight. The lophs of the cheek teeth of *N. complexus* are complicated with minute ridges and crenulations. The premolars of *Monosaulax* are larger than any of the molars, whereas in *Neatocastor* the premolars are approximately equal in size to at least the first molars in early stages of wear.

Xu (1994) included the European species *Steneofiber jaegeri* and *S. depereti,* as well as two Asian species, *Monosaulax changpeinensis* and *M. tungurensis,* as synonyms of *S. hesperus.* He cited three features that united these species and separated them from *Eucastor* (which he cited as a senior synonym of *Monosaulax*): 1) jugal contacts the lacrimal bone and straight masseter ridge (masseteric fossa adjacent to the infraorbital foramen); 2) condyle, coronoid process, and angle of the mandible form straight line in posterior view (not aligned as in *Eucastor*); and 3) *Eucastor* has a cheek tooth pattern with fewer flexi.

Table 1.—*Dental measurements of* Neatocastor hesperus. *Abbreviations: a-p, anteroposterior length; tr, maximum transverse width; * indicates estimated dimensions of permanent premolars in crypt.*

			CM 712	
		CM 711	Right	Left
I_1	a-p	3.68	3.62	3.49
	tr	3.71	3.50	3.41
dP_4	a-p		4.28	3.50
	tr		2.99	3.12
P_4	a-p	5.10	4.50*	
	tr	4.40	3.30*	
M_1	a-p	3.80	3.22	3.47
	tr	4.30	4.15	3.94
M_2	a-p	4.00	3.54	3.49
	tr	4.05	3.82	4.04
M_3	a-p	3.80	3.21	2.96
	tr	3.60	3.30	2.96
I^1	a-p		3.22	3.40
	tr		3.69	3.71
dP^4	a-p			3.40
	tr			3.85
P^4	a-p		3.80*	
	tr		3.80*	
M^1	a-p		3.40	3.20
	tr		4.10	4.00
M^2	a-p		3.00	2.95
	tr		4.00	3.90
M^3	a-p		2.30	2.50
	tr		3.50	3.65

The use of these characters is not consistent with the record of "*Steneofiber hesperus.*" The only known skull of *N. hesperus* is CM 712, and it is damaged in such a way that these particular cranial features are not preserved at all. Similarly, of the three lower jaws of the American beaver, none has all three processes of the mandible preserved (condyle, coronoid, angle), so their alignment is impossible to determine. The right mandible of CM 712 preserves a part of the angle and it is more medial than the remainder of the ascending ramus, at least hinting that the posterior mandibular processes are unlike those of *Steneofiber.* The skull of *N. hesperus* also preserves the root of dP^3 on the right side. In *Steneofiber,* as in all other castorids except *Agnotocastor,* this tooth is lost. As for the number of flexi on the cheek teeth, Xu (1994) may be correct in number, but his discussion and figures do not detail the great amount of complexity in the pattern of *N. hesperus* teeth. The cheek teeth of *Steneofiber,* as well as *Monosaulax* and *Eucastor,* are a series of reentrant valleys separated by smooth, straight lophs. The lophs of the cheek teeth of *Neatocastor* are far more complicated with numerous lophules and tuberosities that are preserved even in worn teeth.

Some cranial features that Xu (1994) did not consider also preclude *Neatocastor* from being a species of *Steneofiber.* The most obvious feature of the skull of *N. hesperus* is the elongation of the rostrum, which it shares with *Agnotocastor.* In the type of *N. hesperus* the upper diastema is 175% the length of the upper tooth row. In *Agnotocastor praetereadens* this ratio is 150%. In the skulls of *Steneofiber* figured by Stirton (1935:fig. 14–18) the ratio of the diastemal length to the tooth row ranges from 100 to 125%. The incisive foramen is also relatively larger in

Neatocastor and *Agnotocastor.* The ratio of the length of the incisive foramen to the length of the upper diastema in *Agnotocastor* and *Neatocastor* is 0.39 and 0.33, respectively. In the figured skulls of *Steneofiber* this ratio is 0.23–0.25, much shorter. The more posterior extent of the nasals on the dorsal skull of *Neatocastor* is not present in skulls of *Steneofiber* where the premaxillary and nasal bones extend posteriorly to the same level as in other castorids.

Wahlert (1977) separated *Agnotocastor* from all other castorids based on two primitive characters: presence of a stapedial foramen on the bulla (lost in other castorids), and posterior palatine foramina entirely within the palatine bone (along palatine–maxillary suture in other castorids). In a skull of *S. castorinus* (AMNH 11010) are two pairs of posterior palatine foramina, a large pair along the palatine–maxillary suture (typical of castorines), and a minute pair posterior to them in the palatine bone. The skull of *N. hesperus* preserves only the anterior portion of the palatine bone on the palate and the entire palatine–maxillary suture is distinguishable. The posterior palatine foramina are posterior to the suture, the condition in *Agnotocastor* and unlike *Steneofiber* and all other castorines. Clearly, *N. hesperus* is not a species of *Steneofiber.*

The European species that Xu (1994) listed as synonyms of "*Steneofiber*" *hesperus* cannot be referred to *Neatocastor.* Not only do the cheek teeth of these species lack the complexity of *N. hesperus,* but they are markedly larger. Wilson (1960) noted that a species he referred to *Anchitheriomys* from the Hemingfordian of Colorado was similar in size to both *Steneofiber depereti* and *S. jaegeri.* This Colorado species is 30% larger than *N. hesperus* (Wilson, 1960:67). Stehlin and Schaub (1951:fig. 80) figured an upper molar of *S. jaegeri* that is nearly 40% larger than the upper molars of *N. hesperus.* Stirton (1935:415) listed dental measurements of "*Steneofiber*" *depereti* that are nearly twice as large as the dental measurements of *N. hesperus* (Table 1). Also, no species of *Steneofiber* is known to have a dP^3 as in *Neatocastor.* These European species clearly are not synonyms of *N. hesperus* and should be retained in *Steneofiber* as originally designated.

The Asian species listed as synonyms of "*S.*" *hesperus* by Xu (1994), likewise, cannot be referred to this species. The early Miocene *Monosaulax changpeiensis* differs from the Montana species in a number of dental features. The P_4 of *M. changpeiensis* is characterized by a deep mesoflexid that bends anteriorly, fusing with a parafossettid that is closed anteriorly (Li, 1962:fig. 1). In a worn P_4 the flexid is closed lingually but the fossettid maintains its long and curved shape. The P_4 of *N. hesperus* has an open anterior flexid, and there is a loph that separates the mesoflexid from the parafossettid. Another feature that separates the P_4 of *M. changpeiensis* from *N. complexus* is the morphology of the metafossettid. In the unworn specimen of *M. changpeiensis* are two small fossettids, and in the worn specimen is a single, small fossettid that is obliquely oriented. The P_4 of *N. hesperus* has only a single metafossettid that is long and buccolingually oriented. The lophs of the cheek teeth of *N. hesperus* preserve a number of minor irregularities not present in the teeth of *M. changpeiensis.* The mesostriids on the molars of *M. changpeiensis* also appear to extend lower on the crowns than those of *N. hesperus* (Li, 1962:pl. 1, fig. 1c).

The later Miocene *Monosaulax tungurensis* is known from a mandible that retains dP_4 along with the molars as does the type of "*S.*" *complexus* (CM 712). The molars of *M. tungurensis* have lophs that are simpler (lack irregularities) than the molars of *N. hesperus.* The dP_4 of *M. tungurensis* consists of two simple fossettids (para- and metafossettid) and a simple mesoflexid and hypoflexid (Li, 1963:pl. 1). The dP_4s of *N. hesperus* (CM 712) are worn to the same level as that of the holotype of *M. tungurensis* but are far more complex. The parafossettid is elongated and bent at a right angle near its center. The mesoflexid is divided into two by what appears to be a mesolophid. The metafossettid is similar to that of the dP_4 of *M. tungurensis* in shape and orientation, but preserves irregular sides, reflecting the generally more complex nature of the lophs of the tooth. There is a steep wall that extends to about the middle of the mandible anterior to P_4 in *M. tungurensis.* The diastema of the mandibles of *N. hesperus* are shallow and gently convex upward. Clearly, these Asian species cannot be referred to *N. hesperus* as suggested by Xu (1994).

Scott (1893) named *Steneofiber montanus* from the Arikareean of Montana based on a maxilla, some lower cheek teeth, and some associated postcranial bones (YPM-PU 10456). Matthew (1902) figured the teeth of *S. montanus* and noted that it had more complex teeth than *Palaeocastor* (= *Steneofiber*) *nebraskensis* and was similar in size to *S. hesperus.* He did not synonymize *S. hesperus* and *S. montanus* because they represented individuals of very different ages (*S. hesperus* young, *S. montanus* old) but noted their great similarity. Later, Stirton (1935) included Scott's species as ?*Agnotocastor montanus,* but cited the holotype as being lost. Both Stirton and Matthew recognized the complexity of the occlusal pattern of the cheek teeth of *S. montanus,* a characteristic of *Neatocastor hesperus.* It is possible that *S. montanus* and *N. hesperus* are synonyms. The holotype of the former (YPM-PU 10456) does exist but the dental elements of the specimen have been lost, so no direct comparison can be made. In the future, if a larger sample of *N. hesperus* or *S. montanus* is discovered, and individuals of the same age as the holotype of the other species are available, then this comparison can be made. If these species do prove synonymous, then the species would have to be referred to *Neatocastor montanus* (Scott).

SYSTEMATIC POSITION OF *NEATOCASTOR*

The most recent classification of the Castoridae listed three subfamilies: Castorinae, Palaeocastorinae, and Castoroidinae (Korth, 1994). The genus *Agnotocastor* was excluded from any of these subfamilies because of its possession of primitive characters of the skull and dentition. Wahlert (1977) noted that the skull of *Agnotocastor* was more primitive than all other castorids. Wahlert cited no derived characters of *Agnotocastor* and left it as a sister group to all other castorids (Wahlert, 1977:fig. 3). Dentally, *Agnotocastor* retains a P^3 which is lost in all other castorids, another primitive retention of the genus (Stirton, 1935). The characters that unite *Agnotocastor* and *Neatocastor,* along with the primitive features of the skull (position of the posterior palatine foramina, at least dP^3 retained), are the elongation of the rostrum, larger incisive foramina, more posterior extent of the nasals, and the greater complexity of the occlusal surface of the cheek teeth. These specializations, as well as the primitively retained characters of the skull cited by Wahlert (1977), are also shared with the problematical genus *Amblycastor* and the Eutypomyidae.

The Eutypomyidae have brachydont to submesodont cheek teeth (lower-crowned than either *Agnotocastor* or *Neatocastor*) with complex occlusal patterns, the last premolars subequal in size to the molars, the upper tooth rows parallel, and P^3 or dP^3 retained; these dental features are shared by *Agnotocastor* and *Neatocastor.* Eutypomyids have elongate rostra, nasals that extend more posteriorly than the premaxillaries dorsally, and retain the stapedial foramen in the bulla (only definitely known in *Agnotocastor* among the former genera) and the posterior palatine foramen is entirely within the palatine bone, features shared by *Agnotocastor* and *Neatocastor.* The only feature used by Wahlert (1977) to separate the Eutypomyidae from the Castoridae was the occlusal pattern of the cheek teeth. The cheek teeth of *Agnotocastor* and *Neatocastor,* while not being as complex as that of *Eutypomys,* are more complex than other castorids. Both *Agnotocastor* and *Neatocastor* have higher-crowned cheek teeth than eutypomyids, and the crowns of the molars taper towards their roots, typical of all castorids. In later stages of wear, because of this tapering of the crowns, the molars are reduced in length (anteroposteriorly) making the premolars appear larger. This "narrowing" of the molars is not present in *Eutypomys.*

The problematical Hemingfordian and Barstovian genus *Amblycastor* (possibly synonymous with *Anchitheriomys*) also shares the elongated rostrum, posterior extension of the nasals, and complex occlusal patterns of the cheek teeth with *Agnotocastor, Neatocastor,* and eutypomyids (Wilson, 1960; Voorhies, 1990). Korth (1994) referred *Amblycastor* and *Anchitheriomys* to the Eutypomyidae based on these characters, whereas previously these latter two genera had been considered castorids (Stirton, 1935; Simpson, 1945). *Amblycastor* has cheek teeth that are at least as high-crowned as those of *Neatocastor.* Voorhies (1990) demonstrated that there was evidence for the presence of a dP^3 *Anchitheriomys* (= *Amblycastor*) *fluminis.* A nearly complete skull of this latter species from the Barstovian of Nebraska (USNM 298914, not yet described fully) has the posterior palatine foramina on this specimen entirely within the palatine bone as in *Agnotocastor, Neatocastor,* and eutypomyids. The cheek teeth of *Amblycastor* and *Anchitheriomys* have several castorid characteristics not present in eutypomyids: 1) premolars are the largest of the cheek teeth; 2) crowns of the molars taper toward their bases (also present in *Agnotocastor* and *Neatocastor*); and 3) the tooth rows diverge posteriorly, although not as strongly as in other castorids (for descriptions of the skull and dentition of *Amblycastor* and *Anchitheriomys* see Stirton, 1935; Wilson, 1960; Voorhies, 1990). The incisors of *Amblycastor* have been described as procumbent (extending anterior to the premaxillaries), similar to those of *Neatocastor* and *Agnotocastor* (Wood, 1937:pl XXVIII, fig. 1), and distinct from those of castorines such as *Steneofiber* and *Castor* (Stirton, 1935: fig. 15, 16; Voorhies, 1990).

Agnotocastor, Neatocastor, and *Amblycastor* retain a primitive cranial feature lost in all other castorids: posterior palatine foramina entirely within palatine bone. Other features of the skull shared by these genera are the relative elongation of the rostrum, the nasals extending farther posterior than the premaxillaries dorsally, and procumbent incisors. These features, along with the complexity of the cheek teeth, unite these three genera. Within this group of genera, *Neatocastor* is clearly intermediate in dental characters. The cheek teeth are higher crowned than in *Agnotocastor* and lower crowned than in *Amblycastor* (and *Anchitheriomys*), and the degree of complexity of the occlusal surface of the cheek teeth of *Neatocastor* is less than in *Agnotocastor* and more complex than in *Amblycastor.* However, the Asian species of *Anchitheriomys* have occlusal patterns of the cheek teeth as complex as those of eutypomyids.

If elongation of the rostrum and complex occlusal pattern of the cheek teeth are considered derived characters, then *Agnotocastor, Neatocastor,* and *Amblycastor* represent a distinct clade among castoroids closely related to the Eutypo-

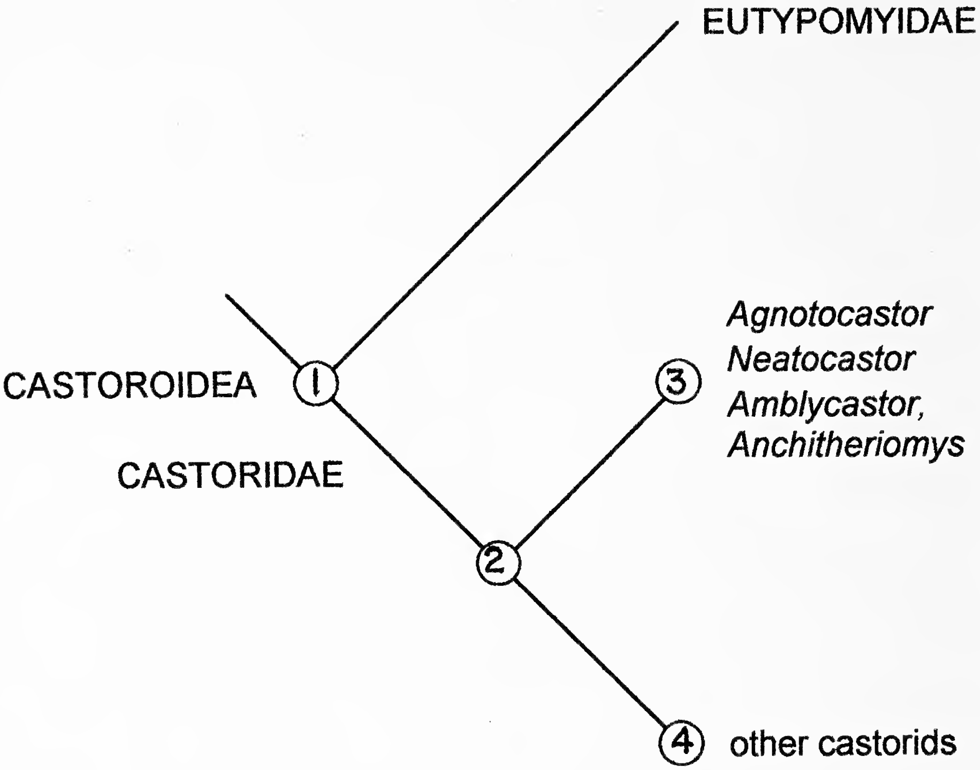


Fig. 3.—Cladogram of proposed relationships. Explanation of nodes: 1, Castoroidea: sciuromorphy; uniserial enamel of incisors; interorbital foramen posterior to optic foramen; sphenopalatine foramen surrounded by maxillary; posterior maxillary foramen enclosed; dorsal palatine foramen in maxillary or along orbitosphenoid–maxillary suture (see Wahlert, 1977:fig. 3). 2, Castoridae: intermediate to large-size rodents; cheek teeth at least mesodont; castorid crown pattern of cheek teeth (= crowns of molars taper towards base; occlusal patterns of cheek teeth series of lophs and reentrant valleys [cusps indistinguishable], patterns become simpler with wear). 3, (unnamed taxon): elongate rostrum; occlusal pattern of cheek teeth complex; upper incisors procumbent; nasals extend further posteriorly than maxillaries dorsally. 4, Palaeocastorinae, Castorinae, Castoroidinae: P^3 and dP^3 lost; stapedial foramen lost; posterior palatine foramen within palatine–maxillary suture; upper tooth rows strongly diverge posteriorly; premolars larger than molars.

myidae. However, if these features are considered primitive for the Castoroidea or convergent with eutypomyids, then these genera represent a primitive group of castorids. The characteristic tapering of the molars that results in a narrowing with age is clearly a dental character that is shared by *Agnotocastor, Neatocastor, Amblycastor,* and all other castorids.

Agnotocastor, Neatocastor, and *Anchitheriomys* represent a distinct subfamily of beavers. A name is being proposed formally elsewhere along with a complete description of the skull of *Anchitheriomys* (Korth and Emry, in press). The relationships of this group of genera are presented in Fig. 3.

Acknowledgments

The specimens described above were loaned by permission of Dr. M. R. Dawson (CM). Assistance in locating the specimens, preparation, and helpful discussion of the locality data of the specimens was provided by A. Tabrum (CM). Drs. J. H. Wahlert (AMMH) and R. J. Emry (USNM) assisted with discussions of cranial anatomy of beavers. Camera and photographic equipment were provided by Dr. J. A. Massare of the State University of New York, College at Brockport.

LITERATURE CITED

DOUGLASS, E. 1901. Fossil Mammalia of the White River beds of Montana. Transactions of the American Philosophical Society, 20:237–279.

HIBBARD, C. W., AND K. A. KEENMON. 1950. New evidence of the Lower Miocene age of the Blacktail Deer Creek Formation in Montana. Contributions to the Museum of Paleontology, University of Michigan, 8:193–204.

KORTH, W. W. 1994. The Tertiary Record of Rodents in North America. Plenum Press, New York, 318 pp.

KORTH, W. W., AND R. J. EMRY. In press. The skull of *Anchitheriomys* and a new subfamily of beavers (Castoridae, Rodentia). Journal of Paleontology.

LI, C. K. 1962. A Tertiary beaver from Changpei, Hopei Province. Vertebrata PalAsiatica, 6:72–77.

———. 1963. A new species of *Monosaulax* from Tung Gur Miocene, Inner Mongolia. Vertebrata PalAsiatica, 7:240–243.

MATTHEW, W. D. 1902. A horned rodent from the Colorado Miocene, with a revision of the mylagauli, beavers, and hares of the American Tertiary. Bulletin of the American Museum of Natural History, 16:291–310.

RASMUSSEN, D. L. 1977. Geology and mammalian paleontology of the Oligocene–Miocene Cabbage Patch Formation, central-western Montana. Unpublished Ph.D. dissert., University of Kansas, 775 pp.

SCOTT, W. B. 1893. The mammals of the Deep River beds. American Naturalist, 27:680.

SIMPSON, G. G. 1945. The principles of classificatoin and a classification of mammals. Bulletin of the American Museum of Natural History, 85:1–350.

STEHLIN, H. G., AND S. SCHAUB. 1951. Die Trigonodontie der simplicidentaten Nager. Schweizerische Paläontologische Abhandlungen, 67:1–385.

STIRTON, R. A. 1935. A review of the Tertiary beavers. University of California Publications in the Geological Sciences, 23:391–458.

VOORHIES, M. R. 1990. Vertebrate paleontology of the proposed Norden Reservoir area, Brown, Cherry and Keya Paha counties, Nebraska. Technical Report 82–09, Division of Archeological Research, University of Nebraska–Lincoln, 731 pp.

WAHLERT, J. H. 1977. Cranial foramina and relationships of *Eutypomys* (Rodentia, Eutypomyidae). American Museum Novitates, 2626:1–8.

WILSON, R. W. 1960. Early Miocene rodents and insectivores from northeastern Colorado. University of Kansas Paleontological Contributions, Vertebrata, 7:1–92.

WOOD, A. E. 1937. The mammalian fauna of the White River Oligocene. Part II. Rodentia. Transactions of the American Philosophical Society, 28:155–269.

WOOD, H. E., II. 1933. A fossil rhinoceros (*Diceratherium armatum* Marsh) from Gallatin County, Montana. Proceedings of the United States National Museum, 82:1–4.

XU, X. 1994. Evolution of Chinese Castoridae. Pp. 77–98, *in* Rodent and Lagomorph Families of Asian Origins and Diversification (Y. Tomida, C. Li, and T. Setoguchi, eds.), National Science Museum, Tokyo, Science Museum Monographs no. 8.

ANNALS OF CARNEGIE MUSEUM
Vol. 65, Number 2, Pp. 181–182 16 May 1996

REVIEW

AUSTRALIAN BEETLES. Lawrence, J. F., and E. B. Britton. 1994. Melbourne University Press, Carlton. x + 192 pp. ISBN 0-522-84519-3. $44.95.

The much-anticipated second edition of Insects of Australia (CSIRO, 1991) replaced and modernized the first edition of 1970. There were many improvements in the new version, not the least of which was the chapter on beetles. The new Coleoptera classification presented was based on detailed study of both larval and adult characters, and was state-of-the-art. However, the second edition had been in the planning and production phase long before its publication in 1991, and therefore contained some information which was obsolete or otherwise faulty. This spinoff volume on Australian beetles, while very similar to the chapter on beetles in the new Insects of Australia, was published to correct some of these problems.

The 35-page introduction to the book is much more than a simple preface, and is divided into several sections: fossil history, habitats of Australian beetles, collecting methods, anatomy of adults, immature stages, biology, and special biogeographic features of Australian beetles. All are treated extensively, and the section on adult anatomy may serve as a reference for the correct use of terms for structures of adult beetles.

The next major part of the book is devoted to the classification and keys to both adults and larvae of Australian beetles. The classification lists all recognized families of beetles, including those not found in Australia, with the number of Australian species (both described and known undescribed) for each. A total of 28,300 species is enumerated in 117 families, with 43 families unknown in Australia. A comparison between this classification and the one in Insects of Australia reveals a few differences of varying importance. For example, the Eucinetiformia has been changed to Scirtiformia, Rhizophagidae to Monotomidae, and Cephaloidae to Stenotrachelidae. Perimylopidae, Boridae, and Pyrochroidae are added to the Australian fauna, while Chalcodryidae, Pedilidae, and Allocorynidae are removed. A brief explanation of the classification is given, with comparisons made to that of Crowson.

The somewhat intimidating key to adults uses 255 couplets, with many families keying out in a number of places, e.g., Tenebrionidae in eight places, and Salpingidae in seven. The larval key is longer, with 266 couplets. Both keys are not strictly dichotomous; some "couplets" are actually triplets or quadruplets. This design is an artifact of using the program DELTA (Description Language for Taxonomy) to store the data on which the keys were based, and creates no practical difficulties in using the keys.

The book's largest part is devoted to the actual treatments of Australian beetle families. Provided for each are diagnostic, abbreviated, descriptions of both larval and adult stages. The names of important structural features are abbreviated, which, although saving space, require some page flipping to and from the list of abbreviations, until they are memorized. After this diagnosis, there is a general discussion of structural peculiarities of the family, included Australian taxa and their classification within the family, a brief account of the natural history, and pertinent references. Within this section, the illustrative material is truly excellent. Each family has at least one representative adult, and for many, also the larva, illustrated. There are 16 plates including scanning electron micrographs of larval and adult structures, and some color paintings and photographs of adult beetles. Within some of the larger families (e.g., Carabidae, Staphylinidae, Scarabaeidae, Cerambycidae, and Chrysomelidae), separate keys are given for subfamilies or tribes.

While this book was written to treat the Australian beetle fauna extensively, its value goes far beyond Australia. It is immediately obvious to the reader that an immense amount of time and many thousands of specimens have gone into the production of this book. The combination of the authoritative text, inclusion of both larval and adult stages, and the superb illustrations make the work a necessity for all serious students of beetle systematics, and the affordable price tag is a welcome change!

DARREN A. POLLOCK, *Rea Postdoctoral Fellow, Section of Invertebrate Zoology.*

INSTRUCTIONS FOR AUTHORS

ANNALS OF CARNEGIE MUSEUM consist of contributions to the earth sciences, life sciences and anthropology, in 30 by 46 picas format (127 by 195 mm or 5 by 7⅝ inches). Submit all manuscripts to the Office of Scientific Publications. Authors should give particular attention to scientific content, format, and general style for the ANNALS. **Manuscripts that do not conform to the style of the ANNALS will be returned to the author immediately.** Every manuscript will be peer reviewed by at least two outside persons. Authors will be asked to subsidize, if funds are available, any or all costs of publication (approximately $100/page printed).

Manuscript style.—Articles should include the following items in this order: title page, abstract, text (with desired headings), acknowledgments, literature cited, tables, figure captions, and copies of illustrations. All manuscripts must be typed ***double-spaced*** on standard 8½ by 11 inch white bond paper, with at least one inch margins all around, and submitted ***in triplicate***—an original for the editors, and two review copies. All pages should be numbered, including tables, literature cited, and the list of figure captions. Only correspondence quality or better dot matrix printouts will be accepted; draft mode is unacceptable. A fixed-space font (e.g., Courier) is preferred.

Title Page. The title, on a separate title page should be brief, include the animal or plant group involved, and appear two to three inches below the top margin. Include the authors name(s) and the affiliations of non-CMNH authors. In the case of multiple authorship indicate the address to which proofs should be sent.

Abstracts. Abstracts should be short, double-spaced and substantive and included at the head of the first page of text.

Text. Do not right justify text or break (hyphenate) a word at the end of a line. ***Footnotes and acknowledgments as footnotes are unacceptable.*** All text is double-spaced.

Tables and figure legends. The list of figure legends and each table should be typed consecutively on individual pages separate from the text. Tables must be double-spaced throughout with **no vertical lines.**

Abbreviations. Refer to the CBE Style Manual for correct abbreviations. Mammalian dentition: use capital letters (I, C, P, M, D, for incisor, canine, premolar, molar, deciduous, respectively) and superscript/subscript numbers (M^2, P_3) to designate upper and lower teeth.

Measurements. Metric units should be used, if possible.

Literature Cited. All references in text must appear in the Literature Cited section. The data (author, date and page) in both citations must agree. ***Do not abbreviate the titles of periodicals or serials.*** The following style, double-spaced, should be used in Literature Cited:

1) Two authors in an institutional series:
   MATTHEW, W. D., AND W. GRANGER. 1923. The fauna of the Houldjin Gravels. American Museum of Natural History Novitates, no. 97: 1–6.
2) Same authors repeated—use three-em dash:
   ———. 1923. The fauna of the Ardyn Obo Formation. American Museum of Natural History Novitates, no. 98:1–5.
3) Same authors plus a third author—repeat all authors:
   MATTHEW, W. D., W. GRANGER, AND G. G. SIMPSON. 1928. Paleocene multituberculates from Mongolia. American Museum of Natural History Novitates, no. 331:1–4.
4) Chapter in an edited volume:
   RAUSCH, R. L. 1963. A review of the distribution of Holarctic mammals. Pp. 29–43, *in* Pacific Basin Biography (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.
6) Book:
   WHITE, M. J. D. 1961. The Chromosomes. Methuen and Co., Ltd., London.
7) Journal articles with usual volume and issue number:
   ANDERSON, W. I. 1969. Lower Mississippian conodonts from northern Iowa. Journal of Paleontology, 43(4):916–928.

Illustrations. All illustrations will be called figures, and are to be numbered in Arabic numerals. Three sets of illustrations are required, one (original artwork) for reproduction, two for reviewers. Xerox copies of photographs for reviewers are usually not acceptable but are adequate for line drawing review copies. Illustrations may not be larger than 72 by 102 picas (305 by 432 mm or 12 by 17 inches). All illustrations must be reducible to a maximum of 127 by 195 mm (30 by 46 picas) without loss of clarity. Line copy should be designed for reduction to ⅔ or ½ of actual size. Typewritten illustration copy will not be accepted. Photographic figures should be submitted at **actual reproduction size,** if possible.

Two or more small figures should be combined for reproduction as a unit or plate, but, if feasible, do not combine halftones and line drawings. Rectangular halftone figures should be abutted, without intervening spaces. The printer will insert narrow white spaces during the reproduction process. Halftone figures with solid black backgrounds will not be accepted unless the author agrees to pay for the printing costs. All plates must have ***minimally*** one inch borders all around. Each plate should be given a protective cover and identified on the back side.

Lettering and/or a magnification scale (linear metric scale) for rectangular halftone figures should be placed directly on the photo, not in a blank space between photos. The scale or lettering for closely cropped photos can be placed in blank areas close to the figure.

Proof.—The author should answer all queried proof marks and check the entire proof copy. Return corrected page proof with the edited manuscript ***promptly*** to the editors.

If an author chooses to make extensive alterations to a paper in proof stage the author or appropriate section will bear the cost. Original manuscripts will not be returned unless requested. Illustrations will be returned to the author.

ISSN 0097-4463

ANNALS of CARNEGIE MUSEUM

THE CARNEGIE MUSEUM OF NATURAL HISTORY
4400 FORBES AVENUE • PITTSBURGH, PENNSYLVANIA 15213

VOLUME 65 30 AUGUST 1996 NUMBER 3

CONTENTS

ARTICLES

Manuscripts, subscriptions, orders for individual numbers, and changes of address should be sent to:

Office of Scientific Publications
Carnegie Museum of Natural History
4400 Forbes Avenue
Pittsburgh, PA 15213-4080
Phone (412) 622-3287
Fax (412) 622-8837
E-mail: schmidtm@clp2.clpgh.org

ANNALS OF CARNEGIE MUSEUM is published quarterly by The Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213-4080, by the authority of the Board of Trustees of Carnegie Institute.

THE CARNEGIE
MUSEUM OF
NATURAL HISTORY

ANNALS OF CARNEGIE MUSEUM

VOL. 65, NUMBER 3, PP. 183–296 30 AUGUST 1996

THE TAXA OF FOSSIL MOLLUSCA INTRODUCED BY HERMANN VON IHERING

JUAN JOSE PARODIZ

Curator Emeritus, Section of Invertebrate Zoology

ABSTRACT

Between 1896 and 1921 Hermann von Ihering described or named 352 taxa of fossil molluscs, from genera to subspecies, and many "varieties." Most of the taxa were from southern Argentina (Patagonia), but some were from Chile, Uruguay, and Brazil. When combined with other species described by Arnold E. Ortmann in 1902, these fossils constitute the basis of our knowledge of the Tertiary malacofauna of the region. Ihering's collection was acquired in 1920 by the Museo Argentino de Ciencias Naturales, and during the 1940s the author organized and catalogued the collection of more than 900 lots.

This paper deals with Ihering's taxa and: 1) updates the taxonomic nomenclature for both genera and species; 2) indicates the correct type localities, many of which were uncertain at the time of description; 3) clarifies the stratigraphic position and geologic age of the deposits where the fossils were found; and 4) reconsiders some of Ihering's conclusions about the origin and distribution of the fauna in relation to climatic changes in the region during the Tertiary.

Ihering's stratigraphy overestimated the age of deposits. There were no intercalations between the Cretaceous and Eocene; Paleocene species were believed to be Cretaceous; marine formations of the Miocene were dated as Eocene, and so on. He also subdivided formations in order to indicate that parts of them were older. The relative ages of strata were based on the proportion of extinct species versus surviving ones. When synonyms are recognized, and many infrasubspecific names eliminated as nontaxonomic variations, such estimation is untenable.

Most of the mid-Tertiary species belong to genera that are represented in the Recent, and from zones warmer than the present climate in the Patagonian and Magellanian regions. Climatic changes were not local phenomena but the consequence of plate tectonics. Movements of plates not only changed their location, but also the orientation of the masses of land by clockwise rotation. The plates, formerly separated, united into a new continent, and rotation reversed to counterclockwise bringing them into their present position. Ihering considered them a single, unique mass, and named them Archhelenis (the northeastern part including Brasilia) and Archiplata (the southwestern part). Although land-bridge theories have been replaced by interpretations from plate tectonics, Ihering's nomenclature for the land masses is still useful and valid.

New combinations are proposed for 32 species, and lectotypes are designated for *Mactra indistincta* Ihering (1897), *Neoinoceramus ameghinoi* Ihering (1902), *Nucula tricesima* Ihering (1897), *Phacoides rocana* Ihering (1907), *Panopea thomasi* Ihering (1914), and *Potamides patagonensis* Ihering (1897). *Aturia* (*Sphenaturia*) *brueggeni* Ihering, 1921, is selected as the type species of *Sphenaturia* Ihering, 1921 (Nautilidae).

INTRODUCTION

Between 1896 and 1921 Hermann von Ihering introduced 352 taxa of fossil Mollusca from the early Tertiary to the Pleistocene of southern South America, including genera, subgenera, species, subspecies, and infrasubspecific taxa. I had the opportunity, in 1940, of organizing this material, verifying the data, and cataloguing the more than 900 lots that constitute Ihering's collection. The present work attempts to update taxonomic nomenclature and synonymy, to clarify the stratigraphic position of strata where the fossils were found, and to indicate the correct type localities.

Submitted 29 January 1990.

Fig. 1.—Hermann von Ihering: born 9 October 1850, died 25 February 1930.

Hermann von Ihering (Fig. 1) was born at Kiel, Germany, on October 9, 1850. He studied at Giessen, Berlin, and Göttingen, and was graduated in medicine and natural sciences. As a young naturalist he went to Italy and practiced at the Naples Zoological Station and at Messina to the south. When he returned to Germany he became an assistant to Professor C. Clauss in Göttingen, was "Privat Dozent" at Erlangen, and finally worked in Leipzig with Professor R. Leuckart. Hermann intended to make his home in the city of Henen (Geissen) by marrying a bourgeois girl, to which his father would not consent. At age 30 he was required to marry, instead, an aristocratic young lady, Anne Maria Clare von Bozel. He projected a trip to South America and his father demanded that, upon his return, he accept a promised professorship at the University of Warsaw in Poland. However, Ihering never took the position. He was already a well-known zoologist when, in 1880, he took permanent residence in Brazil, where he lived for 40 years. He was appointed "Naturalist" of the Museu Nacional at Rio de Janeiro, and later he assumed the responsibility of organizing a new museum in São Paulo, State of Rio Grande do Sul. The Museu Paulista was inaugurated under his direction. His bibliography of this period was considerable, in different branches of natural sciences, published in European journals, and also in his own *Revista do Museu Paulista.* In 1920 he was at the Museu Catharinense, in Florianopolis, Santa Catharina; by that time he had more than 300 scientific publications to his credit. His greatest dedication was to the field of malacology, not only on the taxonomy of living and fossil Mollusca, but also in anatomical research, especially on the nervous system. As early as 1876 he had defined and created the class Amphineura, and recognized the affinities of the Aplacophora to the chitons. His numerous publications on molluscan paleontology, together with A. E. Ortmann's (1902) in the Reports of the Princeton Expedition to Patagonia, laid the foundation of our knowledge of the Tertiary malacofauna of southern South America. Ihering's zoogeographic and paleogeographic studies were epitomized in "Archhelenis und Archinotis" published in Leipzig in 1907.

While residing in São Paulo, Ihering was in permanent correspondence with the Argentine paleontologist Florentino Ameghino, from whom he received the fossil materials that his brother, Carlos Ameghino, collected during 18 years of arduous travels in Patagonia. Carlos Ameghino also provided the geological information on which Florentino Ameghino based the dating of his stratigraphic series which Ihering followed. Those views, however, went through considerable modification by the middle of this century. He had supported, as had other paleogeographers of his time (including Ortmann), the theories of land bridges existing between Africa and South America prior to the Neogene (Ihering, 1900). Current tectonic concepts provide a better explanation for such paleogeographic relationships, but Ihering's nomenclature, given for land masses at the beginning of the Tertiary, is still valid.

A catalogue of the Ihering Collection (Ihering, 1914) was printed when von Ihering left the Museu Paulista in 1914 and took the collection with him (he considered the collection to be his own property). About 1919 the collection was purchased from Ihering by the Buenos Aires Museum. Each lot listed in the published 1914 catalogue was subsequently assigned a number from the Catalogue of Fossil Mollusca in the Museo Argentino de Ciencias Naturales. The numbers preceded by # in the following list are the previously unpublished numbers from that catalogue, which began with the Ihering Collection. A record of those numbers exists as annotations by Parodiz in a copy of Ihering's catalogue (1914) in the library of Carnegie Museum of Natural History (CMNH). All lots and type material were checked by Parodiz in 1940, and during the preparation of this paper in 1987 they were checked again.

During his residence in Brazil, Ihering made frequent trips to the La Plata region, keeping close connection with his collaborators. His last visit to Buenos Aires was in 1919, and it was during that period that his collection of fossils was acquired for the National Museum in that city.

When Ihering returned to Europe at the age of 70, he stayed again for a while at the Naples Zoological Station. Finally he settled in Budingen, and married his second wife Mela Buff, the same person his father had not permitted him to marry half a century before. He died on February 25, 1930.

Although Ihering's fossil collection was founded mainly on Ameghino's specimens, he also received much material from other collectors, geologists, and malacologists. Among those who contributed to the collection were A. E. Ortmann, M. Cossmann, R. A. Philippi, R. Hauthal, S. Roth, and his envoy to Patagonia in 1895, J. Bicego.

The contents of this paper were presented to the Tenth International Congress of Malacology held during August 1989 in Tübingen, Germany.

METHODS

For the taxa listed alphabetically in this paper, the original name is given first followed by references. Then the current combination or senior synonym is given after "=" if differing from the original name, followed in some cases by junior synonyms. The family name on the right side of the citation corresponds to placement of the genus in the current combination. Holotypes are indicated only when the description was based on an original lot consisting of a single specimen. All other type materials are indicated as syntypes, since in many cases the specimen marked "type" in the collection does not coincide with the one figured in the original description, or more than one specimen is marked "type," or the type lot indicated by Ihering in the collection is not from the published type locality. There are several names where no specimen was figured and no specimen is marked as being a type. Finally, in some cases Ihering marked as "type" a better specimen received after the date of description.

In Ihering (1907*a*), species names are separated by commas from a worker's name and associated literature citation. It is therefore not possible to determine if that person and citation are the original author and description of the preceding name, or only a subsequent citation referring to that name. It was necessary to consult those citations directly in order to determine this difference.

The stratigraphical notation of Ihering is given in parentheses on the same line of the reference (usually the last where the author corrected his own earlier assignments), and in the author's original spelling (French, Spanish, or Portuguese). The relative geological age according to current knowledge is given on the line *Stratigraphy*. The catalogue numbers correspond with few exceptions to those given to the collection in the Museo Argentino de Ciencias Naturales.

There are a number of species, subspecies, or "varieties" that Ihering (1914) listed or described which were not found in the collection; in those cases, their absence is clearly stated. The date of publication for names proposed by A. D. d'Orbigny follow Parodiz (1957).

LOCALITIES

Alsina, Valle. Río Negro Province, with strata of the Roca and Salamanca Formations (Paleocene), indicated by Ihering for species he described as "upper cretaceous" or "étage guaraniéen." See also Puente Alsina.

"*Baie*" *de San Julian.* Narrow harbor at San Julian, Santa Cruz.

Bajada de Paraná. Cliff below the city of Paraná, Entre Rios Province. Type section for some species from the Paraná Formation.

Bajo de la Pava. Lowland in the vicinity of Puerto Deseado, with "Sierra Laziar strata" (Laziarense), Araucanean Formation, Pliocene.

Bajo de las Flechas. Lowland near the lower section of the Río Deseado, southeast of Cerro Moro, near the coast of Santa Cruz.

Bajo de San Julian. See *San Julian.*

Boquerón. Punta Boquerón. On Bahía Inútil, Magellan Strait, Tierra del Fuego.

Buentiempo. Cabo Buen Tiempo. Cape Fairweather, southern Santa Cruz; locality first explored by Hatcher (1897). Perforations made by Yacimientos Petroliferos Fiscales (Argentina Oil Bureau) 15 km W of this locality, found continental deposits at 93 m (Santa Cruz Formation), and Tertiary marine deposits at 665 m. See Feruglio, 1949–1950:279.

Camarones, Bahía. Bay immediately north of the Golfo San Jorge.

Cañada de los Artilleros. Long gorge running east from Cerro Cuadrado to the Río Chico in Santa Cruz. Yegua Quemada and Las Cuevas are localities along it.

Cañadón Blanco. South side of Colhue Huapi Lake, Chubut Province.

Carmen Sylva. Tierra del Fuego. Species of this locality are mostly of the Magellanian, and some of the Patagonian formations.

Casamayor, Punta Casamayor. Point on southern part of Golfo San Jorge in Santa Cruz, north of Mazaredo. In geopaleontological bibliography sometimes spelled, *Casa-Maior* or *Casamajor.*

Cerro Bagual or *Cerro de los Baguales.* North of the Río Sehuen Valley west of Mata Amarilla, Santa Cruz. Thick deposits of the Salamanca Formation. Do not confuse with Sierra Baguales which is in south-central Santa Cruz.

Chapadmalal. Creek and town south of Mar del Plata, Buenos Aires Province.

Chico River, Río Chico of Chubut Province. Tributary of Chubut River running northeast from Colhue Huapi Lake, eastern Chubut Province.

Chico River, Río Chico of Santa Cruz. Tributary of Río Sehuen running southeast.

Chocoi, Punta Chocoi. On Magellan Strait at Carelmapu, Chile.

Colhue Huapi. Lake and locality in southeast Chubut Province, east of Lake Muster.

Colloncura, Río. Tributary of the Limay River in southern Neuquen Province.

Corral Foyel. Locality on the Andean zone of Nahuel Huapi, along the Foyel River and Foyel Lake. First explored by the geologist Santiago Roth in 1897–98, and later by R. Hauthal (1898).

Deseado, Puerto Deseado, Port Desire. South of Golfo San Jorge, at the mouth (or *ria*) of Deseado River in Santa Cruz.

Deseado Island. An early Tertiary island in the San Jorge Sea, practically separating northern and southern parts of that sea during the Paleocene.

Fairweather, Cape. See Buentiempo.

Foyel, Rio, Lago. See Corral Foyel.

Foz de Santa Cruz. In Ihering (1914); mouth (or *ria*) of Santa Cruz River.

General Roca. Roca in the geopaleontological literature. Town in the upper Río Negro Valley, east of the junction with Río Limay, which was earlier known as "Fresno Menuco," Río Negro.

Homo Viejo [sic]. Error for Horno Viejo, near Roca, Río Negro.

Jahuel or *Jaguel.* Below the east slope of Sierra Auca Mahuida and Bajo del Palo, south of Río Colorado, Neuquen Province; type section for many species from Paleocene fresh-water deposits.

Jack Harvey. South of Monte Observación and south of Coyle, Santa Cruz.

Jegua Quemada. See Yegua Quemada.

La Cueva or Las Cuevas. Six mi S of the mouth of Río Santa Cruz and north of Río Coyle, near Yegua Quemada, and east of Monte León.

Laziar, Sierra Laziar. 50 km NW of Puerto Deseado, Santa Cruz; type section for species from deposits of the Araucanean Formation, Pliocene.

Lele or *Leleque.* Creek in northwest Chubut Province, at the base of Sierra Leleque, halfway between ñorquinco and Esquel.

Luján. Old city on the Luján River, 100 mi N of Buenos Aires. Pleistocene deposits.

Maiten, Maiten Valle. Río Negro Province.

Malaspina. 25 km W of Bahía Bustamante, northern part of Golfo San Jorge, Chubut Province.

Mata Amarilla. On the north slope of Cerro del Castillo and 20 km E of Park-Aik, Santa Cruz.

Monte Cazador (Capas with *Lahillia luisa*). A number of marine species were described by Wilckens from this locality that were confused with the strata of Salamanca (Paleocene); these are Upper Cretaceous.

Monte Espejo. Marine terrace located near San Julian, Santa Cruz, north of Río Seco and 50 km S of Bahía Laura.

Monte León. South of the mouth of Río Santa Cruz, 5 mi inland from Punta León, Santa Cruz.

Monte Observación. Hill between mouth of Río Santa Cruz and Puerto Coig.

Owen Point. Collecting locality on coast of Santa Cruz, named by Hatcher.

Pan de Azucar. Promontories north of the lower Río Chico Valley, near Gaiman, with Paleocene to Miocene strata, Chubut.

Park-Aik or *Pari-Aike.* Name of an *estancia* (ranch) that was located 20 km W of Mata Amarilla, along the Río Sehuen, Santa Cruz.

Piedra Clavada. A "torreon" or tower produced by eolic erosion of sandstones from the Sehuenan beds, in the Río Sehuen Valley; west of Kohuel Kaike on the railroad between Puerto Deseado and Colonia Las Heras, Santa Cruz.

Puente Alsina. South of Buenos Aires city. Perforation found Miocene strata of the Paraná Formation at a depth of 80 m.

Puerto Militar: now *Puerto Belgrano.* Naval base in southwest Buenos Aires Province at Bahía Blanca. The vicinity is the type section for species of the marine Belgrano Formation, early Pleistocene.

Pueyrredón, Lago. Lake in western Santa Cruz, on the border between Argentina and Chile.

Punta Atlas. Point midway between Rawson and Camarones, Chubut.

Punta Nodales. On the Golfo San Jorge, 20 km N of Comodoro Rivadavia, Chubut Province.

Punta Nueva, Nava, Nova. Point between Bahía Mazaredo and Bahía Bustamante, Golfo San Jorge, Santa Cruz.

Rada Tilly. Harbor near Comodoro Rivadavia, Golfo San Jorge.

Salamanca, Pico. Peak on the Golfo San Jorge, near Bahía Solano, Santa Cruz, between Puerto Viser and Punta Matalinares. Marine Paleocene strata.

San Julian, Bajo de San Julian. Southern Santa Cruz lowlands. Typical strata of the Lower Patagonian Formation (Juliense).

Santa Cruz. Santa Cruz Province. Port at the mouth of the Santa Cruz River. Ihering's references to Santa Cruz for fossils of different strata are not always clear; it may be the locality of that name or some other place in Santa Cruz Province (a Territory at the time).

Santa María da Bocca do Monte. Rio Grande do Sul, Brazil.

Sehuen Aik. Near Mata Amarilla, on the Valley of Río Sehuen, Santa Cruz. Sometimes referred to by Ihering as Sehuen-Ark.

Sehuen River (also called Chalia). Runs from the vicinity of Lago Viedma in Santa Cruz to become a tributary of the Río Chico. The name Chalia was applied for its vicinity to an *estancia* (ranch) of that name near Mata Amarilla.

Shell Gap. A locality mentioned by Ortmann (1902) and named by Hatcher, on the upper section of Río Chico in Santa Cruz, near El Portezuelo.

Tres Puntas. Cape south of Golfo San Jorge, near Deseado, Santa Cruz.

Valcheta, Travesia. Area along the Gualicho River in western Río Negro.

Villarino, Punta Villarino. On Peninsula Valdéz, Chubut.

Yegua Quemada. North of, and very close to, La Cueva, a few miles south of the mouth of the Santa Cruz River, east of Monte León.

STRATIGRAPHIC UNITS

Upper Cretaceous

Senonian–Chubutian

Strata with Lahillia luisa *(Pehuenche–Pehuenchense).*—The complex of Upper Cretaceous deposits, including the *Lahillia luisa* beds, were known to early authors as Chubutiano or Chubutense. According to E. Feruglio (1949–1950) that complex of sediments in southern Patagonia reaches a thickness of 2300 m. Geologists recognize that a considerable hiatus exists between the Senonian and the marine deposits of the Paleocene. The fauna of invertebrates at the end of the Cretaceous showed more global geographic relationships with a complete change in the deposits of the Eocene, with no species affinities. In Ihering's time, the concept of the Paleocene was not yet developed, and the Cretaceous–Tertiary boundary was not established. Marine strata now known as Paleocene were included in the Cretaceous. Even early in this century, authors such as Wichmann (1927) and Windhausen (1918; 1931, in part), parallelled Roca and Salamanca formations with the strata containing *Lahillia luisa.*

Until near the end of the Cretaceous the conditions in the Patagonian region were of continental character. Then epirogenical movements began and continued into the early Tertiary, especially in the area now corresponding to the Golfo San Jorge, which was transformed into a great basin (Feruglio, 1949–1950:17).

Tertiary

Paleocene

Guaranitic.—Ihering, Ameghino, and other early writers on Patagonian stratigraphy used the name "formación guaranitica" for a complex of strata corresponding globally to the Paleocene–Eocene, derived from d'Orbigny's (1842) "Tertiarie Guaranien," "Formación Guaranitica" of Döring (1881–1882), and "Guaranitic Beds" of Hatcher (1897). Other authors included it in the "Pehuenche" (Upper Cretaceous). These sediments contain *Ostrea guaranitica* Ihering (= *Exogyra guaranitica* [Ihering]), *Corbula sehuena* Ihering (= *Eriphyla sehuena* [Ihering]), and *Potamides patagonensis* Ihering; it is recognized as a brackish-water unit of the Paleocene of the Sehuen Valley of Santa Cruz. See Sehuen Formation.

Roca Formation (Rocanense).—The marine deposits of Ihering's (1903) Rocanéen, or Rocanense of other authors, were named after the type locality, the village of General Roca on the left bank of the Río Negro, Río Negro Province. The Roca beds represent the earlier Tertiary ingression of the San Jorge Sea in its northern section. Ihering maintained that the marine Roca was of Upper Cretaceous age. Windhausen (1916) was the first to report that the "Roca horizon corresponds probably to the lowest part of the Tertiary." While the malacofauna of Roca (and Salamanca) appears as a precursor of the subsequent Tertiary marine faunas, and differs from that of the Upper Cretaceous, it contains some characteristic old elements, such as *Odontogryphaea rostrigera* (Ihering), *Odontogryphaea rocana* (Ihering) (= *Odontogryphaea rothi* [Böhm, 1903]), and *Ampullina* (*Pseudotylostoma*) *romeroi* (Ihering).

Río Chico Formation.—This continental formation, named and defined by G. G. Simpson (1933), contains the oldest Patagonian mammal fauna. Land molluscs are very rare (*Thaumastus patagonicus* Parodiz), but the consideration of the strata is important for correlations with marine and fresh-water strata of the Paleocene. It overlies, and is in part coeval with, the marine Salamanca, but the beginning of the Río Chico sedimentation was most probably Danian; its recognized base is laterally equivalent to the Sehuen beds (Montian) and developed considerably during the Thanetian.

Jahuel Formation.—Windhausen (1918) designated this formation as "Capas de Jahuel" strata of that locality, near the eastern slope of Sierra Mahuida, south of the Colorado River in Neuquen. The greater development is in Río Negro, near Roca (Windhausen also called it "lower Roca"). It corresponds to the "Senonian lacustre" of Wichmann (1927) and in part to the Jahuelense of Feruglio (1949–1950). By mechanics of deposition it fills the eroded depressions of Roca, and sometimes is parallel to Río Chico. The deposits are fresh-water, and correlative to the southern brackish-water Sehuenan.

The fresh-water fossils of Jahuel are abundant. The species belong to genera that appear for the first time in Patagonia, some still living such as *Diplodon* and *Cyanocyclas* (= *Neocorbicula*), or extinct such as *Paleoanculosa.* They indicate a migration from the Northern Hemisphere that was correlated with that of the early mammals of Patagonia.

Salamanca Formation.—This is the southern facies of the San Jorge Sea, as Roca was of the north. It is frequently referred to in the literature as Salamanque[i]ano or Salamanquéen. Although both Salamanca and Roca began in the Danian, Salamanca lasted longer into the Montian with greater development. The type section is at Salamanca Peak near the coast of the Golfo San Jorge, Santa Cruz. Feruglio (1949–1950) found the strata underlying the Río Chico Formation, with brackish-water intercalations of the Sehuenan in situations that represent deltaic environments, and with thin layers containing fossil plants indicating transition to the continental conditions that prevailed during the Eocene. Although there is a notable hiatus between the fauna of the Paleocene and the beginning of the Patagonian Formation in the Lower Miocene, there are a number of related species.

Stenzel (1945) still considered Roca and Salamanca as a single mid–upper Paleocene unit. Lithologically the facies are distinguishable: Salamanca sediments are clay and sandstone, and those of the Roca are mostly limestone.

Feruglio (1949–1950:307) identified 67 forms of marine invertebrates which are exclusive to the Salamanca. Ihering described 14 species that occur in the Salamanca Formation, among which *Gryphaea pyrotheriorum* and *Odontogryphaea rostrigera* also occur in the Roca Formation.

Sehuen Formation (Piso Sehuense).—The "Piso Sehuense" or Sehuenéen was first reported by Ameghino as coeval with Roca, later placed above it, and finally (Ameghino, 1906) below Roca–Salamanca. The sequence given by Ihering (1907*a*) was (still considering it Cretaceous): "Pyrotherienne" (now Deseado Formation, base of the Oligocene); disconformity; "Sehuenéen" (now Paleocene, Montian–Thanetian).

The sediments were localized along the Sehuen, also called Chalia River, Santa Cruz. It represents the lateral brackish water of the terrestrial Río Chico Formation, equivalent of what Jahuel is to Roca in the north. It corresponds to the phase of regression of the San Jorge Sea, and the brackish-water *Potamides* and *Eriphyla* are found mixed with *Ostrea* and *Struthiolaria.*

Boca–Levu.—These early marine deposits of the Tertiary of Chile are placed between Paleocene and Eocene (Feruglio, 1949–1950:230, 231).

Eocene

Casamayor Formation.—This is the "capas with *Notostylops*" or Notostylopense in the nomenclature of Ihering and Ameghino. Defined by Simpson (1933), it overlies the Río Chico Formation and at its beginning was lateral to the regression of the San Jorge Sea. Its age is Lower Eocene, and together with the Muster Formation above, was called a unit by most geologists, the "Sarmiento group," or "tuffs with mammals." Molluscs are few but characteristic: *Strophocheilus chubutensis* Ihering, *Strophocheilus hauthali* Ihering (= *Megalobulimus hauthali* [Ihering]), *Paleobulimulus eocenicus* Parodiz, and *Chilina stenostylops* Parodiz, all found in the upper section of the complex (Parodiz, 1949*a*).

Oligocene

Magellanian Formation.—This consists of marine deposits in the southern part of Santa Cruz Province, designated by Hatcher (1897, 1900) as the Magellanian beds, Lower Oligocene. Ihering placed it between the Santa Cruz and the Patagonian formations, but actually it is underlain by both. It represents the beginning of the great marine ingression that continued in the north in the Lower Miocene (the Patagonian Formation). According to Feruglio (1949–1950), who conducted extensive research, the age of the Magellanian must be between the middle and the end of the Oligocene. The separation of the Magellanian and Patagonian is geographical rather than stratigraphical, even if the Patagonian is younger as a whole. In Tierra del Fuego, the Strata of Boquerón at Bahía Inútil are, at their base, equivalent with the Magellanian, but also part of them belong to the Patagonian Formation. A number of forms described by Ihering for the Magellanian (*Glycymeris cuevensis, Turritella ambulacrum sylva, Venericardia sylva,* and *Cominella fueguensis*) were found also in the Patagonian Formation and the Navidad beds of Chile. The greater age assigned by Hatcher for the Magellanian (Lower Oligocene) is probably correct.

Queguay Formation.—This is the "Calizas de Queguay" (Queguay Limestone), the oldest Tertiary deposits known from Uruguay, lying in disconformity over the Asencio sandstones (Upper Cretaceous) and below the Fray Bentos clay (Miocene). Chronologically they are coeval with the Magellanian, and correspond to the lacustrine–eolic system with *Strophocheilus, Paleoanculosa,* and "*Planorbis*" *waltheri.* These strata are found mainly on the Queguay River Valley, north of Paysandú.

Miocene

Santa Cruz Formation.—This vast terrestrial sedimentation began to develop north and lateral to the Upper Magellanian, and continued coeval to the Patagonian Formation, finally overlying it. Ihering (1897*a*) referred the marine fauna he described to the Santacruzense, and in 1907 indicated its relative position to be above, but mostly coeval, with the Patagonian that he considered to be at the Eocene–Oligocene boundary (Ihering, 1907*a*). Feruglio (1949–1950) found it filling also the eroded surfaces of the Patagonian, beginning with the Lower Miocene and progressing upwards thereafter. Its extension into the middle Miocene forms a hiatus between the marine faunas of the Patagonian and the Río Negro formations.

In contrast with the molluscan contents of the Paleocene and Eocene continental formations, no land or fresh-water shells are known from the Santa Cruz Formation. The absence is impressive compared with the abundant fluvio–terrestrial malacofauna in Peruvian, Ecuadorian, and Colombian deposits of the same age (Pilsbry and Brown, 1917; Bristow and Parodiz, 1982).

Lower Miocene Marine Deposits.—Three large marine ingressions, the Oligocene Magellanian, the transition from Upper Oligocene to the early Miocene Patagonian, and the Navidad beds of Chile, covered a vast area. Between the northeastern part of the Patagonian Sea on the coast of Chubut, and the Navidad beds in the northwest, there was a triangular, uncovered peninsula of large dimensions. To the south, the sea covered all the territory down to Tierra del Fuego, intercalated with some areas of terrestrial sedimentation (Santa Cruz Formation).

Patagonian Formation.—D'Orbigny (1842) gave the name of "Tertiaire Patagonien" to all the deposits of marine sedimentation from the north at Paraná, to the south in Patagonia. Above it he placed the "Argile Pampienne" (Pliocene–Pleistocene), and below the "Tertiaire Guaranien." The classification of the sedimentary complex used by Ihering (1897*b*) when he described a large number of fossil Mollusca was the same dichotomy that Ameghino had made the same year: Patagonian and Superpatagonian formations. He also correlated the Patagonian with the terrestrial Santa Cruz Formation, placing both in the Eocene. Thus, most of the species were indicated as being from the "Form. Santacruzense" and, as it is explained in the appendix (Ihering, 1897*b*:317–319), distinguished from the Patagonian Formation which he considered to be relatively older, Upper Eocene. In his larger work of 1907(*a*) he named all these deposits in a global sense as "Pan-Patagonian" in which he established some chronological levels: above was the Superpatagonian made coeval with the Santa Cruz Formation, and better represented at localities such as La Cueva and Yegua Quemada; the middle was occupied by the Monte León strata (Leonense) and the San Julian (Juliense); at the base were the strata of Bahía Camarones (Camaronense) or "Patagonéen inférieur." Such divisions were based only on the relative relationship between the paleontological contents and living species.

Many of the taxa named by Ihering were subspecific or infrasubspecific. The clarification of the taxonomy, as well as the recognition of many synonyms, makes his stratigraphic classification untenable, apart from the fact that the Eocene in Patagonia was predominantly a continental sedimentation. Ortmann (1902), studying the fossils from Hatcher's expedition to Patagonia, concluded that the Patagonian Formation was indivisable and entirely Miocene. Finally, the paleontologist George G. Simpson (1932, 1933, 1935, 1940, 1941), and the geologist Egidio

Feruglio (1933, 1935, 1949, 1950) maintained that the Patagonian Formation cannot be older than Lower Miocene. But very probably the sedimentation, at its base, began as early as the Upper Oligocene, and as such these strata were indicated by modern authors (Del Río and Morra, 1984; Erdmann and Morra, 1985; Morra, 1985) as the San Julian Formation (Ihering's Juliense), and sometimes even older in age. Since the older marine Oligocene is represented by the Magellanian Formation, the base of the Patagonian cannot be older than Upper Oligocene. However, the paleontological contents of the Patagonian (*sensu lato*) in their majority, even those included in the lower level, show features that are characteristically Lower Miocene. In the stratigraphic indications of our list of species, the age is given as such for the Patagonian Formation, although in many cases they belong to the Juliense (such as those materials from the Cañada de los Artilleros). Actually the fauna of the earlier Patagonian Formation is transitional between Upper Oligocene and Lower Miocene. The Navidad beds of Chile are synchronic with the Patagonian Formation.

The Patagonian Formation contains the richest of the Tertiary marine malacofaunas of South America. Feruglio (1949–1950) estimated 325 recognizable species: 153 bivalves, 168 gastropods, four scaphopods, and one cephalopod. Ihering described many species from the Patagonian Formation that belong to genera that today represent elements of warmer climate in the northern zone. Among these are *Abra, Lucina, Sanguinolaria, Aporrhais, Tibia, Laevicardium, Macoma,* and *Glycymeris.* The absence of these and many other genera in the malacofauna of Recent Patagonian and Magellanian regions reflects displacement by plate tectonics rather than "local" changes in temperature.

Collon–Cura Beds (Colloncurense).—These are terrestrial and in part freshwater sediments in the western part of the Chubut Province. Kraglievich (1930) named it "Formación Friaseana" (from Lake Frias) and considered the strata as Oligocene. Simpson (1940) and Feruglio (1949–1950) placed the Collon–Cura in the Middle or Upper Miocene, above the Santa Cruz and Patagonian formations. Molluscs are rare: *Diplodon rothi* Ihering.

Fray Bentos Formation (Fray Bentos Clay).—This consists of strata in Uruguay, on top of the Queguay limestone (Oligocene) and below (hiatus) the Camacho Formation (Pliocene).

Paraná Formation (Paranense of Authors; Also Known as Mesopotamian).—This consists of rich marine sediments in northeastern Argentina. The type section is located in the vicinity of Paraná city, Entre Rios Province, and also found in deep perforations in Buenos Aires and Uruguay. It contains many molluscan genera that denote tropical or semitropical conditions. Authors differed about its age which was indicated as old as Oligocene and as young as Pliocene, but the actual position is in the Upper Miocene. It contains a larger number of extinct species than the next formation, the Araucanean, which is Pliocene.

In Uruguay, the Paraná Formation is particularly represented in the Department of Colonia, where it is known as the Camacho Formation (sandstone), correlated by Caorsi and Goñi (1958:59) to the "Transgresión marina entreriana" but given the age of Pliocene. Also, fossils found at Punta Gorda on the Uruguay River are the same as those from perforations at Chuy on the Atlantic coast which are Miocene in age.

Ihering used the name "Formación Entreriana" as did several other authors. However, the name "Entreriense" or "Entreriano of Patagonia" was also applied to its chronological equivalent in Río Negro, the "Rionegrense" or Río Negro

Formation. More difficult to define is the Araucano–Entreriano complex under which Kraglievich (1930), Simpson (1940), and others united the "Paranense," the "Rionegrense," and the Araucanean formations.

Río Negro Formation (Rionegrense).—The "Rionegrense" was equal to what some authors called the "Entreriense" of northern Patagonia. The type section is Puerto Piramides in Golfo Nuevo, Chubut. There are similarities between the faunas of the Río Negro and Paraná formations. It is relatively younger than Paraná, and corresponds to a later, southern ingressive phase of the Paraná Sea, which marks the boundary between the Miocene and Pliocene, although distinguishable from the Pliocene Araucanean. It has in common with the Paraná Formation species of *Dosinia* and *Lucina,* but the fauna is generally poorer with some characteristic species such as *Amusium cossmanni* Ihering. Of the 52 species known from the Río Negro beds, 23 are exclusive and 26 were known in the Lower Miocene, showing faunistic continuity with chronological changes along the mid-Tertiary Patagonian strand.

Pliocene

Fairweather Beds (Fairweatheriense or Buentiempense).—This stratigraphic unit was reported by Hatcher (1897) for the Miocene of southern Santa Cruz. According to Feruglio (1949–1950) it belongs to the Upper Pliocene. It appears coeval with northern deposits at Chapadmalal as an upper section of the Araucanean complex.

Araucanean Formation.—The "Araucano" is a complex of sediments first observed by Charles Darwin in December 1833 and January 1834. Döring (1881–1882) named it "Tehuelche" of which the larger part belonged to the Pleistocene. It consists of continental sediments and marine terraces of extensive development in the provinces of Chubut and Santa Cruz, particularly at Sierra Laziar (see Feruglio, 1933).

Sierra Laziar Strata (Laziarense).—Most of the fossil Mollusca named by Ihering from the "Araucano" are from Sierra Laziar. Although it contains a good number of extinct species, it shows the transition from the ancient to the Recent fauna; some species or subspecies named by Ihering from this strata are synonyms of Recent ones: *Pupilia aperta tehuelcha* Ihering = *Fissurellidea megatrema* d'Orbigny; *Neomphalius princeps* Ihering = *Tegula patagonica* (d'Orbigny); *Trophon necocheanus* Ihering = *Trophon lamellosus* (Gmelin); *Trophon inornatus gradatus* Ihering = *Trophon varians* (d'Orbigny); *Trophon varians montenus* Ihering = *Trophon varians* (d'Orbigny); *Chione vindex* Ihering = *Protothaca antiqua* (King); *Marcia scutata tehuelcha* Ihering = *Samarangia exalbida* (Chemnitz).

Quaternary

Pleistocene

Belgrano Formation (Belgranense).—This is the first marine ingression of the Pleistocene. It is also known as the "Pampeano marino" of other authors. The sedimentation in the north was coeval with the terrestrial Buenos Aires Formation; the intercalations reveal the oscillation of the Atlantic strand. Geographically it is divided into two sections: Belgrano North, with greater development in Buenos Aires Province with almost all of the species still living; Belgrano South, in southern Santa Cruz, which contains the same species found in the Belgrano

North. The southern section was also called "Deseadense," but that term was used by Kraglievich (1930) and other authors for a different stratigraphic unit of terrestrial deposits.

Buenos Aires Formation (Bonaerense).—This formation consists of very extensive eolic sedimentation, synchronic and alternating with the Belgrano Formation on the coast. It is very poor in land shells: *Peronaeus* (*Lissoacme*) *ameghinoi* (Ihering), *Strophocheilus charruanus* (Frenguelli). In Uruguay, the same coeval deposits are known as "Loess of Arazati."

Querandí Formation (Querandino).—This is the latest of the marine ingressions at the end of the Pleistocene. It was of very short duration but its deposits are found farther inland than Belgrano, up the Paraná River, and of great development in Uruguay where the Belgrano beds are absent. The Querandí Formation coincided with the tectonic movement that produced the great fault of the Paraná, and subsequent marine regression formed the La Plata estuary. It contains species that now live north of that estuary, such as *Diplodon charruanus lujanensis* Ihering (= *Diplodon delodontus* [Lamarck]) in some fresh-water intercalations. In Uruguay it is also known, in part, as the "Clays of Vizcaino."

TERTIARY CLIMATE AND PALEOGEOGRAPHIC CONSIDERATIONS

Ihering's important contribution to the geopaleontological history of South America was the introduction of the concept of different land masses that he named Archhelenis, Archiplata, and Archinotis (Ihering, 1907*b*). These ideas were elaborated two decades earlier than Wegener's 1916 presentation of his continental drift theory (Wegener, 1924).

Of Archhelenis, which in Ihering's paleogeography united Africa with South America, he said (Ihering, 1907*a*:483), "Le continent qui unissait le Brésil à l'Afrique, commencait à disparaître pendant la formation crétacée." That indicates that his idea of Archhelenis was not just of a bridge but of a continent. That same year (Ihering, 1907*b*) he epitomized and developed his ideas in the book "Archhelenis und Archinotis"; in it he illustrated Brasilia and Archiplata united to Africa by Archhelenis, even projecting it into the Indian Ocean in a mass of land of tremendous proportions.

Actually Brasilia was the same as Archhelenis, or part of it, and its tectonic plate had been separated from Africa long before the Cretaceous. It was a large mass of land between the northern sea, Tethys, and the southern, Nereis. Ancient faunistic elements of Gondwanian origin developed into new groups by isolation in Archhelenis. Families which later became the Mycetopodidae and the Strophocheilidae in South America are good examples.

West of Archhelenis was Archiplata, separated by a long, narrow sea. Up to the early Tertiary Archiplata was connected to Archinotis (Antarctica), and the land, with Patagonia at the center, extended as far north as Peru. During the Paleocene there suddenly appeared a large fauna of mammals, fresh-water molluscs, and elements of other zoological groups that were closely related to those of the Cretaceous of North America. The migration must have taken place through some connection between northern and southern regions of the Western Hemisphere. The connection was interrupted during the entire Tertiary and the southern faunas developed in isolation. There is also evidence of identical, or very closely related, species discovered in mid-Tertiary sediments of Antarctica and Patagonia. These are littoral molluscs that indicate a common continental shelf existing between the two regions and a similarity in climatic conditions. Because of the subtropical, sometimes tropical, character of the Tertiary marine malacofauna, Ihering assumed that important climate changes had taken place and that the composition of the faunas was affected sometimes by barriers, sometimes by migrations.

A. E. Ortmann supported the Archhelenis–Archiplata proposition, although he strongly disagreed with Ihering about the age of the Patagonian deposits. After Ortmann's (1902) and Ihering's (1907*a,* 1907*b*) paleontological work, when geologists began to combine their ideas with new concepts of plate tectonics, still they interpreted, as Wegener did in his continental drift theory, the displacement of the South American continent westward as if it had been a solid and unified mass, instead of being formed of different plates originally separated, that included also Archiguiana.

The mechanics of plate tectonics displaced Archiplata in a clockwise direction toward a west–northwest position relative to that which the continent occupies today. It remained connected with Antarctica which was also in lower latitudes. In such position, the east coast of Archiplata was facing more to the south than at present. The gyration must have advanced the tip of the continent to latitude 30–35°S. After the middle Tertiary, the movement of the "pendulum" turned counterclockwise until reaching the Recent position with its tip at latitude 56°S. These oscillating movements explain the climate changes that affected the marine as well as the fresh-water faunas, and their distribution.

The author who first proposed the rotation theory was H. Modell (1950). After many years of studying the taxonomy and geographic distribution of the superfamilies Unionacea and Mutelacea in relation to climate, Modell arrived at a logical conclusion. Modell's schematic illustration (1950:143) seems somewhat exaggerated, but it is supported by many biogeographic facts related to the changes in climate that occurred between the Tertiary and Recent in South America.

The unification of Archhelenis–Archiplata began as early as the first phase of the Andean orogeny on the Andean syncline, but a communication between the Pacific and the new Atlantic Ocean still existed in the Miocene, and probably until the Pliocene. The same gyration that modified the position of the South American continent separated Antarctica, its plate drifting south.

ABBREVIATIONS

ACM	Annals of Carnegie Museum, Pittsburgh.
AJS	American Journal of Science.
AMNBA	Anales del Museo Nacional de Buenos Aires.
ARMGB	Anali del Reale Museu Geologico di Bologna.
ASCA	Anales de la Sociedad Científica Argentina.
BGSA	Bulletin of the Geological Society of America.
BSGF	Bulletin de la Société Geologique de France.
BIGU	Boletín del Instituto Geologico del Uruguay, Montevideo.
CMNH	Carnegie Museum of Natural History, Pittsburgh.
CZMHN	Comunicaciones Zoologicas del Museo de Historia Natural de Montevideo.
ICZN	International Commission on Zoological Nomenclature.
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires.

NDMG	Nachrichtsblätter Deutsche Malakozoologische Gesellschaft, Frankfurt.
NJMGP	Neues Jahrbuch für Mineralogie, Geologie, und Paläontologie, Stuttgart.
NPRMP	Notas Preliminares da Revista do Museu Paulista, São Paulo.
PAPS	Proceedings of the American Philosophical Society.
RMLP	Revista del Museo de La Plata, Argentina.
RMP	Revista do Museu Paulista, São Paulo.

List of New Combinations

abavus Ihering, 1907. *Neomphalius* TROCHIDAE
= *Tegula abava* (Ihering), **new combination**

ameghinoi Ihering, 1907. *Cucullaria.* ARCIDAE
= *Barbatia ameghinoi* (Ihering), **new combination**

ameghinoi Ihering, 1896. *Voluta* VOLUTIDAE
= *Adelomelon ameghinoi* (Ihering), **new combination**

americanus Ihering, 1907. *Neomphalius* TROCHIDAE
= *Tegula americana* (Ihering), **new combination**

burmeisteri Ihering, 1907. *Cymbiola* VOLUTIDAE
= *Adelomelon burmeisteri* (Ihering), **new combination**

camaronesia Ihering, 1907. *Arca* ARCIDAE
= *Anadara camaronesia* (Ihering), **new combination**

cannada Ihering, 1907. *Cymbiola becki* "var." VOLUTIDAE
= *Adelomelon cannada* (Ihering), **new combination, new status**

chicoana Ihering, 1907. *Hadriania jorgensis* "var." MURICIDAE
= *Trophon chicoanus* (Ihering), **new combination, new status**

chubutiana Ihering, 1907. *Scalaria* EPITONIIDAE
= *Epitonium chubutianum* (Ihering), **new combination**

contorta Borchert, 1901. *Modiola* HYRIIDAE
= *Diplodon contortus* (Borchert), **new combination**

dalli Ihering, 1907. *Lyria* VOLUTIDAE
= *Enaeta dalli* (Ihering), **new combination**

dautzembergi Ihering, 1897. *Triton* (*Argobuccinum*)
RANELLIDAE: RANELLINAE
= *Fusitriton dautzembergi* (Ihering), **new combination**

elegans Ortmann, 1900. *Urosalpinx* MURICIDAE: OCENEBRINAE
= *Ocenebra elegans* (Ortmann), **new combination**

jorgensis Ihering, 1907. *Hadriania* MURICIDAE: OCENEBRINAE
= *Crassilabrum jorgensis* (Ihering), **new combination**

juliana Ihering, 1907. *Arca* ARCIDAE
= *Anadara juliana* (Ihering), **new combination**

major Ihering, 1899. *Cancellaria gracilis* "var." CANCELLARIIDAE
= *Naronia major* (Ihering), **new combination, new status**

monoceros Ihering, 1907. *Trophon* MURICIDAE
= *Thais monoceros* (Ihering), **new combination**

multicoronatus Ihering, 1907. *Vermetus* VERMETIDAE
= *Dendropoma multicoronatus* (Ihering), **new combination**

patagonica Ihering, 1897. *Bulla* ?RETUSIDAE
= *Retusa patagonica* (Ihering), **new combination**

paucispina Ihering, 1897. *Pholas* PHOLADIDAE
= *Netastoma paucispina* (Ihering), **new combination**

pyrotheriana Ihering, 1907. *Polynices* NATICIDAE
= *Lunatia pyrotheriana* (Ihering), **new combination**

quemadensis Cossmann, 1899. *Cirsotrema* EPITONIIDAE
= *Opalia quemadensis* (Cossmann), **new combination**

rada Ihering, 1907. *Lotorium* (*Lampusia*) RANELLIDAE: CYMATIINAE
= *Semitriton rada* (Ihering), **new combination**

rocana Ihering, 1907. *Phacoides* LUCINIDAE
= *Lucina rocana* (Ihering), **new combination**

rocanum Ihering, 1907. *Cardium* (*Hemicardium*) CARDIIDAE
= *Trachycardium rocanum* (Ihering), **new combination**

salobris Ihering, 1907. *Cyrena* CORBICULIDAE
= *Cyanocyclas salobris* (Ihering), **new combination**

santacruzense Ihering, 1914. *Cardium* CARDIIDAE
= *Laevicardium santacruzense* (Ihering), **new combination**

santacruzensis Ihering, 1907. *Chenopus* APORRHAIDAE
= *Drepanocheilus santacruzensis* (Ihering), **new combination**

schucherti Ihering, 1914. *Gibbula* ARCHITECTONICIDAE
= *Architectonica schucherti* (Ihering), **new combination**

stromeri Ihering, 1914. *Fusus* RANELLIDAE: RANELLINAE
= *Fusitriton stromeri* (Ihering), **new combination**

tridentata Ihering, 1897. *Cuculearia* [sic] ARCIDAE
= *Barbatia tridentata* (Ihering), **new combination**

usurpator Ihering, 1907. *Lotorium* (*Lampusia*) RANELLIDAE: CYMATIINAE
= *Cymatium usurpator* (Ihering), **new combination.**

LIST OF TAXA

abavus, 1907. *Neomphalius* TROCHIDAE
1907*a*. AMNBA, 14:134, pl. 4, fig. 9a–b.
1914. NPRMP, 1(3):76 (Patagonico Inferior).

= *Tegula abava* (Ihering), **new combination.**

Type Locality.—Southeast of Punta Nova, Golfo San Jorge, Santa Cruz.

Syntypes.—#591, five specimens, coll. Ameghino, 1900.

Stratigraphy.—Lower section of the Patagonian Formation (Lower Miocene).

Remarks.—The shell is higher than in the living *T. patagonica* (d'Orbigny) and therefore more similar to *Calliostoma.*

aequistriata, 1907. *Gibbula cuevensis* "var." ARCHITECTONICIDAE
1907*a*. AMNBA, 14:132. Not figured; diagnosis only.
1914. NPRMP, 1(3):73 (Patagonico Superior).

= *Valdesia dalli* (Ihering).
Type Locality.—Cabo Tres Puntas, Golfo San Jorge, Santa Cruz.
Syntypes.—#573, two specimens, coll. Ameghino, 1900.
Other Lots.—#574, southeast of Punta Nova, one specimen, coll. Ameghino, 1900; #575, Punta Casamayor, two specimens, coll. Ameghino, 1900.
Stratigraphy.—Patagonian Formation (Lower Miocene).

ameghinoi, 1908. *Bulimulus* ORTHALICIDAE: BULIMULINAE

1908. AMNBA, 17:429 (not figured).
1944. Parodiz, CZMHN, 1(17):1–3, pl. 1, fig. 1–6.

= *Peronaeus* (*Lissoacme*) *ameghinoi* (Ihering).
Type Locality.—Chapadmalal, Buenos Aires Province.
Type.—Not in the collection.
Stratigraphy.—Buenos Aires Formation (Pleistocene).
Remarks.—*Bulimulus sporadicus pampa* Ihering is also a synonym.

ameghinoi, 1897. *Cancellaria* CANCELLARIIDAE

1897*b*. RMP, 2:310, pl. 3, fig. 2, and pl. 4, fig. 15.
1907*a*. AMNBA, 14:215. *Admete ameghinoi.*
1914. NPRMP, 1(3):112.

= *Admete ameghinoi* (Ihering).
Type Locality.—Yegua Quemada, Santa Cruz.
Syntypes.—#900, four specimens, coll. Ameghino, 1893.
Stratigraphy.—Patagonia Formation (Lower Miocene).
Remarks.—This species resembles the living *Admete magellanica* Strebel.

ameghinoi, 1907. *Cardium* CARDIIDAE

1907*a*. AMNBA, 14:292, pl. 11, fig. 72a–b.
1914. NPRMP, 1(3):47 (Patagonico Inferior).

Type Locality.—Santa Cruz.
Holotype.—#391, one valve, coll. J. Bicego, 1897 (by monotypy).
Other Lot.—#392, Punta Nova, one specimen, coll. Ameghino, 1900.
Stratigraphy.—Patagonian Formation (Lower Miocene).

ameghinoi, 1907. *Cucullaria* ARCIDAE

1907*a*. AMNBA, 14:233, text fig. 8.
1914. NPRMP, 1(3):16 (Patagonico Inferior).

= *Barbatia* (*Cucullaria*) *ameghinoi* (Ihering), **new combination.**
Type Locality.—Pan de Azucar at San Julian, Santa Cruz.
Holotype.—#99, one valve, coll. Ameghino, 1900 (by monotypy).
Stratigraphy.—Patagonian Formation (Lower Miocene).

ameghinoi, 1907. *Lutraria* MESODESMATIDAE

1907*a*. AMNBA, 14:26, pl. 3, fig. 17a–b.

Type Locality.—Roca, Río Negro.
Type.—Not in the collection.
Stratigraphy.—Roca Formation (Paleocene).

Remarks.—There is an unnumbered specimen in the collection, but not listed in the 1914 catalogue. The illustration is unlike *Lutraria* and resembles a mesodesmatid.

ameghinoi, 1897. *Modiola* MYTILIDAE

1897*b*. RMP, 2:233, pl. 6, fig. 43.
1902. Ortmann, p. 21, pl. 25, fig. 2. *Modiolus*.
1907*a*. AMNBA, 14:275. *Modiolus ameghinoi*.
1914. NPRMP, 1(3):38 (Patagonico Inferior and Superpatagonico).

= *Modiolus ameghinoi* (Ihering).

Syntypes.—#316, two valves, coll. Ameghino, 1893.

Other Lots.—#317, southeast of Punta Nova; #318, Santa Cruz, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—This species was reported by Wilckens (1911) from the Antarctic at Seymour Island. This species resembles *Mytilus pseudochorus* Doello-Jurado, 1922.

ameghinoi, 1902. *Neoinoceramus* MYTILIDAE: MYTILINAE

1902*b*. PAPS, 41(6):134, pl. 19, fig. 3–4.
1907*a*. AMNBA, 14:243, fig. 10.
1914. NPRMP, 1(3):20 (Patagonico Inferior).

Type Locality.—Southeast of Punta Nueva.

Lectotype.—#136, an intact minor valve, corresponding to the figures in the original description, here designated.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—Lot #136 in the Ihering Collection consists of two specimens from Golfo San Jorge, southeast of Punta Nueva. Only one specimen is listed in the catalogue (Ihering, 1914:20) and is a fragment of the paralectotype. It is a single complete large valve, 20 cm long, coll. Ameghino, 1900. Although listed in the catalogue it does not correspond to fig. 3–4 in the original description (Ihering, 1902*b*). The other specimen in Lot #136 is the lectotype designated above, and is not listed in the 1914 catalogue.

ameghinoi, 1907. *Myochlamys centralis* "var." PECTINIDAE

1897*b*. RMP, 2:229, pl. 8, fig. 49. *Pecten centralis*.
1902. Ortmann, 2:114, pl. 21–22, fig. 1a–c (*Pecten proximus*); 2:116, pl. 23, fig. 1a–b (*Pecten centralis*).
1907*a*. AMNBA, 14:253 (Patagonico). *Myochlamys centralis*.

= *Chlamys centralis* Sowerby, 1846.

Type Locality.—Santa Cruz.

Holotype.—#241, specimen received from Ortmann as *P. proximus* (by monotypy).

Other Lot.—#240, Yegua Quemada, six valves, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

ameghinoi, 1902. *Ostrea* OSTREIDAE

1902*a*. AMNBA, 4:114, fig. 4–7.
1903. AMNBA, 9:213.

1907*a*. AMNBA, 14:44 (Salamanquéen).
1914. NPRMP, 1(3):23 (Formación Guaranitica with *Gryphaea pyrotheriorum*).

Type Locality.—West of Río Chico, Chubut.
Syntypes.—#165, one complete specimen and 16 valves.
Other Lot.—#166, Puerto Malaspina, three valves; no indication of collector.
Stratigraphy.—Salamanca Formation (Paleocene).
Remarks.—See *Ostrea rocana* Ihering.

ameghinoi, 1897. *Struthiolaria* STRUTHIOLARIIDAE

1897*b*. RMP, 2:289, text fig. 14.
1900. Ortmann, p. 380. *Struthiolaria chilensis* (not *S. chilensis* Philippi, 1887).
1904. Cossmann, p. 104, pl. 8, fig. 3–4. *Struthiolaria ornata* (not *S. ornata* Sowerby, 1846).
1907*a*. AMNBA, 14:172.
1914. NPRMP, 1(3):95 (Superpatagonico).

Type Locality.—Originally "La Cueva and Santa Cruz."
Syntypes.—#763, Yegua Quemada, designated by Ihering (1914) as "Type lot," 12 specimens, coll. Ameghino.
Other Lots.—#764, Cañada de los Artilleros, coll. Ameghino, 1900; #765, Santa Cruz; #766, Santa Cruz.
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—Two lots were received from Ortmann: #765 as *S. chilensis* Philippi, and #766 as *S. densestriata* Ihering.

ameghinoi, 1903. *Turritella* TURRITELLIDAE

1903. AMNBA, 9:213, pl. 2, fig. 14.
1907*a*. AMNBA, 14:48.
1914. NPRMP, 1(3):89 (Salamanqueano).

Type Locality.—Río Chico, Chubut.
Holotype.—#717, coll. Ameghino, 1900 (by monotypy).
Stratigraphy.—Salamanca Formation (Paleocene).

ameghinoi, 1896. *Voluta* VOLUTIDAE

1896. NDMG, 7:97.
1897*b*. RMP, 2:302, text fig. 17.
1899*b*. Cossmann, p. 125, fig. 18. *Cymbiola.*
1902. Ortmann, p. 233.
1907*a*. AMNBA, 14:209. *Cymbiola.*
1914. NPRMP, 1(3):109 (Superpatagonico).

= *Adelomelon* (*Pachycymbiola*) *ameghinoi* (Ihering), **new combination.**
Type Locality.—La Cueva, Santa Cruz.
Holotype.—#883a, coll. Ameghino (by monotypy).
Other Lots.—#884, La Cueva, a very large specimen, coll. Ameghino; #885, Rada Tilly, San Jorge, one specimen, coll. Ameghino; #886, Golfo San Jorge, one specimen, coll. Ameghino.
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—Specimen #295 differs from typical *ameghinoi,* being more globose and without tuberculae. This species is ancestral to *A.* (*P.*) *feruglioi* (Doello-Jurado, 1931) from the Pliocene and the living *A.* (*P.*) *brasiliana* (Solander, 1786).

Ameghinomya, 1907. VENERIDAE

1907*a*. AMNBA, 1907:71, 306. New subgenus.

= *Protothaca* Dall, 1902.

Type Species.—*Chione argentina* (Ihering, 1897*b*).

Stratigraphy.—Patagonian Formation (Lower Miocene) and Paraná Formation (Upper Miocene).

Remarks.—Close to *Chione* and according to Ihering represented only in the Patagonian, but poorly defined. Although Ihering mentioned *Protothaca* in relation with other forms (see *Chione cossmanni*), he did not compare *Ameghinomya* with *Protothaca.* See *Venus volckmanni argentina.*

ameghinorum, 1907. *Venericardia* ?ARCIDAE

1907*a*. AMNBA, 14:23, pl. 3, fig. 13a–b.
1914. NPRMP, 1(3):42 (Roca).

= ?*Noetia ameghinorum* (Ihering).

Type Locality.—Roca, Río Negro.

Holotype.—#340, an artificial cast received from Florentino Ameghino in 1904 which corresponds to the figured specimen (by monotypy).

Stratigraphy.—Roca Formation (Paleocene).

Remarks.—This species has high umbos anteriorly produced and probably belongs to *Noetia*; unlikely a *Venericardia.*

americanus, 1907. *Neomphalius* TROCHIDAE

1907*a*. AMNBA, 14:134, pl. 4, fig. 7a–b.
1914. NPRMP, 1(3):76 (Superpatagonico).

= *Tegula* (*Promartynia*) *americana* (Ihering), **new combination.**

Type Locality.—Cañada de los Artilleros, Santa Cruz.

Holotype.—#592, coll. Ameghino, 1900 (by monotypy).

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—The shell is high, *Calliostoma*-like but with an umbilicum "circonscrit en dehors par una crete spirale," as in the subgenus *Promartynia* Dall, 1909.

archipatagonica, 1907. *Urosalpinx* MURICIDAE

1897*b*. RMP, 2:297. *Trophon leucostomoides* (not *Triton leucostomoides* Sowerby, 1846).
1907*a*. AMNBA, 14:189, pl. 6, fig. 35.
1914. NPRMP, 1(3):98 (Superpatagonico).

= *Ocenebra* (*Ocinebrina*) *elegans* (Ortmann), **new combination.**

Type Locality.—La Cueva, Santa Cruz.

Holotype.—#795, coll. Ameghino, 1900 (by monotypy).

Other Lot.—#796, Yegua Quemada, one specimen, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—This is a more elongate species than the Recent *Urosalpinx rushi* (Pilsbry).

archiplata "Ihering," 1931. *Bulimus* STROPHOCHEILIDAE

1931. Walther, p. 31, given as "*B. archiplata* Ihering" *in litteris. Nomen nudum.*

= *Strophocheilus charruanus* (Frenguelli, 1930).

Remarks.—See Klappenbach and Olazarri (1966:234) and Parodiz (1969:172, pl. 18, fig. 2).

arenasia, 1907. *Bulla* BULLIDAE

1907*a*. AMNBA, 14:339. New name for *Bulla remondi* in Ortmann (1899:431) and Ortmann (1902: 245, pl. 37, fig. 7a–b), not *Bulla remondi* Philippi, 1887.

Type Locality.—The specimen figured by Ortmann (1902) is from Punta Arenas, Chile.
Stratigraphy.—Magellanian Formation (Lower Oligocene).

arenophila, 1907. *Macrocallista* VENERIDAE

1907*a*. AMNBA, 14:349. New name for *Meretrix iheringi* in Ortmann (1902:142, pl. 28, fig. 5a–b), not *Meretrix iheringi* Cossmann, 1898.

= *?Amiantis arenophila* (Ihering).
Type Locality.—In Ortmann (1902): Punta Arenas, Chile.
Stratigraphy.—Magellanian Formation (Lower Oligocene).

argentina, 1897. *Turritella* TURRITELLIDAE

1897*b*. RMP, 2:286. Not figured (Form. Patagonica).
1907*a*. AMNBA, 14:162. *Turritella ambulacrum argentina.*
1914. NPRMP, 1(3):88. *Turritella ambulacrum argentina.*

= *Turritella ambulacrum* Sowerby, 1846. The different "varieties" of *T. ambulacrum*—*T. a. steinmanni, T. a. pyramidesia,* and *T. a. argentina*—are all the same species.
Type Locality.—Río Santa Cruz, Santa Cruz.
Syntypes.—Not in the collection.
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—The type lot with 17 specimens as reported by Ihering (1914) is not in the collection. The other lot, #709, is a conglomerate.

argentina, 1897. *Venus volckmanni* "var." VENERIDAE

1897*b*. RMP, 2:252, pl. 7, fig. 45.
1904. RMLP, 11:231. *Venus argentina.*
1907*a*. AMNBA, 14:291, 385. *Chione (Ameghinomya) argentina.*
1914. NPRMP, 1(3):55 (Superpatagonico).

= *Protothaca argentina* (Ihering).
Type Locality.—Santa Cruz.
Syntypes.—Not in the collection as listed in Ihering (1914).
Other Lots.—#460, Rada Tilly, two specimens, coll. C. Ameghino, 1900; #461, Trelew, Chubut, a fragment, coll. S. Roth (from "formação entreriana"); #462, Sierra de los Baguales, three casts, coll. Hauthal, 1897; no number, Santa Cruz, one specimen, coll. J. Bicego, 1897.
Stratigraphy.—Patagonian Formation (Lower Miocene) and Paraná Formation (Upper Miocene).
Remarks.—*Venus paranensis* Borchert, 1901:38, pl. 3, fig. 16–18, from Paraná, Entre Rios, is a synonym. E. Feruglio also found it in the Patagonian of Cerro Otto.

argentinus, 1907. *Actaeon* ACTAEONIDAE

1907*a*. AMNBA, 14:117, pl. 4, fig. 2.
1914. NPRMP, 1(3):68 (Superpatagonico).

Type Locality.—Cañada de Los Artilleros, Santa Cruz.
Syntypes.—#545, two specimens, coll. Ameghino, 1900.
Stratigraphy.—Patagonian Formation (Lower Miocene).

Austrocominella, 1907. BUCCINIDAE: PHOTINAE

1907*a*. AMNBA, 14:190, 344. New subgenus.

Type Species.—*Cominella fueguensis* Ihering.
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—Subgenus, "intermediaire entre *Cominella* s.s. et *Ptychosalpinx.*" *Cominella sensu stricto* and other subgenera are from New Zealand; *Ptychosalpinx* is known only from the Miocene of North America.

bagualesia, 1907. *Panopaea* [sic] HIATELLIDAE

1907*a*. AMNBA, 14:325, pl. 13, fig. 86a–b.
1914. NPRMP, 1(3):63.

= *Panopea bagualesia* Ihering.
Type Locality.—Sierra de los Baguales, Santa Cruz [given by Ihering (1914) as Chubut in error].
Holotype.—#511, one cast with part of the shell, coll. Hauthal, 1897 (by monotypy).
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—Feruglio (1949–1950) reported the species from Río Turbio.

Barnea sp. PHOLADIDAE

1914. NPRMP, 1(3):65.

= ?*Cyrtopleura lanceolata* (d'Orbigny, 1846).
Specimens.—#522, one cast, from la Paz, Entre Rios, coll. S. Roth.
Stratigraphy.—Paraná Formation (Upper Miocene).
Remarks.—Similar to *Barnea ornata* Borchert, 1901:45, pl. 4, fig. 3.

bellicosum, 1907. *Calliostoma* TROCHIDAE

1907*a*. AMNBA, 14:439, pl. 17, fig. 117.
1914. NPRMP, 1(3):77 ("Post-Pampeano").

= *Calliostoma militaris* Ihering.
Type Locality.—Puerto Militar (now Puerto Belgrano), Prov. Buenos Aires.
Syntypes.—#597, three specimens, coll. Ameghino, 1905.
Stratigraphy.—Belgrano Formation (Pleistocene). Recent: Rio de Janeiro to Prov. de Buenos Aires.
Remarks.—Clench and Turner (1960:23) listed this species as a synonym of *Calliostoma jucundum* (Gould), but it is actually *C. militaris*; the descriptions of the two species are almost identical.

bicegoi, 1899. *Lotorium* RANELLIDAE: CYMATIINAE

1899*a*. NJMGP, 2:29, pl. 1, fig. 8.
1907*a*. AMNBA, 14:177 (Patagonico).

1914. NPRMP, 1(3):97. *Lotorium* (*Sassia*) *bicegoi*.

= *Cymatium bicegoi* (Ihering).
Type Locality.—Santa Cruz.
Syntypes.—#790, two specimens, coll. J. Bicego.
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—Of this and other species of "*Lotorium*," Ihering (1907*a*:174) said that he did not know the correct stratigraphic position; however, he mentioned Upper Eocene (unlikely) and Superpatagonian.

boehmi, 1907. *Venericardia iheringi* "var." CARDITIDAE

1907*a*. AMNBA, 14:23. Not figured.

= *Venericardia iheringi* Böhm, 1903.
Type Locality.—Roca, Río Negro.
Type.—Not in the collection under this name.
Stratigraphy.—Roca Formation (Paleocene).
Remarks.—The two specimens "plus ventru, moins hault" were included in 1914 in the lot of *Venericardia iheringi* (#355); Ihering added: "Peut-etre c'est une variation individuelle."

borcherti, 1907. *Tritonidea* BUCCINIDAE: PISANIINAE

1907*a*. AMNBA, 14:369. New name for *Turbinella subcraticulata* d'Orbigny *in* Borchert (1901:50, pl. 5, fig. 1–2), not *T. subcraticulata* d'Orbigny.

Type Locality.—Paraná, Entre Rios (Borchert).
Stratigraphy.—Paraná Formation (Upper Miocene).
Remarks.—The genus *Tritonidea* Swainson, 1840, for this species was suggested to Ihering by W. H. Dall.

brüggeni [sic], 1921. *Aturia* (*Sphenaturia*) NAUTILIDAE

1921. Physis, Buenos Aires, 5:76. Not figured.

= *Aturia* (*Sphenaturia*) *brueggeni* Ihering.
Type Locality.—Punta Boquerón, Bahía Inútil, Tierra del Fuego.
Holotype.—Status unknown.
Stratigraphy.—"Estratos de Boquerón" (below Patagonian Formation).
Remarks.—Referring to the holotypes of this species and *A.* (*S.*) *felschi*, Ihering (1921) stated, "Los ejemplares tipicos quedan depositados en este Museo [Museo Argentino de Ciencias Naturales, Buenos Aires]." This species is the type of the subgenus *Sphenaturia* Ihering. Feruglio (1949–1950) places it below the Patagonian.

bullia, 1907. *Melania* PLEUROCERIDAE

1907*a*. AMNBA, 14:464, pl. 18, fig. 127.
1914. NPRMP, 1(3):93 (Salamanqueano).

= *Paleoanculosa bullia* (Ihering), see Parodiz, 1969:125, pl. 12, fig. 7–9; pl. 14, fig. 2; pl. 10, fig. 2–4, 6.
Type Locality.—Río Chico, Chubut.
Holotype.—#753, coll. Ameghino (by monotypy); deposited in CMNH.
Stratigraphy.—Colhue Huapi Formation (Colhuehuapian; Thanetian–Montian, ? Paleocene).

Remarks.—*Melania pehuenchensis* Doello-Jurado (1927:415; see Wichmann, 1927:fig. 77) and *M. ameghiniana* Doello-Jurado (1927:413; see Wichmann, pl. 10, fig. 61–71, and pl. 11, fig. 74) are synonyms of *P. bullia* (Ihering). The holotype was received by Parodiz (1969:pl. 14, fig. 2) in exchange from Dr. Max Birabén, at that time Director of the Museo Argentino de Ciencias Naturales.

burckhardti, 1903. *Cardita* CARDITIDAE

1903. AMNBA, 9:205. New name for *Cardita morganiana* in Burckhardt (1902:216), not *Cardita morganiana* Rathbun, 1875.

Type Locality.—Malargue, near Roca, Río Negro.
Type.—No material described by Burckhardt is in the collection.
Stratigraphy.—Roca Formation (Paleocene).
Remarks.—Specimens from Roca were misidentified by Burckhardt (1902) as *Cardita morganiana* Rathbun, but that species is from the Maria Farinha Formation in Brazil.

burckhardti, 1907. *Dosinia* VENERIDAE

1907*a*. AMNBA, 14:26. New name for *Dosinia brasiliensis* Burckhardt, 1902:216, pl. 4, fig. 8–12, not *D. brasiliensis* White, 1887.
1914. NPRMP, 1(3):50 (Crétacée Supérieur).

Type Locality.—Roca, Río Negro.
Type.—No material described by Burckhardt is in the collection.
Stratigraphy.—Roca Formation (Paleocene).

burckhardti, 1903. *Turritella* TURRITELLIDAE

1903. AMNBA, 9:208, pl. 1, fig. 9.
1907*a*. AMNBA, 14:38.
1914. NPRMP, 1(3):90. *Turritella doeringi* Böhm (Crétacée Supérieur).

= *Turritella doeringi* Böhm, 1903.
Type Locality.—Roca, Río Negro.
Syntypes.—#729, three casts, coll. Santiago Roth.
Stratigraphy.—Roca Formation (Paleocene).

burmeisteri, 1907. *Cymbiola* VOLUTIDAE

1897*b*. RMP, 2:303. *Voluta dorbignyana* Philippi.
1899*a*. NJMGP, 2:33. *Voluta dorbignyana* Philippi.
1902. Ortmann, p. 230, pl. 36, fig. 1 (*V. d'orbignyana*), and p. 232, fig. 37a–b (*V. domeykoana,* not *domeykoana* Philippi).
1907*a*. AMNBA, 14:210. *Cymbiola burmeisteri* Ihering.
1914. NPRMP, 1(3):109–110. *Cymbiola* (*Cymbiola*) *burmeisteri* Ihering and *Cymbiola* (*Miomelon*) *orbignyana* [sic] Philippi (Patagonico).

= *Adelomelon burmeisteri* (Ihering), **new combination.**
Type Locality.—Santa Cruz.
Syntypes.—#880, two specimens plus four casts, Bicego Collection; #881, Sierra de los Baguales, one complete specimen, coll. Hauthal.
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—Ortmann's figures (1902) of *V. dorbignyana* and *V. domeykoana* are similar, and those on pl. 36, fig. 1b, d, e, are juveniles. Figures 1a–1b in Ortmann (1902) are *Adelomelon* (*Pachycymbiola*) *pilsbryi* (Ihering). See *Voluta pilsbryi* Ihering.

burmeisteri, 1907. *Dosinia* VENERIDAE

1907*a*. AMNBA, 14:301, text fig. 13a–b.
1914. NPRMP, 1(3):50 (Patagonico Inferior).

= *Dosinia* (*Dosinella*) *burmeisteri* (Ihering).

Type Locality.—Bajo de San Julian, Santa Cruz.

Holotype.—#416, one valve, coll. Ameghino, 1900 (by monotypy).

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—According to Dall (in consultation with Ihering), this species belongs to the subgenus *Dosinella.*

burmeisteri, 1907. *Psammobia* PSAMMOBIIDAE

1907*a*. AMNBA, 14:312, pl. 11, fig. 81a–b.
1914. NPRMP, 1(3):57 (Patagonico Inferior).

= *Gari burmeisteri* (Ihering).

Type Locality.—Camarones, Chubut.

Syntypes.—#477, only three valves in the collection from the six reported by Ihering (1914).

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—E. Feruglio (1949–1950) reported the species from Río Turbio.

burmeisteri, 1907. *Tellina* TELLINIDAE

1907*a*. AMNBA, 14:27, pl. 3, fig. 16.

Type Locality.—Roca, Río Negro.

Type.—Not in the collection.

Stratigraphy.—Roca Formation (Paleocene).

Remarks.—Ihering (1907*a*) states, "Seulement un moule interne." The figured internal cast appears to be of the subgenus *Strigilla* Turton, 1832, and close to *S. carnaria,* a Recent species ranging from Florida to Bahía Blanca, Argentina. Ihering did not compare this species with living ones because he thought it was from the Cretaceous.

cahuillensis, 1907. *Turritella* TURRITELLIDAE

1907*a*. AMNBA, 14:342. New name for *Turritella affinis* in Hupé, 1854:155 (pl. 2, fig. 7), preoccupied by *Turritella affinis* Müller, 1851, stated by Ihering to be a Cretaceous species.
1914. NPRMP, 1(3):90 ("Terciario de Chili").

Type Locality.—Curaumulli, Valparaiso, Chile.

Syntypes.—#727, received from the Valparaiso Museum, three specimens, are possible syntypes.

Stratigraphy.—Tertiary.

Remarks.—I have not been able to locate a reference for Müller, 1851, as given in Ihering (1907*a*:342). It is possible that Ihering never saw original descriptions for *T. affinis* Müller or *T. affinis* Hupé, and his use of the latter name was based on a questionable identification in Philippi (1887:71). In any event, the name *cahuillensis* reflects the type locality of that name, given by Hupé (1854:155) as Inseln Chiloé, Cahuil, Colchagua. Ihering (1897*b*:289) indicated that Moericke and Steinmann (1896:555) identified a specimen as *T. affinis* Philippi, and without explanation stated his belief that the species was probably the same as *T. affinis* Hupé. This conclusion appears consistent with later placement of "*Turritella af-*

finis R. A. Philippi (*nec* Hupé)" as a synonym of *T. cahuillensis* (Ihering, 1914: 90). Without study of original descriptions and type materials, it is not possible to determine the correct synonymy for specimens identified by various authors as *T. affinis.*

callophyla, 1903. *Exogyra* OSTREIDAE

1903. AMNBA, 9:199. Not figured.
1907*a*. AMNBA, 14:10, 144.
1914. NPRMP, 1(3):20 (Cretáceo Superior, Roca).

Type Locality.—Roca, Río Negro.

Holotype.—#138, one specimen (by monotypy).

Other Lots.—#139, Roca, two complete specimens and five valves, coll. Ameghino, 1907; #140, Río Negro, one specimen, coll. Ameghino, "Cretáceo horizonte mais inferior."

Stratigraphy.—Roca and Salamanca formations.

Remarks.—Feruglio found the species in the Salamancan beds north of Colhue Huapi in the lower valley of the Río Negro in Chubut (Paleocene). Burckhardt (1902:215) referred to it as *Exogyra lateralis* Nilsson; the original *lateralis* of Nilsson is not an *Exogyra,* but a *Gryphaea.*

camaronesia, 1907. *Arca* ARCIDAE

1907*a*. AMNBA, 14:238, text fig. 9.
1914. NPRMP, 1(3):18 (Patagonico Inferior).

= *Anadara camaronesia* (Ihering), **new combination.**

Type Locality.—Camarones, Chubut.

Syntypes.—#104, 34 valves, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—The specimen figured in Ihering (1907*a*) is a juvenile, similar to *Anadara brasiliana* (Lamarck).

camaronesia, 1907. *Crenella divaricata* MYTILIDAE

1907*a*. AMNBA, 14:277, text fig. 11a–b.
1914. NPRMP, 1(3):39 (Patagonico Inferior).

= *Crenella camaronesia* (Ihering).

Type Locality.—Camarones, Chubut.

Syntypes.—#323, 12 valves, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—It differs from *Crenella divaricata* (d'Orbigny), a Recent species ranging from North Carolina to Argentina, by being narrower and more squamose. This species resembles *Crenella duplisensis* Dall of the Tertiary of Florida.

camaronesia, 1907. *Diplodonta villardeboaena* [sic] "var." UNGULINIDAE

1907*a*. AMNBA, 14:290. Not figured.
1914. NPRMP, 1(3):47.

= *Diplodonta vilardeboaena* (d'Orbigny, 1846).

Type Locality.—Camarones, Chubut.

Syntypes.—#390, three valves, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—*Taras* Risso, *nomen dubium* (= *Diplodonta*).

camaronesia, 1907. *Glycimeris* [sic] GLYCYMERIDIDAE

1907*a*. AMNBA, 14:240, pl. 7, fig. 52a–b.
1914. NPRMP, 1(3):18 (Patagonico Inferior).

= *Glycymeris camaronesia* Ihering.

Type Locality.—Camarones, Chubut.

Syntypes.—#121, four large valves (five smaller valves mentioned in Ihering [1914] missing from the collection), coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

camaronesia, 1907. *Leda* NUCULANIDAE

1907*a*. AMNBA, 14:230, pl. 7, fig. 50a–b.
1914. NPRMP, 1(3):14 (Patagonico Inferior).

= *Nuculana* (*Saccella*) *camaronesia* (Ihering).

Type Locality.—Camarones, Chubut.

Syntypes.—#80, one complete specimen (Ihering listed four) plus 22 isolated valves, coll. Ameghino, 1900; #81, south of Colhue Haupi, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—*Leda* Schumacher, 1817 (= *Nuculana* Link, 1807).

camaronesia, 1907. *Tellina patagonica* "var." TELLINIDAE

1907*a*. AMNBA, 14:315. Not figured.
1914. NPRMP, 1(3):58 (Patagonico Inferior).

= *Tellina patagonica* Ihering.

Type Locality.—Camarones, Chubut.

Syntypes.—#487, two valves; coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—The syntype valves differ from each other and represent variation in *T. patagonica.*

camaronesia, 1907. *Tornatina* SCAPHANDRIDAE [CYLICHNIDAE]

1907*a*. AMNBA, 14:119, pl. 4, fig. 3.
1914. NPRMP, 1(3):68 (Patagonico Inferior).

Type Locality.—Camarones, Chubut.

Syntypes.—#547, ten specimens, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

camaronesia, 1907. *Turritella breantiana* "var." TURRITELLIDAE

1907*a*. AMNBA, 14:164, pl. 4, fig. 23.
1914. NPRMP, 1(3):89 (Patagonico Inferior).

= *Turritella breantiana* d'Orbigny, 1847.

Type Locality.—Camarones, Chubut.

Syntypes.—#719, 15 specimens, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—This form was among those reported by Ihering (1899*a*) as *T. breantiana indecussata.* Although both are of the same strata, *T. camaronesia* is found only north of the San Jorge Gulf, while *indecussata* is more abundant south of it.

camaronesia, 1907. *Venericardia* CARDITIDAE

1902. Ortmann, p. 128, fig. 8a–c. *Cardita patagonica* (not *C. patagonica* Sowerby, 1846).
1907*a*. AMNBA, 14:28, pl. 10, fig. 69a–d (Patagonico Inferior).

Type Locality.—Camarones, Chubut.
Syntypes.—#349, 100 valves, coll. Ameghino, 1900.
Stratigraphy.—Patagonian Formation (Lower Miocene).

camaronesium, 1907. *Calliostoma* TROCHIDAE

1907*a*. AMNBA, 14:137, pl. 4, fig. 11. (Only one figure is on plate 4; text says "a–b.")
1914. NPRMP, 1(3):77 (Patagonico Inferior).

Type Locality.—Camarones, Chubut.
Holotype.—#598, coll. Ameghino, 1900 (by monotypy).
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—Ihering compared this species with *Calliostoma santacruzense* Ortmann, but it is more similar to *C. cossmanni* Ortmann.

cannada, 1907. *Cymbiola becki* "var." VOLUTIDAE

1907*a*. AMNBA, 14:211, pl. 6, fig. 42a–b.
1914. NPRMP, 1(3):109 (Superpatagonico).

= *Adelomelon* (*Adelomelon*) *cannada* (Ihering), **new combination; new status.**
Type Locality.—Cañada de los Artilleros, Santa Cruz.
Holotype.—#879, coll. Ameghino, 1900 (by monotypy).
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—This species is ancestral to the living *A.* (*A.*) *becki* (Broderip) and *A.* (*A.*) *barattini* Klappenbach and Ureta, 1966.

cannada,, 1907. *Venericardia* CARDITIDAE

1907*a*. AMNBA, 14:287, pl. 10, fig. 71a–b.
1914. NPRMP, 1(3):42 (Superpatagonico).

Type Locality.—Cañada de los Artilleros, Santa Cruz.
Syntypes.–#344, 38 valves, coll. Ameghino, 1900; #345, Pan de Azucar, one valve, coll. Ameghino, 1900; #346, Bajo San Julian, two valves, coll. Ameghino, 1900; #347, La Cueva, seven valves, coll. Ameghino, 1900; #348, Yegua Quemada, 15 valves, coll. Ameghino, 1900.
Stratigraphy.—Patagonian Formation (Lower Miocene).

cannada, 1907. *Volvulella* RETUSIDAE

1907*a*. AMNBA, 14:119, pl. 4, fig. 4.
1914. NPRMP, 1(3):69 (Superpatagonico).

Type Locality.—Cañada de los Artilleros, Santa Cruz.
Syntypes.—#549, two specimens, coll. Ameghino, 1900.
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—This species resembles the Recent species *V. persimilis* (Mörch) which ranges from North Carolina to Uruguay.

capa, 1907. *Ostrea hemisphaerica* [sic] "var." OSTREIDAE

1907*a*. AMNBA, 14:12. Not figured.
1914. NPRMP, 1(3):22. *Ostrea neuquena capa* (Rocanense).

= *Ostrea neuquena* Ihering.
Type Locality.—Roca, Río Negro.
Syntypes.—#157, five valves, plus three complete.
Stratigraphy.—Roca Formation (Paleocene).
Remarks.—There are no *Ostrea hemispherica* d'Orbigny in the collection. See *Ostrea hemisphaerica* [sic] "var." *paca* Ihering.

caroloameghinoi, 1902. *Aturia* NAUTILIDAE

1902*b*. PAPS, 41(69):134, pl. 19, fig. 1–2.
1907*a*. AMNBA, 14:116; "*caroli-ameghinoi.*"
1914. NPRMP, 1(3):68 (Patagonico Medio).

Type Locality.—Cabo Tres Puntas, Santa Cruz.
Holotype.—#544, coll. Ameghino, 1900 (by monotypy).
Stratigraphy.—Patagonian Formation (Lower Miocene); also in the "Estratos de Boquerón," Tierra del Fuego.

carolodarwini, 1907. *Polynices* NATICIDAE

1907*a*. AMNBA, 14:89. *Nomen nudum*; see *Natica tumbeziana* Ihering.

casa, 1907. *Chione* VENERIDAE

1907*a*. AMNBA, 14:308, pl. 12, fig. 78.
1914. NPRMP, 1(3):55 ("Casa-Maior," Patagonico Inferior).

= *Protothaca antiqua* (King, 1832).
Type Locality.—Punta Casamayor, Santa Cruz.
Holotype.—#456, coll. Ameghino, 1900 (by monotypy).
Other Lot.—#457, Travesia Valcheta, coll. C. Burmeister, one fragment.
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—This is the oldest geological record of the Recent *P. antiqua.*

chalcedonica, 1903. *Cytherea* VENERIDAE

1903. AMNBA, 9:216, pl. 2, fig. 18a–b.
1907*a*. AMNBA, 14:48. *Meretix chalcedonica.*
1914. NPRMP, 1(3):51 (Salamanquéen). ["Posição systematica dubiosa"].

Type Locality.—Colhue Huapi, Chubut.
Syntypes.—#422, three valves, crystalized into chalcedony.
Stratigraphy.—Salamanca Formation (Paleocene).
Remarks.—This species is neither a *Cytherea* nor a *Meretrix*; it most likely belongs in *Pitar.*

chicoana, 1907. *Hadriania jorgensis* "var." MURICIDAE

1907*a*. AMNBA, 14:186, pl. 6, fig. 33a–b.
1914. NPRMP, 1(3):99 (Patagonico Inferior).

= ?*Trophon chicoanus* (Ihering), **new combination.**
Type Locality.—Río Chico, Chubut.

Holotype.—#806, coll. Ameghino, 1900 (by monotypy).
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—Differs from *Nucella jorgensis* (*Hadriania* in Ihering, 1907*a*) and does not belong in that genus.

chicoanus, 1907. *Vermetus* VERMETIDAE

1907*a*. AMNBA, 14:167. New name for *Vermetus* cf. *intortus* in Ortmann (1902:198, pl. 32, fig. 1), not *Serpula intorta* Lamarck, 1818.

= ?*Petaloconchus chicoanus* (Ihering).
Type Locality.—Río Chico, Chubut (Ortmann, 1902). Also from Lake Pueyrredón.
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—*Vermetus intortus* (Lamarck) is a European species currently placed in *Petaloconchus* H. C. Lea, 1843.

chubutensis, 1903. *Rostellaria* ?APORRHAIDAE

1903. AMNBA, 9:220, pl. 2, fig. 17.
1907*a*. AMNBA, 14:29. *Aporrhais* (Rocanéen).
1914. NPRMP, 1(3):94 (Salamanquéen).

Type Locality.—Río Chico, Chubut.
Syntypes.—#756, two specimens, coll. Ameghino, 1900.
Stratigraphy.—Salamanca Formation (Paleocene).
Remarks.—Ihering transferred this species to the *Aporrhais* but it is more likely a species of *Struthiolaria.*

chubutensis, 1904. *Strophocheilus* STROPHOCHEILIDAE

1904. RMLP, 2:241, pl. 2, fig. 13–14 ("Notostylops" beds).
1907*a*. AMNBA, 14:463.
1914. NPRMP, 1(3):70 (Cretáceo Superior, "Notostylopeano").
1969. Parodiz, ACM, 40:170.

Type Locality.—Cañadón Blanco, south side of Lake Colhue Huapi, Chubut.
Lectotype.—#560, cast, coll. Ameghino (reported in error as Hauthal by Ihering (1914).
Stratigraphy.—Casamayor Formation (Lower Eocene).
Remarks.—The lectotype was designated by Parodiz (1949*b*:181, fig. 1a) as the specimen figured in Ihering (1904, pl. 2, fig. 13). Parodiz (1949*b*) also clarified the status of 15 paralectotypes. As for *S. hauthali,* the collector of the type lot was C. Ameghino, not Hauthal as reported by Ihering (1914). Three of the paralectotypes from Río Chico, Chubut (#560), became the holotype and paratypes for *Strophocheilus avus* Parodiz (1949*b*:181), a name later synonymized with *S.* (*Megalobulimus*) *hauthali* (Ihering) by Parodiz (1969).

chubutiana, 1907. *Scalaria* EPITONIIDAE

1907*a*. AMNBA, 14:364, pl. 14, fig. 99.

= *Epitonium chubutianum* (Ihering), **new combination.**
Type Locality.—Puerto Piramides, Chubut.
Type.—Not in the collection.
Stratigraphy.—Río Negro Formation (Upper Miocene).

Remarks.—Ihering (1907*a*:465) reported this species in a perforation from Puente Alsina at 73 m.

clarae, 1907. *Ostrea* OSTREIDAE

1907*a*. AMNBA, 14:10, pl. 1, fig. 6a, pl. 2, fig. 6a–c.
1914. NPRMP, 1(3):22 (Roca).

Type Locality.—Roca, Río Negro.
Syntypes.—#158, six valves, coll. Ameghino, 1904.
Stratigraphy.—Roca Formation (Paleocene).
Remarks.—Another lot is in the collection from Park-Aik (1907) or "Par-aiqu" (1914, one valve, "formação guaranitica, classificação incerta").

clessini, 1907. *Turbonilla* PYRAMIDELLIDAE: TURBONILLINAE

1907*a*. AMNBA, 14:145. New name for *Turbonilla iheringi* Clessin (1900:174, pl. 36, fig. 7), not *T. iheringi* Cossmann (1899*a*:235, pl. 10, fig. 12), and not *T. iheringi* Clessin (1900:168–169, pl. 35, fig. 5).

Type Locality.—"Südbrasilien, lgt. v. Ihering, Mus. Berol.," as given in Clessin (1900:174).
Stratigraphy.—Patagonia Formation (Lower Miocene).
Remarks.—Clessin (1900) separately described two specimens under the name *Turbonilla iheringi* without mention of their primary junior homonymy with each other and with the senior valid name *T. iheringi* Cossmann, 1899. Ihering (1907*a*) observed that Clessin's material consisted of two species, the first of which he let stand as *T. iheringi* Clessin (1900:168) despite its junior status to *T. iheringi* Cossmann. The other species (*T. iheringi* Clessin, 1900:174) was named *Turbonilla clessini* by Ihering. He noted that Cossmann had already used *T. iheringi,* and without regard for priority of the available names he offered *Turbonilla eopatagonica* as an unnecessary replacement name for the valid senior name, *T. iheringi* Cossmann. *Turbonilla iheringi* Clessin (1900:168) remains a junior homonym of Cossmann's name, and requires a replacement name.

colhuapensis, 1903. *Diplodon* HYRIIDAE

1903. AMNBA, 9:217, fig. 2.
1907*a*. AMNBA, 14:466 (". . . depots qui sont probablement tertiares.")
1914. NPRMP, 1(3):36 (Cretáceo).
1969. Parodiz, ACM, 40:53–54.

Type Locality.—Colhue Huapi, Chubut.
Lectotype.—#295, coll. Ameghino; in CMNH.
Stratigraphy.—Sehuen Formation (Paleocene).
Remarks.—The lectotype was designated by Parodiz, 1969:54, pl. 1, fig. 1, 3–4 (fig. 2 is a paratype) based on material received in exchange from Dr. Max Birabén, at that time Director of the Museo Argentino de Ciencias Naturales. This species will be included in a new genus (Parodiz, in preparation).

Cominella sp. BUCCINIDAE: PHOTINAE

1914. NPRMP, 1(3):105 (Patagonico).

Locality.—Punta Atlas, Chubut.
Specimens.—#859, coll. Ameghino.

Stratigraphy.—Patagonian Formation (Lower Miocene).

concors, 1902. *Gryphaea* GRYPHAEIDAE

1902*a*. AMNBA, 4:11, 114, fig. 1–3 (Formation Guaranitique).
1903. AMNBA, 9:210.
1904. RMLP, 11:210.
1907*a*. AMNBA, 14:8, 43 (Salamanquéen).
1914. NPRMP, 1(3):21 ("étage guaraniéen").

Type Locality.—Valle Alsina, Chubut.
Syntypes.—#144, five valves, coll. G. Burmeister, 1887.
Other Lot.—#145, Pico Salamanca, two valves.
Stratigraphy.—Salamanca Formation (Paleocene).

confinis, 1897. *Marginella* MARGINELLIDAE

1897*b*. RMP, 2:307, pl. 3, fig. 8 (Formação Santacruzense).
1907*a*. AMNBA, 14:200. *Neoimbricaria* (Superpatagonico).

= *Neoimbricaria quemadensis* (Ihering).
Type Locality.—La Cueva, Santa Cruz.
Holotype.—#866, coll. Ameghino (by monotypy).
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—*Marginella gracilior* Ihering is another synonym of *N. quemadensis* (Ihering).

consimilis, 1897. *Natica* NATICIDAE

1897*b*. RMP, 2:283, text fig. 12 (Formação Santacruzense).
1899*a*. NJMGP, 2:28. *Natica famula* Philippi.
1907*a*. AMNBA, 14:156. *Polynices magellanica* "var."
1914. NPRMP, 1(3):85. *Polynices magellanica* (*consimilis*) (Superpatagonico).

= *Lunatia magellanica* Hombron and Jacquinot, 1834.
Type Locality.—La Cueva, Santa Cruz.
Syntypes.—#672, two specimens, coll. Ameghino; #673, San Jorge, ten specimens, coll. J. Bicego; #674, Golfo San Jorge, two specimens, coll. Ameghino; #675, Deseado (Formación Araucana), one specimen, coll. Ameghino, 1900.
Stratigraphy,—Patagonian Formation (Lower Miocene) and also Araucanean Formation (Pliocene).
Remarks.—*Natica famula* Philippi referred to by Ihering (1899*a*) is a species from Chile, different from *consimilis,* although it is also found in Santa Cruz (#668–#670 in the Ihering Collection). It is related to a longer species, *Lunatia pyrotheriorum* Ihering from the Patagonian.

Conus sp. CONIDAE

1907*a*. AMNBA, 14:448.

= *Conus clenchi* Martins, 1943. Recent.
Locality.—Reported from "Pampien de Puerto Militar aff. *C. portoricanus* Hwass." The type locality of *Conus clenchi* Martins is Puerto Deseado, Santa Cruz.
Stratigraphy.—Belgrano Formation (Lower Pleistocene).
Remarks.—*Conus carcellesi* Martins, 1945, is a synonym of *C. clenchi* according to Rios (1975:124).

Corbiculella, 1907. CORBICULIDAE

1907*a*. AMNBA, 14:462, 469. New subgenus of *Corbicula* Megerle.
1969. Parodiz, ACM, 40:98. Subgenus of *Neocorbicula* Fischer.

Type Species.—*Corbicula tenuis* Ihering.
Stratigraphy.—Paraná Formation (Upper Miocene).

cossmanni, 1907. *Amussium* [sic] PROPEAMUSSIIDAE

1907*a*. AMNBA, 14:260, pl. 9, fig. 59a–b.
1914. NPRMP, 1(3):35 (Patagonico).

= *Amusium cossmanni* Ihering.
Type Locality.—Punta Atlas, Chubut.
Holotype.—#288, one valve, coll. R. Valentin, 1897 (by monotypy).
Stratigraphy.—Paraná Formation (Entre Rios) and Río Negro Formation (Rionegrense) in Chubut (Upper Miocene).
Remarks.—Ihering (1907*a*) remarked that this species was found together with *Ostrea hatcheri* Ortmann. *Amusium cossmanni* resembles *Amusium darwinianum* (d'Orbigny), which is also from the Paraná Formation.

cossmanni, 1907. *Chione* VENERIDAE

1907*a*. AMNBA, 14:350. New name for *Venus chiloensis* in Ortmann (1900:378) and Ortmann (1902: 137, pl. 27, fig. 10), not *Venus chiloensis* Philippi, 1887.

= ?*Protothaca cossmanni* (Ihering).
Type Locality.—Punta Arenas, Chile (Ortmann).
Stratigraphy.—?Lower Miocene.
Remarks.—Ihering (1907*a*:350) remarked that *chiloensis* belongs to *Protothaca* while *cossmanni* has the sculpture of *Chione,* but that is not a generic definition.

cossmanni, 1907. *Cominella* BUCCINIDAE: PHOTINAE

1902. Ortmann, p. 209, pl. 39, fig. 18. *Buccinum obesum* var. *minor* (Philippi).
1907*a*. AMNBA, 14:191 (Santacruzense).
1914. NPRMP, 1(3):105.

= *Cominella minor* (Philippi, 1887).
Type Locality.—Santa Cruz.
Holotype.—#857, received from Ortmann (by monotypy).
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—Feruglio (1949–1950) reported the species for Río Turbio.

cossmanni, 1907. *Lima* LIMIDAE

1907*a*. AMNBA, 14:264, pl. 9, fig. 62.
1914. NPRMP, 1(3):29. *Lima* (*Limatula*) (Patagonico Inferior).

Type Locality.—Punta Nova (Nueva), Golfo San Jorge.
Syntypes.—#225, three valves, coll. Ameghino; #226, Casamayor, one valve, coll. Ameghino, 1900.
Other Lot.—#227, ". . . valva isolada que foi examinada pelo snr. Cossmann." (Ihering, 1914).
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—The three species of *Lima* described by Ihering are all from the

same type locality and same stratigraphic position, but they are easily distinguished.

cossmanni, 1907. *Proscaphella* VOLUTIDAE

1907*a*. AMNBA, 14:206, pl. 6, fig. 41a–b.
1914. NPRMP, 1(3):110. *Cymbiola* (*Miomelon*) (Patagonico).

= *Adelomelon* (*Pachycymbiola*) *cossmanni* (Ihering).
Type Locality.—Santa Cruz.
Syntypes.—#888, two specimens, coll. J. Bicego.
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—Ihering (1907*a*): "... intermediaire entre *P. gracilis* et *quemadensis.*"

cossmanni, 1903. *Rostellaria* APORRHAIDAE

1903. AMNBA, 9:219, pl. 2, fig. 15.
1907*a*. AMNBA, 14:49. *Aporrhais* (Salamanquéen).
1914. NPRMP, 1(3):94 (Salamanqueano).

= *Aporrhais cossmanni* (Ihering).
Type Locality.—Río Chico, Chubut.
Syntypes.—#757, two specimens (Ihering [1907*a*]: "L'unique exemplaire"), coll. Ameghino, 1900.
Stratigraphy.—Salamanca Formation (Paleocene).
Remarks.—The syntypes have the siphonal canal and peristoma missing but the body whorl is of *Aporrhais.*

cossmanni, 1907. *Scalaria* EPITONIIDAE

1907*a*. AMNBA, 14:141, pl. 4, fig. 12. Primary junior homonym of *Scalaria* (*Nodiscala*) *cossmanni* de Boury, 1889.
1914. NPRMP, 1(3):80. *Cirsotrema quemadense* [sic] Cossmann (Superpatagonico).

= *Opalia* (*Nodiscala*) *quemadensis* (Cossmann), **new combination.**
Type Locality.—Yegua Quemada, Santa Cruz.
Holotype.—#616, coll. Ameghino, 1900 (by monotypy).
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—*Opalia* (*Nodiscala*) *eolis* Clench and Turner, 1950, is a closely related species.

cossmanni, 1907. *Tenagodus* SILIQUARIIDAE

1907*a*. AMNBA, 14:166, pl. 5, fig. 25.
1914. NPRMP, 1(3):91 (Superpatagonico).

= *Siliquaria cossmanni* (Ihering).
Type Locality.—Cañada de los Artilleros, Santa Cruz.
Holotype.—#743, a small fragment of tube, coll. Ameghino, 1900 (by monotypy).
Stratigraphy.—Patagonian Formation (Lower Miocene).

crucis, 1907. *Solen* SOLENIDAE

1897*b*. RMP, 2:263. *Solen elytron* Philippi.
1907*a*. AMNBA, 14:318, pl. 12, fig. 83.

1914. NPRMP, 1(3):59 (Superpatagonico).

Type Locality.—Yegua Quemada, Santa Cruz.
Holotype.—#491, coll. Ameghino (by monotypy).
Other Lot.—#492, Rada Tilly, Golfo San Jorge, one specimen, coll. Ameghino.
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—This species resembles *Solen scalprum* Broderip.

cruzensis, 1907. *Genotia* TURRIDAE

1907*a*. AMNBA, 14:222. New name for *Genotia cuevensis* in Ortmann (1902:240, pl. 37, fig. 2), not *Genota cuevensis* Ihering, 1897 (Superpatagonico).

= *Genota cuevensis* (Ihering).
Type Locality.—Mouth of the Santa Cruz River (Ortmann).
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—This name was unnecessarily proposed for large forms correctly identified by Ortmann (1902) as *Genota cuevensis* Ihering. *Genotia* Fischer, 1883 (= *Genota* H. and A. Adams, 1853).

cruzialis, 1907. *Phacoides promaucana* "var." LUCINIDAE

1907*a*. AMNBA, 14:288, pl. 13, fig. 90a–b.
1914. NPRMP, 1(3):45 (Superpatagonico).

= *Lucina cruzialis* (Ihering).
Type Locality. Yegua Quemada, Santa Cruz.
Syntypes.—#374, coll. Ameghino.
Other Lots.—#375, Santa Cruz, three specimens, coll. J. Bicego, 1897; #376, Jack Harvey, one specimen; #377, Pan de Azucar, two specimens, coll. Ameghino, 1900; #378, Casamayor, 11 specimens, coll. Ameghino, 1900; #379, Cabo Tres Puntas, one valve, coll. Ameghino, 1900; #380, Punta Nodales, three specimens, coll. Ameghino, 1900; "Region de Sur," Golfo San Jorge, two casts, coll. Ameghino, 1900.
Stratigraphy.—Patagonian Formation (Lower Miocene).

cuevensis, 1897. *Genota* TURRIDAE

1897*b*. RMP, 2:313, pl. 3, fig. 10.
1902. Ortmann, p. 240, pl. 37, fig. 2. *Genota cuevensis.*
1907*a*. AMNBA, 14:222. *Genotia.*
1914. NPRMP, 1(3):113 (Superpatagonico).

Type Locality.—La Cueva, Santa Cruz.
Holotype.—#911, coll. Ameghino (by monotypy).
Other Lots.—#912, Cabo Tres Puntas, one specimen, coll. Ameghino; #913, Golfo San Jorge, coll. Ameghino.
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—See note on *G. cruzensis* for *Genota* vs. *Genotia.*

cuevensis, 1897. *Gibbula fracta* "var." ARCHITECTONICIDAE

1897*b*. RMP, 2:274, pl. 3, fig. 2.
1907*a*. AMNBA, 14:131. *Gibbula cuevensis* (Patagonico Superior).
1914. NPRMP, 1(3):72 (Superpatagonico).

= *Valdesia dalli* (Ihering).

Type Locality.—La Cueva, Santa Cruz.
Holotype.—#571, coll. Ameghino (by monotypy).
Other Lot.—#572, Cañada de los Artilleros, six specimens, coll. Ameghino.
Stratigraphy.—Patagonian Formation (Lower Miocene).

cuevensis, 1897. *Pectunculus pulvinatus* "var." GLYCYMERIDIDAE

1897*b*. RMP, 2:238, pl. 7, fig. 46 and pl. 8, fig. 50 (Form. santacruzensis).
1907*a*. AMNBA, 14:240, 345, 373. *Glycimeris cuevensis* [sic].
1914. NPRMP, 1(3):19 (Superpatagonico and Magellanico).

= *Glycymeris cuevensis* (Ihering).

Type Locality.—La Cueva, Santa Cruz.

Syntypes.—#122, two valves, coll. Ameghino.

Other Lots.—#123, Yegua Quemada, six valves; #124, Santa Cruz, one valve, coll. J. Bicego; #125, Manantial Salado, one valve, coll. Ameghino, 1900; #126, Cañada de los Artilleros, two large valves and 30 smaller valves, coll. Ameghino, 1900; #127, Puerto Piramides, Chubut, one valve, coll. Ameghino, 1903 (label says "from Dr. F. Lahille"); #128, "Fin de Barrancas"[?], three valves from Dr. Lahille; #129, Punta Arenas (Magellanico), one specimen received from Ortmann under the name *Pectunculus ibari* Philippi.

Stratigraphy.—Magellanian (Lower Oligocene) and Patagonian Formation (Lower Miocene).

Remarks.—E. Feruglio (1949–1950) found the species at Río Turbio. *Glycymeris pulvinatus* Lamarck from the Tertiary of Europe has no connection with *G. cuevensis.*

cuevensis, 1897. *Turbonilla* PYRAMIDELLIDAE

1897*b*. RMP, 2:276, text fig. 11 (Formação Santacruzense).
1907*a*. AMNBA, 14:144.
1914. NPRMP, 1(3):81 (Superpatagonico).

Type Locality.—La Cueva, Santa Cruz.
Holotype.—#635, coll. Ameghino (by monotypy).
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—See note under *Turbonilla observationis* (Ihering).

Cymbiola (*Pachycymbiola*) sp. VOLUTIDAE

1914. NPRMP, 1(3):110 (Formação Entreriana ou Araucana).

= *Adelomelon* (*Pachycymbiola*) *feruglioi* (Doello-Jurado, 1931).

Locality.—The undetermined species of Ihering is from Puerto Piramides, Chubut; the type of *C. feruglioi* Doello-Jurado is from Sierra Laziar, Santa Cruz.

Specimens.—#887, one incomplete specimen, coll. Hauthal.

Stratigraphy.—Sierra Laziar (Laziarense), Araucanean Formation (Pliocene).

Remarks.—This species is intermediate between *Adelomelon* (*Pachycymbiola*) *ameghinoi* (Ihering) and *A.* (*P.*) *brasiliana* (Solander).

dalli, 1907. *Calliostoma* TROCHIDAE

1907*a*. AMNBA, 14:437, pl. 17, fig. 114a–c. (Deseado Formation).
1914. NPRMP, 1(3):77 (Pampeano).

= *Calliostoma militaris* Ihering.

Type Locality.—Puerto Militar, Prov. Buenos Aires.

Syntypes.—#602, three specimens, coll. Ameghino, 1905.

Stratigraphy.—Belgrano Formation (Lower Pleistocene).

Remarks.—*Calliostoma dalli* Ihering (1907*a*), *C. amazonicum* Finlay (1930), and *C. quequensis* Carcelles (1944) are all synonyms of *C. militaris.* See *C. bellicosum* Ihering.

dalli, 1907. *Crassinella* CRASSATELLIDAE

1907*a*. AMNBA, 14:280, text fig. 12a–b.
1914. NPRMP, 1(3):41 (Patagonico Inferior).

Type Locality.—Camarones, Chubut.

Syntypes.—#334, 100 valves (the one figured is a right valve, 4.5 × 4 mm), coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—See *C. acutus* Dall from the Pliocene of Florida.

dalli, 1897. *Cucullaea* CUCULLAEIDAE

1897*b*. RMP, 2:241, pl. 7, fig. 47, and pl. 8, fig. 54 (Formação Santacruzense).
1907*a*. AMNBA, 14:232. *Cucullaea alta* Sowerby.
1914. NPRMP, 1(3):14. *Cucullaea alta* Sowerby (Patagonico).

= *Cucullaea alta* Sowerby, 1846.

Type Locality.—Jack Harvey, Santa Cruz.

Type.—Not in the collection.

Other Lots.—#84, one complete specimen, coll. Ameghino, 1900; #85, two valves; #86, Santa Cruz, two casts, coll. J. Bicego; #87, Camarones, two fragments attached to *Ostrea,* coll. Ameghino, 1900; #88, Cañada de los Artilleros, one valve, coll. Ameghino, 1900; #89, Punta Casamayor, one valve, coll. Ameghino, 1900; #90, Cabo Tres Puntas, coll. Ameghino, 1905; #91, Cabo Tres Puntas, coll. Ameghino, 1900; #92, Punta Nueva, one complete specimen, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

dalli, 1897. *Gibbula* ARCHITECTONICIDAE

1897*b*. RMP, 2:273, pl. 3, fig. 1, and pl. 4, fig. 13 (Formação Santacruzense).
1902. Ortmann, p. 171, pl. 31, fig. 9a–b.
1907*a*. AMNBA, 14:131.
1914. NPRMP, 1(3):73 (Superpatagonico).

= *Valdesia dalli* (Ihering).

Type Locality.—Jack Harvey, Santa Cruz.

Syntypes.—#576, four specimens, coll. Ameghino.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—This is the large form of *G. cuevensis* (= *dalli*); see also *Gibbula cuevensis* and *Gibbula cuevensis fracta* Ihering. See Del Río (1985) for the description of the genus *Valdesia.*

dalli, 1907. *Lithodomus patagonica* [sic] MYTILIDAE: LITHOPHAGINAE

1907*a*. AMNBA, 14:275.
1914. NPRMP, 1(3):39 (Patagonico Medio).

= *Lithophaga patagonica* (d'Orbigny, 1846).

Type Locality.—Rada Tilly, Golfo San Jorge.

Holotype.—#320, by original designation, "exemplaire typique 32 mm," two paratypes, coll. Ameghino, 1901, found perforating *Ostrea hatcheri.*

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—This species resembles *Lithodomus platensis* Philippi (1893) from the Paraná Formation.

dalli, 1907. *Lyria* VOLUTIDAE

1907*a*. AMNBA, 14:204, pl. 14, fig. 9.
1914. NPRMP, 1(3):108 (Patagonico Medio).

= *Enaeta dalli* (Ihering), **new combination.**

Type Locality.—Cabo Tres Puntas, Santa Cruz.

Holotype.—#874 (a very small specimen), coll. Ameghino, 1905 (by monotypy).

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—On consultation with H. W. Dall, Ihering placed this species in *Lyria.* There is another lot, #875, assumed to be a different species by Ihering, but too incomplete for description.

dalli, 1907. *Phacoides* LUCINIDAE

1907*a*. AMNBA, 14:284. Not figured.
1914. NPRMP, 1(3):46 (Superpatagonico).

= *Lucina dalli* (Ihering).

Type Locality.—Cañada de los Artilleros, Santa Cruz.

Syntypes.—#386, six valves, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—*Phacoides* Blainville, 1825 (= *Lucina* Bruguière, 1797).

dalli, 1907. *Venericardia* CARDITIDAE

1907*a*. AMNBA, 14:413, pl. 16, fig. 108a–b.
1914. NPRMP, 1(3):43 (Formação Araucana).

Type Locality.—Sierra Laziar, Santa Cruz.

Syntypes.—#353, three valves, coll. Ameghino, 1900.

Stratigraphy.—Araucanean Formation (Lower Pliocene).

dautzembergi, 1897. *Triton* (*Argobuccinum*) RANELLIDAE: RANELLINAE

1897*b*. RMP, 2:293, text fig. 16 (Formação Santacruzense).
1907*a*. AMNBA, 14:176. *Lotorium.*
1914. NPRMP, 1(3):97. *Lotorium* (*Lampusia*) (Superpatagonico).

= *Fusitriton dautzembergi* (Ihering), **new combination.**

Type Locality.—Yegua Quemada, Santa Cruz.

Holotype.—#791, the specimen is small, juvenile (by monotypy).

Stratigraphy.—Patagonian Formation (Lower Miocene).

densestriata, 1897. *Struthiolaria ornata* "var." STRUTHIOLARIIDAE

1897*b*. RMP, 2:292, text fig. 15.
1907*a*. AMNBA, 14:171.
1914. NPRMP, 1(3):95 (Patagonico Medio–Inferior).

= *Struthiolaria ornata* Sowerby (1846).

Type Locality.—Not reported in the original description, but the specimens of the "var." in the "type lot" were labelled as being from Santa Cruz.

Syntypes.—#769, seven specimens, coll. Ameghino.

Other Lots.—#770, Pan de Azucar, coll. Ameghino; #771, Manantial Salado, three specimens, coll. Ameghino; #772, Cabo Tres Puntas, six specimens, coll. Ameghino; #773, Sierra de los Baguales, eight specimens, coll. Ameghino; #774, Corral Foyel, three specimens, coll. Hauthal; #775, Golfo San Jorge, five specimens, coll. Ameghino.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—Of *Struthiolaria ornata* Sowerby (1846:260, pl. 4, fig. 62) there are also five lots in the Ihering Collection: #777, Santa Cruz, 11 specimens, coll. J. Bicego; #778, ten specimens, coll. Hatcher, received from Ortmann; #779, "Foz do Río Santa Cruz," one specimen received from Ortmann; #780, La Cueva in conglomerate; #781, Cañada de los Artilleros, one specimen, coll. Ameghino. From Park-Aik, Río Sehuen there is one cast, #782, collected by C. Ameghino, and labelled as "*Struthiolaria* sp." which is probably *S. ornata* (see *Struthiolaria prisca*).

derbyi*, 1907. *Diplodon HYRIIDAE

1907*a*. AMNBA, 14:466, pl. 18, fig. 128 (Cretaceous).
1914. NPRMP, 1(3):36 (Terciario).
1969. Parodiz, ACM, 40:82, pl. 8, fig. 3, *Fossula derbyi* (Ihering).

= *Fossula derbyi* (Ihering).

Type Locality.—Santa María da Bocca do Monte, Rio Grande do Sul, Brasil.

Holotype.—#297, upper portion of a valve, coll. Orville A. Derby (by monotypy).

deseadense*, 1914. *Calliostoma ?TURBINIDAE

1914. NPRMP, 1(3):77, pl. 3, fig. 12 (Formação Araucana).

Type Locality.—Deseado, Santa Cruz.

Holotype.—#603, coll. Ameghino, 1900 (by monotypy).

Stratigraphy.—Araucanean Formation (Pliocene)

Remarks.—This species is not a *Calliostoma,* but rather more like *Turbo.* The holotype is a broken specimen but in the figure it shows complete ornamentation.

deseadensis*, 1907. *Myochlamys PECTINIDAE

1907*a*. AMNBA, 14:410, pl. 15, fig. 102a–b.
1914. NPRMP, 1(3):30 (Formação Araucana).

= *Chlamys deseadensis* (Ihering).

Type Locality.—Sierra Laziar.

Syntypes.—#242, 12 valves.

Stratigraphy.—(Laziarense) Araucanean Formation (Lower Pliocene).

deuterolivella*, 1907. *Volvaria MARGINELLIDAE

1907*a*. AMNBA, 14:197. New name for *Marginella oliviformis* in Ortmann (1900:376), not *Marginella oliviformis* Tuomey and Holmes, 1857.
1914. NPRMP, 1(3):106. *Marginella* (*Volvaria*) *deuterolivella* (Patagonico).

= ?*Marginella* (*sensu lato*) *deuterolivella* (Ihering).

Type Locality.—Mouth of Santa Cruz River (Ortmann).

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—Specimens of this species were misidentified as *Marginella olivella* Reeve, 1865, by Ortmann (1902:225, pl. 35, fig. 3a, b). This species is more elongated than any living species of *Marginella* from the southwestern Atlantic, and is *Columbella*-like in shape. There is one specimen (#863, Golfo San Jorge, coll. Ameghino) in the Ihering Collection.

dubiosa, 1907. *Gibbula* ARCHITECTONICIDAE

1907*a*. AMNBA, 14:130, pl. 4, fig. 91a–b.
1914. NPRMP, 1(3):73 (Patagonico Medio).

= *Valdesia dalli* (Ihering).

Type Locality.—Golfo San Jorge.

Holotype.—#577, (by monotypy).

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—This species was based on a distorted specimen of "*Gibbula*" *dalli.*

dynastes, 1907. *Nucula* NUCULIDAE

1907*a*. AMNBA, 14:3, pl. 1, fig. 2a–b (Rocanéen).
1914. NPRMP, 1(3):12 (Roca, Cretáceo Superior, Roca).

Type Locality.—General Roca, Río Negro.

Syntypes.—#64, two casts, received from Ameghino in 1905.

Stratigraphy.—Roca Formation (Paleocene).

elongata, 1914. *Panopaea* [sic] *nucleus* HIATELLIDAE

1914. NPRMP, 1(3):64. Not figured (Cretáceo Superior, Roca).

= *Panopea nucleus* (Ihering).

Type Locality.—Corral Foyel.

Holotype.—#517, one cast, coll. Hauthal (by monotypy).

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—There is another specimen in the collection (MACN #2480), Foyel River. Ihering's brief diagnosis indicates a form higher than *nucleus* with the margin slightly convex (Ihering: ". . . me parece uma variedade").

Entacanthus, 1907. MURICIDAE

1907*a*. AMNBA, 14:14:183. New subgenus of *Trophon* Montfort.

= *Thais* (*Stramonita*) Schumacher, 1817.

Type Species.—*Trophon monoceros* Ihering.

Stratigraphy.—Patagonian Formation (Lower Miocene).

entreriana, 1907. *Anomalocardia* VENERIDAE

1907*a*. AMNBA, 14:386.
1914. NPRMP, 1(3):57 (Formação Entreriana).

Type Locality.—Paraná, Entre Rios.

Syntypes.—#476, five valves, Bravard coll.

Remarks.—The syntypes were identified by Borchert (1901:39, pl. 3, fig. 12–

21) as *Venus brasiliana* (Gmelin). The specimens were sent to W. H. Dall who confirmed it to be a different species but still very similar to *Anomalocardia brasiliana* (Gmelin).

entreriana, 1907. *Dosinia* VENERIDAE

1901. Borchert, p. 36. *Dosinia patagonica,* not *Dosinia patagonica* Philippi, 1893.
1907*a*. AMNBA, 14:383. Not figured.

= *Dosinia meridionalis* Ihering.
Type Locality.—Paraná, Entre Rios (Borchert).
Type.—Not in the collection.
Stratigraphy.—Paraná Formation (Upper Miocene); also in the Patagonian Formation.
Remarks.—Ihering (1907*a*): "J'ai examiné la coquille décrite par Borchert et vérifie quelle n'est pas identique avec *Dosinia patagonica.*"

entreriana, 1907. *Leda* NUCULANIDAE

1901. Borchert, p. 32, *Leda patagonica,* not *Leda patagonica* d'Orbigny, 1846.
1907*a*. AMNBA, 14:371. Not figured.

= *Nuculana entreriana* (Ihering).
Type Locality.—Paraná, Entre Rios (Borchert).
Type.—Not in the collection.
Stratigraphy.—Paraná Formation (Upper Miocene).
Remarks.—Other "*Leda*" in the collection are only from Patagonia, not from Paraná.

entrerianus, 1907. *Tagelus gibbus* PSAMMOBIIDAE: SOLECURTINAE

1901. Borchert, p. 21, pl. 3, fig. 26. *Solecurtus platensis* d'Orbigny.
1907*a*.—AMNBA, 14:387. Not figured.

= *Tagelus plebeius* (Solander, 1823). Recent.
Type Locality.—Paraná, Entre Rios (Borchert).
Stratigraphy.—Paraná Formation (Upper Miocene).
Remarks.—*Solecurtus platensis* d'Orbigny, *Tagelus gibbus* of authors, and *T. plebeius* (Solander) are all synonyms for the same species which is widely distributed in the western Atlantic.

eopatagonica, 1907. *Turbonilla* PYRAMIDELLIDAE: TURBONILLINAE

1907*a*. AMNBA, 14:144. New name for *Turbonilla iheringi* in Cossmann (1899*a*:235, pl. 10, fig. 12), not *T. iheringi* (Clessin, 1902).
1914. NPRMP, 1(3):82 (Superpatagonico).

= *Turbonilla iheringi* Cossmann, 1899.
Type Locality.—Yegua Quemada, Santa Cruz.
Stratigraphy.—Patagonia Formation (Lower Miocene).
Remarks.—This name is an unnecessary replacement name for *T. iheringi* Cossmann. The only specimen in the collection is #636, collected by Ameghino in 1900, and therefore not the type of Cossmann's "*T. iheringi*" described in 1899. The four species of *Turbonilla* named by Ihering, *T. clessini, T. cuevensis, T. observationis,* and *T. eopatagonica* (= *T. iheringi* Cossmann) are all similar

to the Recent *Turbonilla* (*Pyrgiscus*) *uruguayensis* Pilsbry. See Remarks section under *T. clessini.*

espejoana "Ihering," 1902. *Chlamys* PECTINIDAE

1902. Ameghino, ASCA, 54:224. *Nomen nudum.*

= *Pecten praenuncius* Ihering, 1897*b*.

eupatagonica, 1907. *Myochlamys* PECTINIDAE

1907*a*. AMNBA, 14:259, pl. 9, fig. 58.
1914. NPRMP, 1(3):30 (Superpatagonico).

= *Chlamys eupatagonicus* (Ihering).
Type Locality.—Cañada de los Artilleros, Santa Cruz.
Holotype.—#243, coll. Ameghino, 1900 (by monotypy).
Stratigraphy.—Patagonian Formation (Lower Miocene).

eupyga, 1907. *Chione* VENERIDAE

1907*a*. AMNBA, 14:310, pl. 12, fig. 80.
1914. NPRMP, 1(3):55 (Patagonico Superior).

Type Locality.—San Julian, Santa Cruz.
Holotype.—#452, coll. Ameghino, 1900 (by monotypy).
Other Lot.—#453, Rada Tilly, Santa Cruz, coll. S. Roth, reported from "Roca."
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—The specimen described and figured by Ihering is a fragment of a valve in poor condition for correct identification; it may belong in *Chione meridionalis* Sowerby.

faira, 1907. *Ostrea* OSTREIDAE

1907*a*. AMNBA, 14:406.
1914. NPRMP, 1(3):25 (Formação Araucana).

Type Locality.—Cabo Fairweather (Buentiempo) Santa Cruz.
Syntypes.—#196, two large specimens received from Ortmann.
Stratigraphy.—Araucanean Formation (Pliocene).
Remarks.—*Ostrea ingens* in Ortmann (1902:99, pl. 18, fig. 1a–b) is in part this species.

fairus, 1907. *Trophon inornatus* MURICIDAE

1907*a*. AMNBA, 14:402.
1914. NPRMP, 1(3):100 (Formação Araucana).

= *Trophon* (*Austrotrophon*) *lamellosus* (Gmelin, 1791).
Type Locality.—Cabo Fairweather (Buentiempo), Santa Cruz.
Syntypes.—#810, two specimens, coll. Hatcher, received from Ortmann.
Stratigraphy.—Araucanean Formation (Pliocene).

felschi, 1921. *Aturia* (*Sphenaturia*) NAUTILIDAE

1921. Physis, Buenos Aires, 5:76.

Type Locality.—Punta Chocoi, Carelmapu, Chile.

Holotype.—Collected by J. Flesch; status unknown.

Stratigraphy.—"Estratos de Boquerón" (below Patagonian Formation).

Remarks.—Referring to the holotypes of this species and *A.* (*S.*) *brueggeni,* Ihering (1921) stated, "Los ejemplares tipicos quedan depositados en este Museo [Museo Argentino de Ciencias Naturales, Buenos Aires]."

filipponei [sic], 1907. *Lotorium* RANELLIDAE: CYMATIINAE

1907*a*. AMNBA, 14:443, pl. 17 (text states in error "XVIII") fig. 22a–b.

= *Cymatium* (*Cabestana*) *felipponei* (Ihering), emendation.

Type Locality.—Maldonado, Uruguay.

Type.—Not in the collection.

Stratigraphy.—Querandí Formation (Pleistocene).

Remarks.—Ihering mentioned another specimen (1907*a*) from Punta Carretas, Montevideo, also received from F. Felippone of Uruguay.

Fimbria sp. LUCINIDAE

1897*b*. RMP, 2:219.

Specimens.—Not in the collection.

Remarks.—A single valve from Yegua Quemada, Santa Cruz, which Ihering said was *Corbis*-like, but different from "*Fimbria*" *patagonica* (Philippi). *Corbis patagonica* Philippi is of questionable taxonomic position. *Fimbria* M. von Muhlfeld, 1811; not Bohadsch, 1761 (= *Corbis* Cuvier, 1817).

fissocostalis, 1899. *Pecten* PECTINIDAE

1899*a*. NJMGP, 2:11, pl. 1, fig. 1.
1907*a*. AMNBA, 14:255. *Myochlamys.*
1914. NPRMP, 1(3):31 (Patagonico).

= *Chlamys* (*Zygochlamys*) *fissocostalis* (Ihering); see Morra (1985).

Type Locality.—Santa Cruz.

Syntypes.—#244, two complete specimens and four valves, coll. J. Bicego, 1897.

Other Lot.—#245, fragment of a large valve, coll. Bicego; probably same locality.

Stratigraphy.—Patagonian Formation (Lower Miocene).

foyela, 1914. *Myochlamys* PECTINIDAE

1914. NPRMP, 1(3):33, pl. 1, fig. 3 (Patagonico).

= *Chlamys foyela* (Ihering).

Type Locality.—Corral Foyel, Neuquen.

Syntypes.—#273, three valves and pieces in conglomerate, coll. Hauthal.

Stratigraphy.—Patagonian Formation (Lower Miocene).

fracta, 1897. *Gibbula* ARCHITECTONICIDAE

1897*b*. RMP, 2:273, pl. 3, fig. 2 (Formação Santacruzense).
1907*a*. AMNBA, 14:131, "et Var. *cruzis*" not described.
1914. NPRMP, 1(3):73 (Superpatagonico); the specimen figured in 1897 is identified here as *cuevensis.*

= ?*Valdesia fracta* (Ihering).

Type Locality.—Yegua Quemada, Santa Cruz.

Holotype.—#578, one specimen in fragments (by monotypy).

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—Another specimen from the same locality is reported as *Gibbula diametralis* Cossmann. The differentiation of "*G.*" *fracta cuevensis* is very difficult; all specimens from the same area of Golfo San Jorge are probably individual variations.

fraus, 1907. *Diplodon* HYRIIDAE

1907*a*. AMNBA, 14:467, pl. 18, fig. 129. Unnecessary replacement name for *Modiola contorta* Borchert, 1901:27, pl. 2, fig. 3–4, not *Unio contortus* Heude.
1969. Parodiz, ACM, 40:74, pl. 7, fig. 5.

= *Diplodon contortus* (Borchert, 1901), **new combination.**

Type Locality.—Paraná, Entre Rios (Borchert).

Holotype.—Examined by Parodiz in 1971 in the Senckenberg Museum, Frankfurt.

Stratigraphy.—Paraná Formation (Upper Miocene).

Remarks.—The name *contorta* is not preoccupied in *Diplodon*; therefore, *Diplodon fraus* Ihering, based on the type of *Modiola contorta* Borchert, is an unnecessary replacement name in that genus. This species belongs to the *Diplodon parallelipipedon* group.

freti, 1907. *Venericardia sulcolunularis* CARDITIDAE

1907*a*. AMNBA, 14:347. Not figured.

Type Locality.—Carmen Sylva, Tierra del Fuego.

Type.—Not in the collection.

Stratigraphy.—Magellanian Formation (Lower Oligocene).

fuegina, 1907. *Struthiolaria chilensis* STRUTHIOLARIIDAE

1907*a*. AMNBA, 14:343. Not figured.

= *Struthiolaria chilensis* Philippi, 1887.

Type Locality.—Carmen Sylva, Tierra del Fuego.

Stratigraphy.—Magellanian Formation (Lower Oligocene).

Remarks.—There are no specimens in the collection under the name *fuegina,* but there is one specimen of *S. chilensis,* labelled by Ihering as "cotypo," from Matanzas, Tertiary of Chile, received from R. A. Philippi. *Struthiolaria chilensis* is related to *S. nordenskjoldi* Wilckens, 1911, from the Tertiary of Seymour Island, Antarctica.

fueguensis, 1907. *Cominella* BUCCINIDAE: PHOTINAE

1907*a*. AMNBA, 14:343, pl. 14, fig. 97a–b.
1908. Steinmann and Wilckens, 4(6):60, pl. 7, fig. 3–5. *Cominella obesa* "var." *fueguina.*
1914. NPRMP, 1(3):105 (Superpatagonico).

= *Cominella* (*Austrocominella*) *fueguensis* Ihering.

Type Locality.—Barrancas de Carmen Sylva, Tierra del Fuego.

Syntypes.—#858, two specimens, coll. Backhausen.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—This species is the type of the subgenus *Austrocominella* Ihering, 1907. It was also found by Feruglio at Río Turbio.

gibber, 1907. *Tellina* TELLINIDAE

1907*a*. AMNBA, 14:456, pl. 18, fig. 126a–b.
1914. NPRMP, 1(3):59 (Pampeano and post-Pampeano).

Type Locality.—Puerto Militar (Puerto Belgrano), Buenos Aires Province.

Syntypes.—#488, four valves from what Ihering indicates as Pampeano, and one valve post-Pampeano, coll. Ameghino.

Stratigraphy.—Belgrano Formation (Pleistocene) and Recent.

Remarks.—The Recent distribution of this species is from Rio de Janeiro to Chubut.

golfina, 1907. *Gibbula iheringi* "var." BUCCINIDAE: PHOTINAE

1907*a*. AMNBA, 14:133. Not figured.
1914. NPRMP, 1(3):74 (Patagonico).

= *Gibbula iheringi* Cossmann, 1899.

Type Locality.—Cabo Tres Puntas, Santa Cruz.

Holotype.—#582, coll. Ameghino, 1900 (by monotypy).

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—Ihering commented "Un des exemplaires que je possede" probably referring to *G. iheringi* Cossmann from Yegua Quemada, of which the "var." *golfina* is a synonym.

golfonia, 1914. *Cominella* BUCCINIDAE: PHOTINAE

1914. NPRMP, 1(3):105, pl. 3, fig. 5 (Patagonico Medio).

= *Cominella* (*Austrocominella*) *golfonia* Ihering.

Type Locality.—Cabo Tres Puntas, Santa Cruz.

Syntypes.—#860, seven specimens, coll. Ameghino.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—*Cominella iheringi* Feruglio, 1935, from the Salamanca Formation has affinities with this species.

gracilior, 1897. *Marginella* MARGINELLIDAE

1897*b*. RMP, 2:308, text fig. 18 (Formação Santacruzense).
1907*a*. AMNBA, 14:200. *Neoimbricaria*.
1914. NPRMP, 1(3):107 (Superpatagonico).

= *Neoimbricaria quemadensis* (Ihering).

Type Locality.—Yegua Quemada, Santa Cruz.

Holotype.—#867, coll. Ameghino, 1900 (by monotypy).

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—See *Marginella confinis* Ihering and *Marginella quemadensis* Ihering.

gracilior, 1896. *Voluta* VOLUTIDAE

1896. NDMG, 7:96. New name for *Voluta gracilis* in Philippi (1887), not *Voluta gracilis* Swainson, 1842.
1897*b*. RMP, 2:305. *Voluta philippianus* Dall.

1907*a*. AMNBA, 14:206. *Proscaphella gracilior* (Patagonico).
1914. NPRMP, 1(3):110. *Cymbiola* (*Miomelon*) *gracilior*.

= *Miomelon gracilior* (Ihering).
Type Locality.—Santa Cruz.
Syntypes.—#889, Santa Cruz, one specimen and one cast, coll. J. Bicego, 1897.
Stratigraphy.—Patagonian Formation (Lower Miocene).

gracilis, 1897. *Cancellaria* CANCELLARIIDAE

1897*b*. RMP, 2:310, pl. 3, fig. 11 (Formação Santacruzense).
1907*a*. AMNBA, 14:213.
1914. NPRMP, 1(3):111 (Superpatagonico).

Type Locality.—La Cueva, Santa Cruz.
Holotype.—#896, coll. Bicego, 1897 (by monotypy).
Other Lot.—#897, Cañada de los Artilleros, two specimens, coll. Ameghino.
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—*Cancellaria gracilis observatoria* Ihering is a synonym.

gradata, 1907. *Trophon inornatus* "var." MURICIDAE

1907*a*. AMNBA, 14:402. *Nomen nudum.*

Remarks.—The name *gradata* described on the same page was given to one of the two specimens of *T. inornatus fairus*. See also *Trophon varians gradata* Ihering, 1897.

gradata, 1897. *Trophon varians* "var." MURICIDAE

1897*b*. RMP, 2:297, 323 (Pan-Patagonico).
1907*a*. AMNBA, 14:403.
1914. NPRMP, 1(3):101. *T. varians "gradatus"* (Formação Araucana).

= *Trophon varians* (d'Orbigny, 1841).
Type Locality.—"Entre S. Jorge e Deseado," Santa Cruz.
Holotype.—#833, coll. Ameghino (by monotypy).
Other Lots (as Trophon varians*).*—#829, San Juan [sic] must be San Julian, four specimens, coll. Ameghino; #830, Sierra Laziar, ten specimens, coll. Ameghino; #831, Monte Espejo, five specimens, coll. Ameghino; #832, Golfo San Jorge, "Pampeano," five specimens, coll. Ameghino.
Stratigraphy.—Araucanean Formation (Pliocene) and Belgrano Formation (Pleistocene); Recent, common.

guaranitica, 1899. *Ostrea* OSTREIDAE

1899*b*. ASCA, 47:63–64 (Piso Sehuense, Formación Guaranitica).
1902*a*. AMNBA, 7:116.
1903. AMNBA, 9:213.
1907*a*. AMNBA, 14:50 (Sehuenéen).
1914. NPRMP, 1(3):2 (Guaranien).

= *Exogyra guaranitica* (Ihering).
Type Locality.—Park-Aik (Sehuen-Aik) Sehuen Valley, Santa Cruz.
Syntypes.—One lot of nine specimens is in the collection with one specimen, #149, marked as "type."
Stratigraphy.—Sehuenan Formation (Paleocene).

Remarks.—An incomplete specimen in the Ihering Collection, #150 from San Juan Creek, Santa Ana, Misiones, was identified as *guaranitica* but probably does not belong in the same Patagonian species. Ihering (1907*a*:52) stated that "Les huîtres de San Juan. . .ne peuvent non plus servir pour reconnaître l'âge géologique, de depôts respectifs [Upper Cretaceous or Tertiary]." The name "*guaranitica*" was taken from an ethnic root of the north, and is confusing for a Patagonian species. See Stratigraphic Units.

guassus [sic], 1907. *Psammobia* PSAMMOBIIDAE

1907*a*. AMNBA, 14:312, pl. 14, fig. 95 (Patagonico).
1914. NPRMP, 1(3):57. *Psammobia guassu* (Patagonico Inferior).

= *Gari guassu* Ihering (*guassus* is a typographical error).
Type Locality.—Bajo de San Julian, Santa Cruz.
Holotype.—#478, one large cast, coll. Ameghino (by monotypy).
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—Ihering (1914) explained that the word "guassú" in Tupi language means large and can be used, Latinized, as an adjective; but Tupi are Indians of southern Brazil, and why the word was used for a Patagonian species is difficult to understand.

hauthali, 1907. *Mytilus chorus* "var." MYTILIDAE

1897*b*. RMP, 2:232, pl. 9, fig. 55. *Mytilus* aff. *chorus.*
1902. Ortmann, p. 120, pl. 25, fig. 1a–b.
1907*a*. AMNBA, 14:273. *Mytilus chorus* "var." *hauthali.*

= *Chloromya hauthali* (Ihering).
Type Locality.—Mayten, Río Chubut.
Syntypes.—#304, three specimens in a conglomerate, coll. Hauthal.
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—This species has affinities with *Mytilus pseudochorus* Doello-Jurado, 1922.

hauthali, 1904. *Strophocheilus* MEGALOBULIMIDAE

1904. RMLP, 11:14, pl. 2, fig. 12.
1907*a*. AMNBA, 14:463 (Notostylopéen).
1914. NPRMP, 1(3):70 (Cretáceo Superior).
1949*b*. Parodiz, Physis, 20:183. *Megalobulimus hauthali* (Ihering).
1969. Parodiz, ACM, 40:175

= *Megalobulimus hauthali* (Ihering).
Type Locality.—Cañadón Blanco, between the rivers Senguer and Chubut.
Type Material.—Lectotype, #557, coll. Ameghino (not Hauthal); three paralectotypes, same data as lectotype.
Stratigraphy.—Casamayor Formation (Lower Eocene); also Musters Formation (for Colhue Huapi, Astraponotense of authors; Upper Eocene).
Remarks.—The lectotype was subsequently designated by Parodiz (1969:176). As in the case of *Strophocheilus chubutensis,* the collector of the type lot was C. Ameghino, not Hauthal as reported by Ihering (1914); the original label is in the handwriting of C. Ameghino, and indicates "capas de *Astraponotus,*" not *Notostylops. Strophocheilus avus* Parodiz (1949*b*) was synonymized with *S.* (*Megalobulimus*) *hauthali* (Ihering) by Parodiz (1969).

hauthali**,** 1907. *Turritella* TURRITELLIDAE

1907*a*. AMNBA, 14:163, pl. 5, fig. 22.
1914. NPRMP, 1(3):90 (Patagonico Inferior).

Type Locality.—Camarones, Chubut.

Syntypes.—#731, six specimens, coll. Ameghino.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—This species has affinities with *Turritella malaspina* Ihering of the Salamanca Formation.

huttoni**,** 1907. *Cardium* CARDIIDAE

1907*a*. AMNBA, 14:291.

Holotype.—A single example sent to Ihering by F. W. Hutton; not in the collection.

Type Locality.—Waipara, New Zealand.

Stratigraphy.—Miocene.

Remarks.—Briefly diagnosed in the discussion of *Cardium philippi* Ihering. Ihering (1907*a*) proposed the new name *C. huttoni* for a specimen from the Miocene of Waipara, New Zealand, sent by F. W. Hutton and misidentified as *Cardium multiradiatum* Sowerby, 1833 (not Philippi, 1887). The type may have been returned to Hutton, but this is not certain. Also see *Cardium philippii* Ihering.

improvisa**,** 1914. *Columbella* (*Anachis*) COLUMBELLIDAE

1914. NPRMP, 1(3):106. Not figured (Superpatagonico).

Type Locality.—Yegua Quemada, Santa Cruz.

Syntypes.—#861, seven specimens, coll. Ameghino.

Stratigraphy.—Patagonian Formation (Lower Miocene).

indecussata**,** 1899. *Turritella breantiana* "var." TURRITELLIDAE

1897*b*. RMP, 2:288. *Turritella breantiana* d'Orbigny.
1899*a*. NJMGP, 2:26. *Turritella b.* "var." *indecussata.*
1907*a*. AMNBA, 14:164, pl. 5, fig. 23, *T. breantiana.*
1914. NPRMP, 1(3):89 refers to fig. 23 of 1907*a* as *T. indecussata.*

= *Turritella breantiana* d'Orbigny, 1847.

Type Locality.—Santa Cruz.

Holotype.—#4229, coll. J. Bicego, 1895 (by monotypy).

Other Lots.—#721, Manantial Salado, one specimen, coll. Ameghino; #722, Bajo de las Flechas, Santa Cruz, one specimen, coll. Ameghino; #723, Punta Casamayor, one specimen, coll. Ameghino; #724, Golfo San Jorge, one specimen, coll. Ameghino; #725, Cabo Tres Puntas, two specimens, coll. Ameghino; #726, Cañada de los Artilleros, four specimens, coll. Ameghino.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—There are no lots labelled as *T. breantiana* in the collection to compare with "var." *indecussata. Turritella iheringi* Cossmann, 1898, and *T. tricincta* Ihering, 1897 (not *T. tricincta* Hutton, 1873), are synonyms of *T. breantiana* d'Orbigny, 1847.

indistincta**,** 1897. *Mactra* MACTRIDAE

1897*b*. RMP, 2:262, text fig. 3 (Formação Santacruzense).
1907*a*. AMNBA, 14:320.

1914. NPRMP, 1(3):60 (Superpatagonico).

= *Mactra patagonica* d'Orbigny, 1846.

Type Locality.—Yegua Quemada, Santa Cruz.

Lectotype.—#497, the only specimen that remains in the collection from the three valves reported by Ihering (1914), coll. Ameghino, 1905, here designated.

Stratigraphy.—Patagonian Formation (Lower Miocene).

jeguaensis, 1897. *Tellina* TELLINIDAE

1897*b*. RMP, 2:260, pl. 5, fig. 33 (Formação Santacruzense).
1907*a*. AMNBA, 14:315. ?"var." of "*striata*" Turton.
1914. NPRMP, 1(3):58 (Superpatagonico).

Type Locality.—Yegua Quemada, Santa Cruz.

Syntypes.—#484, three specimens, coll. Ameghino, 1895.

Other Lot.—#485, Cañada de los Artilleros, one valve, coll. Ameghino.

Stratigraphy.—Patagonian Formation (Lower Miocene).

jorgea, 1914. *Mactra* MACTRIDAE

1914. NPRMP, 1(3):60, pl. 2, fig. 6a–b (Patagonico Inferior).

Type Locality.—Southeast of Punta Nova (Nueva), Santa Cruz.

Syntypes.—#496, two specimens, crystalized into chalcedony, coll. Ameghino, 1905.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—The hinge area of the specimens is missing, for which reason Ihering stated "duvidosa a sua posição systematica." The valves are shorter but with the apex higher than in *Mactra patagonica* d'Orbigny.

jorgensis, 1907. *Bulla patagonica* "var." ?RETUSIDAE

1907*a*. AMNBA, 14:121. Not figured.
1914. NPRMP, 1(3):69 (Supra e Patagonico Medio).

= ?*Retusa patagonica* (Ihering), **new combination.**

Locality.—Punta Casamayor, Santa Cruz.

Holotype.—#554, coll. Ameghino, 1900 (by monotypy).

Other Lot.—#553, one specimen, Golfo San Jorge, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

jorgensis, 1907. *Cardium pisum* "var." CARDIIDAE

1907*a*. AMNBA, 14:294. Not figured.
1914. NPRMP, 1(3):48 (Patagonico Medio).

= *Cardium jorgensis* Ihering, 1907, **new status.**

Type Locality.—Cabo Tres Puntas, Santa Cruz.

Holotype.—#405, coll. Ameghino, 1905 (by monotypy).

Stratigraphy.—Patagonian Formation (Lower Miocene).

jorgensis, 1907. *Hadriania* MURICIDAE: OCENEBRINAE

1907*a*. AMNBA, 14:185, pl. 6, fig. 32a–b.
1914. NPRMP, 1(3):99 (Patagonico Medio a Inferior).

= *Crassilabrum jorgensis* (Ihering), **new combination.**

Type Locality.—Punta Casamayor, Santa Cruz.

Holotype.—#804, coll. Ameghino, 1900 (by monotypy).

Other Lot.—#805, two specimens, Río Chico, Chubut, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—The valid generic name is *Crassilabrum* Jousseaume, 1880. The replacement name *Antimurex* Cossmann, 1903, on grounds of preoccupation, is not valid because the presumed senior homonym *Crassilabrum* Megerle in Scudder (1882*a*:88 and 1882*b*:81) is a *nomen nudum.*

jorgensis, 1907. *Pecten* PECTINIDAE

1907*a.* AMNBA, 14:258, pl. 9, fig. 57a, d.
1914. NPRMP, 1(3):34. *Myochlamys* (Patagonico Medio).

= *Chlamys* (*Zygochlamys*) *jorgensis* (Ihering); see Morra (1985).

Type Locality.—Punta Casamayor, Santa Cruz.

Syntypes.—#274, one complete specimen plus one valve, coll. Ameghino.

Other Lots.—#275, same locality, one valve, coll. Ameghino, 1900; #276, Punta Nodales, three valves, coll. Ameghino, 1900; #277, Punta Nova (Nueva), one intact specimen and six other valves, coll. Ameghino, 1900; #278, Fondo del Bajo de San Julian, Santa Cruz, one valve, coll. Ameghino, 1900; #279, Río Chico, Chubut, one valve, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—Found also at Cerro Otto by E. Feruglio.

jorgensis, 1907. *Pleurotoma* TURRIDAE

1907*a.* AMNBA, 14:220, pl. 7, fig. 47.
1914. NPRMP, 1(3):113 (Patagonico Inferior).

Type Locality.—Cabo Tres Puntas, Santa Cruz.

Holotype.—#906, incomplete specimen, coll. Ameghino, 1900 (by monotypy).

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—A more elongated species than *Pleurotoma santacruzensis* Ihering, otherwise very similar (both species based on a single specimen).

jorgensis, 1907. *Polynices* NATICIDAE

1907*a.* AMNBA, 14:158, pl. 5, fig. 19.
1914. NPRMP, 1(3):84 (Patagonico Medio).

= *Polynices famula* (Philippi).

Type Locality.—Cabo Tres Puntas, Santa Cruz.

Holotype.—#671, coll. Ameghino, 1900 (by monotypy).

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—Ihering (1907*a*:158) states, "Cette espèce paraît voisine de la *P. famula* Phil., mais . . . l'overture plus grand. . . ." In the unique specimen the aperture is broken, but all other visible characters are equal to *famula,*

juliana, 1907. *Arca* ARCIDAE

1907*a.* AMNBA, 14:238, pl. 7, fig. 5a–b.
1914. NPRMP, 1(3):18 (Patagonico Inferior).

= *Anadara juliana* (Ihering), **new combination.**

Type Locality.—Pan de Azucar, Santa Cruz (Formação Patagonica Inferior).

Holotype.—#115, single valve, coll. Ameghino, 1900 (by monotypy).
Stratigraphy.—Patagonian Formation (Lower Miocene).

juliana, 1907. *Bullinella* SCAPHANDRIDAE [CYLICHNIDAE]

1907*a*. AMNBA, 14:121, pl. 4, fig. 6.
1914. NPRMP, 1(3):69 (Superpatagonico).

= *Cylichna juliana* (Ihering).
Type Locality.—Cañada de los Artilleros, San Julian, Santa Cruz.
Syntypes.—#555, nine specimens, coll. Ameghino, 1900.
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—*Bullinella* Newton, 1891 (= *Cylichna* Lovén, 1846). The peristoma in this species is very thick and marginated.

juliana, 1907. *Calyptraea pileus* "var." CREPIDULIDAE

1907*a*. AMNBA, 14:148. Not figured.
1914. NPRMP, 1(3):83 (Patagonico Inferior).

= *Calyptraea pileus* Lamarck, 1822.
Type Locality.—Fondo del Bajo de San Julian, Santa Cruz.
Holotype.—#654, coll. Ameghino, 1900 (by monotypy).
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—The description of the "var." was not comparative and insufficient for recognition of a distinct form, but the type specimen corresponds to *Calyptraea pileus* Lamarck ranging from the middle Tertiary to Recent. Do not confuse with *Calyptraea pileolus* d'Orbigny (= *Trochita americana* Gray).

juliana, 1907. *Cerithiopsis* CERITHIOPSIDAE

1907*a*. AMNBA, 14:169, text fig. 7.
1914. NPRMP, 1(3):92 (Superpatagonico).

Type Locality.—Cañada de los Artilleros, Santa Cruz.
Holotype.—#750, coll. Ameghino, 1900 (by monotypy).
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—In its large number of whorls and deep sutures it resembles the Recent *Cerithiopsis exilis* (C. B. Adams, 1850) which ranges from the Antilles to Brazil, but the whorls are less convex.

juliana, 1907. *Corbula pulchella* CORBULIDAE

1907*a*. AMNBA, 14:322, pl. 12, fig. 81a–c.
1914. NPRMP, 1(3):62. *Corbula pulchella hatcheri* Ortmann (Superpatagonico, Patagonico Inferior).

= *Corbula hatcheri* Ortmann, 1900.
Type Locality.—Punta Nova (Nueva) Santa Cruz.
Syntypes.—#504, four specimens, coll. Ameghino, 1900.
Other Lots.—#503, Mouth of Santa Cruz River, one specimen of *C. hatcheri* received from Ortmann; #505, south of Colhue Huapi, one specimen plus one valve, coll. Ameghino, 1900; #506, Golfo San Jorge, five specimens, coll. Ameghino, 1900; #507, Camarones, 60 specimens, coll. Ameghino, 1900; #508, Cañada de los Artilleros, 15 specimens, coll. Ameghino, 1900.
Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—This species has similarities with the living *Corbula lyoni* Pilsbry; Recent, Buenos Aires and Uruguay.

juliana, 1907. *Dentalium sulcosum* "var." DENTALIIDAE

1907*a*. AMNBA, 14:224.
1914. NPRMP, 1(3):67. *Dentalium sulcosum julianum* (emend.) (Patagonico Superior).

Type Locality.—Cañada de los Artilleros, Santa Cruz.
Syntypes.—#541, ten specimens, coll. Ameghino, 1900.
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—See *Dentalium sulcosum camaronesis.*

juliana, 1907. *Myochlamys* PECTINIDAE

1902. Ameghino, ASCA, 54:224 (*in litteris* as *Chlamys*).
1907*a*. AMNBA, 14:253, pl. 8, fig. 56a–b. *Myochlamys.*
1914. NPRMP, 1(3):34 (Patagonico Inferior, Medio).

= *Chlamys juliana* (Ihering).
Type Locality.—Southeast of Punta Nova (Nueva), Santa Cruz.
Holotype.—#280, coll. Ameghino, 1900 (by monotypy).

Other Lots.—#281, Pan de Azucar, one valve, coll. Ameghino, 1900; #282, Punta Casamayor, one valve, coll. Ameghino, 1900; #283, north of Río Seco and San Julian, Santa Cruz, one valve, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

juliana, 1907. *Neoimbricaria quemadensis* "var." MARGINELLIDAE

1907*a*. AMNBA, 14:199. Not figured.
1914. NPRMP, 1(3):108 (Superpatagonico).

= *Neoimbricaria quemadensis* (Ihering).
Type Locality.—San Julian, Santa Cruz.
Syntypes.—#871, 15 specimens, coll. Ameghino, 1900.
Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—This form was diagnosed within the discussion of *N. quemadensis* as having an obsolete spiral sulcus, but this is a character extremely variable in *quemadensis* and other species. A synonym of this species is *N. gracilior* (Ihering).

juliana, 1907. *Urosalpinx elegans* "var." MURICIDAE: OCENEBRINAE

1907*a*. AMNBA, 14:187, pl. 6, fig. 34a–b.
1914. NPRMP, 1(3):98. *Urosalpinx elegans* Ortmann (Superpatagonico).

= *Ocenebra* (*Ocinebrina*) *elegans* (Ortmann), **new combination.**
Type Locality.—Cañada de los Artilleros, Santa Cruz.
Syntypes.—#799, ten specimens, coll. Ameghino, 1900.
Other Lot.—#798, Yegua Quemada, Santa Cruz, two specimens, C. Ameghino.
Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—The species *U. elegans* Ortmann does not belong in *Urosalpinx* but rather with *Ocinebrina* Jousseaume, 1880. What Ihering describes as "var." *juliana* are juveniles and not distinct from *elegans.*

julianum, 1907. *Pitar* VENERIDAE

1907*a*. AMNBA, 14:302, pl. 11, fig. 74a–b.
1914. NPRMP, 1(3):51 (Patagonico Inferior).

Type Locality.—Bajo de San Julian (in the original "Baie de San Julian") Santa Cruz.

Syntypes.—#424, three fragments of valves, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—The incomplete valves do not show well the configuration of the shells, but from the umbo and cardinal area they are clearly a species of *Pitar*. E. Feruglio (1949–1950) mentions the species for Río Turbo.

julianus, 1907. *Vermetus* ANNELIDA: POLYCHAETA

1907*a*. AMNBA, 14:166, pl. 5, fig. 6.
1914. NPRMP, 1(3):92 (Patagonico Inferior).

Type Locality.—Manantial Salado, San Julian.

Syntypes.—#745, a conglomerate with several individuals.

Other Lots.—#746, Pan de Azucar, Santa Cruz, numerous in rock, coll. Ameghino, 1900; #747, Cañada de los Artilleros, three specimens, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—These are not molluscs but probably tubes of polychaetes (Annelida).

juliensis, 1907. *Pododesmus* ANOMIIDAE

1907*a*. AMNBA, 14:267, pl. 10, fig. 65a–b.
1914. NPRMP, 1(3):27 (Patagonico Inferior).

Type Locality.—Pan de Azucar, Santa Cruz.

Syntypes.—#217, Manantial Salado, six valves, coll. Ameghino, 1900; #219, Cabo Tres Puntas, Santa Cruz, one valve, coll. Ameghino, 1905.

Stratigraphy.—Patagonian Formation (Lower Miocene).

kokeni, 1899. *Crassatella* CRASSATELLIDAE

1899*a*. NJMGP, 2:17, pl. 2, fig. 2.
1907*a*. AMNBA, 14:279. *Crassatellites.*
1914. NPRMP, 1(3):40 (Patagonico Inferior).

Type Locality.—Santa Cruz.

Syntypes.—#325, five valves, coll. J. Bicego.

Other Lots.—#326, Cabo Tres Puntas, three valves, coll. Ameghino, 1900; #327, Punta Casamayor, two specimens, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

lacustris, 1907. *Hadriania* MURICIDAE: OCENEBRINAE

1907*a*. AMNBA, 14:185. New name for material misidentified as *Urosalpinx pyriformis* (Ihering) in Ortmann (1902:220, pl. 34, fig. 11), not *Trophon pyriformis* Ihering, 1897*b*.
1914. NPRMP, 1(3):99. *Hadriania hatcheri* Ortmann (Patagonico Medio).

= *Crassilabrum hatcheri* (Ortmann, 1900).

Other Lots.—#802, Punta Casamayor, one specimen, C. Ameghino, 1900.; #803, Punta Nodales, one specimen, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

lahillei*, 1907. *Calliostoma TROCHIDAE

1907*a*. AMNBA, 14:440, pl. 17, fig. 118 ("Pampeano").

= *Calliostoma jucundum* (Gould, 1849).

Type Locality.—Punta Villarino, Chubut.

Type.—Not in the collection.

Remarks.—Included by Ihering among the species from the "Pampeano" (Pleistocene), this is not a fossil.

lahillei*, 1907. *Pitar VENERIDAE

1907*a*. AMNBA, 14:303, pl. 11, fig. 75a–b. Not fully described but reported as a new, Recent species in the discussion of *Pitar julianum*.

Remarks.—This form, being Recent, is not in the collection but the figures show a higher shell than the living *Pitar rostrata* (Koch). As the latter species is extremely variable, *P. lahillei* may be only an individual variation. See *Pitar lahillei ortmanni*.

laziarina*, 1907. *Amiantis VENERIDAE

1903. Ameghino, ASCA, 54:190. *Cytherea laziarina* Ihering, *in litteris*.
1907*a*. AMNBA, 14:414, pl. 16, fig. 110. *Amiantis*.
1914. NPRMP, 1(3):54 (Tehuelche Medio).

Type Locality.—Sierra Laziar, Santa Cruz.

Syntypes.—#431, "*Chione*" *laziarina* on label, seven valves, coll. Ameghino, 1900.

Stratigraphy.—Araucanean Formation (Lower Pliocene).

laziarina*, 1907. *Myochlamys PECTINIDAE

1897*b*. RMP, 2:323. *Pecten* aff. *centralis* Sowerby.
1902. Ameghino, ASCA, 54:190. *Pseudoamusium laziarium, nomen nudum.*
1907*a*. AMNBA, 14:409, pl. 16, fig. 104a–b.
1914. NPRMP, 1(3):35 (Formação Araucana).

= *Chlamys laziarina* (Ihering).

Type Locality.—Sierra Laziar, Santa Cruz.

Syntypes.—#284, four valves, coll. Ameghino, 1900; #285, Bajo de la Pava, Santa Cruz, one valve, coll. Ameghino, 1897.

Stratigraphy.—Araucanean Formation (Lower Pliocene).

laziarium*, 1907. *Calliostoma TROCHIDAE

1907*a*. AMNBA, 14:399, pl. 16, fig. 105a–b.
1914. NPRMP, 1(3):78 (Formação Araucana).

Type Locality.—Sierra Laziar, Santa Cruz.

Holotype.—#606, coll. Ameghino, 1900 (by monotypy).

Stratigraphy.—Araucanean Formation (Lower Pliocene).

levuana*, 1907. *Calyptraea CREPIDULIDAE

1907*a*. AMNBA, 14:523. New name for *Trochita araucana* in Philippi (1887:87), not *Trochita araucana* Lesson, 1831.
1914. NPRMP, 1(3):84. *Calyptraea pueyrredona* (Patagonico).

= *Calyptraea pueyrredona* Ihering.

Type Locality.—Lago Pueyrredón, Santa Cruz.

Syntypes.—#666, two specimens, Lagoa Pueyrredón, coll. Hatcher, received from Ortmann as *Galerus araucanus,* labelled as "cotypes."

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—Ihering mistakenly proposed two new names, *C. levuana* and *C. pueyrredona,* for the species misidentified by Philippi (1887) as *Trochita araucana* Lesson. The name *C. levuana* Ihering is therefore a junior objective synonym and Ihering did not list it in his 1914 catalogue, but placed the corresponding lot under *C. pueyrredona.* There are five other lots of *Calyptraea* sp. similar to lot #666 in the Ihering Collection without indication of locality.

longior, 1897. *Crassatella* CRASSATELLIDAE

1897*b*. RMP, 2:247, pl. 5, fig. 34, pl. 6, fig. 37 (Formação Santacruzense).
1902. Ortmann, p. 125, pl. 27, fig. 2. *Crassatellites.*
1907*a*. AMNBA, 14:272. *Crassatellites.*
1914. NPRMP, 1(3):40 (Superpatagonico).

Type Locality.—Yegua Quemada, Santa Cruz.

Holotype.—#328, one valve, coll. Ameghino, 1900 (by monotypy).

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—Other lot reported by Ihering (1914) from Punta Casamayor is missing from the collection. According to Feruglio (1949–1950), *C. longior* has affinities to *Crassatella chubutiensis* Feruglio. *Crassatellites* Krueger, 1823, is an unavailable name (= *Crassatella* Lamarck, 1799).

luciferus, 1904. *Helcioniscus* PATELLIDAE: NACELLINAE

1904. RMLP, 11:235, fig. 7–8.
1907*a*. AMNBA, 14:123 (araucaniense).
1914. NPRMP, 1(3):71 (Araucano ou Pampeana).

= *Cellana lucifera* (Ihering).

Type Locality.—Río Deseado, Santa Cruz.

Syntypes.—#563, two specimens, coll. S. Roth.

Stratigraphy.—"Deseado beds" coeval and equivalent to the Belgrano Formation in the north (Lower Pleistocene).

Remarks.—*Helcioniscus* Dall, 1871 (= *Cellana* H. Adams, 1869).

lujanensis, 1907. *Diplodon charruanus* HYRIIDAE

1907*a*. AMNBA, 14:468. Not figured.
1914. NPRMP, 1(3):36 ("Pampeano superior").

= *Diplodon delodontus* (Lamarck, 1819).

Type Locality.—Luján, Buenos Aires Province ("Post-Pampeano").

Syntypes.—One specimen marked "type" exists at the Museum Senckenberg, Frankfurt; in the Ihering Collection there are two other valves (#294), both also marked as "type." Neither of these are *charruanus.*

Stratigraphy.—Upper Buenos Aires Formation (Pleistocene).

Remarks.—See Parodiz (1973). I have observed fossil *Diplodon* specimens, from Luján and other places, in strata indicated as "Lujanense" (Upper Pleistocene) and none of them are similar to *D. charruanus* (d'Orbigny), but belong to various species including *D. delodontus* (Lamarck), *D. piceus* (Lea), and *D. rhu-*

acoicus (d'Orbigny). See Parodiz, 1968:7. *Unio charruanus* "var." *lujanensis* Döring (1884:328) is a *nomen nudum.*

madryna, 1907. *Ostrea* OSTREIDAE

1907*a*. AMNBA, 14:407, pl. 15, fig. 101a–d.
1914. NPRMP, 1(3):25 (Formação Araucana).

Type Locality.—Puerto Madryn, Bahía Nueva, Chubut.

Syntypes.—#197, seven isolated valves, coll. Ameghino, 1900.

Stratigraphy.—Araucanean Formation (Pliocene).

Remarks.—*Ostrea madryna* is intermediate between *O. hatcheri* Ortmann and *O. orbignyi* Ihering.

magellanica, 1899. *Pinna semicostata* "var." PINNIDAE

1899*a*. NJMGP, 2:213. *Pinna.*
1907*a*. AMNBA, 14:242. *Atrina magellanica.*
1914. NPRMP, 1(3):19 (Patagonico Medio).

= *Atrina magellanica* (Ihering).

Type Locality.—Santa Cruz.

Syntypes.—#131, ten valves (fragments); #132, Cabo Tres Puntas, two incomplete specimens, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene); also Magellanian Formation (Lower Oligocene) (Feruglio, 1949–1950, at Epuyen and Arroyo Nireco).

magellanica, 1907. *Ringicula* RINGICULIDAE

1907*a*. AMNBA, 14:120, pl. 4, fig. 5.
1914. NPRMP, 1(3):69 (Patagonico Inferior).

Type Locality.—Camarones, Chubut.

Syntypes.—#550, two incomplete specimens, coll. Ameghino.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—This species is similar to the Recent *R. semistriata* (d'Orbigny), but with fewer whorls and larger shell.

major, 1899. *Cancellaria gracilis* "var." CANCELLARIIDAE

1899*a*. NJMGP, 2:35, pl. 2, fig. 10.
1907*a*. AMNBA, 14:215, pl. 7, fig. 43. *Sveltia major.*
1914. NPRMP, 1(3):111 (Superpatagonico).

= *Naronia* (*Sveltia*) *major* (Ihering), **new combination.**

Type Locality.—Santa Cruz.

Holotype.—#898, in clayish rock containing specimens of *Struthiolaria ameghinoi,* coll. J. Bicego, 1895 (by monotypy).

Stratigraphy.—Patagonian Formation (Lower Miocene).

malaspina, 1903. *Turritella* TURRITELLIDAE

1903. AMNBA, 9:217, pl. 2, fig. 13.
1907*a*. AMNBA, 14:48.
1914. NPRMP, 1(3):91 (Salamanqueano).

Type Locality.—Malaspina, Chubut.

Syntypes.—#735, three specimens, coll. Ameghino, 1900.

Stratigraphy.—Salamanca Formation (Paleocene).

Remarks.—Feruglio (1949–1950) mentioned the species from Cañadón Perdido, north of Comodoro Rivadavia. It has affinities with *T. australis* Ihering of the Patagonian Formation.

Marginella sp. MARGINELLIDAE

1914. NPRMP, 1(3):106 (Formação Entreriana).

Locality.—La Paz, Entre Rios.

Specimens.—#862, cast of an unidentifiable species, coll. S. Roth.

Stratigraphy.—Paraná Formation (Upper Miocene).

Marginella (*Volvaria*) sp. MARGINELLIDAE

1914. NPRMP, 1(3):107.

Locality.—Cabo Tres Puntas, Santa Cruz.

Specimen.—#864, one specimen, coll. Ameghino.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—*Volvaria* Jousseaume, 1875 (= *Volvarina* Hinds, 1844).

matanzasense, 1907. *Dentalium* ?DENTALIIDAE

1907*a*. AMNBA, 14:224. New name for *Dentalium sulcosum* in Philippi, 1887, not *D. sulcosum* Sowerby, 1846.

1914. NPRMP, 1(3):66 ("Terciario antiguo").

Type Locality.—Matanzas, Chile.

Type.—#531, one specimen received from R. A. Philippi.

Stratigraphy.—Probably Navidad Formation (Miocene).

matthewi, 1914. *Siphonalia* FASCIOLARIIDAE: FUSININAE

1914. NPRMP, 1(3):102, pl. 3, fig. 14 (Patagonico).

= *Fusinus subrectum* (Ihering).

Type Locality.—Golfo San Jorge, Santa Cruz.

Holotype.—#845a, one cast, distorted by pressure, with fragments of the shell, coll. Ameghino (by monotypy).

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—This species and *S. nodocincta* Ihering are both synonyms of *Fusinus subrectum* (Ihering).

mendozana, 1907. *Exogyra ostracina* OSTREIDAE

1907*a*. AMNBA, 14:37, text fig. 1 (étage Rocanéen).

= *Exogyra mendozana* Ihering.

Type Locality.—"Territorios Nacionales al Sud de Mendoza"; = present Neuquen Province, or Río Negro.

Holotype.—#4455 (by monotypy).

Stratigraphy.—Roca Formation (Paleocene).

Remarks.—Label data on the type: "from Fl. Ameghino collection found 15 April [1882]." Not listed in catalogue (Ihering, 1914). The specimen was found together with *Gryphaea burckhardti* Böhm which is known from the Roca Formation.

meridionalis, 1897. *Dosinia* VENERIDAE

1897*b*. RMP, 2:256, pl. 6, fig. 41 (Formação Santacruzense).
1907*a*. AMNBA, 14:300.
1914. NPRMP, 1(3):51 (Superpatagonico).

Type Locality.—Yegua Quemada, Santa Cruz.

Syntypes.—#419, five valves, coll. Ameghino; #420, Cañada de los Artilleros, one small valve, coll. Ameghino; #421, Paraná, three casts and fragments of valves, coll. J. Bicego, 1895.

Stratigraphy.—Patagonian Formation (Lower Miocene); Paraná Formation (Upper Miocene); Araucanean Formation (Pliocene); Recent.

militaris, 1907. *Calliostoma* TROCHIDAE

1907*a*. AMNBA, 14:438, pl. 17, fig. 116 (Pampeano).

Type Locality.—Puerto Militar (now Puerto Belgrano), Prov. Buenos Aires).

Syntypes.—Described from two specimens; neither are in the Ihering Collection or his 1914 catalogue under this name; the lot used in the description of *C. militaris* is under *C. dalli* in the Ihering Collection, labelled with an incorrect locality (Deseado). Priority of *C. militaris* over *C. dalli* follows Clench and Turner (1960:75).

Stratigraphy.—Belgrano Formation (Pleistocene).

militaris, 1907. *Tornatina* SCAPHANDRIDAE [CYLICHNIDAE]

1907*a*. AMNBA, 14:435, pl. 17, fig. 133 (Pampeano).

= *Tornatina candei* (d'Orbigny, 1841). See Carcelles and Parodiz, 1938.

Type Locality.—Puerto Militar (now Puerto Belgrano), Prov. Buenos Aires.

Syntypes.—Two specimens, coll. Ameghino.

Stratigraphy.—Belgrano Formation (Pleistocene); Recent.

monoceros, 1907. *Trophon* MURICIDAE

1907*a*. AMNBA, 14:183, pl. 14, fig. 92.
1914. NPRMP, 1(3):98. *Entacanthus* (Patagonico).

= *Thais* (*Stramonita*) *monoceros* (Ihering), **new combination.**

Type Locality.—Santa Cruz.

Syntypes.—#801, two specimens, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

montenus, 1907. *Trophon varians* MURICIDAE

1907*a*. AMNBA, 14:404. Not figured.
1914. NPRMP, 1(3):101 (Formação Araucana).

= *Trophon varians* (d'Orbigny, 1841).

Type Locality.—Monte Espejo, Santa Cruz.

Syntypes.—#834, three specimens.

Stratigraphy.—Araucanean Formation (Pliocene).

Remarks.—In the original description two specimens were cited, but only one specimen was noted in the 1914 catalogue.

multicoronatus, 1907. *Vermetus* VERMETIDAE

1907*a*. AMNBA, 14:167, pl. 5, fig. 27.
1914. NPRMP, 1(3):92 (Patagonico Inferior).

= *Dendropoma multicoronatus* (Ihering), **new combination.**

Type Locality.—North of Río Seco (this may be the same as Monte Espejo).

Syntypes.—#748, three specimens (Río Seco and San Julian mixed).

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—The fragments of the tubes seem to belong in the genus *Dendropoma* Mörch, 1861 (*nomina conservanda* over *Spiroglyphus* Daudin, 1800; *Siphonium* Gray, 1847. The only species known in the southwestern Atlantic is *D. irregularis* (d'Orbigny).

multicostata, 1897. *Cucullaea* CUCULLAEIDAE

1897*b*. RMP, 2:240, pl. 4, 20 and pl. 5, fig. 29.
1899*a*. NJMGP, 2:13.
1904. RMLP, 11:9, pl. 1, fig. 2–4.
1907*a*. AMNBA, 14:232.
1914. NPRMP, 1(3):15 (Patagonico Inferior and Superpatagonico).

Type Locality.—La Cueva, Santa Cruz.

Holotype.—#93, coll. Ameghino (by monotypy).

Other Lots.—#94, Santa Cruz, three valves, coll. Bicego, 1897; #95, Cañada de los Artilleros, one valve, coll. Ameghino, 1900; #96, Punta Casamayor, six complete specimens and five valves, coll. Ameghino, 1900; #97, Sierra de los Baguales, four specimens, coll. Hauthal.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Myochlamys, 1907. PECTINIDAE

1907*a*. AMNBA, 14:106, 251. New genus.

Remarks,—Genus-group name proposed to replace *Chlamys* Röding, 1798, which was thought to be invalid. The type species of *Chlamys* Röding is *Pecten islandicus* Müller, 1776, by subsequent designation of Hermannsen, 1846, and that species would also be the type species of *Myochlamys* Ihering. Since names from the Bolten Collection are now accepted by the ICZN as authored by Röding (1798), *Myochlamys* Ihering is an unnecessary replacement name and junior objective synonym of *Chlamys* Röding. In any event, *Myochlamys* Ihering, 1907, is preoccupied by *Myochlamys* Fairmaire, 1876 (Insecta: Coleoptera).

necocheanus, 1907. *Trophon* MURICIDAE

1907*a*. AMNBA, 14:404, pl. 14, fig. 106 (Formação Araucano).
1914. NPRMP, 1(3):100. *Trophon laciniatus necocheanus*.

= *Trophon* (*Austrotrophon*) *lamellosus* (Gmelin, 1791).

Type Locality.—Necochea, Prov. of Buenos Aires.

Type.—Not in the collection.

Stratigraphy.—Araucanean Formation (Pliocene); Recent.

Remarks.—Lot #823 contains two specimens from Sierra Laziar and was labelled by Ihering as "Type," but this does not agree with the type locality published in the original description. The two specimens are juveniles of *T. lamellosus* (Gmelin). Feruglio (1949–1950:268) reported the affinities of *T. necocheanus* Ihering with *T. disparides* Wilckens (1911) from Seymour Island in the Antarctic.

negroina, 1907. *Chlamys patagonensis* "var." PECTINIDAE

1907*a*. AMNBA, 14:22, pl. 3, fig. 11 (étage Rocanéen).

= *Chlamys patagonensis* (d'Orbigny, 1842).

Type Locality.—Río Negro, kilometers 1216 and 1217.

Type.—Not in the collection and not listed in the 1914 catalogue.

Stratigraphy.—?Roca Formation.

Remarks.—Ihering (1907*a*) said he could not "Juger définitivement de la relation de cette forme avec *Ch. patagonensis* de la formation patagonienne."

neuquena, 1907. *Ostrea* OSTREIDAE

1899*b*. ASCA, 47:64. *Ostrea hemispherica* d'Orbigny.
1907*a*. AMNBA, 14:45, text fig. 3a–c.
1914. NPRMP, 1(3):22 (Cretáceo Superior).

Type Locality.—Roca, Río Negro (not Neuquen as the species-group name suggests).

Syntypes.—Those specimens figured in Ihering (1907*a*:text fig. 3a–c) including one marked #151.

Other Lots.—#152, San Juan, Puerto Santa Ana, Misiones, northeast Argentina, fragment reported from "Formación Guaranitica" of uncertain identification; #153, Roca, Río Negro; #154, Malaspina, Santa Cruz, five valves; #155, "Cretáceo de Río Negro Kilometro 1216," two valves, coll. Ameghino, 1904.

Stratigraphy.—Roca and Salamanca formations (Paleocene).

Remarks.—E. Feruglio also found the species in the "Salamanqueano" of the valley of the Río Chico. The valves from Misiones are fragments of *O. guaranitica* Ihering; those from kilometer 1216 on the Río Negro were probably from or near Roca. *Ostrea hemispherica capa* Ihering and *O. h. paca* Ihering are synonyms of this name.

nodocincta, 1907. *Siphonalia* FASCIOLARIIDAE: FUSININAE

1897*b*. RMP, 2:3299. *Siphonalia* aff. *nodosa* Martens.
1907*a*. AMNBA, 14:193, pl. 6, fig. 37. *Siphonalia nodocincta.*
1914. NPRMP, 1(3):102 (Patagonico Medio).

= *Fusinus subrectus* (Ihering).

Type Locality.—Cabo Tres Puntas, Santa Cruz.

Holotype.—#841, coll. Ameghino, 1900 (by monotypy).

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—The type specimen has only the upper part of the aperture preserved and the siphonal canal is missing. On the Argentine coast (Recent) the genus is represented by *Fusinus frenguelli* (Carcelles, 1953). The species most similar to *F. subrectus* is *F. brasiliensis* (Grabau, 1903).

nodosoplicatus, 1897. *Pecten* PECTINIDAE

1897*b*. RMP, 2:227, pl. 5, fig. 36 (Formação Santacruzense).
1907*a*. AMNBA, 14:256. *Myochlamys.*
1914. NPRMP, 1(3):31 (Patagonico Medio–Superior).

= *Chlamys* (*Zygochlamys*) *nodosoplicatus* (Ihering); see Morra (1985).

Type Locality.—La Cueva, Santa Cruz.

Syntypes.—#251, four valves, coll. Ameghino, 1900.

Other Lots.—#252, Yegua Quemada, Santa Cruz, five valves, coll. Ameghino, 1900; #253, Monte Espejo, Santa Cruz, one valve, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—The name was first given in Ihering (1897*b*:227) as *Pecten nodosopiicatus* [sic], an incorrect original spelling for *P. nodosoplicatus.*

nucleus, 1899. *Glycimeris* [sic] HIATELLIDAE

1899*a*. NJMGP, 2:23, pl. 1, fig. 7.
1907*a*. AMNBA, 14:326, pl. 12, fig. 85a–b. *Panopaea* [sic].
1914. NPRMP, 1(3):62 (Patagonico).

= *Panopea nucleus* (Ihering).

Type Locality.—Cabo Tres Puntas, Santa Cruz.

Holotype.—#515, coll. Ameghino (by monotypy).

Other Lots.—#513, Santa Cruz, one specimen, coll. J. Bicego, 1895, reported by Ihering (1914) as type but is not from type locality; #514, Corral Foyel, one cast, coll. Hauthal; #516, Sierra de los Baguales, one cast, coll. Hauthal; #4464, San Julian, coll. Ameghino; #2480, Río Foyel, coll. Ameghino.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—This species is related to *Panopea nucleoides* Wilckens (1911) from the Tertiary of Antarctica.

observationis, 1907. *Turbonilla* PYRAMIDELLIDAE

1907*a*. AMNBA, 14:144. New name for one of the specimens of *Turbonilla cuevensis* misidentified by Ortmann (1902:174, pl. 33, fig. 8a–b), not *Turbonilla cuevensis* Ihering, 1897*b*.

Type Locality.—Monte Observación, Santa Cruz.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—A questionable species; Ihering (1907*a*:144) states, "Espèce intermediaire entre *T. cuevensis* and *T. Iheringi.*"

observatoria, 1907. *Cancellaria gracilis* "var." CANCELLARIIDAE

1907*a*. AMNBA, 14:214. New name for specimens of *C. gracilis* as figured by Ortmann (1902:235, pl. 36, fig. 3a–b).

= *Cancellaria gracilis* (Ihering).

Type Locality.—Monte Observación, Santa Cruz.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—No description; in the discussion of *Cancellaria gracilis* Ihering as "différente par les caracteres de l'overture"; these characters are insufficient to identify the form.

observatoria, 1907. *Nucula* NUCULIDAE

1907*a*. AMNBA, 14:227, pl. 7, fig. 49a–b.
1914. NPRMP, 1(3):13 (Patagonico Superior).

Type Locality.—Monte Observación, Santa Cruz.

Holotype.—#70, one specimen within a lot of *Nucula semiornata* d'Orbigny received from Ortmann (by monotypy).

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—Ihering (1914:13) gives the type locality as Camarones from specimens collected by C. Ameghino in 1900, but the original description (Ihering, 1907*a*:227) states the type locality was Monte Observación from which the species derives its name. *Nucula semiornata* d'Orbigny, 1846, of which *N. reticularis* Ortmann, 1902, is a synonym, is also found at both localities.

octocostatum, 1897. *Dentalium* DENTALIIDAE

1897*b*. RMP, 2:266, pl. 4, fig. 16 (Formação Santacruzense).
1907*a*. AMNBA, 14:225. *Dentalium octocostellatum* Pilsbry and Sharp.
1914. NPRMP, 1(3):66 (Patagonico Inferior–Superior).

= *Dentalium octocostellatum* Pilsbry and Sharp, 1898.

Type Locality.—Yegua Quemada, Santa Cruz.

Syntypes.—#532, nine specimens, coll. Ameghino, 1894.

Other Lots.—#533, 24 specimens, Camarones, coll. Ameghino, 1900; #534, Cañada de los Artilleros, 100 specimens, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—*Dentalium octocostellatum* Pilsbry and Sharp (1898:211) replaced *D. octocostatum* Ihering which was preoccupied by *Dentalium octocostatum* Fraas, 1867.

Odontogryphaea, 1903. GRYPHAEIDAE

1903. AMNBA, 9:194. New subgenus of *Gryphaea* Lamarck.
1907*a*. AMNBA, 14:43, 44.
1945. Stenzel, BGSA, 56(12, pt. 2):1202.

Type Species.—*Gryphaea rostrigera* Ihering, by subsequent designation of Stenzel, 1945.

Stratigraphy.—Salamanca Formation (Paleocene).

Remarks.—Ihering made *Odontogryphaea* a subgenus of *Gryphaea* Lamarck for the early Tertiary species with crenulated margins. Stenzel considered it a genus, with *Gryphaea rostrigera* Ihering as the type species. According to Stenzel *Odontogryphaea* is convergent with *Gryphaea* but not closely related. Outside Patagonia *Odontogryphaea* is known from the Lower Eocene of the southeastern United States (*O. thirsae* [Gabb, 1862]; see Palmer and Brann, 1965:225) and from the Paleocene of France and India (Stenzel, 1945).

orbignyi, 1897. *Ostrea* OSTREIDAE

1897*b*. RMP, 2:222, pl. 9, fig. 52 (Formação Santacruzense).
1907*a*. AMNBA, 14:17, pl. 2, fig. 9 (spelled *d'orbignyi*).
1914. NPRMP, 1(3):24 (Patagonico and Superpatagonico).

Type Locality.—La Cueva, Santa Cruz.

Syntypes.—#186, six valves, coll. Ameghino, 1904.

Other Lots.—#187, Santa Cruz, two valves, coll. Ameghino; #188, Yegua Quemada, one valve, coll. Ameghino; #189, Sierra de los Baguales, five valves, coll. Hauthal; #190, Deseado, one valve, coll. S. Roth; #191, Deseado, three valves, coll. S. Roth.

Stratigraphy.—Patagonian Formation (Lower Miocene).

ortmanni, 1907. *Leda* NUCULANIDAE

1907*a*. AMNBA, 14:229. New name for *Leda oxyrhyncha* in Ortmann (1902:83, pl. 23, fig. 2a–b), not *Leda oxyrhyncha* Philippi, 1887.

= *Nuculana ortmanni* (Ihering).

Type Locality.—Santa Cruz and Río Negro (Ortmann).
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—See *Leda camaronesia* for note on *Nuculana.*

ortmanni, 1899. *Lucina* LUCINIDAE

1899*a*. NJMGP, 2:18, pl. 2, fig. 3.
1902. Ortmann, p. 131, pl. 27, fig. 5.
1907*a*. AMNBA, 14:289, *Phacoides.*
1914. NPRMP, 1(3):46 (Patagonico Inferior–Medio).

= *Lucina ortmanni* (Ihering).
Type Locality.—Cabo Tres Puntas, Santa Cruz.
Syntypes.—#384, five valves, coll. Ameghino.
Other Lots.—#382, Santa Cruz, five specimens (labelled "typo"); #383, Bajo de San Julian, one specimen, coll. Ameghino, 1900.
Stratigraphy.—Patagonian Formation (Lower Miocene).

ortmanni, 1907. *Marcia* VENERIDAE

1907*a*. AMNBA, 14:304. New name for *Venus navidadis* in Ortmann (1902:141, pl. 27, fig. 12), not *Venus navidadis* Philippi, 1887.
1914. NPRMP, 1(3):52. *Marcia navidadis* Philippi.

= *Samarangia navidadis* (Philippi).
Type Locality.—Talcahuano, Chile (Philippi, 1887).
Type.—#433, one specimen, received from the Valparaiso Museum.
Stratigraphy.—Tertiary Inferior of Chile (Philippi, 1887).

ortmanni, 1907. *Pitar lahillei* VENERIDAE

1907*a*. AMNBA, 14:453, pl. 18, fig. 124a–b.
1914. NPRMP, 1(3):51 (Pampeano).

= *Pitar rostrata* (Koch, 1844).
Type Locality.—L'ouest de Cabo Tres Puntas, Santa Cruz (probably Sierra Laziar).
Syntypes.—#425, nine valves, coll. Ameghino, 1900.
Other Lot.—#426, one valve, coll. Ameghino, 1900.
Stratigraphy.—Araucanean Formation (Pliocene).
Remarks.—Feruglio (1949–1950, vol. 3:81) reports the species from the Pliocene of San Julian. It is common in the Recent. See *Pitar lahillei* Ihering.

ortmanni, 1907. *Polynices* NATICIDAE

1907*a*. AMNBA, 14:157, pl. 5, fig. 18. New name for *Natica ovoidea* in Ortmann (1902:380), not *Natica ovoidea* Philippi, 1887.
1914. NPRMP, 1(3):85 (Patagonico–Superpatagonico).

= *Polynices famula* (Philippi).
Type Locality.—Santa Cruz (specimens figured by both Ortmann and Ihering).
Other Lots.—#676, Yegua Quemada, coll. Ameghino, 1900; #677, two specimens, coll. J. Bicego, 1897.
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—*Polynices jorgensis* Ihering is also a synonym.

ortmanni, 1907. *Tellina* PSAMMOBIIDAE

1907*a*. AMNBA, 14:313, 315. New name for *Tellina tehuelcha* in Ortmann (1902:147, pl. 29, fig. 3), not *Tellina tehuelcha* Ihering, 1899.
1914. NPRMP, 1(3):58. *Sanguinolaria tehuelcha* (Ihering).

= *Sanguinolaria tehuelcha* (Ihering).
Type Locality.—Shell Gap at Río Chico, Santa Cruz (Ortmann).
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—There is no material in the Ihering Collection under this name, and only the type lot is curated under the corresponding *Tellina tehuelcha* Ihering.

ortmanni, 1907. *Urosalpinx* MURICIDAE

1907*a*. AMNBA, 14:188. New name for material misidentified as *Urosalpinx leucostomoides* (Sowerby) in Cossmann (1899*a*:pl. 10, fig. 7), not *Triton leucostomoides* Sowerby (1846:383, fig. 60).
1914. NPRMP, 1(3):98 (Superpatagonico).

Type Locality.—Yegua Quemada, Santa Cruz.
Syntypes.—#800, four specimens, coll. Ameghino, 1900.
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—This species resembles *Urosalpinx archipatagonica* Ihering from the same locality. It is synonymous with *Urosalpinx "pleurotomoides"* Cossmann (1903:50), *lapsus calami* and misidentification of *U. leucostomoides* (Sowerby).

osborni, 1914. *Gibbula* ?TROCHIDAE

1914. NPRMP, 1(3):75, pl. 3, fig. 11 (Patagonico Inferior).

Type Locality.—Pan de Azucar, Santa Cruz.
Holotype.—#590, coll. Ameghino, 1900 (by monotypy).
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—It may not be a *Gibbula*; it is more *Turbo*-like; probably a new genus.

paca, 1907. *Ostrea hemisphaerica* [sic] "var." OSTREIDAE

1907*a*. AMNBA, 14:12. Not figured (Roca).
1914. NPRMP, 1(3):22. *Ostrea neuquena paca* (Roca, Cretáceo Superior).

= *Ostrea neuquena* Ihering.
Type Locality.—Roca, Río Negro.
Syntypes.—#156, three valves, coll. A. Romero, 1903.
Stratigraphy.—Roca Formation (Paleocene).

pachychila, 1907. *Bulla* BULLIDAE

1907*a*. AMNBA, 14:363. New name for *Bulla* aff. *elegans* in Borchert (1901:47, pl. 4, fig. 7), not *Bulla elegans* Gray, 1825 (= *Haminea guildingi* [Sowerby]).

Type Locality.—Paraná, Entre Rios.
Stratigraphy.—Paraná Formation (Upper Miocene).
Remarks.—Ihering (1907*a*:363) states, "La détermination de Borchert est conséquent inexacte, non seulement pour l'espèce, mais aussi pour le genre au sousgenre. . .."

palaeopatagonica, 1903. *Cardita* CARDITIDAE

1903. AMNBA, 9:215, fig. 12.
1907*a*. AMNBA, 14:24, 47. *Venericardia* (Rocanéen et Patagonéen).

Type Locality.—Río Chico, Chubut.
Holotype.—#360, coll. Ameghino, 1900 (by monotypy).
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—Ihering (1904) referred to another specimen, a cast from Roca, which is not listed in the 1914 catalogue and was not found in the collection. The species has affinities with *Venericardia inequalis* Philippi, also from the Patagonian Formation. It is similar to "*Cardita*" *iheringi* Böhm, 1903:72 (= *Cardita burckhardti* Ihering; see Burckhardt, 1902:216, fig. 1–7).

pampa, 1914. *Bulimulus sporadicus* ORTHALICIDAE: BULIMULINAE

1914. NPRMP, 1(3):70–71. Not figured.
1944. Parodiz, CZMHN, 1(17):1–2, fig. 2–3. *Peronaeus* (*Lissoacme*) *ameghinoi* (Ihering).

= *Peronaeus* (*Lissoacme*) *ameghinoi* (Ihering). See *Bulimulus ameghinoi* Ihering.
Type Locality.—"Buenos Aires."
Syntypes.—#562, coll. Ameghino, 1910.
Stratigraphy.—Buenos Aires Formation (Pleistocene).
Remarks.—The type locality of *P.* (*L.*) *ameghinoi* is Chapadmalal, Buenos Aires Province; the specimens of *B. pampa* are probably from Luján where Ameghino made extensive collections. The species *ameghinoi* occurs in the region of San Matias Gulf as the subspecies *P.* (*L.*) *ameghinoi madrynensis* Parodiz, 1944.

pampa, 1914. *Siphonaria lessoni* SIPHONARIIDAE

1914. NPRMP, 1(3):69. Not figured (Pampeano Inferior).

= *Siphonaria lessoni* (Blainville, 1826).
Type Locality.—"Buenos Aires" probably near or at Chapadmalal.
Syntypes.—#556, two specimens, coll. Ameghino, 1910.
Stratigraphy.—Belgrano Formation (Lower Pleistocene); Recent.

pampeana, 1907. *Bullia gradata* NASSARIIDAE

1907*a*. AMNBA, 14:445. Not figured.
1914. NPRMP, 1(3):105 (Pampeano).
1933. Feruglio, ARMGB, 8 bis:236, 239.
1939. Parodiz, Physis, 17:754, fig. 3–4. *Buccinanops.*

= *Buccinanops gradatum* (Deshayes, 1844).
Type Locality.—Puerto Militar, Prov. Buenos Aires.
Syntypes.—#855, 19 specimens, coll. Ameghino, 1910.
Stratigraphy.—Belgrano Formation (Lower Pleistocene); also Recent and common from Uruguay to northern Patagonia.

pampeana, 1907. *Chione* VENERIDAE

1907*a*. AMNBA, 14:454, pl. 18, fig. 125a–b.
1914. NPRMP, 1(3):56.

Type Locality.—San Julian, Santa Cruz.
Syntypes.—#468, 18 valves, coll. Ameghino, 1900.
Stratigraphy.—Deseado beds coeval with the Belgrano Formation (Pleistocene).
Remarks.—This is most likely a synonym of *Protothaca antiqua* (King), the specimens in the type lot being slightly more elongated.

panensis, 1914. *Arca* ?ARCIDAE

1914. NPRMP, 1(3):16–17, pl. 2, fig. 1 (Formação Patagonica).

Type Locality.—Pan de Azucar, Santa Cruz.

Holotype.—#109, a cast, coll. Ameghino, 1900 (by monotypy).

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—The unique specimen is an incomplete cast of questionable specific determination, but not likely an *Arca.*

panis, 1907. *Panopaea* [sic] HIATELLIDAE

1907*a.* AMNBA, 14:327, pl. 13, fig. 87.
1914. NPRMP, 1(3):64, pl. 2, fig. 9a–b (Patagonico Inferior).

= *Panopea panis* Ihering.

Type Locality.—Pan de Azucar, Santa Cruz.

Holotype.—#518, corresponding to the specimen figured in Ihering (1914), coll. Ameghino, 1900 (by monotypy).

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—Ihering (1914:64) wrote that the species was not figured until 1914, but he did figure a specimen in 1907 without mentioning it in the text. The two figures (1907*a* and 1914) appear slightly different, but the former is a photograph and the latter is a drawing. The original description is based on "l'unique exemplaire" interpreted here as the specimen figured in the 1914 catalogue. *Panope* and *Panopaea* of authors are misspellings of *Panopea.*

patagonensis, 1907. *Pododesmus* ANOMIIDAE

1907*a.* AMNBA, 14:266, pl. 9, fig. 63a–b.
1914. NPRMP, 1(3):27 (Patagonico Inferior).

Type Locality.—Pan de Azucar, Santa Cruz.

Syntypes.—#213, six valves.

Other Lots.—#214, Pan de Azucar, Santa Cruz, four valves, coll. Ameghino, 1900; #215, Río Chico, Chubut, one valve, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

patagonensis, 1897. *Potamides* POTAMIDIDAE

1897*b.* RMP, 2:315, text fig. 20 (first of two figures numbered 20; the other figure numbered 20 on page 316 is *Ostrea pyrotheriorum.*)
1899*b.* ASCA, 47:67. *Melania* sp.
1907*a.* AMNBA, 14:52.
1914. NPRMP, 1(3):92 (Salamanqueano).
1969. Parodiz, ACM, 40:152.

Type Locality.—"Lehuen-ark" error for Sehuen Aik (e), Valley of Sehuen River.

Lectotype.—#749, the specimen figured by Ihering (1897*b*:text fig. 20) is here designated the lectotype. The type lot consisted of nine syntypes.

Stratigraphy.—Sehuenan Formation (Paleocene). The name *P. patagonensis* was mentioned frequently in geological literature by Ameghino, Windhausen, Frenguelli, Feruglio, and others, and some of the references may correspond to *Potamides chaliana* Parodiz, 1969.

patagonensis, 1903. *Rostellaria* STROMBIDAE

1903. AMNBA, 9:209. Not figured.
1904. RMLP, 11:239, pl. 2, fig. 11.
1907*a*. AMNBA, 14:29. *Aporrhais* (Rocanéen).
1914. NPRMP, 1(3):94 (Salamanqueano).

= *Tibia patagonensis* (Ihering).

Type Locality.—Roca, Río Negro.

Syntypes.—#759, two casts, specimens collected by C. Ameghino and S. Roth in the same lot.

Stratigraphy.—Roca Formation (Paleocene).

Remarks.—*Aporrhais rocai* Böhm, 1903:72, is synonymous but unavailable (*nomen nudum*). Both *Rostellaria patagonensis* and *R. rocai* were from the same locality and strata, and known only by internal casts; the variations in both species show similarities. *Rostellaria* Lamarck, 1799 (= *Tibia* Röding, 1798).

patagonica, 1907. *Abra* SEMELIDAE

1907*a*. AMNBA, 14:316, pl. 2, fig. 82a–b.
1914. NPRMP, 1(3):59 (Patagonico Inferior).

= ?*Abra uruguayensis* (Pilsbry, 1879). Recent.

Type Locality.—Camarones, Chubut.

Syntypes.—#489, 25 valves, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

patagonica, 1897. *Arca* ARCIDAE

1897*b*. RMP, 2:235, pl. 4, fig. 25, and pl. 5, fig. 30.
1902. Ortmann, p. 93, pl. 25, fig. 3a–b.
1907*a*. AMNBA, 14:236. *Arca umbonata* Lamarck.
1914. NPRMP, 1(3):18 (Superpatagonico).

= *Arca umbonata* Lamarck.

Type Locality.—Yegua Quemada, Santa Cruz.

Type.—The type lot containing four valves reported by Ihering (1914) is not in the collection.

Other Lots.—#118, Cabo Tres Puntas, coll. Ameghino, 1900; #119, Cañada de los Artilleros, 25 valves, coll. Ameghino, 1900; #120, San Julian, one specimen, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

patagonica, 1897. *Bulla* ?RETUSIDAE

1897*b*. RMP, 2:271, text fig. 8 (Formação Santacruzense).
1902. Ortmann, p. 246, pl. 37, fig. 8a, c.
1907*a*. AMNBA, 14:121.
1914. NPRMP, 1(3):69 (Superpatagonico).

= ?*Retusa patagonica* (Ihering), **new combination.**

Type Locality.—Yegua Quemada, Santa Cruz.

Syntypes.—#551, 25 specimens, coll. Ameghino.

Other Lot.—#552, Cañada de los Artilleros, 12 specimens, coll. Ameghino.

Stratigraphy.—Patagonian Formation (Lower Miocene).

patagonica, 1907. *Lahillia angulata* CARDIIDAE

1897*b*. RMP, 2:257, text fig. 2 on p. 258. *Amathusia angulata* Philippi.
1907*a*. AMNBA, 14:294. *Lahillia angulata patagonica* Ihering.
1914. NPRMP, 1(3):50 (Patagonico Inferior–Super).

= *Lahillia angulata* (Philippi, 1887).

Type Locality.—Sierra de los Baguales, Santa Cruz.

Holotype.—#413, cast with portion of the shell, coll. Hauthal (by monotypy).

Other Lots.—#412, Santa Cruz, one cast, coll. J. Bicego, 1897; #414, Yegua Quemada, one valve, large, 21 cm, but broken.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—In the collection there is also a cast in plaster of Paris, #4462, from the specimen (?type) of *Amathusia angulata* sent to Ihering by Philippi from Navidad, Chile. Cossmann (1899*c*:134) listed the species as *Iheringia angulata* (Philippi).

patagonica, 1907. *Lima* LIMIDAE

1907*a*. AMNBA, 14:262, pl. 9, fig. 60.
1914. NPRMP, 1(3):29 (Patagonico Medio–Inferior).

Type Locality.—Punta Nueva, Santa Cruz.

Syntypes.—#230, nine valves, coll. Ameghino, 1900; #231, Golfo San Jorge, one valve, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

patagonica, 1897. *Tellina* TELLINIDAE

1897*b*. RMP, 2:261, pl. 5, fig. 261 (Formação Santacruzense).
1907*a*. AMNBA, 14:315.
1914. NPRMP, 1(3):59 (Superpatagonico).

Type Locality.—Yegua Quemada, Santa Cruz.

Syntypes.—#486, three valves, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—See *Tellina patagonica camaronesia* Ihering.

patagonica, 1897. *Voluta* MARGINELLIDAE

1897*b*. RMP, 2:306, pl. 3, fig. 6 (Formação Santacruzense).
1907*a*. AMNBA, 14:200. *Neoimbricaria.*
1914. NPRMP, 1(3):107.

= *Neoimbricaria patagonica* (Ihering), as figured in Wenz, 1938:1297, fig. 3701.

Type Locality.—Yegua Quemada, Santa Cruz.

Syntypes.—#868, five specimens, coll. Ameghino.

Stratigraphy.—Patagonian Formation (Lower Miocene).

patagonica, 1907. *Vulpecula* COSTELLARIIDAE [VEXILLIDAE]

1907*a*. AMNBA, 14:199, pl. 7, fig. 48a–b.
1914. NPRMP, 1(3):107 (Patagonico Medio).

= *Vexillum patagonicus* (Ihering).

Type Locality.—Golfo San Jorge, Santa Cruz.

Holotype.—#865, coll. Ameghino, 1900 (by monotypy).

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—*Vulpecula* Blainville, 1824 (= *Vexillum* Röding, 1798).

patagonicum, 1907. *Cardium* CARDIIDAE

1907*a*. AMNBA, 14:293, pl. 11, fig. 73.
1914. NPRMP, 1(3):48 (Patagonico).

Type Locality.—Santa Cruz.
Holotype.—#396, coll. J. Bicego, 1897 (by monotypy).
Other Lot.—#397, Cabo Tres Puntas, three valves, coll. Ameghino, 1900.
Stratigraphy.—Patagonian Formation (Lower Miocene).

patagonicus, 1907. *Actaeon* ACTAEONIDAE

1907*a*. AMNBA, 14:117, pl. 4, fig. 1.
1914. NPRMP, 1(3):68 (Superpatagonico).

Type Locality.—Cañada de los Artilleros, Santa Cruz.
Syntypes.—#546, two specimens, coll. Ameghino, 1900.
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—A very distinct, more elongated species than *Actaeon argentinus* Ihering from the same locality and strata, and perhaps not congeneric.

patagonicus, 1907. *Crassatellites* CRASSATELLIDAE

1907*a*. AMNBA, 14:279.
1914. NPRMP, 1(3):40 (Patagonico Inferior).

= *Crassatella kokeni* Ihering.
Type Locality.—Camarones, Chubut.
Syntypes.—#332, two valves, coll. Ameghino, 1900.
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—Ihering named *C. patagonicus* as being different only in size from *C. kokeni* as figured by Ortmann (1902:123, pl. 38, fig. 10). He gave neither description nor illustrations of *C. patagonicus. Crassatellites* Krueger, 1823 (= *Crassatella* Lamarck, 1799).

patagonicus, 1904. *Helcioniscus luciferus* PATELLIDAE: NACELLINAE

1904. RMLP, 11:285. Not figured.
1907*a*. AMNBA, 14:436.
1914. NPRMP, 1(3):436 (Formação Pampeana).

= *Cellana lucifera* (Ihering).
Type Locality.—Deseado, Santa Cruz.
Syntypes.—#564, two specimens, coll. Ameghino, 1900.
Stratigraphy.—"Deseadense," Pleistocene marine of Deseade (= Belgrano Formation).
Remarks.—See *Helcioniscus luciferus* Ihering.

paucicostata, 1907. *Scalaria rugulosa* "var." EPITONIIDAE

1907*a*. AMNBA, 14:140. Not figured.
1914. NPRMP, 1(3):81 (Patagonico Inferior).

= *Opalia* (*Nodoscala*) *rugulosa* (Sowerby, 1846).
Type Locality.—Manantial Salado, Santa Cruz.
Holotype.—#631, coll. Ameghino, 1900 (by monotypy).
Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—"*Scalaria*" *rugulosa* Sowerby, 1846, is a species of wide distribution from New Zealand to Chile and is also abundant in the Tertiary of Patagonia in Chubut and Santa Cruz.

pauciradiata, 1899. *Cardium philippii* CARDIIDAE

1899*a*. NJMGP, 2:15.
1907*a*. AMNBA, 14:104, 291. *Cardium philippii pauciradiatum.*
1914. NPRMP, 1(3):48 (Patagonico).

= *Cardium philippii* Ihering.

Type Locality.—Santa Cruz.

Syntypes.—#402, three valves, coll. Bicego, 1897.

Stratigraphy.—In Ihering's table (1907*a*:104) the provenance of *pauciradiata* is uncertainly indicated. Probably Patagonian Formation (Lower Miocene).

Remarks.—There is one additional specimen in the Ihering Collection, #2481, from Río Foyel, collector unknown.

paucispina, 1897. *Pholas* PHOLADIDAE

1897*b*. RMP, 2:265, text fig. 5 (Formação Santacruzense).
1907*a*. AMNBA, 14:329. *Barnea paucispina* (Ihering).
1914. NPRMP, 1(3):65 (Superpatagonico).

= ?*Netastoma paucispina* (Ihering), **new combination.**

Type Locality.—Yegua Quemada, Santa Cruz.

Syntype.—#521, only one of the three valves mentioned by Ihering (1914); coll. Ameghino.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—The specimen figured in Ihering (1897*b*) is a restoration. *Nettastomella* Carpenter, 1865, is an unnecessary replacement name for *Netastoma* Carpenter, 1864.

paucisquamatus, 1907. *Pododesmus* ANOMIIDAE

1907*a*. AMNBA, 14:268, pl. 10, fig. 10a–b.
1914. NPRMP, 1(3):27 (Patagonico Inferior).

Type Locality.—Southeast of Punta Nueva, Santa Cruz.

Holotype.—#220, coll. Ameghino, 1900 (by monotypy).

Stratigraphy.—Patagonian Formation (Lower Miocene).

pazensis, 1914. *Pododesmus* ?ANOMIIDAE

1914. NPRMP, 1(3):28, pl. 2, fig. 2 (Formação Entreriana).

Type Locality.—La Paz, Entre Rios.

Holotype.—#223, coll. S. Roth (by monotypy).

Stratigraphy.—Paraná Formation (Upper Miocene).

Remarks.—Ihering (1914:28) states, ". . . esta descripção ha de ser considerada como provisoria." The generic position of this species is uncertain, but it is not a species of *Pododesmus.*

percrassa, 1897. *Ostrea* OSTREIDAE

1897*b*. RMP, 2:221, text fig. 1 (and pl. 9, fig. 53 as *Ostrea patagonica* of authors; the true *O. patagonica* d'Orbigny in the plate is fig. 52).

1902. Hauthal, RMLP, 10:46. *Ostrea hatcheri* Ortmann.
1902. Ortmann, p. 99. *Ostrea ingens* in part.
1907*a*. AMNBA, 14:18. *Ostrea hatcheri* Ortmann.
1914. NPRMP, 1(3):23. *Ostrea hatcheri* (Patagonico Superior).

= *Ostrea hatcheri* Ortmann, 1897.

Type Locality.—Santa Cruz.

Syntypes.—#173, five of the six valves in original type lot are present in the collection.

Other Lots.—The name is preoccupied by *Ostrea percrassa* Conrad, 1840, a Miocene species from North America. There are other lots in the collection under *Ostrea hatcheri,* #174–183, from different localities including Puerto Madryn, Camarones, Pan de Azucar, north of Río Seco, Río Chico of Chubut, Punta Nodales, southeast of Punta Nueva, and Deseado, collected by S. Roth, J. Bicego, and C. Ameghino. There are a total of 90 specimens in these lots.

Stratigraphy.—Patagonian Formation (Lower Miocene).

perplana, 1897. *Tellina* PSAMMOBIIDAE

1897*b*. RMP, 2:259, pl. 6, fig. 39 (Formação Santacruzense).
1907*a*. AMNBA, 14:313. *Sanguinolaria.*
1914. NPRMP, 1(3):58 (Superpatagonico).

= ?*Psammotella perplana* (Ihering).

Type Locality.—La Cueva, Santa Cruz.

Syntype.—#481, only one specimen remaining of the three listed by Ihering (1914), coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Phacoides sp. LUCINIDAE: MILTHINAE

1914. NPRMP, 1(3):46.

= *Miltha iheringiana* Doello-Jurado (1919:558).

Locality.—La Paz, Entre Rios.

Specimens.—One specimen from Puerto Madryn, Chubut, coll. J. Bicego, 1897; there are three other casts in the collection, #388 from La Paz, Entre Rio, coll. S. Roth.

Stratigraphy.—The species is known from both Paraná Formation of Entre Rios and Río Negro Formation of Chubut (Upper Miocene).

philippii, 1897. *Cardium* CARDIIDAE

1897*b*. RMP, 2:249, pl. 6, fig. 40 (Formação Santacruzense).
1907*a*. AMNBA, 14:291.
1914. NPRMP, 1(3):48 (Superpatagonico).

Type Locality.—Yegua Quemada, Santa Cruz.

Holotype.—#398, one valve, C. Ameghino (by monotypy).

Other Lots.—#399, Yegua Quemada, Santa Cruz, six valves, coll. Ameghino; #400, Santa Cruz, three casts, coll. J. Bicego, 1897; #401, Cañada de los Artilleros, one valve, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—This is *Cardium multiradiatum* (in part) in Philippi (1887:171, pl. 38, fig. 9), not *Cardium multiradiatum* Sowerby, 1833. See also *Cardium huttoni* Ihering.

philippii, 1907. *Gibbula* ?RAPHISTOMATIDAE

1907*a*. AMNBA, 14:132, pl. 4, fig. 6a–c.
1914. NPRMP, 1(3):74 (Patagonico Medio).

Type Locality.—Cabo Tres Puntas, Santa Cruz.
Syntypes.—#585, four specimens, coll. Ameghino, 1900.
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—This species belongs to the Pleurotomariacea, and to a genus similar to *Trophidostropha* Longstoff from the European Carboniferous, but probably undescribed. E. Feruglio collected it at Epuyen.

piconus, 1907. *Pecten* PECTINIDAE

1907*a*. AMNBA, 14:46, text fig. 4.
1914. NPRMP, 1(3):36 (Salamanqueano).

Type Locality.—Pico Salamanca, Santa Cruz.
Holotype.—#292, single valve, coll. Ameghino, 1909 (by monotypy).
Stratigraphy.—Salamanca Formation (Paleocene).
Remarks.—This species may belong in *Pecten sensu lato*; its taxonomic position is questionable.

pilsbryi, 1899. *Voluta* VOLUTIDAE

1899*a*. NJMGP, 2:34, pl. 12, fig. 9.
1902. Ortmann, pl. 37, fig. 1a–b.
1907*a*. AMNBA, 14:210. *Cymbiola.*
1914. NPRMP, 1(3):109 (Superpatagonico).

= *Adelomelon* (*Pachycymbiola*) *pilsbryi* (Ihering).
Type Locality.—Santa Cruz.
Syntypes.—#883, one specimen plus two casts, coll. J. Bicego, 1897.
Stratigraphy.—Patagonian Formation (Lower Miocene).

pisum, 1907. *Lima* LIMIDAE

1907*a*. AMNBA, 14:263, pl. 9, fig. 61a–c. *Limatula.*

Type Locality.—Southeast of Punta Nueva, Santa Cruz.
Syntypes.—#228, 16 valves, coll. Ameghino, 1900; #229, Punta Casamayor, 12 valves, coll. Ameghino, 1900.
Stratigraphy.—Patagonian Formation (Lower Miocene).

plata, 1907. *Cardita* CARDITIDAE

1907*a*. AMNBA, 14:451, pl. 18, fig. 23a–b.

= *Carditamera plata* (Ihering).
Type Locality.—Monte Hermoso, Prov. de Buenos Aires.
Type.—Not in the collection.
Stratigraphy.—Belgrano Formation (Lower Pleistocene) and Querandinan (Upper Pleistocene); Recent.

plicifera, 1897. *Marginella* MARGINELLIDAE

1897*b*. RMP, 2:308, text fig. 19.
1902. Ortmann, p. 225, fig. 2 (with supplementary description).

1907*a*. AMNBA, 14:200. *Neoimbricaria*.
1914. NPRMP, 1(3):107. *Neoimbricaria* (Superpatagonico).

= ?*Neoimbricaria plicifera* (Ihering).
Type Locality.—Yegua Quemada, Santa Cruz.
Holotype.—#869, coll. Ameghino, 1900 (by monotypy).
Stratigraphy.—Patagonian Formation (Lower Miocene).

portenia, 1907. *Myochlamys patagonensis* PECTINIDAE

1907*a*. AMNBA, 14:377. Not figured.

= *Chlamys patagonensis portenia* (Ihering).
Type Locality.—Puente Alsina, Buenos Aires, from a perforation 80 m deep.
Type.—Not in the collection.
Stratigraphy.—Paraná Formation (Upper Miocene).

Remarks.—In the original description Ihering stated that he received several specimens from Ameghino.

praenuncius, 1897. *Pecten* PECTINIDAE

1897*b*. RMP, 2:230. Not figured.
1902. Ameghino, ASCA, 54:224. *Chlamys espejoana* Ihering, *in litteris*.
1907*a*. AMNBA, 14:251, pl. 7, fig. 54. *Myochlamys*.
1914. NPRMP, 1(3):33 (Patagonico Inferior–Superpatagonico).

= *Chlamys praenuncius* (Ihering).
Type Locality.—Punta Nova (Nueva), Santa Cruz.
Syntypes.—#268, a complete specimen, eight valves.

Other Lots.—#269, Monte Espejo, four valves, coll. Ameghino; #270, Yegua Quemada, Santa Cruz, two valves, coll. Ameghino.

Stratigraphy.—Patagonian Formation (Lower Miocene).

princeps, 1907. *Neomphalius* TROCHIDAE

1907*a*. AMNBA, 14:135, pl. 4, fig. 8a–b.
1914. NPRMP, 1(3):76 (Patagonico Medio).

= *Tegula patagonica* (d'Orbigny, 1840).
Type Locality.—Punta Casamayor, Santa Cruz.
Holotype.—#594, coll. Ameghino, 1900 (by monotypy).
Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—Ihering did not compare this species with *T. patagonica* which is known from the Araucanean Formation (Pliocene), and from Rio de Janeiro to northern Patagonia (Recent).

prisca, 1907. *Modiolarca* ?GAIMARDIIDAE

1907*a*. AMNBA, 14:276, pl. 14, fig. 94.
1914. NPRMP, 1(3):39 (Patagonico Medio).

= ?*Gaimardia prisca* (Ihering).
Type Locality.—Southeast of Punta Nueva, Santa Cruz.
Holotype.—#322, coll. Ameghino, 1900 (by monotypy).
Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—The holotype is a very poor specimen for correct generic identification.

prisca, 1907. *Olivancillaria* OLIVIDAE

1907*a*. AMNBA, 14:370, text fig. 15.
1914. NPRMP, 1(3):108 (Formação Entreriana).

Type Locality.—Paraná, Entre Rios.

Holotype.—#873, one cast, coll. S. Roth (by monotypy).

Stratigraphy.—Paraná Formation (Upper Miocene).

Remarks.—This is *Oliva reticularis brasiliana* in Borchert (1901:47, pl. 4, fig. 8), not *O. reticularis* Lamarck, 1811, or *O. brasiliana* Lamarck, 1811. Similar to the Recent species *Olivancillaria elongata* (Fischer, 1807) from Brazil and Uruguay.

prisca, 1907. *Struthiolaria* STRUTHIOLARIIDAE

1907*a*. AMNBA, 14:28, pl. 3, fig. 18 (Crétacée Supérieur).

Type Locality.—Roca, Río Negro.

Type.—Not in the collection under this name.

Stratigraphy.—Roca Formation (Paleocene).

Remarks.—The type material was stated to consist of "un moule externe mal conserve." One specimen in the collection, #782 from Park-Aik, is not well preserved and was listed by Ihering (1914:96); it may be this species. See *Struthiolaria ornata* "var." *densestriata.*

Proscaphella, 1907. VOLUTIDAE

1907*a*. AMNBA, 14:205. New genus.

Type Species.—*Voluta gracilior* Ihering (= *V. gracilis* Philippi, 1887).

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—= *Miomelon* Dall, 1907 (type species: *Volutilithes philippianus* Dall; = *V. gracilis* Philippi, 1887).

pruniformis, 1907. *Marginella* MARGINELLIDAE

1907*a*. AMNBA, 14:370. New name for *Marginella* aff. *prunum* in Borchert (1901:48, pl. 6, fig. 11), not *Marginella prunum* Swainson, 1822.

Type Locality.—Paraná, Entre Rios (Borchert).

Stratigraphy.—Paraná Formation (Upper Miocene).

pseudopatagonica, 1899. *Cardita* CARDITIDAE

1899*a*. NJMGP, 2:16.
1907*a*. AMNBA, 14:283. *Venericardia patagonica* (Sowerby).
1914. NPRMP, 1(3):44. *Venericardia pseudopatagonica* (Superpatagonico).

= *Venericardia patagonica* (Sowerby).

Type Locality.—La Cueva, Santa Cruz (in Ihering [1914] changed to Yegua Quemada).

Syntypes.—#365, two specimens, coll. Ameghino.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—This species was based on juveniles of *V. patagonica.*

pseudopatagonica, 1907. *Corbula* CORBULIDAE

1907*a*. AMNBA, 14:388. Not figured; new name for *Corbula patagonica* in Borchert (1901:44, pl. 4, fig. 31–32), not *Corbula patagonica* d'Orbigny, 1846.

Type Locality.—Paraná, Entre Rios (Borchert).
Stratigraphy.—Paraná Formation (Upper Miocene).

Pseudotylostoma, 1903. NATICIDAE

1903. AMNBA, 9:207. New genus.

Type Species.—*Pseudotylostoma romeroi* Ihering.
Stratigraphy.—Roca Formation (Paleocene).
Remarks.—See *Pseudotylostoma romeroi.*

pueyrredona, 1907. *Calyptraea* CREPIDULIDAE

1907*a*. AMNBA, 14:149. New name for *Trochita araucana* in Philippi (1887:87, pl. 11, fig. 1), not *Trochita araucana* Lesson, 1831.
1914. NPRMP, 1(3):84 (Patagonico).

Type Locality.—Northwest Santa Cruz at Lake Pueyrredón.
Syntypes.—#666, two specimens, coll. Hatcher, received from Ortmann.
Stratigraphy.—Patagonian and Navidad formations (Feruglio, 1949–1950) (Lower Miocene).
Remarks.—This species was misidentified as *Galerus araucanus* by Ortmann (1902:181, pl. 32, fig. 7a–b). *Trochita araucana* Lesson is a synonym of *Calyptraea radians* Lamarck. In the same publication (1907*a*:253) Ihering gave another new name, *Calyptraea levuana,* for the species misidentified as *Trochita araucana* by Philippi (1887).

pueyrredona, 1907. *Leda* NUCULANIDAE

1907*a*. AMNBA, 14:229. New name for *Leda errazurizi* in Ortmann (1902:84, pl. 26, fig. 3a–b), not *Nucula errazurizi* Philippi (1887:189, pl. 41, fig. 11).
1914. NPRMP, 1(3):14 (Formação Patagonica).

= *Nuculana pueyrredona* (Ihering).
Type Locality.—Lago Pueyrredón, Santa Cruz (Ortmann).
Syntypes.—#83, two valves received from Ortmann and reported as "cotypos" are in collection.
Stratigraphy.—Patagonian and Navidad formations (Lower Miocene).

pueyrredona, 1907. *Venericardia* CARDITIDAE

1907*a*. AMNBA, 14:286. New name for *Cardita volckmanni* in Ortmann (1902:126, pl. 26, fig. 6), not *Cardita volckmanni* Philippi, 1887 ("Terciario antiguo").
1914. NPRMP, 1(3):45. *Venericardia volckmanni* (Philippi).

= *Venericardia volckmanni* (Philippi).
Type Locality.—Lago Pueyrredón, Santa Cruz, as Ihering referred to specimens listed in Ortmann (1902). The type locality for *Cardita volckmanni* Philippi is Tubul, Chile.
Stratigraphy.—?Navidad Formation (?Miocene).
Remarks.—One valve received from Philippi (Lot #372) is in the Ihering Collection under *volckmanni,* not under *pueyrredona.*

puntana, 1907. *Pecten patagonensis* PECTINIDAE

1897*b*. RMP, 2:226. *Pecten patagonensis* d'Orbigny.
1907*a*. AMNBA, 14:257. *Myochlamys patagonensis puntana.*

1914. NPRMP, 1(3):32 (Formação Entreriana Patagonico).

= *Chlamys patagonensis* (d'Orbigny, 1842).
Type Locality.—Golfo San Jorge, Punta Nova (Nueva), Santa Cruz.
Syntypes.—#267, 12 valves, coll. Ameghino, 1900.
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—Curated in the Ihering Collection under *Myochlamys patagonensis puntana.*

puntarenasensis, 1907. *Polynices* NATICIDAE

1907*a*. AMNBA, 14:341. New name for *Natica chiloensis* in Ortmann (1899:431) and Ortmann (1902, pl. 186, fig. 1a–b), not *Natica chiloensis* Philippi, 1887.
1914. NPRMP, 1(3):85 (Magellanico Inferior).

Type Locality.—Punta Arenas, Chile (Ortmann).
Syntypes.—#678, three specimens received from Ortmann and reported as "cotypes" are in the collection.
Stratigraphy.—Magellanian Formation (Lower Oligocene).

puntasium, 1907. *Calliostoma* TROCHIDAE

1907*a*. AMNBA, 14:136, pl. 4, fig. 10a–c.
1914. NPRMP, 1(3):79 (Patagonico Medio).

Type Locality.—Cabo Tres Puntas, Santa Cruz.
Types.—Not in the collection.
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—Ihering compared *C. puntasium* to *Calliostoma rioense* Dall (= *C. jucundum* [Gould]), but considering the nature of the columella in the illustration it appears to belong in the subgenus *Kombologion* Clench and Turner, 1960. Two specimens were listed in the 1914 catalogue.

pyramidesia, 1907. *Turritella ambulacrum* TURRITELLIDAE

1907*a*. AMNBA, 14:367. Not figured.
1914. NPRMP, 1(3):88 (Formação Entreriana).

= *Turritella ambulacrum* Sowerby, 1846.
Type Locality.—Puerto Piramides, Chubut.
Holotype.—#710, coll. Ameghino, 1903 (by monotypy).
Other Lot.—#711, Trelew, Chubut, three specimens, coll. S. Roth.
Stratigraphy.—Río Negro Formation (Upper Miocene) and also Camacho Formation in Uruguay which is coeval with the Paraná and Río Negro formations.
Remarks.—Although this material is both allopatric and allochronic with nominotypical *T. ambulacrum,* it is not different and the name is placed in synonymy. *Turritella ambulacrum* Sowerby of southern range in Santa Cruz is represented in the collection by ten lots from different localities. See also *T. steinmanni* Ihering, *T. argentina* Ihering, and *T. ambulacrum sylva* Ihering.

pyramidesium, 1907. *Pecten oblongus* PECTINIDAE

1907*a*. AMNBA, 14:375. Not figured.
1914. NPRMP, 1(3):36. *Pecten oblongus* Bravard (Formação Entreriana).

= *Chlamys oblongus pyramidesium* (Ihering).
Type Locality.—Puerto Piramides, Chubut.

Types.—Not in the collection.
Other Lot.—#291, *Pecten oblongus* Bravard, three specimens, coll. S. Roth, 1903.
Stratigraphy.—Paraná and Río Negro formations (Upper Miocene).
Remarks.—Ihering (1907) reports specimens from this locality collected by Ameghino in 1903, but none are in the collection under this name; only "*Pecten*" *oblongus* from Entre Rios.

pyriformis, 1897. *Trophon* MURICIDAE

1897*b*. RMP, 2:295, pl. 3, fig. 5 (Formação Santacruzense).
1907*a*. AMNBA, 14:183, pl. 5, fig. 31.
1914. NPRMP, 1(3):101 (Superpatagonico).

Type Locality.—Yegua Quemada, Santa Cruz.
Syntypes.—#828, one specimen and one fragment (juveniles), coll. Ameghino.
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—These may belong in *Trophon lamellosus* (Gmelin).

pyrotheriana, 1907. *Polynices* NATICIDAE

1907*a*. AMNBA, 14:154, pl. 5, fig. 17.
1914. NPRMP, 1(3):85, pl. 3, fig. 13 (Patagonico Inferior).

= *Lunatia pyrotheriana* (Ihering), **new combination.**
Type Locality.—Camarones, Chubut.
Syntypes.—#679, six large specimens and nine smaller, coll. Ameghino.
Stratigraphy.—Patagonian Formation (Lower Miocene), also known from the Magellanian Formation (Lower Oligocene) of Río Turbio.

pyrotheriorum, 1897. *Ostrea* GRYPHAEIDAE

1897*b*. RMP, 2:315, text fig. 20 on p. 316 [there are two figures numbered 20, the first on page 315 is *Potamides patagonensis*].
1902*a*. AMNBA, 4:116. *Gryphaea* (Salamanqueano).
1903. Tournouër, BSGF, 3:473.
1907*a*. AMNBA, 14:44. *Gryphaea.*
1914. NPRMP, 1(3):21 (Cretáceo Superior "salamanquéen").

= *Gryphaea pyrotheriorum* (Ihering).
Type Locality.—Mamelones de Pinedo (also known as Tetas de Pinedo), Santa Cruz.
Syntypes.—#146, one complete specimen and one valve.
Stratigraphy.—Roca and Salamanca formations (Paleocene).
Remarks.—The species was also mentioned by Tournouër (1903) from Colhue Huapi, and by Feruglio (1949–1950) from Punta Peligros and Puerto Viser.

quadrisulcata, 1897. *Perna* ISOGNOMONIDAE

1897*b*. RMP, 2:231, pl. 9, fig. 54 (Superior formationis patagonicae).
1902. Ortmann, p. 97, pl. 24, fig. 2a–b (Lake Pueyrredón).
1907*a*. AMNBA, 14:243.
1914. NPRMP, 1(3):20 (Superpatagonico).

Type Locality.—La Cueva, Santa Cruz.
Holotype.—#134, single valve, coll. Ameghino (by monotypy).
Other Lot.—#135, Cabo Tres Puntas, two valves.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—Lot #135 was reported by Ihering (1914) as "typo" but it was collected by C. Ameghino in 1900, after the original description and from a different locality. This species is only tentatively placed in *Perna.*

quemadensis, 1907. *Fusus* FASCIOLARIIDAE: FUSININAE

1907*a*. AMNBA, 1907 14:195, pl. 6, fig. 39.
1914. NPRMP, 1(3):103 (Superpatagonico).

= ?*Fusinus quemadensis* (Ihering).

Type Locality.—Yegua Quemada, Santa Cruz.

Holotype.—#850, coll. Ameghino (by monotypy).

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—*Fusus* of authors (= *Fusinus* Rafinesque, 1815); the canal in this species is very short. This species resembles *Fusinus pilsbryi* (Ortmann) which was originally described in the genus *Fusus* (Ortmann, 1900:375).

quemadensis, 1897. *Glycimeris* [sic] HIATELLIDAE

1897*b*. RMP, 2:264, text fig. 4 on p. 265 (Formação Santacruzense).
1907*a*. AMNBA, 14:328. *Panopaea* [sic].
1914. NPRMP, 1(3):63 (Superpatagonico).

= *Panopea quemadensis* (Ihering).

Type Locality.—Yegua Quemada, Santa Cruz.

Holotype.—#519, a restored valve, coll. Ameghino (by monotypy).

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—This is a species close to the Recent *Panopea abbreviata* Valenciennes, 1839.

quemadensis, 1897. *Marginella* MARGINELLIDAE

1897*b*. RMP, 2:307, pl. 3, fig. 9, and pl. 4, fig. 14.
1907*a*. AMNBA, 14:199, pl. 6, fig. 40a–b. *Neoimbricaria.*
1914. NPRMP, 1(3):107. *Neoimbricaria* "*guemadesia*" (Patagonico).

= *Neoimbricaria quemadensis* (Ihering).

Type Locality.—Yegua Quemada, Santa Cruz.

Holotype.—#870, coll. Ameghino (by monotypy).

Stratigraphy.—Patagonian Formation (Lower Miocene).

quemadensis, 1897. *Pecten* PECTINIDAE

1897*b*. RMP, 2:228, pl. 6, fig. 38 (Formação Santacruzense).
1907*a*. AMNBA, 14:256. *Myochlamys.*
1914. NPRMP, 1(3):33 (Superpatagonico).

= *Chlamys* (*Zygochlamys*) *quemadensis* (Ihering).

Type Locality.—Yegua Quemada, Santa Cruz.

Syntypes.—#271, five valves, coll. Ameghino; #272, Las Cuevas, one specimen, coll. Ameghino.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—Lot #272 was reported as "typo" in Ihering (1914), but it was collected after the original description and from a different locality. See Morra (1985).

quemadensis, 1897. *Terebra costellata* "var." TEREBRIDAE

1897*b*. RMP, 2:311 (Formação Santacruzense).
1902. Ortmann, p. 236, pl. 36, fig. 5. *Terebra costellata* Sowerby.
1907*a*. AMNBA, 14:216. *Terebra quemadensis.*
1914. NPRMP, 1(3):112 (Superpatagonico).

= *Terebra quemadensis* Ihering.

Type Locality.—Yegua Quemada, Santa Cruz.

Holotype.—#901, coll. Ameghino (by monotypy).

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—The type locality of *Terebra costellata* Sowerby is Navidad, Chile; *T. quemadensis* is a different species. See *T. costellata santacruzensis* Ihering.

quemadensis, 1896. *Voluta* VOLUTIDAE

1896. NDMG, 7:97.
1897*b*. RMP, 2:304, pl. 3, fig. 7 (Formação Santacruzense).
1899*a*. NJMGP, 2:34.
1907*a*. AMNBA, 14:207. *Proscaphella.*
1914. NPRMP, 1(3):111. *Cymbiola* (*Miomelon*) (Superpatagonico).

= *Miomelon quemadensis* (Ihering).

Type Locality.—Yegua Quemada, Santa Cruz.

Holotype.—#892, coll. Ameghino (by monotypy).

Other Lot.—#893, Manantial Salado, Santa Cruz, two incomplete specimens, reported as *Cymbiola* sp. aff. to *quemadensis,* coll. Ameghino.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—Ihering (1897*b*) stated that this species may be synonymous with *V. philippiana* Dall, which is a synonym of *Adelomelon gracilior* (Ihering, 1896).

querandina, 1907. *Turbonilla* PYRAMIDELLIDAE: TURBONILLINAE

1907*a*. AMNBA, 14:442, pl. 17, fig. 121 (Pampeano Superior).

= *Turbonilla* (*Pyrgiscus*) *uruguayensis* Pilsbry, 1897.

Type Locality.—Bahía Blanca, formation pampienne supérieur.

Type.—Not in the collection.

Stratigraphy.—Querandí Formation (Late Pleistocene). Recent in Uruguay and Buenos Aires Province.

rada, 1907. *Lotorium* (*Lampusia*) RANELLIDAE: CYMATIINAE

1907*a*. AMNBA, 14:175, pl. 5, fig. 29a–b (text states fig. 26 in error).
1914. NPRMP, 1(3):97 (Superpatagonico).

= *Semitriton rada* (Ihering), **new combination.**

Type Locality.—Rada Tilly, Santa Cruz.

Syntypes.—#793, three specimens, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—This species resembles *Semitriton dennanti* (Tale) from the Eocene of Australia but has a shorter spire and stronger nodulous cords.

rada, 1914. *Marcia* VENERIDAE: SAMARANGIINAE

1914. NPRMP, 1(3):53, pl. 1, fig. 5a–b (Superpatagonico).

= ?*Samarangia exalbida* (Chemnitz, 1795).

Type Locality.—Rada Tilly, Santa Cruz.
Holotype.—#438, juvenile, coll. Ameghino (by monotypy).
Other Lots.—Unnumbered, Sierra de los Baguales, seven casts, coll. Hauthal.
Stratigraphy.—Patagonian Formation (Lower Miocene); Recent.

radana, 1907. *Myochlamys geminata* "var." PECTINIDAE

1907*a*. AMNBA, 14:255. Not figured.
1914. NPRMP, 1(3):35 (Patagonico Inferior).

= *Chlamys geminata* (Sowerby, 1846).
Type Locality.—Rada Tilly, Santa Cruz.
Syntype.—#287, only one specimen reported as "cotypo" in the collection, C. Ameghino, 1900.
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—There was another specimen mentioned in the description from Piedra Clavada but it was not in the collection. Although there are no specimens of *Chlamys geminata* Sowerby in the collection, Ihering (1907*a*) mentioned the species had been collected at several localities: Bajo de San Julian, Manantial Salado, Pan de Azucar, Monte Espejo, Punta Nodales, Punta Nueva, and Camarones. Feruglio (1949–1950) found the species *geminata* at all levels of the Patagonian, but listed the form *radana* with doubt.

rionegrensis, 1903. *Modiola* MYTILIDAE

1903. AMNBA, 9:205. Not figured.
1904. RMLP, 11:233, pl. 1, fig. 5.
1907*a*. AMNBA, 14:38. *Modiolus.*
1914. NPRMP, 1(3):39 (Cretáceo Superior).

Type Locality.—Roca, Río Negro.
Syntypes.—#319, two specimens, coll. S. Roth.
Stratigraphy.—Roca Formation (Paleocene).
Remarks.—This is probably a *Brachidontes* Swainson.

rionegrensis, 1903. *Ostrea* OSTREIDAE

1903. AMNBA, 9:202, pl. 1, fig. 5a–b (text shows 5–6).
1907*a*. AMNBA, 14:14, pl. 2, fig. 7; see also p. 46 (Rocanéen).
1914. NPRMP, 1(3):22 (Cretáceo Superior).

Type Locality.—Roca, Río Negro.
Syntypes.—#160, four valves, coll. S. Roth.
Other Lots.—#161, Roca, two valves, coll. Ameghino, 1904; #162, Homo Viejo [sic] for Horno Viejo near Roca, ten valves, coll. Ameghino, 1904.
Stratigraphy.—Roca Formation (Paleocene).
Remarks.—The specimen figured in Ihering (1907*a*) differs from the original of Ihering (1903). In the Danian of Cerro Dorotea, in the Magellanian region, the species is characteristic (Feruglio, 1949–1950).

rioplatensis, 1907. *Columbella* COLUMBELLIDAE

1907*a*. AMNBA, 14:369. New name for *Columbella acuta* in Borchert (1901:50, pl. 5, fig. 3.), not *Anachis acuta* Stearns, 1873.

= ?*Anachis moleculina* (Duclos, 1840).

Type Locality.—Entre Rios (Borchert).
Stratigraphy.—?Paraná Formation (Upper Miocene).
Remarks.—On consultation with W. H. Dall, Ihering confirmed that *C. acuta* Stearns was a synonym of *C. albella* Dall and different from *C. rioplatensis.* The name *rioplatensis* given by Ihering might refer to deep perforations in the zone of La Plata River (?Puente Alsina) 230 ft deep.

rocana, 1903. *Cucullaea* CUCULLAEIDAE

1903. AMNBA, 9:204, pl. 1, fig. 7.
1907. NPRMP, 14:35 (Rocanéen).

Type Locality.—Roca, Río Negro.
Type.—Not in the collection.
Stratigraphy.—Roca Formation (Paleocene).
Remarks.—In the work of 1914, no *Cucullaea* were listed from the Paleocene of Roca as indicated in the original description.

rocana, 1903. *Gryphaea* GRYPHAEIDAE

1903. AMNBA, 9:198. Not figured.
1907*a*. AMNBA, 14:7, pl. 1, fig. 5a–b (Rocanéen), and p. 36.
1914. NPRMP, 1(3):20. *Gryphaea rothi* Böhm.

= ?*Odontogryphaea rothi* (Böhm, 1903).
Type Locality.—Roca, Río Negro.
Stratigraphy.—Roca Formation (Paleocene).
Remarks.—The description of *G. rothi* Böhm appeared a few weeks before *G. rocana* Ihering. *Gryphaea rocana* was based upon specimens figured by Burckhardt (1902:214, pl. 3, fig. 1–3) as *Gryphaea* aff. *pitcheri,* not *G. pitcheri* Morton, 1834.

rocana, 1907. *Phacoides* LUCINIDAE

1907*a*. AMNBA, 14:25, pl. 3, fig. 5 (Rocanéen).
1914. NPRMP, 1(3):46.

= *Lucina* (*Lucinisca*) *rocana* (Ihering), **new combination.**
Type Locality.—Roca, Río Negro.
Lectotype.—#385, the only specimen in the collection of the three listed in the original description, coll. Ameghino, 1904, here designated the lectotype.
Stratigraphy.—Roca Formation (Paleocene).
Remarks.—*Phacoides* Blainville, 1825 (= *Lucina* Bruguière, 1797).

rocana, 1903. *Ostrea* OSTREIDAE

1902. Burckhardt, p. 214, pl. 2, fig. 11–19. *Ostrea* aff. *bomilcaris* Coquand.
1903. AMNBA, 9:203. *Ostrea rocana.* Not figured.
1907*a*. AMNBA, 14:13. *O. ameghinoi rocana.*
1914. NPRMP, 1(3):23. *O. ameghinoi rocana* (Rocanéen).

Type Locality.—Roca, Río Negro.
Holotype.—#167, coll. Ameghino, 1901 (by monotypy).
Other Lots.—#168, Roca, eight valves, coll. S. Roth; #169, Neuquen, one well-preserved specimen; #170, Roca, one complete specimen, coll. Ameghino, 1904; #171, same five valves; #172, km 1216–1218, Río Negro, one valve.

Stratigraphy.—Roca Formation (Paleocene).

rocanum, 1907. *Cardium* (*Hemicardium*) CARDIIDAE

1907*a*. AMNBA, 14:25, pl. 3, fig. 14a–b (Rocanéen).

= *Trachycardium rocanum* (Ihering), **new combination.**
Type Locality.—Roca, Río Negro.
Type.—Not in the collection; the figured specimen is an internal cast.
Stratigraphy.—Roca Formation (Paleocene).

rochai, 1907. *Tylostoma* NATICIDAE

1907*a*. AMNBA, 14:40, text fig. 2 ("Cretaceous").

= *Ampullina* (*Pseudotylostoma*) *rochai* (Ihering).
Type Locality.—Rio Grande do Norte, Brasil.
Type.—Not in the collection; the single described specimen was collected by Francisco da Rocha.
Stratigraphy.—Probably Paleocene.

romeroi, 1903. *Nautilus* NAUTILIDAE

1903. AMNBA, 9:191, pl. 1, fig. 1 (Crétacée Supérieur).
1907*a*. AMNBA, 14:41 (Rocanéen).
1914. NPRMP, 1(3):68 (Cretáceo Superior de Roca).

Type Locality.—Roca, Río Negro.
Syntype.—#543, labelled "cotypo," coll. Ameghino, 1901.
Stratigraphy.—Roca Formation (Paleocene).

romeroi, 1903. *Pseudotylostoma* NATICIDAE

1903. AMNBA, 9:207, pl. 1, fig. 8.
1907*a*. AMNBA, 14:39.
1914. NPRMP, 1(3):87.

= *Ampullina* (*Pseudotylostoma*) *romeroi* (Ihering). See Wenz, 1938:1028.
Type Locality.—Roca, Río Negro.
Syntype.—#693, one cast labelled "cotypo," coll. Ameghino, 1904[!].
Stratigraphy.—Roca Formation (Paleocene).
Remarks.—Although the label for the syntype states the specimen was from C. Ameghino, 1904, the catalogue (Ihering, 1914) names Colonel A. Romero as the collector.

rostrigera, 1902. *Gryphaea concors* "var." GRYPHAEIDAE

1902*a*. AMNBA, 4:113. Not figured.
1903. AMNBA, 9:211, pl. 2, fig. 10.
1907*a*. AMNBA, 14:43. *Gryphaea rostrigera* (Salamanqueano).
1945. Stenzel, BGSA, 56(12, pt. 2):1202. *Odontogryphaea.*

= *Odontogryphaea rostrigera* (Ihering).
Type Locality.—West of Río Chico, Chubut.
Syntypes.—#147, two complete specimens and six valves.
Other Lots.—#148, Puerto Malaspina, Chubut, one complete specimen and ten valves.

Stratigraphy.—Salamanca Formation (Paleocene).

Remarks.—This species is the type species of the genus *Odontogryphaea* Ihering.

rothi, 1904. *Diplodon* HYRIIDAE

1904. RMLP, 11:232, pl. 1, fig. 6.
1907*a*. AMNBA, 14:466.
1914. NPRMP, 1(3):37 ("Terciario antiguo").
1969. Parodiz, ACM, 40:69, pl. 7, fig. 4.

Type Locality.—Arroyo Lele, N. W. Chubut.

Syntypes.—#299, not in collection; the lectotype is deposited at CMNH (see *Remarks*).

Stratigraphy.—Colloncura beds (Simpson, 1933; Feruglio, 1949–1950), = Friasean Formation (Kraglievich, 1930). Upper Miocene.

Remarks.—The lectotype was designated by Parodiz (1969) from a specimen in Lot #299 in the Ihering Collection received in exchange from Dr. Max Birabén, at that time Director of the Museo Argentino de Ciencias Naturales. The species is also found at Arroyo Lepa given as "type," coll. Hauthal.

rothi, 1903. *Rostellaria* STROMBIDAE

1903. AMNBA, 9:204.
1904. RMLP, 11:12, pl. 2, fig. 9–10.
1907*a*. AMNBA, 14:28.
1914. NPRMP, 1(3):94 (Salamanqueano).

= *Tibia rothi* (Ihering).

Type Locality.—Roca, Río Negro.

Syntypes.—#760, nine casts, coll. S. Roth; #761, a "Variety," three casts, coll. Ameghino–S. Roth.

Stratigraphy.—Roca Formation (Paleocene).

Remarks.—See note under *Rostellaria patagonensis.* There are two lots in the collection under *Rostellaria* "sp." (undetermined species), #762 consisting of two casts from Valle Alsina, Chubut, coll. Ameghino, and #4233, a single cast from Roca, coll. S. Roth.

salamanca, 1903. *Chlamys* PECTINIDAE

1903. AMNBA, 9:214, pl. 1, fig. 11.
1907*a*. AMNBA, 14:47. *Myochlamys* (Salamanqueano).

Type Locality.—Pico Salamanca, Santa Cruz.

Syntypes.—#286, one complete specimen, seven valves, coll. Ameghino, 1900.

Stratigraphy.—Salamanca Formation (Paleocene).

Remarks.—This species appears to be ancestral to *Chlamys patagonicus* (d'Orbigny). Feruglio (1949–1950) reports it from the Valley of the Río Chico.

salobris, 1907. *Cyrena* CORBICULIDAE

1907*a*. AMNBA, 14:413, pl. 16, fig. 109 (Formação Araucana).
1914. NPRMP, 1(3):41.
1969. Parodiz, ACM, 40:95, fig. 14–15. *Neocorbicula.*

= *Cyanocyclas salobris* (Ihering), **new combination.**

Type Locality.—Sierra Laziar, Santa Cruz.

Type Material.—#336, lectotype and one paralectotype, coll. Ameghino; subsequent designation by Parodiz, 1969.

Stratigraphy.—Araucanean Formation (Lower Pliocene).

Remarks.—*Cyanocyclas* Blainville, 1818, and *Neocorbicula* Fischer, 1887, are subjective synonyms. This synonymy was not recognized correctly in Parodiz and Hennings (1965). I prefer to treat *Cyanocyclas* as a genus distinct from *Corbicula* because species of the former have a pallial sinus, longer siphons, and are restricted to the Neotropical region. Living species of *Cyanocyclas* are viviparous.

santacruzense, 1914. *Cardium* CARDIIDAE

1914. NPRMP, 1(3):49, pl. 1, fig. 4a–b.

= *Laevicardium santacruzense* (Ihering), **new combination.**

Type Locality.—Yegua Quemada, Santa Cruz.

Holotype.—#411, a broken valve, coll. Ameghino (by monotypy).

Stratigraphy.—Patagonia Formation (Lower Miocene).

santacruzensis, 1907. *Chenopus* APORRHAIDAE

1907*a.* AMNBA, 14:170. New name for *Aporrhais araucana* in Ortmann (1902:200, pl. 33, fig. 9), not *Aporrhais araucana* Philippi, 1887, from the Tertiary of Chile.

= *Drepanocheilus santacruzensis* (Ihering), **new combination.**

Type Locality.—Santa Cruz (Ortmann).

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—This species differs from *D. araucanus* (Philippi) by having axial instead of spiral sculpture.

santacruzensis, 1907. *Pleurotoma* TURRIDAE

1907*a.* AMNBA, 14:219, pl. 7, fig. 46.
1914. NPRMP, 1(3):113 (Superpatagonico).

Type Locality.—Yegua Quemada, Santa Cruz.

Holotype.—#907, incomplete specimen, coll. J. Bicego, 1897 (by monotypy).

Other Lot.—#908, Cañada de los Artilleros, one specimen, coll. Ameghino.

Stratigraphy.—Patagonian Formation (Lower Miocene).

santacruzensis, 1897. *Polynices* NATICIDAE

1897*b.* RMP, 2:280. *Natica solida* Sowerby, 1846 (not *N. solida* Blainville, 1825).
1907*a.* AMNBA, 14:152, pl. 5, fig. 5. *Polynices santacruzensis.*
1914. NPRMP, 1(3):86 (Superpatagonico).

Type Locality.—Cañada de los Artilleros, Santa Cruz.

Syntypes.—#680, seven specimens.

Other Lots.—#681, Yegua Quemada, coll. Ameghino; #682, La Cueva, 12 specimens, coll. Ameghino.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—The species has affinities with *Polynices lacteus* (Guilding, 1830) which is Recent and ranges from North Carolina to Brazil. See note on *Natica tumbeziana* Ihering.

santacruzensis, 1899. *Tellina* TELLINIDAE: MACOMINAE

1899*a.* NJMGP, 2:22, pl. 2, fig. 5.
1907*a.* AMNBA, 14:314. *Macoma.*

1914. NPRMP, 1(3):58. *Macoma* (Patagonico).

= *Macoma santacruzensis* (Ihering).
Type Locality.—Santa Cruz.
Syntypes.—#483, four casts, coll. J. Bicego, 1897.
Stratigraphy.—Patagonian Formation (Lower Miocene).

santacruzensis, 1897. *Terebra costellata* "var." TEREBRIDAE

1897*b*. RMP, 2:311. *Terebra costellata* Sow. ?"var."
1907*a*. AMNBA, 14:216. *Terebra quemadensis santacruzensis.*
1914. NPRMP, 1(3):112. *Terebra quemadensis santacruzensis* (Superpatagonico).

= *Terebra santacruzensis* Ihering.
Type Locality.—La Cueva, Santa Cruz.
Holotype.—#902, coll. Ameghino, 1895 (by monotypy).
Other Lot.—#903, Cañada de los Artilleros, three specimens.
Stratigraphy.—Patagonian Formation (Lower Miocene).

santacruzensis, 1897. *Trophon laciniatus* MURICIDAE

1897*b*. RMP, 2:294, pl. 3, fig. 4.
1907*a*. AMNBA, 14:182.
1904. RMLP, 11:230. *Trophon laciniatus.*
1914. NPRMP, 1(3):100 (Patagonico Inferior–Medio).

= *Trophon* (*Austrotrophon*) *lamellosus* (Gmelin, 1791).
Type Locality.—La Cueva, Santa Cruz.
Holotype.—#811, coll. Ameghino, 1895 (by monotypy).

Other Lots.—#812, Yegua Quemada, two specimens, coll. Ameghino; #814, Manantial Salado, four specimens, coll. Ameghino; #815, Pan de Azucar, four specimens, coll. Ameghino; #816, Owen Point, four specimens, received from Ortmann; #817, Cañada de los Artilleros, three specimens, coll. Ameghino; #818, Rada Tilly, one specimen, coll. Ameghino; #819, Punta Nodales, one specimen, coll. Ameghino; #820, Punta Casamayor, one specimen, coll. Ameghino; #822, Corral Foyel, one cast, coll. Hauthal.

Stratigraphy.—Patagonian Formation (Lower Miocene).

saxicava, 1907. *Barnea* PHOLADIDAE

1907*a*. AMNBA, 14:325, pl. 14, fig. 96.
1914. NPRMP, 1(3):63 (Patagonico Inferior).

Type Locality.—Bahía Camarones, Chubut.
Type.—Not in the collection.
Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—This species was based on an unique specimen listed in Ihering (1914), and because of the unsatisfactory illustration the species is of questionable status.

schucherti, 1914. *Gibbula* ARCHITECTONICIDAE

1914. NPRMP, 1(3):74, pl. 3, fig. 10a–b (Patagonico Inferior).

= *Architectonica schucherti* (Ihering), **new combination.**
Type Locality.—Manantial Salado, Santa Cruz.
Holotype.—#856, coll. Ameghino, 1900 (by monotypy).

Other Lots.—#587, Cabo Tres Puntas, three specimens, coll. Ameghino, 1900; #588, Rada Tilly, one cast, coll. Ameghino, 1900; #589, Sierra de los Baguales, two casts, coll. Hauthal.

Stratigraphy.—Patagonian Formation (Lower Miocene).

scutata, 1907. *Marcia* VENERIDAE: SAMARANGIINAE

1907*a*. AMNBA, 14:303, pl. 11, fig. 76.
1914. NPRMP, 1(3):52 (Patagonico).

= *Samarangia scutata* (Ihering).

Type Locality.—Punta Casamayor, Santa Cruz.

Holotype.—#737, coll. Ameghino (by monotypy).

Other Lot.—#435, Santa Cruz, eight casts, coll. Bicego, 1897.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—This species is close to the Recent *Samarangia exalbida* (Chemnitz, 1795). See also "*Marcia*" *scutata tehuelcha* Ihering.

sehuena, 1907. *Corbula* ?CORBICULIDAE

1907*a*. AMNBA, 14:51, text fig. 5 (Formation "Guaranitica").
1914. NPRMP, 1(3):62 (Cretáceo Superior).
1949–1950. Feruglio 1:258, 273, 274. *Eriphyla.*
1969. Parodiz, ACM, 40:101. *Eriphyla* (Paleocene).

= *Eriphyla sehuena* (Ihering).

Type Locality.—Mata Amarilla on the Sehuen River (also called Chalia), Santa Cruz (delimited by Parodiz, 1969).

Lectotype.—#509, coll. Ihering, deposited at CMNH (see *Remarks*).

Stratigraphy.—Sehuenan beds (Paleocene).

Remarks.—A lectotype was designated by Parodiz (1969) from Lot #509 based on specimens from the Ihering Collection received in exchange from Dr. Max Birabén, at that time Director of the Museo Argentino de Ciencias Naturales. *Eriphyla* Gabb, 1864, is known from the Mesozoic of the Archiplata of Bolivia and Ecuador, and also from the Tertiary in the Puca Formation (Paleocene).

sierrana, 1907. *Panopaea* [sic] HIATELLIDAE

1902. Ortmann, p. 154, pl. 30, fig. 2. *Panopaea* [sic] *quemadensis* Ihering.
1907*a*. AMNBA, 14:328, pl. 13, fig. 38.
1914. NPRMP, 1(3):65 (Patagonico).

= *Panopea*? *quemadensis* (Ihering).

Type Locality.—Sierra de los Baguales, Santa Cruz.

Holotype.—#520, one cast, coll. Hauthal (by monotypy).

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—The type cast is only an upper portion not showing the characteristic surface that Ihering mentioned in the original description.

Sphenaturia, 1921. NAUTILIDAE

1921. Physis, 5:76. New subgenus of *Aturia* Bronn.

Type Species.—*Aturia* (*Sphenaturia*) *brueggeni* Ihering, here designated.

Stratigraphy.—"Estratos de Boquerón" (below Patagonian Formation).

Remarks.—Described as a subgenus of *Aturia* Bronn, 1838, without original selection of a type species.

splendida, 1897. *Cytherea* VENERIDAE

1897*b*. RMP, 2:255, pl. 6, fig. 42 (Formação Santacruzense).
1907*a*. AMNBA, 14:302.
1914. NPRMP, 1(3):51. *Macrocallista iheringi* Cossmann (Superpatagonico).

= *Macrocallista iheringi* (Cossmann, 1895) (= *Amiantis* Carpenter, originally *Meretrix* Lamarck).

Type Locality.—Yegua Quemada, Santa Cruz.

Syntypes.—#423, 11 valves, one separated with a label: "*C. explendida* [sic] = *C. iheringi* Cossmann."

Stratigraphy.—Patagonian Formation (Lower Miocene).

steinmanni, 1897. *Turritella* TURRITELLIDAE

1897*b*. RMP, 2:289. Not figured.
1907*a*. AMNBA, 14:162. *Turritella ambulacrum steinmanni.*
1914. NPRMP, 1(3):88. *Turritella ambulacrum steinmanni* (Patagonico and Superpatagonico).

= *Turritella ambulacrum* Sowerby, 1846.

Type Locality.—Santa Cruz.

Holotype.—#712, coll. Ameghino (by monotypy).

Other Lots.—#713, Casamayor, three specimens, coll. Ameghino; #714, Manantial Salado, five specimens, coll. Ameghino; #715, Camarones, 40 specimens, coll. Ameghino.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—*Turritella ambulacrum argentina* Ihering is also a synonym. Ihering (1897*b*:332) referred to *T.* cf. *steinmanni* from the Paraná Formation, which in Ihering (1907*a*) was included in the synonymy of *T. americana* Bravard, a common species of the Upper Miocene.

striatissima, 1903. *Rostellaria* STRUTHIOLARIIDAE

1903. AMNBA, 9:219, pl. 2, fig. 16.
1907*a*. AMNBA, 14:49. *Aporrhais striatissima.*
1914. NPRMP, 1(3):94 (Salamanqueano).

= *Struthiolaria striatissima* (Ihering).

Type Locality.—Río Chico, Chubut.

Syntypes.—#768, two specimens, coll. Ameghino.

Stratigraphy.—Salamanca Formation (Paleocene).

Remarks.—Other *Rostellaria* in the Ihering Collection correspond by priority to *Tibia,* but *striatissima* has the characteristics of a *Struthiolaria.*

striatolamellata, 1897. *Venus* VENERIDAE

1897*b*. RMP, 2:253, pl. 7, fig. 44 (Formação Santacruzense).
1902. Ortmann, p. 140, pl. 28, fig. 4. *Venus darwini* Ortmann.
1907*a*. AMNBA, 14:305. *Marcia.*
1914. NPRMP, 1(3):53. *Marcia* (Superpatagonico).

= *Samarangia*? *exalbida* (Chemnitz, 1795).

Type Locality.—Yegua Quemada, Santa Cruz.

Syntypes.—#437, four valves, coll. Ameghino.

Stratigraphy.—Patagonian Formation (Lower Miocene); also Recent.

Remarks.—This species resembles *Venus navidaensis* Philippi from the Tertiary of Chile. "*Marcia*" *pupilla* Feruglio, 1935, from the Salamanca Formation is also very similar to *striatolamellata.*

stromeri, 1914. *Fusus* RANELLIDAE: RANELLINAE

1914. NPRMP, 1(3):104. Not figured (Patagonico Medio).

= *Fusitriton stromeri* (Ihering), **new combination.**

Type Locality.—Cabo Tres Puntas, Santa Cruz.

Syntypes.—#851, two specimens, coll. Ameghino; #852, southeast of Punta Nueva, one specimen, coll. Ameghino.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—Ihering (1907*a*:194) assigned the specimens from Cabo Tres Puntas to *Fusus archimedis* Ortmann (1900:374).

Struthiolaria sp. STRUTHIOLARIIDAE

1914. NPRMP, 1(3):96.

Locality.—Pio [Piso] Sehuen (Cretáceo superior).

Specimens.—#782, from Park-Aik, Santa Cruz, coll. Ameghino.

Stratigraphy.—Sehuenan Formation (Paleocene).

Remarks.—The "piso" Sehuen (Sehuenan) is a fresh–brackish-water stratigraphic unit of the Paleocene. The specimen, not well preserved, must be from debris of the Salamanca; it was not reported by Ihering (1907*a*), and probably is *S. prisca* Ihering.

subrecta, 1899. *Siphonalia dilatata* FASCIOLARIIDAE: FUSININAE

1899*a*. NJMGP, 2:30.
1902. Ortmann, p. 211, pl. 34, fig. 4. *Siphonalia domeykoana* (Philippi).
1907*a*. AMNBA, 14:192. *Siphonalia subrecta.*
1914. NPRMP, 1(3):102 (Patagonico Medio–Super).

= *Fusinus subrectum* (Ihering).

Type Locality.—Santa Cruz.

Syntypes.—#842, five specimens, coll. J. Bicego, 1895.

Other Lots.—#843, Santa Cruz, one specimen received from Ortmann. #844, Cabo Tres Puntas, five specimens, coll. Ameghino; #845, Cañada de los Artilleros, six specimens, coll. Ameghino.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—*Siphonalia nodocincta* Ihering and *S. matthewi* Ihering are synonyms of this name.

subtenuis, 1897. *Natica* NATICIDAE

1897*b*. RMP, 2:284, text fig. 13 (Formação Santacruzense).
1907*a*. AMNBA, 14:157. *Polynices.*
1914. NPRMP, 1(3):86 (Superpatagonico).

Type Locality.—Yegua Quemada, Santa Cruz.

Holotype.-#692, coll. Ameghino, 1895 (by monotypy).

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—This species has affinities with *P. ortmanni* Ihering. It was reported by Wilckens (1911) from the Tertiary of Seymour Island, Antarctica, and may belong in *Magnatica* Marwick (1924:545), a genus described from the Miocene of New Zealand.

subtrigona, 1907. *Glycimeris* [sic] GLYCYMERIDIDAE

1907*a*. AMNBA, 14:241, pl. 7, fig. 53a–b (in text as fig. 23).
1914. NPRMP, 1(3):19 (Patagonico Inferior).

= *Glycymeris subtrigona* Ihering.

Type Locality.—Camarones, Chubut.

Syntypes.—#130, 32 valves, coll. Ameghino, 1900.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—*Glycymeris* Da Costa, 1778, was considered a *nomina conservanda* by the ICZN (Opinion 1414).

suburbana, 1907. *Crassatellites* CRASSATELLIDAE

1907*a*. AMNBA, 14:381, pl. 14, fig. 100a–b.

= *Crassatella suburbana* (Ihering).

Type Locality.—Puente Alsina, a suburb south of Buenos Aires city, from a perforation, 230 ft.

Type.—Not in the collection.

Stratigraphy.—Paraná Formation (Upper Miocene).

Remarks.—The only valve was described in great detail. There was no indication of collector (probably Ameghino).

subventricosa, 1897. *Eulima* EULIMIDAE

1897*b*. RMP, 2:274, text fig. 9.
1907*a*. AMNBA, 14:142.
1914. NPRMP, 1(3):81 (Superpatagonico).

Type Locality.—Yegua Quemada, Santa Cruz.

Syntypes.—#632, two specimens, coll. Ameghino.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—This species is a large (20 mm in length) ?*Eulima,* a rarity among the Patagonian gastropods, fossil or Recent.

sulcolunularis, 1907. *Venericardia* CARDITIDAE

1907*a*. AMNBA, 14:285, pl. 10, fig. 70a–b.
1914. NPRMP, 1(3):45 (Patagonico Medio).

Type Locality.—Bajo de las Flechas, Santa Cruz.

Holotype.—#367, coll. Ameghino, 1900 (by monotypy).

Other Lots.—#366, Golfo San Jorge, one complete specimen and four valves, coll. Ameghino, 1900; #368, Golfo San Jorge, three valves; #369, Pan de Azucar, two valves.

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—In the 1914 catalogue a lot from Golfo San Jorge was listed as "Typo." This species resembles *Venericardia cossmanni* Ihering.

suturalis, 1897. *Odostomia* ?PYRAMIDELLIDAE

1897*b*. RMP, 2:275, text fig. 19 (Formação Santacruzense).
1902. Ortmann, p. 173, pl. 33, fig. 7a–b.

1907*a*. AMNBA, 14:143, pl. 4, fig. 13.
1914. NPRMP, 1(3):81 (Superpatagonico).

Type Locality.—Yegua Quemada, Santa Cruz.
Holotype.—#633, one specimen, coll. Ameghino (by monotypy).
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—The type specimen is the one figured in Ihering (1907*a*). The original figure of 1897*b* is much different and must be an error. The acute spire and long "goniostome-like" aperture are unlike any Recent species.

sylva, 1907. *Turritella ambulacrum* TURRITELLIDAE

1907*a*. AMNBA, 14:342. Not figured.
1914. NPRMP, 1(3):89 (Magellanico).

= *Turritella ambulacrum* Sowerby, 1846.
Type Locality.—Carmen Sylva, Chile.
Syntypes.—#716, two specimens, received from C. Backhausen.
Stratigraphy.—Magellanian Formation (Lower Oligocene).
Remarks.—Only two specimens remain of the five mentioned in the original description. See *Turritella ambulacrum argentina* Ihering, *T. a. steinmanni* Ihering, and *T. a. pyramidesia* Ihering.

sylva, 1907. *Venericardia* CARDITIDAE

1907*a*. AMNBA, 14:346, pl. 14, fig. 98a–b (Magellanico).

Type Locality.—Carmen Sylva, Chile.
Type.—Not in the collection.
Stratigraphy.—Magellanian Formation (Lower Oligocene).

tehuelcha, 1907. *Cucullaea* CUCULLAEIDAE

1907*a*. AMNBA, 14:5, pl. 1, fig. 3a–b (Rocanéen).

Type Locality.—Roca, Río Negro.
Type.—Not in the collection.
Stratigraphy.—Roca Formation (Paleocene).
Remarks.—This species was based on a cast and the generic assignment is uncertain. The locality indicates the Roca Formation, but there are no *Cucullaea* from the Paleocene in the Ihering Collection.

tehuelcha, 1914. *Marcia scutata* VENERIDAE: SAMARANGIINAE

1914. NPRMP, 1(3):53. Not figured; title of original description states "*subsp. n.,*" but description says "variedade" (Formação Araucana).

= ?*Samarangia exalbida* (Chemnitz, 1795).
Type Locality.—Between San Jorge and Deseado, Santa Cruz.
Holotype.—#436, coll. Ameghino, 1900 (by monotypy).
Stratigraphy.—Araucanean Formation (Pliocene); Recent.

tehuelcha, 1907. *Psammobia* PSAMMOBIIDAE

1907*a*. AMNBA, 14:417, pl. 17, fig. 112a–b.
1914. NPRMP, 1(3):58 (Formação Araucana).

= *Gari tehuelcha* (Ihering).

Type Locality.—Sierra Laziar, Santa Cruz.
Syntypes.—#480, three valves, coll. Ameghino, 1900.
Stratigraphy.—Araucanean Formation (Lower Pliocene).
Remarks.—*Psammobia* Lamarck, 1817, is a synonym of *Gari* Schumacher, 1817.

tehuelcha, 1907. *Pupilia aperta* FISSURELLIDAE

1907*a*. AMNBA, 14:399. Not figured.
1914. NPRMP, 1(3):72 (Formação Araucana).

= *Fissurellidea megatrema* d'Orbigny, 1841.
Type Locality.—Sierra Laziar, Santa Cruz.
Holotype.—#566, coll. Ameghino, 1900 (by monotypy).
Stratigraphy.—Araucanean Formation (Lower Pliocene); also Recent.
Remarks.—The species described by Sowerby (1892) as *Pupilia aperta* was from South Africa.

tehuelcha, 1899. *Tellina* PSAMMOBIIDAE

1899*a*. NJMGP, 2:21, pl. 2, fig. 4.
1907*a*. AMNBA, 14:313. *Sanguinolaria.*
1914. NPRMP, 1(3):58. *Sanguinolaria* (Patagonico).

= *Sanguinolaria tehuelcha* (Ihering).
Type Locality.—Santa Cruz.
Holotype.—#482, cast with pieces of the original valve, coll. Ameghino, 1900 (by monotypy).
Stratigraphy.—Patagonian Formation (Lower Miocene).

tehuelchana, 1907. *Venericardia* CARDITIDAE

1902. Ameghino, ASCA, 54:190. *Cardita tehuelchana* Ihering, *in litteris.*
1907*a*. AMNBA, 14:412, pl. 16, fig. 107a–b. *Venericardia.*
1914. NPRMP, 1(3):45 (Formação Araucana).

Type Locality.—Sierra Laziar, Santa Cruz.
Syntypes.—#371, 16 valves, coll. Ameghino.
Stratigraphy.—Araucanean Formation (Lower Pliocene).

tehuelchum, 1907. *Calliostoma* TROCHIDAE

1907*a*. AMNBA, 14:437, pl. 17, fig. 115a–b.
1914. NPRMP, 1(3):74 (Pampeano).

= *Calliostoma consimilis* Smith, 1881. Recent.
Type Locality.—Puerto Deseado, Santa Cruz.
Holotype.—#615, coll. Ameghino, 1907 (by monotypy).
Stratigraphy.—Deseado beds, corresponds to the Belgrano Formation of the north (Pleistocene).
Remarks.—The original description indicates a unique specimen, but Ihering (1914) list two specimens in error.

tenuis, 1907. *Corbicula* CORBICULIDAE

1907*a*. AMNBA, 14:468, pl. 18, fig. 13c.
1914. NPRMP, 1(3):41 (Formação Entreriana).

1920. Frenguelli, 24:108.
1969. Parodiz, ACM, 40:98, pl. 10, fig. 12, 13. *Neocorbicula tenuis* (Ihering).

Type Locality.—Paraná, Entre Rios.

Syntypes.—#337, four valves, labelled as "cotypos."

Other Lot.—#338, La Paz, Entre Rios, conglomerate with numerous impressions of valves, coll. S. Roth.

Stratigraphy.—Paraná Formation (Upper Miocene).

Remarks.—Frenguelli (1920) said that he found "thousands" of badly preserved shells in the deposits at Paraná; these were probably *Cyanocyclas limosa* (Maton), as *Corbicula tenuis* is very rare in collections. Ihering said that the specimens were found in a mass of clay from the Bravard collection that also contained *Diplodon fraus* Ihering. *Corbicula tenuis* Ihering is the type species of the subgenus *Corbiculella* Ihering, 1907.

thomasi, 1914. *Panopaea* [sic] HIATELLIDAE

1914. NPRMP, 1(3):63, pl. 2, fig. 8a–b (Cretáceo Superior).

= *Panopea thomasi* Ihering.

Type Locality.—Río Chico, Chubut.

Type Material.—#474, two casts, coll. Ameghino. The figured specimen, 27 mm long, is here designated the lectotype.

Stratigraphy.—Salamanca Formation (Paleocene).

trespunta, 1907. *Cerithiopsis* CERITHIOPSIDAE

1907*a*. AMNBA, 14:168, text fig. 6.
1908. Cossmann, p. 104. *Colina trespunta* (Ihering).
1914. NPRMP, 1(3):93 (Patagonico Medio).

Type Locality.—Cabo Tres Puntas, Santa Cruz.

Holotype.—#751, coll. Ameghino (by monotypy).

Stratigraphy.—Patagonian Formation (Lower Miocene).

Remarks.—*Cerithiopsis emersoni* (C. B. Adams, 1839), Recent, is a very similar species occurring from Massachusetts to Brazil.

tricesima, 1897. *Nucula* NUCULIDAE

1897*b*. RMP, 2:243, pl. 4, fig. 21, and pl. 5, fig. 27.
1907*a*. AMNBA, 14:226 (Superpatagonico).
1914. NPRMP, 1(3):13 (Superpatagonico).

Type Locality.—La Cueva, Santa Cruz.

Lectotype.—#75, coll. Ameghino, 1895. The original description reports three specimens, broken; only one remains in the collection, and is here designated the lectotype.

Stratigraphy.—Patagonian Formation (Lower Miocene).

tricincta, 1897. *Turritella* TURRITELLIDAE

1897*b*. RMP, 2:pl. 3, fig. 3 (Formação Santacruzense).
1902. Ortmann, p. 135, pl. 31, fig. 14a–b. *Turritella breantiana* d'Orbigny.
1907*a*. AMNBA, 14:165, pl. 5, fig. 24. *Turritella iheringi* Cossmann.
1914. NPRMP, 1(3):90. *Turritella iheringi* Cossmann (Superpatagonico).

= ?*Turritella breantiana* d'Orbigny, 1847.

Type Locality.—Yegua Quemada, Santa Cruz.
Syntypes.—#732, ten specimens, coll. Ameghino.
Other Lots.—#733, La Cueva, one specimen, coll. Ameghino; #734, Cañada de los Artilleros, 18 specimens, coll. Ameghino.
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—There are no specimens in the collection under *Turritella tricincta* and all material of that species are labelled *T. iheringi* as listed in the catalogue (Ihering, 1914:90–91).

tridentata, 1897. *Cuculearia* [sic] ARCIDAE

1897*b*. RMP, 2:237, pl. 4, fig. 22, and pl. 5, fig. 28.
1907*a*. AMNBA, 14:233. *Cucullaria.*
1914. NPRMP, 1(3):15.

= *Barbatia tridentata* (Ihering), **new combination.**
Type Locality.—Yegua Quemada, Santa Cruz.
Syntypes.—#98, two broken valves, coll. Ameghino, 1895.
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—The original description reports "an unique specimen." "*Cuculearia*" was an error for *Cucullaria.*

tumbeziana, 1907. *Natica* NATICIDAE

1907*a*. AMNBA, 14:153. New name for *Natica darwini* in Philippi (1887:80, pl. 9, fig. 28), not *Natica darwini* Hutton, 1886 (the latter in turn a new name for *Natica solida* Sowerby [1846]), not *Natica solida* Blainville (1825).

Type Locality.—"Formation Crétacée, Chile" (Philippi, 1887).
Stratigraphy.—Probably the Navidad Formation (Miocene).
Remarks.—In the collection there is a single cast from Lebu, Chile, received from R. A. Philippi as "*Polynices*" *darwini* Hutton, but no specimens labelled as *N. tumbeziana.* Ihering (1907*a*:89) said that "*Polynices Carolodarwini* Ih. ['est substitué dans la Nouvelle-Zelandé] par *P. darwini* Hutton." I have not found any previous reference to *Polynices carolodarwini.*

unifascialis, 1897. *Pleurotoma discors* "var." TURRIDAE

1897*b*. RMP, 2:312. Discussed under *Pleurotoma discors* Sowerby.
1902. Ortmann, p. 239, pl. 36, fig. 7a–b. *Pleurotoma discors* "Var."
1907*a*. AMNBA, 14:219, pl. 7, fig. 45. *Pleurotoma unifascialis.*
1914. NPRMP, 1(3):113 (Superpatagonico).

Type Locality.—Yegua Quemada, Santa Cruz.
Holotype.—#909, coll. Ameghino (by monotypy).
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—This species probably belongs in *Bathystoma. Pleurotoma* Link, 1807 (= *Turris* Röding, 1798).

usurpator, 1907. *Lotorium* (*Lampusia*) RANELLIDAE: CYMATIINAE

1907*a*. AMNBA, 14:175, pl. 5, fig. 28a–b.
1914. NPRMP, 1(3):98 (Superpatagonico).

= *Cymatium usurpator* (Ihering), **new combination.**
Type Locality.—Rada Tilly, Santa Cruz.

Syntypes.—#794, two specimens, coll. Ameghino, 1900.
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—*Cymatium usurpator* (Ihering) and *C. rada* (Ihering) are both from the same locality and strata, but they can be distinguished by their shape and sculpture.

valchetanus, 1907. *Pododesmus* ANOMIIDAE

1907*a*. AMNBA, 14:267, pl. 10, fig. 64a–b.
1914. NPRMP, 1(3):27 (Patagonico).

Type Locality.—"Travesia" Valcheta, Gualicho River, Río Negro.
Syntypes.—#216, seven upper valves (12 were listed in the original description), coll. C. Burmeister, 1887.
Stratigraphy.—Patagonian Formation (Lower Miocene).

vindex, 1907. *Chione* VENERIDAE

1907*a*. AMNBA, 14:416, pl. 16, fig. 11a–b.
1914. NPRMP, 1(3):55 (Formación Araucana).

= *Protothaca antiqua* (King).
Type Locality.—Sierra Laziar, Santa Cruz.
Holotype.—#454, one broken valve, coll. Ameghino (by monotypy).
Stratigraphy.—Araucanean Formation (Lower Pliocene); Recent.

waltheri "Ihering," 1931. *Planorbis* PLANORBIDAE

1931. Walther, BIGU, 13:192. Name credited to Ihering *in litteris*.
1958. Caorsi and Goñi, BIGU, 37:58.
1969. Parodiz, ACM, 40:165, pl. 18, fig. 1. *Taphius walteri* (emended as *waltheri*).

= *Taphius waltheri* Parodiz (= *Biomphalaria waltheri* [Parodiz]).
Remarks.—Describing *Taphius walteri* [sic] (= *waltheri*; Parodiz, 1969), I used the name which was a *nomen nudum* in Walther (1931) because it was frequently mentioned as such in the Uruguayan geological literature. *Taphius* Adams and Adams, 1855, is the most abundant genus of South American planorbids; the name was arbitrarily synonymized by the ICZN under the African *Biomphalaria* Preston, 1910, on the grounds that the two genera are anatomically the same, but disregarding the 50-year rule for conservation of names. The type locality for *Taphius walteri* [sic] Parodiz, 1969, is Palmitas, Soriano, southeastern Uruguay, from the Fray Bentos Formation (Miocene). The holotype in CMNH is a specimen collected by A. Berro in 1927.

whitei, 1903. *Pseudotylostoma* NATICIDAE

1903. AMNBA, 9:307. New name for *Tylostoma torrubiae* in White, 1887, not *T. torrubiae* Sharpe, 1849.

= *Ampullina* (*Pseudotylostoma*) *whitei* (Ihering).
Type Locality.—Sergipe, Brazil.
Stratigraphy.—?"Upper Cretaceous."

wilckensi, 1907. *Ostrea* OSTREIDAE

1907*a*. AMNBA, 14:13, pl. 2, fig. 10a–b, and pl. 3, fig. 10c.
1914. NPRMP, 1(3):23 ("cretáceo superior horizonte medio").

Syntypes.—#163, two valves.
Stratigraphy.—Roca Formation (Paleocene).

Zygochlamys, 1907. PECTINIDAE

1907*a*. AMNBA, 14:250. New subgenus of *Chlamys* Röding.

Type Species.—*Chlamys geminata* Sowerby.
Stratigraphy.—Patagonian Formation (Lower Miocene).
Remarks.—This subgenus includes *C. fissocostatus* Ihering, *C. nodosoplicatus* Ihering, *C. quemadensis* Ihering, and *C. jorgensis* Ihering. For a revision of *Zygochlamys,* see Morra (1985).

Synonymic List of Fossil Taxa Described by Ihering

All names proposed by Ihering are organized below in a synonymic list following the classification of Vaught (1989). The placement of some fossil taxa follows Wenz (1938). Names of the species group and of the genus group are alphabetically arranged under higher categories (family level and above). Original combinations of names proposed by Ihering are in boldface; all synonyms are indented below the name considered valid. In some cases, combinations are unknown or tentative, and this uncertainty is indicated by placing the genus-group name within quotation marks (e.g., "*Gibbula*").

PHYLUM ANNELIDA
Class Polychaeta
***"Vermetus" julianus* Ihering, 1907**

PHYLUM MOLLUSCA
Class Gastropoda
Subclass Prosobranchia
Order Archaeogastropoda
Superfamily Pleurotomarioidea
Family Raphistomatidae
***"Gibbula" philippii* Ihering, 1907**

Superfamily Fissurelloidea
Family Fissurellidae
Fissurellidea megatrema d'Orbigny, 1841
***Pupilia aperta tehuelcha* Ihering, 1907**

Superfamily Patelloidea
Family Fissurellidae
Cellana lucifera (Ihering, 1904)
***Helcioniscus luciferus* Ihering, 1904**
***Helcioniscus luciferus patagonicus* Ihering, 1904**

Superfamily Trochoidea
Family Trochidae
***Calliostoma camaronesium* Ihering, 1907**
Calliostoma consimilis Smith, 1881
***Calliostoma tehuelchum* Ihering, 1907**
***Calliostoma militaris* Ihering, 1907**
Calliostoma amazonicum Finlay, 1930

Calliostoma bellicosum **Ihering, 1907**
Calliostoma dalli **Ihering, 1907**
Calliostoma quequensis Carcelles, 1944
Calliostoma jucundum (Gould, 1849)
Calliostoma lahillei **Ihering, 1907**
Calliostoma laziarium **Ihering, 1907**
Calliostoma puntasium **Ihering, 1907**
“Gibbula” osborni **Ihering, 1914**
Tegula patagonica (d’Orbigny, 1840)
Neomphalius princeps **Ihering, 1907**
Tegula abava (Ihering, 1907), **new combination**
Neomphalius abavus **Ihering, 1907**
Tegula (*Promartynia*) *americana* (Ihering, 1907), **new combination**
Neomphalius americanus **Ihering, 1907**

Family Turbinidae
“Calliostoma” deseadense **Ihering, 1914**

Order Mesogastropoda
Superfamily Cerithioidea
Family Potamididae
Potamides patagonensis **Ihering, 1897**

Family Pleuroceridae
Paleoanculosa bullia (Ihering, 1907)
Melania bullia **Ihering, 1907**
Melania pehuenchensis Doello-Jurado, 1927
Melania ameghiniana Doello-Jurado, 1927

Family Turritellidae
Turritella ambulacrum Sowerby, 1846
Turritella ambulacrum sylva **Ihering, 1907**
Turritella ambulacrum pyramidesia **Ihering, 1907**
Turritella argentina **Ihering, 1897**
Turritella steinmanni **Ihering, 1897**
Turritella ameghinoi **Ihering, 1903**
Turritella breantiana d’Orbigny, 1847
Turritella breantiana **“var.”** ***camaronesia*** **Ihering, 1907**
Turritella breantiana **“var.”** ***indecussata*** **Ihering, 1899**
Turritella iheringi Cossmann, 1898
Turritella tricincta **Ihering, 1897**
Turritella doeringi Böhm, 1903
Turritella burckhardti **Ihering, 1903**
Turritella cahuillensis **Ihering, 1907**
Turritella hauthali **Ihering, 1907**
Turritella malaspina **Ihering, 1903**

Family Siliquariidae
Siliquaria cossmanni (Ihering, 1907)
Tenagodus cossmanni **Ihering, 1907**

- Family Vermetidae
  - *Dendropoma multicoronatus* (Ihering, 1907), **new combination**
    - ***Vermetus multicoronatus* Ihering, 1907**
  - *Petaloconchus chicoanus* (Ihering, 1907)
    - ***Vermetus chicoanus* Ihering, 1907**

- Superfamily Stromboidea
  - Family Struthiolariidae
    - ***Struthiolaria ameghinoi* Ihering, 1897**
    - *Struthiolaria chilensis* Philippi, 1887
      - ***Struthiolaria chilensis fuegina* Ihering, 1907**
    - *Struthiolaria ornata* Sowerby (1846)
      - ***Struthiolaria ornata* "var." *densestriata* Ihering, 1897**
    - ***Struthiolaria prisca* Ihering, 1907**
      - ***Struthiolaria* sp., Ihering, 1914**
    - *Struthiolaria striatissima* (Ihering, 1903)
      - ***Rostellaria striatissima* Ihering, 1903**
  - Family Aporrhaidae
    - ***Rostellaria chubutensis* Ihering, 1903**
    - *Aporrhais cossmanni* (Ihering, 1903)
      - ***Rostellaria cossmanni* Ihering, 1903**
    - *Drepanocheilus santacruzensis* (Ihering, 1907), **new combination**
      - ***Chenopus santacruzensis* Ihering, 1907**
  - Family Strombidae
    - *Tibia patagonensis* (Ihering, 1903)
      - ***Rostellaria patagonensis* Ihering, 1903**
      - *Aporrhais rocai* Böhm, 1903, *nomen nudum*
    - *Tibia rothi* (Ihering, 1903)
      - ***Rostellaria rothi* Ihering, 1903**

- Superfamily Crepiduloidea
  - Family Crepidulidae
    - *Calyptraea pileus* Lamarck, 1822
      - ***Calyptraea pileus* "var." *juliana* Ihering, 1907**
    - ***Calyptraea pueyrredona* Ihering, 1907**
      - ***Calyptraea levuana* Ihering, 1907** [junior objective synonym]

- Superfamily Naticoidea
  - Family Naticidae
    - *Ampullina* (*Pseudotylostoma*) Ihering, 1903
      - ***Pseudotylostoma* Ihering, 1903**
    - *Ampullina* (*Pseudotylostoma*) *rochai* (Ihering, 1907)
      - ***Tylostoma rochai* Ihering, 1907**
    - *Ampullina* (*Pseudotylostoma*) *romeroi* (Ihering, 1903)
      - ***Pseudotylostoma romeroi* Ihering, 1903**
    - *Ampullina* (*Pseudotylostoma*) *whitei* (Ihering, 1903)
      - ***Pseudotylostoma whitei* Ihering, 1903**
    - *Lunatia magellanica* Hombron and Jacquinot, 1834
      - ***Natica consimilis* Ihering, 1897**
    - *Lunatia pyrotheriana* (Ihering, 1907), **new combination**
      - ***Polynices pyrotheriana* Ihering, 1907**

- ***Polynices carolodarwini* Ihering, 1907** [*nomen nudum*]
- *Polynices famula* (Philippi, 1887)
  - ***Polynices jorgensis* Ihering, 1907**
  - ***Polynices ortmanni* Ihering, 1907**
- ***Polynices puntarenasensis* Ihering, 1907**
- ***Polynices santacruzensis* Ihering, 1897**
- ***Natica subtenuis* Ihering, 1897**
- ***Natica tumbeziana* Ihering, 1907**

Superfamily Tonnoidea
- Family Ranellidae
  - *Cymatium bicegoi* (Ihering, 1899)
    - ***Lotorium bicegoi* Ihering, 1899**
  - *Cymatium* (*Cabestana*) *felipponei* (Ihering, 1907) [emendation]
    - ***Lotorium filipponei* [sic] Ihering, 1907**
  - *Cymatium usurpator* (Ihering, 1907), **new combination**
    - ***Lotorium* (*Lampusia*) *usurpator* Ihering, 1907**
  - *Fusitriton dautzembergi* (Ihering, 1897), **new combination**
    - ***Triton* (*Argobuccinum*) *dautzembergi* Ihering, 1897**
  - *Fusitriton stromeri* (Ihering, 1914), **new combination**
    - ***Fusus stromeri* Ihering, 1914**
  - *Semitriton rada* (Ihering, 1907), **new combination**
    - ***Lotorium* (*Lampusia*) *rada* Ihering, 1907**

Superfamily Cerithiopsoidea
- Family Cerithiopsidae
  - ***Cerithiopsis juliana* Ihering, 1907**
  - ***Cerithiopsis trespunta* Ihering, 1907**

Superfamily Epitonioidea
- Family Epitoniidae
  - *Epitonium chubutianum* (Ihering, 1907), **new combination**
    - ***Scalaria chubutiana* Ihering, 1907**
  - *Opalia* (*Nodiscala*) *quemadensis* (Cossmann), **new combination**
    - ***Scalaria cossmanni* Ihering, 1907**
  - *Opalia* (*Nodoscala*) *rugulosa* (Sowerby, 1846)
    - ***Scalaria rugulosa* "var." *paucicostata* Ihering, 1907**

Superfamily Eulimoidea
- Family Eulimidae
  - ***Eulima subventricosa* Ihering, 1897**

Order Neogastropoda
- Superfamily Muricoidea
  - Family Muricidae
    - *Crassilabrum jorgensis* (Ihering, 1907), **new combination**
      - ***Hadriania jorgensis* Ihering, 1907**
    - *Crassilabrum hatcheri* (Ortmann, 1900)
      - ***Hadriania lacustris* Ihering, 1907**
    - *Ocenebra* (*Ocinebrina*) *elegans* (Ortmann, 1900), **new combination**
      - ***Urosalpinx archipatagonica* Ihering, 1907**
      - ***Urosalpinx elegans* "var." *juliana* Ihering, 1907**

Thais (*Stramonita*) Schumacher, 1817
  ***Trophon* (*Entacanthus*) Ihering, 1907**
Thais (*Stramonita*) *monoceros* (Ihering, 1907), **new combination**
  ***Trophon monoceros* Ihering, 1907**
Trophon chicoanus (Ihering, 1907), **new combination**
  ***Hadriania jorgensis* "var." *chicoana* Ihering, 1907**
***Trophon inornatus* "var." *gradata* Ihering, 1907** [*nomen nudum*]
Trophon lamellosus (Gmelin, 1791)
  ***Trophon inornatus fairus* Ihering, 1907**
  ***Trophon laciniatus santacruzensis* Ihering, 1897**
  ***Trophon necocheanus* Ihering, 1907**
***Trophon pyriformis* Ihering, 1897**
Trophon varians (d'Orbigny, 1841)
  ***Trophon varians* "var." *gradata* Ihering, 1897**
  ***Trophon varians montenus* Ihering, 1907**
***Urosalpinx ortmanni* Ihering, 1907**
  Urosalpinx "pleurotomoides" Cossmann, 1903

Family Buccinidae
***Cominella* (*Austrocominella*) Ihering, 1907**
***Cominella fueguensis* Ihering, 1907**
Cominella minor (Philippi, 1887)
  ***Cominella cossmanni* Ihering, 1907**
***Cominella golfonia* Ihering, 1914**
***Cominella* sp., Ihering, 1914** [unidentifiable]
Gibbula iheringi Cossmann, 1899
  ***Gibbula iheringi* "var." *golfina* Ihering, 1907**
***Tritonidea borcherti* Ihering, 1907**

Family Columbellidae
***Columbella (Anachis) improvisa* Ihering, 1914**
Anachis moleculina (Duclos, 1840)
  ***Columbella rioplatensis* Ihering, 1907**

Family Nassariidae
Buccinanops gradatum (Deshayes, 1844)
  ***Bullia gradata pampeana* Ihering, 1907**

Family Fasciolariidae
Fusinus quemadensis (Ihering, 1907)
  ***Fusus quemadensis* Ihering, 1907**
Fusinus subrectum (Ihering, 1899)
  ***Siphonalia dilatata subrecta* Ihering, 1899**
  ***Siphonalia nodocincta* Ihering, 1907**
  ***Siphonalia matthewi* Ihering, 1914**

Family Volutidae
Adelomelon ameghinoi (Ihering, 1896), **new combination**
  ***Voluta ameghinoi* Ihering, 1896**
Adelomelon burmeisteri (Ihering, 1907), **new combination**
  ***Cymbiola burmeisteri* Ihering, 1907**
Adelomelon cannada (Ihering, 1907), **new combination**

Cymbiola becki ''var.'' cannada Ihering, 1907
Adelomelon cossmanni (Ihering, 1907)
Proscaphella cossmanni Ihering, 1907
Adelomelon feruglioi (Doello-Jurado, 1931)
Cymbiola (*Pachycymbiola*) sp., Ihering, 1914
Adelomelon (*Pachycymbiola*) *pilsbryi* (Ihering, 1899)
***Voluta pilsbryi* Ihering, 1899**
Enaeta dalli (Ihering, 1907), **new combination**
***Lyria dalli* Ihering, 1907**
Miomelon Dall, 1907
***Proscaphella* Ihering, 1907**
Miomelon gracilior (Ihering, 1896)
***Voluta gracilior* Ihering, 1896**
Miomelon quemadensis (Ihering, 1896)
***Voluta quemadensis* Ihering, 1896**

Family Olividae
***Olivancillaria prisca* Ihering, 1907**

Family Marginellidae
Marginella (*sensu lato*) *deuterolivella* (Ihering, 1907)
***Volvaria deuterolivella* Ihering, 1907**
Neoimbricaria quemadensis (Ihering, 1897)
***Marginella confinis* Ihering, 1897**
***Marginella gracilior* Ihering, 1897**
***Marginella quemadensis* Ihering, 1897**
***Neoimbricaria quemadensis* ''var.'' *juliana* Ihering, 1907**
***Marginella pruniformis* Ihering, 1907**
***Marginella* sp., Ihering, 1914** [unidentifiable]
***Marginella* (*Volvaria*) sp., Ihering, 1914** [unidentifiable]
Neoimbricaria patagonica (Ihering, 1897
***Voluta patagonica* Ihering, 1897**
Neoimbricaria plicifera (Ihering, 1897)
***Marginella plicifera* Ihering, 1897**

Family Costellariidae [Vexillidae]
Vexillum patagonicus (Ihering, 1907)
***Vulpecula patagonica* Ihering, 1907**

Superfamily Cancellarioidea
Family Cancellariidae
Admete ameghinoi (Ihering, 1897)
***Cancellaria ameghinoi* Ihering, 1897**
***Cancellaria gracilis* Ihering, 1897**
***Cancellaria gracilis* ''var.'' *observatoria* Ihering, 1907**
Naronia (*Sveltia*) *major* (Ihering, 1899), **new combination, new status**
***Cancellaria gracilis* ''var.'' *major* Ihering, 1899**

Superfamily Conoidea
Family Conidae
Conus clenchi Martins, 1943

***Conus* sp., Ihering, 1907**
Conus carcellesi Martins, 1945

Family Turridae
***Genota cuevensis* Ihering, 1897**
***Genotia cruzensis* Ihering, 1907**
***Pleurotoma discors* "var." *unifascialis* Ihering, 1897**
***Pleurotoma jorgensis* Ihering, 1907**
***Pleurotoma santacruzensis* Ihering, 1907**

Family Terebridae
Terebra quemadensis Ihering, 1897
***Terebra costellata* "var." *quemadensis* Ihering, 1897**
Terebra santacruzensis Ihering, 1897
***Terebra costellata* "var." *santacruzensis* Ihering, 1897**

Subclass Heterobranchia
Superfamily Architectonicoidea
Family Architectonicidae
Architectonica schucherti (Ihering, 1914), **new combination**
***Gibbula schucherti* Ihering, 1914**
Valdesia dalli (Ihering, 1897)
***Gibbula cuevensis* "var." *aequistriata* Ihering, 1907**
***Gibbula dalli* Ihering, 1897**
***Gibbula dubiosa* Ihering, 1907**
***Gibbula fracta* "var." *cuevensis* Ihering, 1897**
Valdesia fracta (Ihering, 1897)
***Gibbula fracta* Ihering, 1897**

Superfamily Pyramidelloidea
Family Pyramidellidae
***Odostomia suturalis* Ihering, 1897**
***Turbonilla clessini* Ihering, 1907**
Turbonilla iheringi Clessin, 1900:174 [primary junior homonym]
***Turbonilla cuevensis* Ihering, 1897**
Turbonilla iheringi Cossmann, 1899
***Turbonilla eopatagonica* Ihering, 1907** [unnecessary replacement name]
Turbonilla iheringi Clessin, 1900:168 [primary junior homonym without replacement name]
***Turbonilla observationis* Ihering, 1907**
Turbonilla uruguayensis Pilsbry, 1897
***Turbonilla querandina* Ihering, 1907**

Subclass Opisthobranchia
Order Cephalaspidea
Superfamily Philinoidea
Family Actaeonidae
***Actaeon argentinus* Ihering, 1907**
***Actaeon patagonicus* Ihering, 1907**

Family Ringiculidae
  ***Ringicula magellanica* Ihering, 1907**

Family Scaphandridae
  Cylichna juliana (Ihering, 1907)
    ***Bullinella juliana* Ihering, 1907**
  ***Tornatina camaronesia* Ihering, 1907**
  Tornatina candei d'Orbigny, 1841
    ***Tornatina militaris* Ihering, 1907**

Family Bullidae
  ***Bulla arenasia* Ihering, 1907**
  ***Bulla pachychila* Ihering, 1907**

Family Retusidae
  Retusa patagonica (Ihering, 1897), **new combination**
    ***Bulla patagonica* Ihering, 1897**
    ***Bulla patagonica* "var." *jorgensis* Ihering, 1907**
  ***Volvulella cannada* Ihering, 1907**

Subclass Pulmonata
  Order Basommatophora
    Superfamily Siphonarioidea
      Family Siphonariidae
        Siphonaria lessoni (Blainville, 1826)
          ***Siphonaria lessoni pampa* Ihering, 1914**

    Superfamily Planorboidea
      Family Planorbidae
        Biomphalaria waltheri (Parodiz, 1969)
          ***Planorbis waltheri* "Ihering," ex Walther, 1931**
          Taphius walteri [sic] Parodiz, 1969 [incorrect original spelling]
          Taphius waltheri Parodiz, 1969 [emendation]

  Order Stylommatophora
    Suborder Sigmurethra
      Superfamily Orthalicoidea
        Family Orthalicidae
          Peronaeus (*Lissoacme*) *ameghinoi* (Ihering, 1908)
            ***Bulimulus ameghinoi* Ihering, 1908**
            ***Bulimulus sporadicus pampa* Ihering, 1914**
            Peronaeus (*Lissoacme*) *ameghinoi madrynensis* Parodiz, 1944

      Superfamily Strophocheiloidea
        Family Strophocheilidae
          Strophocheilus charruanus (Frenguelli, 1930)
            ***Bulimus archiplata* "Ihering" ex Walther, 1931** [*nomen nudum*]
          ***Strophocheilus chubutensis* Ihering, 1904**

        Family Megalobulimidae
          Megalobulimus hauthali (Ihering, 1904)
            ***Strophocheilus hauthali* Ihering, 1904**
            Strophocheilus avus Parodiz, 1949

Class Cephalopoda
  Subclass Nautiloidea
    Order Nautilida
        Family Nautilidae
          ***Aturia caroloameghinoi* Ihering, 1902**
          ***Aturia (Sphenaturia)* Ihering, 1921**
          Aturia (Sphenaturia) brueggeni Ihering, 1921
            ***Aturia (Sphenaturia) brüggeni* [sic] Ihering, 1921**
          ***Aturia (Sphenaturia) felschi* Ihering, 1921**
          ***Nautilus romeroi* Ihering, 1903**

Class Bivalvia
  Subclass Protobranchia
    Order Nuculoida
      Superfamily Nuculoidea
        Family Nuculidae
          ***Nucula dynastes* Ihering, 1907**
          ***Nucula observatoria* Ihering, 1907**
          ***Nucula tricesima* Ihering, 1897**

      Superfamily Nuculanoidea
        Family Nuculanidae
          Nuculana camaronesia (Ihering, 1907)
            ***Leda camaronesia* Ihering, 1907**
          Nuculana entreriana (Ihering, 1907)
            ***Leda entreriana* Ihering, 1907**
          Nuculana ortmanni (Ihering, 1907)
            ***Leda ortmanni* Ihering, 1907**
          Nuculana pueyrredona (Ihering, 1907)
            ***Leda pueyrredona* Ihering, 1907**

  Subclass Pteriomorphia
    Order Arcoida
      Superfamily Arcoidea
        Family Arcidae
          Anadara camaronesia (Ihering, 1907), **new combination**
            ***Arca camaronesia* Ihering, 1907**
          Anadara juliana (Ihering, 1907), **new combination**
            ***Arca juliana* Ihering, 1907**
          ***Arca panensis* Ihering, 1914**
          Arca umbonata Lamarck, 1819
            ***Arca patagonica* Ihering, 1897**
          Barbatia (Cucullaria) ameghinoi (Ihering, 1907), **new combination**
            ***Cucullaria ameghinoi* Ihering, 1907**
          Barbatia tridentata (Ihering, 1897), **new combination**
            ***Cuculearia* [sic] *tridentata* Ihering, 1897**
          Noetia ameghinorum (Ihering, 1907)
            ***Venericardia ameghinorum* Ihering, 1907**

        Family Cucullaeidae
          Cucullaea alta Sowerby, 1846

- ***Cucullaea dalli* Ihering, 1897**
- ***Cucullaea multicostata* Ihering, 1897**
- ***Cucullaea rocana* Ihering, 1903**
- ***Cucullaea tehuelcha* Ihering, 1907**

- Superfamily Limopsoidea
  - Family Glycymerididae
    - *Glycymeris camaronesia* Ihering, 1907
      - ***Glycimeris* [sic] *camaronesia* Ihering, 1907**
    - *Glycymeris cuevensis* (Ihering, 1897)
      - ***Pectunculus pulvinatus* "var." *cuevensis* Ihering, 1897**
    - *Glycymeris subtrigona* Ihering, 1907
      - ***Glycimeris* [sic] *subtrigona* Ihering, 1907**

- Order Mytiloida
  - Superfamily Mytiloidea
    - Family Mytilidae
      - *Crenella camaronesia* (Ihering, 1907)
        - ***Crenella divaricata camaronesia* Ihering, 1907**
      - *Chloromya hauthali* (Ihering, 1907)
        - ***Mytilus chorus* "var."** *hauthali* Ihering, 1907
      - *Lithophaga patagonica* (d'Orbigny, 1846)
        - ***Lithodomus patagonica* [sic] *dalli* Ihering, 1907**
      - "*Modiola*" *rionegrensis* Ihering, 1903
      - *Modiolus ameghinoi* (Ihering, 1897)
        - ***Modiola ameghinoi* Ihering, 1897**
      - ***Neoinoceramus ameghinoi* Ihering, 1902**

- Order Pterioida
  - Suborder Pteriina
    - Superfamily Pterioidea
      - Family Isognomonidae
        - ***Perna quadrisulcata* Ihering, 1897**

  - Suborder Pinnina
    - Superfamily Pinnoidea
      - Family Pinnidae
        - *Atrina magellanica* (Ihering, 1899)
          - ***Pinna semicostata* "var." *magellanica* Ihering, 1899**

- Order Limoida
  - Superfamily Limoidea
    - Family Limidae
      - ***Lima cossmanni* Ihering, 1907**
      - ***Lima patagonica* Ihering, 1907**
      - ***Lima pisum* Ihering, 1907**

- Order Ostreoida
  - Suborder Ostreina
    - Superfamily Ostreoidea
      - Family Ostreidae
        - ***Exogyra callophyla* Ihering, 1903**
        - *Exogyra guaranitica* (Ihering, 1899)

- ***Ostrea guaranitica* Ihering, 1899**
- *Exogyra mendozana* Ihering, 1907
  - ***Exogyra ostracina mendozana* Ihering, 1907**
- ***Ostrea ameghinoi* Ihering, 1902**
- ***Ostrea clarae* Ihering, 1907**
- ***Ostrea faira* Ihering, 1907**
- *Ostrea hatcheri* Ortmann, 1897
  - ***Ostrea percrassa* Ihering, 1897**
- ***Ostrea madryna* Ihering, 1907**
- ***Ostrea neuquena* Ihering, 1907**
  - ***Ostrea hemisphaerica* [sic] "var." *capa* Ihering, 1907**
  - ***Ostrea hemisphaerica*** [sic] "var." ***paca* Ihering, 1907**
- ***Ostrea orbignyi* Ihering, 1897**
- ***Ostrea rionegrensis* Ihering, 1903**
- ***Ostrea rocana* Ihering, 1903**
- ***Ostrea wilckensi* Ihering, 1907**

Family Gryphaeidae

- ***Gryphaea concors* Ihering, 1902**
- *Gryphaea pyrotheriorum* (Ihering, 1897)
  - ***Ostrea pyrotheriorum* Ihering, 1897**
- *Odontogryphaea* Ihering, 1903
  - ***Gryphaea* (*Odontogryphaea*) Ihering, 1903**
- *Odontogryphaea rostrigera* (Ihering, 1902)
  - ***Gryphaea concors* "var." *rostrigera* Ihering, 1902**
- *Odontogryphaea rothi* (Böhm, 1903)
  - ***Gryphaea rocana* Ihering, 1903**

Suborder Pectinina

Superfamily Pectinoidea

Family Pectinidae

- *Chlamys* Röding, 1798
  - ***Myochlamys* Ihering, 1907** [unnecessary replacement name; preoccupied]
- ***Chlamys* (*Zygochlamys*) Ihering, 1907**
- *Chlamys centralis* Sowerby, 1846
  - ***Myochlamys centralis* "var." *ameghinoi* Ihering, 1907**
- *Chlamys deseadensis* (Ihering, 1907)
  - ***Myochlamys deseadensis* Ihering, 1907**
- *Chlamys eupatagonicus* (Ihering, 1907)
  - ***Myochlamys eupatagonica* Ihering, 1907**
- *Chlamys fissocostalis* (Ihering, 1899)
  - ***Pecten fissocostalis* Ihering, 1899**
- *Chlamys foyela* (Ihering, 1914)
  - ***Myochlamys foyela* Ihering, 1914**
- *Chlamys geminata* (Sowerby, 1846)
  - ***Myochlamys geminata* "var." *radana* Ihering, 1907**
- *Chlamys jorgensis* (Ihering, 1907)
  - ***Pecten jorgensis* Ihering, 1907**
- *Chlamys juliana* (Ihering, 1907)
  - ***Myochlamys juliana* Ihering, 1907**

Chlamys laziarina (Ihering, 1907)
  ***Myochlamys laziarina* Ihering, 1907**
Chlamys nodosoplicatus (Ihering, 1897)
  ***Pecten nodosopiicatus* [sic] Ihering, 1897** [incorrect original spelling]
  ***Pecten nodosoplicatus* Ihering, 1897**
Chlamys patagonensis (d'Orbigny, 1842)
  ***Pecten patagonensis puntana* Ihering, 1907**
  ***Chlamys patagonensis* "var." *negroina* Ihering, 1907**
Chlamys patagonensis portenia (Ihering, 1907)
  ***Myochlamys patagonensis portenia* Ihering, 1907**
Chlamys praenuncius (Ihering, 1897)
  ***Chlamys espejoana* "Ihering" ex Ameghino, 1902** [*nomen nudum*]
  ***Pecten praenuncius* Ihering, 1897**
Chlamys oblongus pyramidesium (Ihering, 1907)
  ***Pecten oblongus pyramidesium* Ihering, 1907**
Chlamys quemadensis (Ihering, 1897)
  ***Pecten quemadensis* Ihering, 1897**
***Chlamys salamanca* Ihering, 1903**
***Pecten piconus* Ihering, 1907**

Family Propeamussiidae
Amusium cossmanni Ihering, 1907
  ***Amussium* [sic] *cossmanni* Ihering, 1907**

Superfamily Anomioidea
Family Anomiidae
***Pododesmus juliensis* Ihering, 1907**
***Pododesmus patagonensis* Ihering, 1907**
***Pododesmus paucisquamatus* Ihering, 1907**
***Pododesmus pazensis* Ihering, 1914**
***Pododesmus valchetanus* Ihering, 1907**

Subclass Paleoheterodonta
Order Unionoida
Superfamily Unionoidea
Family Hyriidae
***Diplodon colhuapensis* Ihering, 1903**
Fossula derbyi (Ihering, 1907)
  ***Diplodon derbyi* Ihering, 1907**
Diplodon contortus (Borchert, 1901), **new combination**
  ***Diplodon fraus* Ihering, 1907** [unnecessary replacement name]
Diplodon delodontus (Lamarck, 1819)
  ***Diplodon charruanus lujanensis* Ihering, 1907**
***Diplodon rothi* Ihering, 1904**

Subclass Heterodonta
Order Veneroida
Superfamily Lucinoidea
Family Lucinidae
***Fimbria* sp., Ihering, 1897** [unidentifiable]

- *Lucina cruzialis* (Ihering, 1907)
  - ***Phacoides promaucana* "var." *cruzialis* Ihering, 1907**
- *Lucina dalli* (Ihering, 1907)
  - ***Phacoides dalli* Ihering, 1907**
- *Lucina ortmanni* (Ihering, 1899)
  - ***Lucina ortmanni* Ihering, 1899**
- *Lucina rocana* (Ihering, 1907), **new combination**
  - ***Phacoides rocana* Ihering, 1907**
- *Miltha iheringiana* Doello-Jurado (1919)
  - ***Phacoides* sp., Ihering, 1914**

Family Ungulinidae

- *Diplodonta vilardeboaena* (d'Orbigny, 1846)
  - **Diplodonta *villardeboaena* [sic] "var." camaronesia Ihering, 1907**

Superfamily Carditoidea

Family Carditidae

- ***Cardita burckhardti* Ihering, 1903**
- ***Cardita palaeopatagonica* Ihering, 1903**
- *Carditamera plata* (Ihering, 1907)
  - ***Cardita plata* Ihering, 1907**
- ***Venericardia camaronesia* Ihering, 1907**
- ***Venericardia cannada* Ihering, 1907**
- ***Venericardia dalli* Ihering, 1907**
- *Venericardia iheringi* Böhm, 1903
  - ***Venericardia iheringi* "var." *boehmi* Ihering, 1907**
- *Venericardia patagonica* (Sowerby, 1846)
  - ***Cardita pseudopatagonica* Ihering, 1899**
- ***Venericardia sulcolunularis* Ihering, 1907**
- ***Venericardia sulcolunularis freti* Ihering, 1907**
- ***Venericardia sylva* Ihering, 1907**
- ***Venericardia tehuelchana* Ihering, 1907**
- *Venericardia volckmanni* (Philippi, 1887)
  - ***Venericardia pueyrredona* Ihering, 1907**

Superfamily Crassatelloidea

Family Crassatellidae

- ***Crassinella dalli* Ihering, 1907**
- ***Crassatella kokeni* Ihering, 1899**
  - ***Crassatellites patagonicus* Ihering, 1907**
- ***Crassatella longior* Ihering, 1897**
- *Crassatella suburbana* (Ihering, 1907)
  - ***Crassatellites suburbana* Ihering, 1907**

Superfamily Cardioidea

Family Cardiidae

- ***Cardium ameghinoi* Ihering, 1907**
- ***Cardium huttoni* Ihering, 1907**
- ***Cardium patagonicum* Ihering, 1907**
- ***Cardium philippii* Ihering, 1897**
  - ***Cardium philippii pauciradiata* Ihering, 1899**

    Cardium jorgensis Ihering, 1907, **new status**
        ***Cardium pisum* "var."** ***jorgensis* Ihering, 1907**
    Laevicardium santacruzense (Ihering, 1914), **new combination**
        ***Cardium santacruzense* Ihering, 1914**
    Lahillia angulata (Philippi, 1887)
        ***Lahillia angulata patagonica* Ihering, 1907**
    Trachycardium rocanum (Ihering, 1907), **new combination**
        ***Cardium (Hemicardium) rocanum* Ihering, 1907**

Superfamily Mactroidea
  Family Mactridae
    Mactra patagonica d'Orbigny, 1846
        ***Mactra indistincta* Ihering, 1897**
    ***Mactra jorgea* Ihering, 1914**

  Family Mesodesmatidae
  ***Lutraria ameghinoi* Ihering, 1907**

Superfamily Solenoidea
  Family Solenidae
    ***Solen crucis* Ihering, 1907**

Superfamily Tellinoidea
  Family Tellinidae
    Macoma santacruzensis (Ihering, 1899)
        ***Tellina santacruzensis* Ihering, 1899**
    ***Tellina burmeisteri* Ihering, 1907**
    ***Tellina gibber* Ihering, 1907**
    ***Tellina jeguaensis* Ihering, 1897**
    ***Tellina patagonica* Ihering, 1897**
        ***Tellina patagonica* "var."** ***camaronesia* Ihering, 1907**

  Family Semelidae
    Abra uruguayensis (Pilsbry, 1879)
        ***Abra patagonica* Ihering, 1907**

  Family Psammobiidae
    Gari burmeisteri (Ihering, 1907)
        ***Psammobia burmeisteri* Ihering, 1907**
    Gari guassu (Ihering, 1907)
        ***Psammobia guassus* [sic] Ihering, 1907**
    Gari tehuelcha (Ihering, 1907)
        ***Psammobia tehuelcha* Ihering, 1907**
    Psammotella perplana (Ihering, 1897)
        ***Tellina perplana* Ihering, 1897**
    Sanguinolaria tehuelcha (Ihering, 1899)
        ***Tellina ortmanni* Ihering, 1907**
        ***Tellina tehuelcha* Ihering, 1899**
    Tagelus plebeius (Solander, 1823)
        ***Tagelus gibbus entrerianus* Ihering, 1907**
    Solecurtus platensis d'Orbigny, 1846

Superfamily Gaimardioidea
- Family Gaimardiidae
    - *Gaimardia prisca* (Ihering, 1907)
        - ***Modiolarca prisca* Ihering, 1907**

Superfamily Corbiculoidea
- Family Corbiculidae
    - *Eriphyla sehuena* (Ihering, 1907)
        - ***Corbula sehuena* Ihering, 1907**
    - ***Corbicula (Corbiculella)* Ihering, 1907**
    - *Corbicula (Corbiculella) tenuis* Ihering, 1907
        - ***Corbicula tenuis* Ihering, 1907**
    - *Cyanocyclas salobris* (Ihering, 1907)
        - ***Cyrena salobris* Ihering, 1907**

Superfamily Veneroidea
- Family Veneridae
    - *Amiantis arenophila* (Ihering, 1907)
        - ***Macrocallista arenophila* Ihering, 1907**
    - ***Amiantis laziarina* Ihering, 1907**
    - ***Anomalocardia entreriana* Ihering, 1907**
    - ***Chione eupyga* Ihering, 1907**
    - ***Chione pampeana* Ihering, 1907**
    - **''*Cytherea*'' *chalcedonica* Ihering, 1903**
    - ***Dosinia burckhardti* Ihering, 1907**
    - *Dosinia (Dosinella) burmeisteri* (Ihering, 1907)
        - ***Dosinia burmeisteri* Ihering, 1907**
    - ***Dosinia meridionalis* Ihering, 1897**
    - ***Dosinia entreriana* Ihering, 1907**
    - *Macrocallista iheringi* (Cossmann, 1895)
        - ***Cytherea splendida* Ihering, 1897**
    - ***Pitar julianum* Ihering, 1907**
    - ***Pitar lahillei* Ihering, 1907**
    - *Pitar rostrata* (Koch, 1844)
        - ***Pitar lahillei ortmanni* Ihering, 1907**
    - *Protothaca* Dall, 1902
        - ***Chione (Ameghinomya)* Ihering, 1907**
    - *Protothaca antiqua* (King, 1832)
        - ***Chione casa* Ihering, 1907**
        - ***Chione vindex* Ihering, 1907**
    - *Protothaca argentina* (Ihering, 1897)
        - ***Venus volckmanni* ''var.'' *argentina* Ihering, 1897**
        - *Venus paranensis* Borchert, 1901
    - *Protothaca cossmanni* (Ihering, 1907)
        - ***Chione cossmanni* Ihering, 1907**
    - *Samarangia navidadis* (Philippi, 1887)
        - ***Marcia ortmanni* Ihering, 1907**
    - *Samarangia exalbida* (Chemnitz, 1795)
        - ***Venus striatolamellata* Ihering, 1897**
        - ***Marcia rada* Ihering, 1914**
        - ***Marcia scutata tehuelcha* Ihering, 1914**

Samarangia scutata (Ihering, 1907)
  ***Marcia scutata* Ihering, 1907**

Order Myoida
  Suborder Myina
    Superfamily Myoidea
      Family Corbulidae
        Corbula hatcheri Ortmann, 1900
          ***Corbula pulchella juliana* Ihering, 1907**
        ***Corbula pseudopatagonica* Ihering, 1907**

    Superfamily Hiatelloidea
      Family Hiatellidae
        Panopea bagualesia Ihering, 1907
          ***Panopaea* [sic] *bagualesia* Ihering, 1907**
        Panopea nucleus (Ihering, 1899)
          ***Glycimeris* [sic] *nucleus* Ihering, 1899**
          ***Panopaea* [sic] *nucleus elongata* Ihering, 1914**
        Panopea panis Ihering, 1907
          ***Panopaea* [sic] *panis* Ihering, 1907**
        Panopea quemadensis (Ihering, 1897)
          ***Glycimeris* [sic] *quemadensis* Ihering, 1897**
          ***Panopaea* [sic] *sierrana* Ihering, 1907**
        Panopea thomasi Ihering, 1914
          ***Panopaea* [sic] *thomasi* Ihering, 1914**

    Superfamily Pholadoidea
      Family Pholadidae
        Cyrtopleura lanceolata (d'Orbigny, 1846)
          ***Barnea* sp., Ihering, 1914**
        ***Barnea saxicava* Ihering, 1907**
        Netastoma paucispina (Ihering, 1897), **new combination**
          ***Pholas paucispina* Ihering, 1897**

Class Scaphopoda
  Order Dentaliida
      Family Dentaliidae
        ***Dentalium sulcosum* "var." *juliana* Ihering, 1907**
        ***Dentalium matanzasense* Ihering, 1907**
        Dentalium octocostellatum Pilsbry and Sharp, 1898
          ***Dentalium octocostatum* Ihering, 1897** [preoccupied name]

ACKNOWLEDGMENTS

I acknowledge with gratitude the use of facilities at the Museo Argentino de Ciencias Naturales in Buenos Aires, and the assistance of the late Directors, Dr. Max Birabén and Dr. José María Gallardo, and the Curator of Invertebrate Paleontology, Mrs. Nora Cabaleri. I am indebted to Dr. John E. Rawlins, Section of Invertebrate Zoology, CMNH, Pittsburgh, Pennsylvania, for his valuable suggestions and revisions of various drafts of this paper, and Mary Ann Daman of the same Section for technical assistance with the preparation of the manuscript. Bernadette G. Callery, Kenneth J. Boss, and Richard I. Johnson provided information on references not available at CMNH. I also wish to pay tribute to the memory of Dr. Egidio Feruglio, who, during many decades of arduous exploration, contributed so much to our knowledge of Patagonian geology.

LITERATURE CITED

Ameghino, F. 1902. L'Age des formations sédimentaires de Patagonie. Anales de la Sociedad Científica Argentina, 54:161–180, 220–249, 283–242.

———. 1906. Les formations sédimentaires du Crétacée Supérieur et du Tertiaire de Patagonia. Anales del Museo Nacional de Buenos Aires, 8:1–568.

BÖHM, J. 1903. Fossilien von General Roca am Rio Negro [without title under "Protokole"; title in index]. Zeitschrift der Deutsche Geologische Gesellschaft, 54:71–72.

BORCHERT, A. 1901. Die Molluskenfauna das Alter der Paraná-Stuffe. Neues Jahrbuch für Mineralogie, Geologie, und Paläontologie (Stuttgart), 14:1–78.

BRISTOW, A., AND J. J. PARODIZ. 1982. The stratigraphic paleontology of the Tertiary non-marine sediments of Ecuador. Bulletin of Carnegie Museum, 19:1–53.

BURCKHARDT, C. 1902. Le gisement supracrétacique de Roca. Revista del Museo de La Plata, Zoología, 10:207–223, 4 pl.

CAORSI, J. H., AND Q. J. GOÑI. 1958. Geología Uruguaya. Boletín del Instituto Geologico del Uruguay, 33:1–73.

CARCELLES, A. 1944. Catálogo de los Moluscos marinos de Puerto Quequén. Revista del Museo de La Plata, Zoología, 3(241):233–310.

CARCELLES, A., AND J. J. PARODIZ. 1938. Moluscos del contenido estomacal de *Astropecten cingulatus*. Physis (Buenos Aires), 12:255–266.

CLENCH, W. J., AND R. D. TURNER. 1950. The genera *Sthenorytis, Cirsotrema, Acirsa, Opalia,* and *Amaea* in the western Atlantic. Johnsonia, 2(29)221–246.

———. 1960. The genus *Calliostoma* in the western Atlantic. Johnsonia, 4(40):1–80.

CLESSIN, S. 1900. Eulimidae. Parts 456–460, pp. 121–200, *in* Systematisches Conchylien-Cabinet von Martini und Chemnitz (edition of H. C. Kuester), Band 1, Abteilung 28.

COSSMANN, M. 1899*a*. Description de quelques coquilles de la formation Santacruzienne en Patagonie. Journal de Conchyliologie, 47(3):223–242.

———. 1899*b*. Essais de Paléoconchologie comparée. Livre 3. Paris, 201 pp., 8 pl.

———. 1899*c*. Rectifications de nomenclature. Revue Critique de Paléozoologie (Paris), 3:133–139, 176–178.

———. 1903. Essais de Paléoconchologie comparée. Livre 5. Paris, 215 pp., 9 pl.

———. 1904. Essais de Paléoconchologie comparée. Livre 6. Paris, 151 pp.

———. 1908. Rectifications de nomenclature. Revue Critique de Paléozoologie (Paris), 12:64–268.

DEL RIO, C. J. 1985. Primera mención de la subfamilia Architectonicinae en el Terciario de la Patagonia (Republica Argentina). Ameghiniana (Buenos Aires), 22(3–4):263–268.

DEL RIO, C., AND G. A. MORRA. 1984. Representantes de la subfamilia Pseudomelaxinae en el Terciario de Patagonia. Ameghiniana (Buenos Aires), 22(1–2):111–115.

DOELLO-JURADO, M. 1919. Une nouvelle espèce de "*Miltha*" du tertiaire du l'Argentine. Physis (Buenos Aires), 4:558–562.

———. 1922. Un nuevo *Mytilus* fósil del Terciario de Patagonia. Anales de la Sociedad Científica Argentina, 94:86–90.

———. 1927. Noticia preliminar sobre los moluscos fósiles de agua dulce mencionados por Wichmann. Boletín de la Academia Nacional de Ciencias (Córdoba, Argentina), 30:407–416.

———. 1931. Una nueva especie de *Voluta* fósil de Patagonia. Anales del Museo Nacional de Buenos Aires, 36:515–519.

DÖRING, A. 1881–1882. Informe Oficial de la Comisión Científica Agregada al Estado Mayor General de la Expedición al Río Negro. Buenos Aires, 3:299–530.

———. 1884. Estudios Hidrognosticos. Boletín de la Academia Nacional de Ciencias (Córdoba, Argentina), 6:328.

ERDMANN, S., AND G. A. MORRA. 1985. Nuevos moluscos de la Formación San Julian. Ameghiniana (Buenos Aires), 22(3–4):289–295.

FERUGLIO, E. 1933. I terrazi marini della Patagonia. Anali del Reale Museu Gelogico di Bologna, 8(bis):236.

———. 1935. Relaciones estratigráficas y faunísticas entre los estratos cretáceos y terciarios in la región del Lago Argentino y en la del Golfo de San Jorge. Boletín Informativo de Petroleos (Buenos Aires), nos. 120 and 130.

———. 1949–1950. Descripción Geológica de la Patagonia. Publication of the Yacimientos Petroliferos Fiscales (Buenos Aires), 3 volumes, 1112 pages.

FRENGUELLI, J. 1920. Contribución al conocimiento de la geología de Entre Rios. Boletín de la Academia Nacional de Ciencias (Córdoba, Argentina), 24:55–256.

HATCHER, J. B. 1897. On the geology of southern Patagonia. American Journal of Science, 4:327–354.

———. 1900. Die Conchylien der Patagonischen Formation, von H. v. Ihering. Compte-rendu, Science, 11(268):263–266 [as cited in Ihering, 1907*a*].

HAUTHAL, R. 1898. Ueber patagonisches Tertiär etc. [sic]. Zeitschrift der Deutschen Geologischen Gesellschaft, 50:436–440.

———. 1902. [Communication and Table I]. Pp. 45–47, *in* Contribuciones á la Palaeophytologia Argentina. III. Sobre la existencia de una Dakota-Flora en la Patagonia Austro–Occidental (Cerro Guido, Governación de Santa Cruz) (F. Kurtz). Revista del Museo de La Plata, 10:45–60.

HUPÉ, L. H. 1854. Fauna Chilena—Moluscos. *In* Historia Física y Política de Chile (C. Gay). Zoología (Santiago), 8:1–500, Volume 2, Atlas.

IHERING, H. VON. 1896. Zur Kenntnis der südamerikanischen *Voluta* und ihrere Geschichte. Nachrichtsblätter Deutsche Malakozoologische Gesellschaft (Frankfurt), 7:93–99.

———. 1897*a*. Zur Geschichte der marinen Fauna von Patagonia. Zoologischer Anzeiger, 20:530–535.

———. 1897*b*. Os Moluscos dos terrenos Terciarios da Patagonia. Revista do Museu Paulista (São Paulo), 2:217–382.

———. 1899*a*. Die Conchylien der Patagonisches Formation. Neues Jahrbuch für Mineralogie, Geologie, und Paläontologie, 2:1–46.

———. 1899*b*. Descripción de la *Ostrea guaranitica.* Anales de la Sociedad Científica Argentina, 47:63–64.

———. 1900. The History of the Neotropical Region. Science, 1900:857–864.

———. 1902*a*. Historia de las Ostras Argentinas. Anales del Museo Nacional de Buenos Aires, 4: 109–123.

———. 1902*b*. On the molluscan fauna of the Patagonian Tertiary. Proceedings of the American Philosophical Society, 41:132–137.

———. 1903. Les mollusques des terrains crétaciques supérieurs de l'Argentina orientale. Anales del Museo Nacional de Buenos Aires, 9:193–229.

———. 1904. Nuevas observaciones sobre moluscos cretáceos y terciarios de Patagonia. Revista del Museo de La Plata, Zoología, 11:227–242.

———. 1907*a*. Les mollusques fossiles du Tertiaire et du Crétacée Supérieur de l'Argentine. Anales del Museo Nacional de Buenos Aires, 14:1–611.

———. 1907*b*. Archhelenis und Archinotis. W. Engelmann, Leipzig. 350 pp.

———. 1908. Mollusques du pampéen de Mar del Plata et Chapadmalal. Anales del Museo Nacional de Buenos Aires, 17:429.

———. 1914. Catálogo de moluscos Cretáceos e Terciarios da Argentina da colleção do author [with appendix in German]. Notas Preliminares da Revista do Museu Paulista (São Paulo), 1(3):1–148.

———. 1921. Nautilidos del Terciario de Chile y Argentina. Physis (Buenos Aires), 5:76.

KLAPPENBACH, M., AND O. OLAZARRI. 1966. Notas sobre Strophocheilidae: *Strophocheilus charruanus* (Frenguelli). Revista de la Facultad de Humanidades y Ciencia (Montevideo), 22:233–238.

KRAGLIEVICH, L. 1930. La Formación Friaseana. Physis (Buenos Aires), 10:127–161.

MARTINS, E. A. 1943. Uma nova especie de Molusco do genero *Conus* do Brasil (*C. clenchi*). Boletim do Museu Nacional do Rio de Janeiro, 128:1–8.

———. 1945. *Conus carcellesi,* un nuevo gastropodo marino de la Rep. Argentina. Notas del Museo de La Plata, 10:259–264.

MARWICK, J. 1924. The Tertiary and Recent Naticidae and Naricidae of New Zealand. Transactions and Proceedings of the New Zealand Institute, Wellington, 55:545–579.

MODELL, H. V. 1950. Südamerikanische Najaden der Gattungen *Castalia, Schleschiella* und *Ecuadorea.* Archiv für Molluskenkunde, 79:135–146.

MOERICKE, W., AND G. STEINMANN. 1896. Die Tertiärer Bildungen dem nordelischen Chile und ihre Fauna. Neues Jahrbuch für Mineralogie, Geologie, und Paläontologie, 10:553–586.

MORRA, G. A. 1985. Revisión de *Zygochlamys* Ihering. Ameghiniana (Buenos Aires), 22(3–4):300.

ORBIGNY, A. D. D'. 1842 [1835–1846]. Voyage dans l'Amérique Méridionale, Paris. 3(3):1–290, Geologie; 3(4):1–188, Paléontologie; 5(3):1–758, Mollusques.

ORTMANN, A. E. 1897. On some of the large oysters of the Patagonia. American Journal of Science, (4)4(154):355–356, pl. 9.

———. 1899. The fauna of the Magellanian beds of Punta Arenas, Chile. American Journal of Science, (4)8(158):427–432.

———. 1900. Synopsis of the collections of invertebrate fossils made by the Princeton Expedition to southern Patagonia. American Journal of Science, (4)10(160):368–381.

———. 1902. Tertiary invertebrates. Reports of the Princeton Expedition to Patagonia, 2(2):45–332.

PALMER, K. V. W., AND D. C. BRANN. 1965. Catalogue of the Paleocene and Eocene Mollusca of the southern and eastern United States. Pelecypoda, Amphineura, Cephalopoda. Bulletins of American Paleontology (Ithaca, New York), 48(1):1–471.

PARODIZ, J. J. 1939. Dorsaninae Argentinas y Uruguayas. Physis (Buenos Aires), 17:745–768.

———. 1944. El genero *Bulimulus* en el Territorio de La Pampa y en la Patagonia meridional. Comunicaciones Zoologicas del Museo Historia Natural de Montevideo, 1(17):1–8.

———. 1949*a*. Un nuevo gastrópodo terrestre del Eoceno de Patagonia. Physis (Buenos Aires), 20: 174–179.

———. 1949*b*. Notas sobre *Strophocheilus* fósiles de Argentina. Physis (Buenos Aires), 20:181–184.

———. 1957. Centenario de d'Orbigny. Neotropica, 3(10):1–6.

———. 1962. Los Moluscos marinos de Pleistoceno Rioplatense. Comunicaciones de Sociedad Malacologica del Uruguay (Montevideo), 1(2):29–46.

———. 1968. Annotated catalogue of the genus *Diplodon* (Unionacea, Hyriidae). Sterkiana, 30:1–22.

———. 1969. The Tertiary non-marine Mollusca of South America. Annals of Carnegie Museum, 40:1–242.

———. 1973. The species complex of *Diplodon delodontus* (Lamarck). Malacologia, 14:247–270.

———. 1982. Distribution and origin of the South American continental molluscs. Malacologia, 22: 421–425.

PARODIZ, J. J., AND L. HENNINGS. 1965. The *Neocorbicula* of the Paraná–Uruguay Basin. Annals of Carnegie Museum, 38:69–96.

PHILIPPI, R. A. 1887. Fósiles Terciarios y Cuartarios de Chile. Santiago, Chile, 256 pp. [Also in German: Die Tertiaren und Quartarien Versteinerugen Chiles. Leipzig].

PILSBRY, H. A., AND A. P. BROWN. 1917. Oligocene fossils from the neighborhood of Cartagena, Colombia. Proceedings of the Academy of Natural Sciences (Philadelphia), 69:32–41.

PILSBRY, H. A., AND B. SHARP. 1898. Scaphopoda. Manual of Conchology, 17:xxxii + 348 pp., 48 pl.

RIOS, E. C. 1975. Brazilian Marine Mollusks Iconography. Fundacão Universidade do Rio Grande, Brazil, 331 pp.

[RÖDING, P. F.]. 1798. Museum Boltenianum. Catalogus cimeliorum e tribus regnis naturae quae olim collegerat Joa. Fried Bolten, M.D.p.d. Pars Secunda continens Conchylia Testacea univalvia, bivalvia & multivalvia. Anonymously published, Hamburg, viii + 199 pp.

SCUDDER, S. H. 1882*a*. Nomenclator Zoologicus. I. Supplemental List of Genera in Zoology. Government Printing Office, Washington, D. C. xxi + 376 pp.

———. 1882*b*. Nomenclator Zoologicus. II. Universal Index to Genera in Zoology. Government Printing Office, Washington, D. C. 340 pp.

SIMPSON, G. G. 1932. The supposed occurrences of Mesozoic mammals in South America. American Museum Novitates, 530:1–9.

———. 1933. Stratigraphic nomenclature of the Tertiary of central Patagonia. American Museum Novitates, 644:1–13.

———. 1935. Occurrence and relationships of the Río Chico fauna of Patagonia. American Museum Novitates, 818:1–21.

———. 1940. Review of the mammal-bearing Tertiary of South America. Proceedings of the American Philosophical Society, 83:649–709.

———. 1941. The Eogene of Patagonia. American Museum Novitates, 1120:1–16.

SOWERBY, G. B. 1833. [New species]. Pp. 83–85, *in* [. . .new species of shells contained in the collection made by Mr. Cuming . . .] (W. J. Broderip and G. B. Sowerby). Proceedings of the Zoological Society of London, 1833:82–85.

———. 1846. Descriptions of Tertiary fossil shells from South America. Pp. [249]–264, *in* Geological Observations in South America (C. Darwin). Smith, Elder and Co., London, vii + 279 pp.

STEINMANN, G., AND O. WILCKENS. 1908. Kreide- und Tertiärfossilien aus den Magellanslandern gesammelt von der Schwedischen Expedition. Arkiv för Zoologi (Stockholm), 4(6):1–118, 7 pl.

STENZEL, H. B. 1945. Oysters of the *Odontogryphaea* and *Flemingostrea* stock. Bulletin of the Geological Society of America, 56(12, pt.2):1202.

TOURNOUËR, A. 1903. Note sur la géologie et la paléontologie de la Patagonia. Bulletin de la Société Geologique de France, 3:463–473.

VAUGHT, K. C. 1989. A Classification of the Living Mollusca. American Malacologists, Inc., Melbourne, Florida, xii + 195 pp.

WALTHER, K. 1931. Sedimentos geliticos y clastogeliticos del Cretáceo Superior y Terciario Uruguayos. Boletín del Instituto Geologico y Perforaciones (Montevideo, Uruguay), 13:1–92.

WEGENER, A. 1924. The Origin of Continents and Oceans [English translation of third German edition (1922)]. Methuen and Co., London, xx + 212 pp.

WENZ, W. 1938. Gastropoda. Teil 1. Allgemeiner Teil und Prosobranchia. Handbuch der Paläozoologie, Band 6, Gebrüder Borntraeger, Berlin, viii + 1,639 pp.

WHITE, C. A. 1887. Contribução a paleontología do Brasil. Archivos do Museu Nacional, Rio de Janeiro, 7:1–273.

WICHMANN, R. 1927. Sobre la facies lacustre senoniana de los estratos con dinosaurios y su fauna. Boletín de la Academia Nacional de Ciencias (Córdoba, Argentina), 30:383–406.

WILCKENS, O. 1911. Die Mollusken der antarktischen Tertiärformation. *In* Nordenskjöld Schwedische Südpolar-Expedition, 1901–1903, 13:1–42, 1 pl.

WINDHAUSEN, A. 1916. Yacimientos petroliferos de la zona Andina. Boletín de la Dirección de Minas, Buenos Aires (Series B, Geology), 15:1.27.

———. 1918. The problem of the Cretaceous–Tertiary in South America. American Journal of Science, 45:1–53.

———. 1931. Geología Argentina. Volume 2: Historical—Stratigraphic. Editorial Peuser, Buenos Aires, Argentina.

ANNALS OF CARNEGIE MUSEUM
Vol. 65, Number 3, Pp. 297–303 30 August 1996

TWO NEW SPECIES OF *XYRIS* FROM CUBA

Armando Urquiola Cruz[1]

Robert Kral[2]
Research Associate, Section of Botany

Abstract

Two new species of *Xyris* (Xyridaceae) are described and illustrated, both endemic to western Pinar del Río Province, Cuba. Differences between these and two closely related species, *X. navicularis* Griseb. and *X. bicarinata* Griseb., are discussed. A key to the four species is included.

Resumen

Se describen e ilustran dos especies nuevas de *Xyris* (Xyridaceae) endémicas del occidente de Pinar del Río Provincia, Cuba. Se discuten las diferencias entre éstas y la cercana *X. navicularis, X. bicarinata,* además se dan las claves para las mismas.

Introduction

During an examination of material of Xyridaceae for the Flora of the Greater Antilles, the senior author had difficulty with some morphologic extremes of what previously had been identified as *Xyris navicularis,* particularly with samples gotten by him and others from far western Pinar del Río Province. Further fieldwork by him in western Pinar del Río has served not only to confirm extreme variation, but also to find populations of two related and yet distinctly different species. These two novelties, now sufficiently vouchered, are described, figured, and discussed below. Since there are also some character states in this complex of species that are shared by yet another Cuban endemic, *X. bicarinata* Griseb., we include and compare that species also.

Institutional abbreviations in text follow Holmgren et al., 1990.

Description of New Species

Xyris bissei Urquiola & Kral, **species novum**
(Fig. 1)

Herba perennis, densicaespitosa; radices fibrosa. **Caules** breves. **Folia** principalia anguste linearia, 8–15 cm longa, erecta vel anguste flabellate expansa, vaginis scaporum longiora. **Laminae** foliorum compressae, tortae, 2–3 mm latae, vaginis 3–4-plo longiores, longitudine subtiliter multinervosae, brunneolo-ferrugineae vel testaceae; apices gradatim, tum abrupte incurvato-acuti, leviter incrassati; margines cartilagineo-incrassati, grosse papillosi vel scabrelli; vaginae integrae, carinatae, carinibus ad apicem leviter papillosis, lateribus valde longitudinae multicostatae, basi brunneae, glabrae, valde pluricostatae, marginibus in laminas gradatim convergentibus, ad apicem ligulam erectam vel excurvatam acutam 1.5–

---

[1] Departamento de Biología, Instituto Superior Pedagógico de Pinar del Río, Cuba.
[2] Department of Biology, Vanderbilt University, Nashville, Tennessee.
Submitted 19 June 1995.

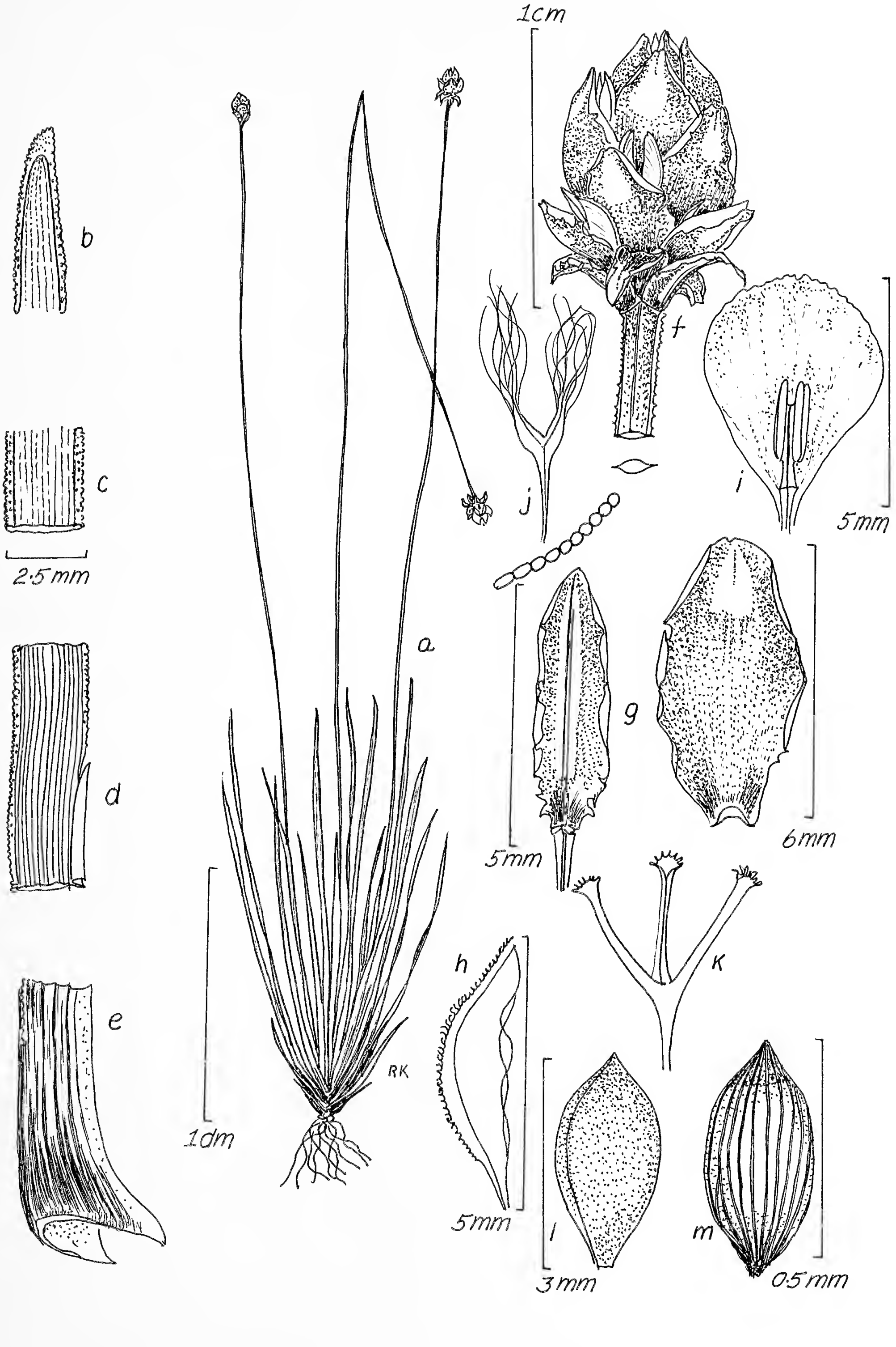
2 mm longam fascientes, infime gradatim dilatatae. **Vaginae scaporum** laxae, valde convolutae sed apertae, laminis brevibus. **Scapi** erecti, subfiliformes, torti et flexuosi, vulgo bicostati, distaliter parum compressi aut ovales, 0.7–1 mm lati, costis duas angustata scabropapillatas fascientes. **Spicae** obovoideae, late ovoideae ubi maturae, 8–13 mm longae, pluriflorae, breviter attenuatae; bracteae laxe spiraliter imbricatae, tenues, pallide brunneolae, margine late scariosae, involuto-laceratescens; bracteae steriles ca. 4, mox valde excurvatae vel recurvatae, oblongo-ellipticae vel anguste ovatae, 5–5.5 (–6) mm, areis dorsalibus linearibus bracteam aequantibus, viridis, unicostalis; bracteae fertiles late ovatae aut ellipticae, 5.5–6.5 mm longae, ecarinatae, leviter convexae, ad apicem obtusae et areis dorsalibus brevibus, ovatis, indistinctis, dilutis, ad apicem leviter carinatis. **Sepala lateralia** libera, subequilateralia, valde curvata, elliptica, ca. 5 mm longa, acuta, ala carinali firma, prominente crispato-ciliolata. **Laminae petalorum** late rhombeo-orbiculatae, luteolae, margine denticulatae. **Staminodia** bibrachiata, brachiis longipenicillata. **Antherae** oblongae, ca. 2 mm longae, profunde bifidae et auriculatae; filiis brevis, 0.5–0.6 mm longis. **Capsula** ellipsoideae vel anguste obovoideae, 3 mm longae, apiculatae, pallide cinereo-brunneolae; placenta marginalis. **Semina** numerosa, ellipsoidea, 0.5 mm longa, pallide brunneola, translucida, longitudine valde multicostata.

Slender but stiff and densely cespitose, hard-based perennial 20–60 cm high. Roots coarse, fibrous. Stems short. Principal foliage leaves ascending or in narrow fans, longer than the scape sheaths, 8–15 cm long; blades linear, flat, 2–3 mm wide, narrowed gradually to an incurved-acute, slightly thickened tip, the edges cartilaginous-thickened, scabridulous-papillate, the surface smooth, finely nerved, greenish-brown; sheaths entire, keeled, ⅓–¼ as long as blades, with edges forming an erect or slightly excurved scarious ligule 1.5–2 mm long at narrowed base of blade, and gradually dilating downward, the base smooth, deep brown, strongly few-costate, the keel costa papillate-scabridulous. Scape sheaths loosely tubular, strongly convolute but open, short-bladed. Scapes wiry, twisted and flexuous, mostly two-costate, distally slightly compressed or oval, 0.7–1 mm wide, the costae forming two strong, scabro-papillate edges. Spikes ovoid, maturing broadly ovoid, 8–13 mm long, of several spirally and loosely imbricate, thin, light-brown bracts; sterile bracts mostly four, elliptic to narrowly ovate, 5–5.5 (–6) mm long, broadly acute, soon strongly excurved or recurved, lacerate, with pale or pale green, narrowly elliptic, elongate dorsal areas, carinate; fertile bracts broadly ovate or elliptic, 5.5–6.5 mm long, ecarinate, slightly convex with indistinct, ovate, paler, apically low-carinate dorsal areas, the apex obtuse or slightly emarginate, the thin borders strongly involute, becoming strongly lacerate. Lateral sepals free, subequilateral, strongly curvate, elliptic, ca. 5 mm long, acute, the firm but broad keel prominently crisped-ciliate. Petal blades rhombic-orbicular, 5 mm long, yellow, low-toothed. Staminodia bibrachiate, the branches long-penicillate. Anthers oblong, ca. 2 mm long, deeply bifid and auriculate, on short filaments 0.5–0.6 mm long. Capsule ellipsoid or narrowly obovoid, 3 mm long, apiculate, pale gray-

---

→

Fig. 1.—*Xyris bissei* (*Urquiola et al. 7876*). a. Habit sketch; b. leaf tip; c. leaf midblade; d. leaf blade-sheath junction; e. leaf base; f. spike; g. lowest spike bract (left), -fertile bract (right); h. lateral sepal; i. petal blade and stamen; j. staminode and enlarged apical sector of beard hair (below); k. stylar apex; l. capsule; m. seed.


1cm
b
c
2·5mm
d
e
a
1dm
RK
f
j
i
5mm
g
5mm
6mm
k
h
5mm
l
3mm
m
0·5mm

brown, the placentation parietal. Seeds ellipsoid, 0.5 mm long, pale amber, translucent, with ca. ten strong, horizontal, parallel ribs per side.

Type.—**CUBA. Pinar del Río:** Pinares sobre arenas blancas, próximo a la Laguna de Los Carneros, Santa Teresa, Guane, m.s.m. 5, 12 Apr. 1993, *A. Urquiola, A. Urquiola f., E. Lezcano, R. Novo 7876* (holotype: HPPR; isotypes: GH, HAJB, HAC, NY, VDB).

Etymology.—This species is named in honor of the late Johannes Bisse, an exceptional worker on the Cuban flora and teacher of many present-day Cuban botanists.

Xyris mantuensis Urquiola & Kral, **species novum**
(Fig. 2)

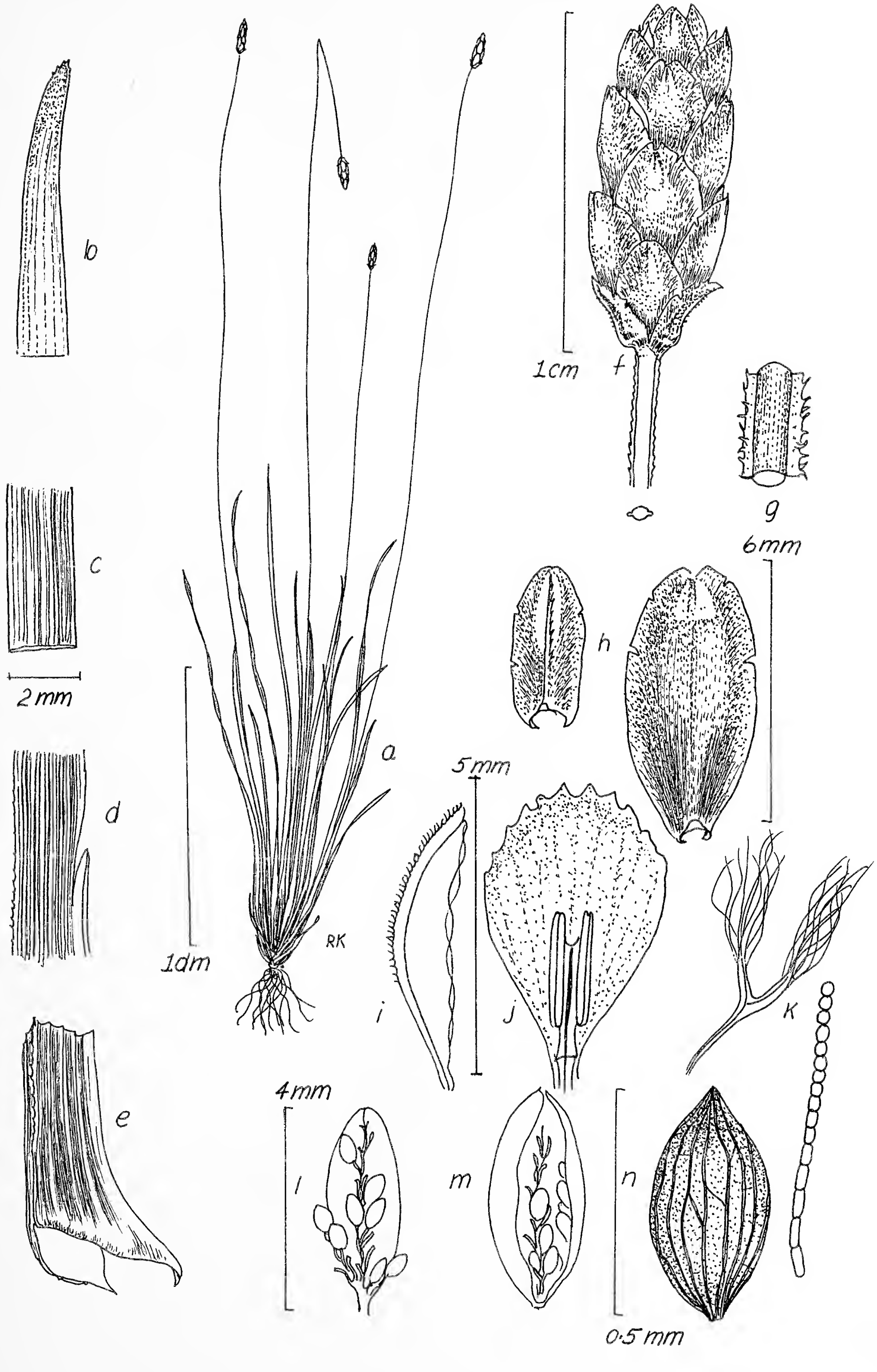
Herba perennis, gracilis, densicaespitosa; radices fibrosa. **Caules** breves. **Folia principalia** anguste linearia, 15–20 (–25) cm longa, erecta vel anguste flabellate expansa, vaginis scaporum longiora. **Laminae foliorum** compressae, tortae vel rectae, 1–2 (–3) mm latae, vaginis 4–5-plo longiores, integrae, longitudine subtiliter multinervosae, olivaceae; apices gradatim decrescentes, anguste acuti, vulgo prominente scabro-papillatae; margines tenues, a basin dorsaliter papillosi vel ciliatae; vaginae integrae, carinatae, carinibus ad apicem leviter scabridis, lateribus valde longitudine multicostatae, basi atroferrugineae aut brunneolae, nitidae, marginibus in laminas gradatim convergentibus, ad apicem ligulam erectam vel excurvatam acutam 1.5–2 mm longam fascientes, infime gradatim, tum abrupte dilatatae. **Vaginae scaporum** laxae, conduplicatae, a medio ad apicem apertae, laminis breves. **Scapi** erecti, subfiliformes, torti et flexuosi, a basin teres, multicostali, apicem versus vulgo bicostati, ca. 1 mm lati, plerumque costis duas alas valde papillosas aut ciliatas fascientes. **Spicae** anguste ellipsoideo-cylindricae vel lanceoloideae, 1.2–1.6 cm longae, pluriflorae; bracteae steriles mox 4, pari infimo oblongo, valde carinato, carinis scabridis, obtuso, 3–3.5 mm longo, paribus intimis fertilibus leviter breviores, in fertiles gradatim transientes; bracteae fertiles obovatae vel late ellipticae, 5.5–6 mm longae, integrae tum laceratae, convexae, areis dorsalibus late ovatis, brevis, indistinctis, subapice carinatis. **Sepala lateralia** libera, subequilateralia, valde aut leviter curvata, 3.5–5 mm longa, acuta; ala carinali a medio ad apicem ciliolata. **Laminae petalorum** obovatae, ca. 5 mm longae, late rotundatae, serratae. **Staminodia** bibrachiata, brachiis longipenicillatis. **Antherae** oblongae, ca. 2 mm longae, profunde retusae et auriculatae; fila lata, ca. 7 mm longa. **Capsula** ellipsoidea, 4 mm longa, placentatio parietalis. **Semina** ellipsoidea, apiculata, 0.5 mm longa, translucida, longitudine valde multicostata.

Herb perennial, slender, densely cespitose, hard-based, 30–45 cm high. Roots coarsely fibrous. Stems short. Principal foliage leaves ascending in narrow fans, 15–20 (–25) cm long; blades flattened, twisted or straight, narrowly linear, 1–2.5 (–3) mm wide, tapering gradually to slightly thickened, incurved, narrowly acute tip, the margin slightly if at all thickened, papillate to ciliate at least toward base,

---

→

Fig. 2.—*Xyris mantuensis* (*Urquiola et al. 7880*). a. Habit sketch; b. leaf apex; c. leaf midblade; d. leaf blade-sheath junction; e. leaf base; f. spike; g. extreme example of midscape costa; h. lower spike bract (left), -fertile bract (right); i. lateral sepal; j. petal blade, stamen; k. staminode and enlarged apical sector of beard hair (below right); l. capsule valve, adaxial side; m. capsule, valves pulled apart; n. seed.


b
c
2 mm
d
e
1dm
RK
a
1cm
f
g
6mm
h
5 mm
i
j
k
4mm
l
m
n
0·5 mm

surface smooth, greenish-maroon with several low nerves, blade base narrowed at junction with sheath; sheaths entire, multicostate, keeled distally, keel costa strongly scabro-ciliate, at blade junction producing an erect to excurved ligule 1.5–2 mm, gradually, then abruptly dilating downsheath to a broad base, distally pale yellow-green, proximally deep red-brown or brownish, lustrous. Scape sheath conduplicate but loose, open most of its length, and with a short, linear blade similar to foliage leaf. Scapes subfiliform, twisted and flexuous, proximally terete, several-costate, costae narrow but strong, distally with fewer, often two, costae, ca. 1 mm wide, the strong costae forming edges, these commonly intermittently papillate to strongly tuberculate-scabrid, or retrorsely so. Spikes narrowly ellipsoid-cylindric or lanceoloid, 1.2–1.6 cm long, of many subdecussately arranged, loosely imbricate, ascending, tan to brown bracts with indistinct dorsal areas; sterile bracts usually four, the lower pair oblong, 3–3.5 mm long, blunt, carinate, the keel raised and scabrid, the upper pair slightly longer, broader; fertile bracts broadly elliptic or narrowly obovate, convex, 5.5–6 mm long, entire aging lacerate, the paler dorsal area with a low carina subapically. Lateral sepals free, subequilateral, strongly or slightly curved, 3.5–5 mm long, the broadly rounded apex coarsely toothed. Petal blades obovate, ca. 5 mm long, broadly rounded, serrate. Staminodia bibrachiate, branches long-penicillate-hairy. Anthers oblong, ca. 2 mm long, deeply bifid and auriculate, the connective broad, on short flattened filaments ca. 0.7 mm long. Capsule ellipsoid, 4 mm long, placentation three-parietal. Seeds broadly ellipsoid, 0.5 mm long, amber, with ca. ten strong, mostly parallel ribs per side.

Type.—**CUBA. Pinar del Río:** Pinares sobre arenas blancas de Playa La Cana, Mantua, m.s.m. 5, 1 Jan. 1994, *A. Urquiola & A. Urquiola f. 7880* (holotype HPPR; isotypes GH, HAC, HAJB, NY, VDB).

Etymology.—This species is named for the type locality.

DISCUSSION

There are two other species of *Xyris* in the Antilles with which the two new species could be confused and which can co-occur with them in the white sand savanna or pineland ecosystems of Pinar del Río, namely *X. navicularis* Grisebach (as mentioned), the nearest morphologically to *X. mantuensis,* and *X. bicarinata* Grisebach, which resembles *X. bissei* in spike and somewhat in leaf. These four species are compared by means of the following key:

1a. Mature (seeding) spikes broadly ovoid or obovoid, with at least the lower bracts strongly excurved or recurved.
  2a. Leaf blades narrowly linear or filiform, 1–2 mm wide, the edges thickened, often with a median furrow, smooth or nearly so, and not in color contrast with the rest of the blade, medially with 1–3 strongly raised nerves, the others lower or indistinct . . . . . *X. bicarinata*
  2b. Leaf blades linear, 2–5 mm wide, the edges a narrow or strong, cartilaginous, smooth to papillate band in pale contrast with the rest of the blade, the faces with more and less strongly raised nerves.
    3a. Bracts aging lacerate and also strongly revolute-inrolled; blades of principal leaves mostly 2–3 mm wide, their margins moderately to strongly papillate or rugulose-papillate; scape costae mostly papillate or scabridulous. . . . . *X. bissei*
    3b. Bracts aging lacerate but scarcely if at all revolute; blades of principal leaves 2–5 mm wide, their margins mostly smooth, rarely sparsely papillate; scape costae smooth to sparsely papillate . . . . *X. navicularis*
1b. Mature (seeding) spikes narrowly ovoid to lanceoloid or ellipsoid-cylindric, the bracts (spreading-) ascending to erect.
  4a. Spikes lance-cylindric, narrowly ellipsoid, or cylindric, 0.4–0.7 cm thick, mostly widest

at or near middle; leaf sheath apex with ligule 1–1.5 mm long; margins of leaf blades remotely papillate to papillate or even scabrociliate; the most prominent scape costae papillate to intermittently scabrociliate, often retrorsely so . . . . *X. mantuensis*

4b. Spikes ovoid to lance-ovoid or broadly cylindric, 0.7–1.0 cm thick; leaf sheath apex with ligule 0.2–0.5 mm long or ligule lacking; margins of leaf blades smooth, rarely sparsely papillate; scape costae smooth or sparsely or distantly papillate. . . . . *X. navicularis*

Of the four species treated in the key above, only *X. navicularis* is found outside Cuba, appearing in savanna or pine savanna in Belize, Honduras, Nicaragua, and (rarely) in Venezuela. The rest are confined to white-sand savannas in western Cuba. There all four occur, but the two novelties are thus far known only from a few populations within a very narrow area of far western Pinar del Río.

LITERATURE CITED

HOLMGREN, P. K., N. H. HOLMGREN, AND L. C. BARNETT. 1990. Index Herbariorum. Part I: The Herbaria of the World. Eighth Edition. Regnum Vegetabile, 120:1–693.

ANNALS OF CARNEGIE MUSEUM

VOL. 65, NUMBER 3, PP. 305–321 30 AUGUST 1996

A NEW PLESIADAPIFORM (MAMMALIA: PLESIADAPIFORMES) FROM THE EARLY EOCENE OF THE BIGHORN BASIN, WYOMING

KENNETH D. ROSE[1]
Research Associate, Section of Vertebrate Paleontology

THOMAS M. BOWN[2]
Research Associate, Section of Vertebrate Paleontology

ABSTRACT

Dentaries of a very small, specialized plesiadapiform from the lower Eocene Willwood Formation are the basis for a new genus and species, *Picromomys petersonorum.* It was the smallest known plesiadapiform, weighing only about 10 g. Like some other plesiadapiforms, the new taxon has a strongly procumbent, hypertrophied medial incisor, followed by very reduced dentition between the incisor and P_4. Unlike all other plesiadapiforms, it has a unique semimolariform P_4 reminiscent of M_1 in picrodontids, as well as lower molars bearing an accessory trigonid cusp anterobuccal to the protoconid. The closest known relative of *Picromomys* appears to be Bridgerian *Alveojunctus,* and we group these two genera here in the new family Picromomyidae. Picromomyids share derived similarities with several plesiadapiform families but are probably most closely related to either Micromomyidae or uintasoricine Microsyopidae.

INTRODUCTION

Field work in early Wasatchian strata of the Willwood Formation of the Bighorn Basin in 1994 yielded dentaries of a highly distinctive new plesiadapiform. The new form is unusual in several respects, including a highly modified lower fourth premolar, presence of an accessory trigonid cusp on M_{1-2}, and its extremely small size. It also shares numerous derived traits with various plesiadapiforms assigned to four different families, but there is no compelling evidence to support a special relationship to any one particular family. Hence homoplasy must account for many of the similarities. The only strongly supported relationship is to the poorly known Bridgerian species *Alveojunctus minutus,* and even this alliance is based on very limited evidence. The latter has been considered to be a uintasoricine microsyopid (Bown, 1982; Gunnell, 1989), but its apparent similarities to microsyopids could well be convergent, for it also shares potential synapomorphies with other families. The new taxon and *Alveojunctus* are here placed in a new family of plesiadapiforms because of their unusual specializations and the lack of an unequivocal relationship to any known family of plesiadapiforms.

Recognition of new species of fossil mammals from the lower Eocene Willwood Formation is not unusual, despite more than a century of field work in these strata. Discovery of new genera or families, however, is considerably rarer. It

---

[1] Department of Cell Biology and Anatomy, The Johns Hopkins University School of Medicine, Baltimore, Maryland 21205.

[2] Adjoint Associate Professor, Department of Geological Sciences, University of Colorado, Boulder, Colorado 80309.

Submitted 30 October 1995.

serves as a reminder that we still have much to learn about mammalian diversity during the Wasatchian—even in well-studied sequences.

Abbreviations used in text are: AMNH, American Museum of Natural History, New York, New York; USGS, US Geological Survey, Denver, Colorado; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; YPM-PU, Peabody Museum, Yale University, New Haven, Connecticut.

SYSTEMATIC PALEONTOLOGY

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

Picromomyidae, **new family**

Type Genus.—*Picromomys,* new genus.

Included Genera.—Type genus and *Alveojunctus.*

Distribution.—Wasatchian–Bridgerian (early–middle Eocene) of Wyoming.

Diagnosis.—Diminutive plesiadapiforms having the following combination of features: very low-crowned lower molars with shallow hypoflexids, low and anteriorly canted trigonids, and hypoconulids shifted towards entoconids but separated by a distinct entoconid notch; P_4 larger than M_1 and with open, anteriorly canted trigonid and large, squared talonid with fully buccal cristid obliqua and no hypoflexid; anterobuccal cingulids poorly developed or absent.

Discussion.—Although *Picromomys* and *Alveojunctus* are extremely rare and their known fossils very fragmentary, they share several unusual features that suggest close relationship. Moreover, they are dentally so distinctive that they cannot reasonably be assigned to any named family. No other plesiadapiforms have modified P_4 in the same way. Nonetheless, there can be little doubt that both are plesiadapiforms (see Discussion following description of the new species), and there are derived resemblances to members of four different families: Micromomyidae, Microsyopidae, Picrodontidae, and Paromomyidae (see below). In no case are the similarities very compelling, however, and the likelihood that most of them result from convergence is equally plausible.

It is possible that more complete material will strengthen the alliance of Picromomyidae with one of those families—most probably Micromomyidae or Microsyopidae, to judge from present evidence—and eventually warrant reclassification (e.g., as a subfamily of Micromomyidae or a tribe of Uintasoricinae). However, family level separation seems justified by the kind and extent of dental apomorphies present in picromomyids. Many plesiadapiforms exhibit modifications of antemolar teeth while retaining rather conservative molars. In particular, a specialized, usually hypertrophied P_4 characterizes several plesiadapiform families (viz. Carpolestidae, Paromomyidae, Micromomyidae), each of which has modified this tooth in a different manner. The defining specializations of picromomyids are comparable to any of these.

Bridgerian *Alveojunctus* is known from only a small number of isolated teeth (Fig. 1) representing two or three loci, P_4, M_2(?), and possibly M_3. The single molar (the holotype) known from the Aycross Formation was identified as M_1 by Bown (1982), but in comparison with the new species appears more likely to be M_2. As noted by Bown, an M_3 from the early Bridgerian Cathedral Bluffs Tongue (Wasatch Formation, Green River Basin), referred to cf. *Niptomomys* sp. by West and Dawson (1973), may also belong to *Alveojunctus.* These two molars are distinctive and differ from those of the new species in uniquely having the trigonid basin conjoined with the talonid basin through a deep trigonid notch. P_4 of *Al-*

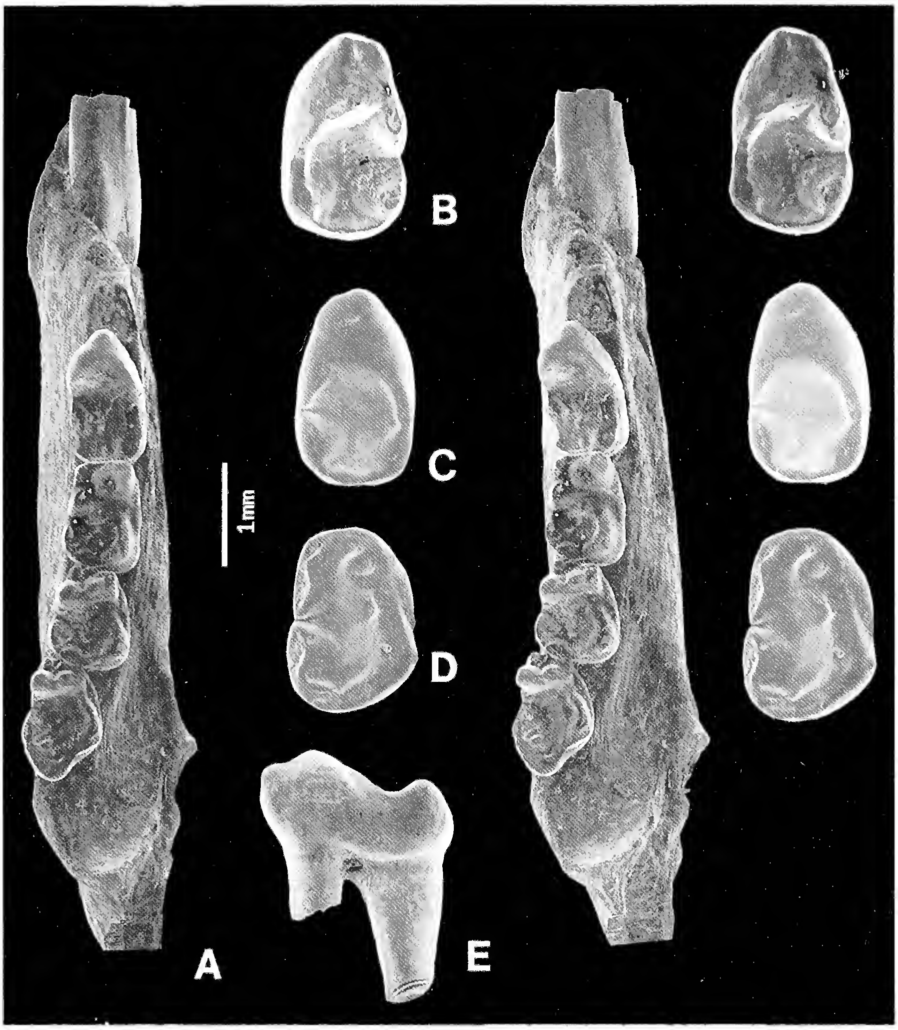


Fig. 1.—SEM stereopairs of picromomyids. A, *Picromomys petersonorum,* n. gen. and sp., holotype (USNM 487900), right dentary with base of I_1 and P_4–M_3 in occlusal view. B–E, *Alveojunctus minutus.* B, unworn left P_4 (USNM 250589); C, worn right P_4 (USNM 251446); D, right M_2?, holotype (USGS 2005); B–D in occlusal view. E, left P_4 (USNM 250589) in buccal view.

veojunctus differs from that of the new species in having a talonid with a clear basin and a particularly prominent entoconid, which is often swollen into the basin.

Picromomys, new genus

Type and Only Known Species.—Picromomys petersonorum, new species.

Diagnosis.—Very small plesiadapiform (M_1 length = 1.1 mm, just over half the linear dimensions of *Alveojunctus*) with enlarged, nearly horizontal medial incisor and only two small teeth between I_1 and P_4. Differs from *Alveojunctus* and all other plesiadapiforms in having a prominent cusp-like expansion on M_{1-2} anterobuccal to the protoconid. P_4 trigonid with poorly defined blunt cusps. P_4 talonid about same length as trigonid and wider than trigonid, as in *Alveojunctus*; and flat (without basin), sloping posterolingually, and lacking distinct hypoconulid and entoconid, all in contrast to *Alveojunctus*.

Distribution.—Wasatchian (early Eocene) of Wyoming.

Etymology.—Greek *pikros,* bitter, in allusion to the superficial resemblance of P_4 to the first lower molar of Paleocene *Picrodus,* + *Omomys,* middle Eocene primate and suffix commonly used for small primitive primates and plesiadapiforms.

Picromomys petersonorum, **new species**

(Fig. 1, 2)

Holotype.—USNM 487900, right dentary with P_4–M_3, base of I_1, and two alveoli between incisor and P_4; left dentary with base of I_1, incomplete P_4, and all other alveoli. Only known specimen; collected by T. M. Bown in 1994. The two dentaries are assumed to represent the same individual because they are the same size, are similarly worn, and were found together in situ during quarrying, within about 1 cm of each other.

Locality and Horizon.—A stage 1 paleosol in meander-belt mudstones at USGS locality D-2035 in the Dorsey Creek badlands, SE ¼ Sec. 12, T.50 N., R.95 W., Big Horn County, Wyoming; 390 m-level of the Willwood Formation, early Wasatchian. See Bown and Kraus (1987) and Bown et al. (1994) for further information on Willwood sediments and stratigraphy.

Diagnosis.—As for genus.

Etymology.—For Ted and LaDean Peterson of Worland, Wyoming, in recognition of years of friendship and generous assistance to our expedition.

Description.—The dentary appears relatively deep because of the very low-crowned molars, but it is actually comparatively shallower than in some paromomyids. Two mental foramina are present, the larger one positioned below the front of P_4 and the other under the trigonid of M_1. The cheek tooth row is not perfectly straight in superior view, but forms a gentle arc directed slightly mediad at the posterior end, a common configuration in plesiadapiforms.

The lower dentition consists of a hypertrophied, procumbent anterior tooth, assumed to be I_1, and six postcanine teeth. The base of I_1, present in both dentaries, is oriented essentially horizontally; the crowns of both are missing. The limited portion preserved, however, provides significant information bearing on the affinities of *Picromomys.* The tooth is laterally compressed, with an elliptical cross section that is almost flat medially and convex laterally. A faint horizontal ridge is present on the anterolateral aspect near the broken edge of I_1, whereas the dorsal aspect is smoothly rounded. The preserved part of the incisor approximates that of paromomyids and micromomyids more closely than that of other plesiadapiforms, such as carpolestids or plesiadapids. Moreover, it is distinctly different from the diagnostic lanceolate lower incisor of microsyopids (including *Navajovius, Arctodontomys, Microsyops, Niptomomys,* and *Uintasorex*). In the latter group, the incisor has an abrupt dorsal expansion just distal to its base, and the crown is rotated medially. As a result, the homologue of the lateral crest in other plesiadapiform incisors is reoriented to form a sharp dorsal margin in microsyopids, and what was the "dorsal" surface faces medially. This sharp dorsal margin is absent in *Picromomys.*

Only two alveoli are present between I_1 and P_4, making *Picromomys* one of the most derived plesiadapiforms in terms of antemolar reduction. The dimensions and orientation of the two alveoli make it probable that they held two single-rooted teeth rather than a single, large double-rooted premolar. The first alveolus is smaller and slightly lower than the one behind, and is separated from I_1 by a short diastema. The inclined position of this alveolus suggests that it housed a somewhat procumbent tooth whose crown projected mesially over the front of its root, similar to the condition in apatemyids, carpolestids, and the micromomyid *Tinimomys,* as well as in some soricids, but not so closely appressed to I_1 as in uintasoricines. The homologies of this tooth are equivocal in *Picromomys* and several of the other taxa; here it is tentatively identified as P_2, but it could just as well be I_2 or

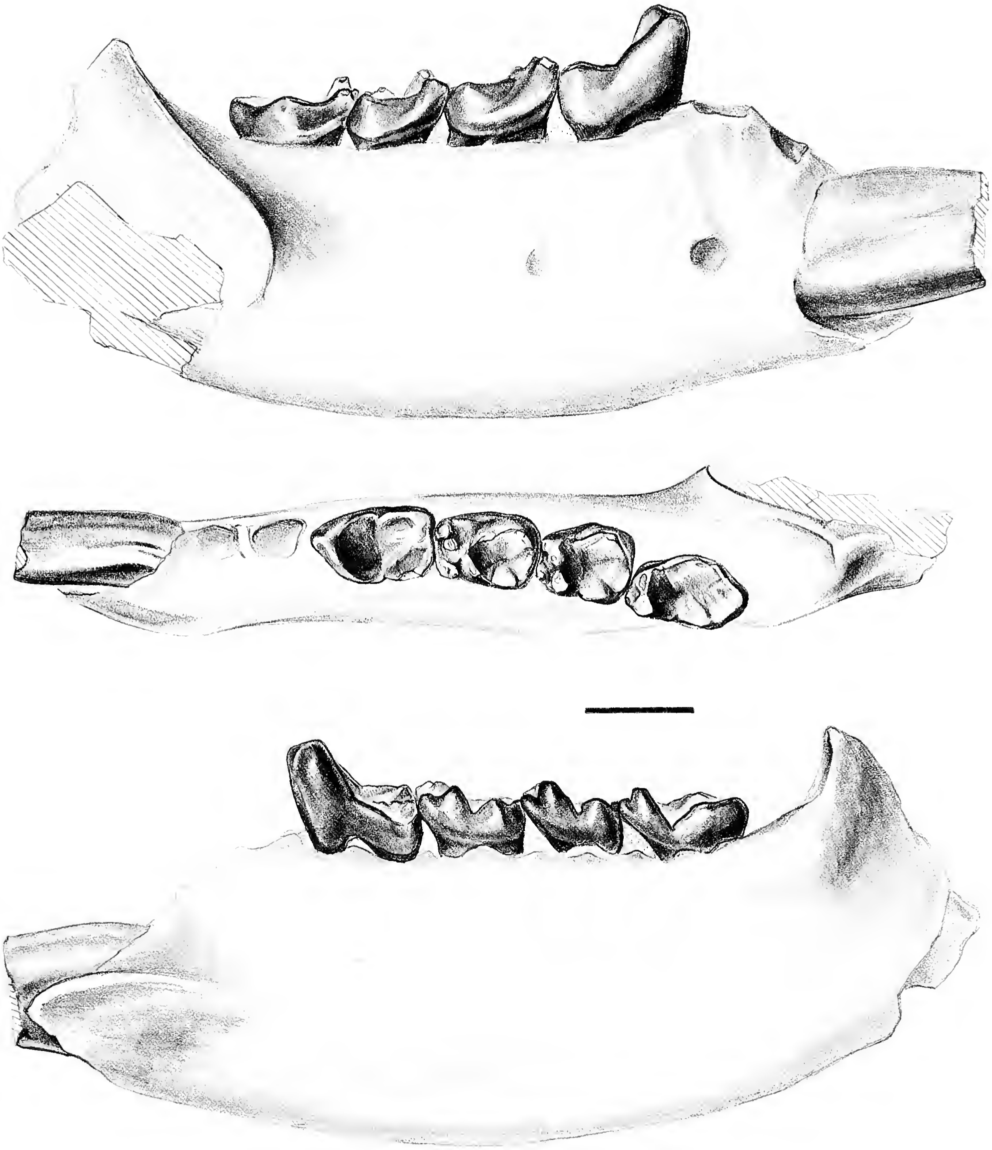


Fig. 2.—*Picromomys petersonorum,* n. gen. and sp., holotype right dentary (USNM 487900) in lateral, occlusal, and medial views. Scale = 1 mm.

the canine. The second alveolus is elliptical and somewhat larger, and probably held a tooth (P_3) with a fused double root as in *Uintasorex.*

P_4 is the most distinctive tooth and, apart from the noted resemblance to *Alveojunctus,* is unique in form among plesiadapiforms. The trigonid is tall but anteriorly canted, with a compact and wedge-shaped summit bearing blunt, ill-defined cusps or, more precisely, crests. The crests form a trefoil or Y-shaped pattern, a short anterior arm representing the paracristid, and a longer posterolingually directed arm joining an indistinct metaconid, which is indicated by a subtle swelling on the back of the trigonid. Near the midpoint (site of the protoconid?) a lower, blunt crest projects posterobuccally and merges into a sharper crest that descends the posterolateral wall of the trigonid. There it meets the talonid just lateral to the cristid obliqua on the buccal tooth margin, producing a faint hint of a hypoflexid. The unusual appearance of the trigonid probably results from a combination of wear and weakly defined cusps, and has been interpreted in part by comparison with a series of unworn and worn P_4s of *Alveojunctus* (see Fig. 1), its closest morphological counterpart.

The talonid of P_4 is about the same length as the trigonid and is slightly broader than long. The cristid obliqua is high and fully buccal and the entocristid is much lower. These crests meet the straight postcristid at right angles, and all three crests are situated on the periphery of the talonid, barely elevated above the enclosed surface. The hypoconid, a rounded conical swelling at the posterolateral corner of the tooth, is the highest point on the talonid and the only distinct cusp. Nonetheless, it is hardly any higher than the cristid obliqua. From the hypoconid, the postcristid slopes medially to a low point at the lingual margin, where it meets the entocristid. This is normally the location of the entoconid in plesiadapiforms and other mammals that have well-developed P_4 talonids, but in *Picromomys* it is the lowest part of the talonid. From there, the entocristid ascends gradually to its highest point at the posterolingual border of the trigonid; hence, there is no talonid notch. Neither hypoconulid nor entoconid cusps are discernible, although a small bump of enamel near the hypoconid may be the remnant of a hypoconulid. Rather than having a basin, the talonid is flat. It is distinctly lower lingually than buccally, and bears an irregular fold of enamel that crosses diagonally from just inside the hypoconid to the anterolingual corner. P_4 lacks cingulids.

The lower molars are very low crowned, with trigonids that are sharply canted anteriorly and appear anteroposteriorly constricted in lateral view. Although of roughly similar dimensions, the molars increase in length in the sequence $M_2 < M_1 < M_3$. The standard trigonid cusps are bunodont, the metaconid tallest and the paraconid low and reduced, closely resembling the arrangement in *Tinimomys.* The trigonids are transversely narrow and become progressively more compressed anteroposteriorly from M_1 to M_3. The most distinctive feature of the molars is an autapomorphous cusp-like swelling, with a well-developed, beveled wear facet, situated just anterobuccal to the protoconid. It is large and columnar on M_1, somewhat smaller on M_2, and barely visible on M_3. Apatemyids also have an accessory trigonid cusp anterior to the protoconid, but the resemblance to *Picromomys* is quite superficial.

The molar talonids are increasingly broader and have increasingly deeper basins from M_1 to M_3. The talonid of M_1 is slightly longer than wide, whereas that of M_2 is wider than long. The talonid of M_3 is slightly broader still, but the third lobe is only moderately expanded, unlike the enlarged third lobe of paromomyids and plesiadapids. The cristid obliqua joins the trigonid near the protoconid on M_1 and is progressively more buccal on M_{2-3}, resulting in very shallow hypoflexids. A faint mesoconid is present on M_1. The hypoconulid and entoconid are especially prominent on M_{1-2}. The hypoconulid is lenticular or crescentic, not round or conical like the hypoconid on M_2, and is distinctly shifted toward the entoconid but separated from the latter by a distinct, shallow notch. These conditions are closely approximated in uintasoricine microsyopids (*Uintasorex* more than *Niptomomys*) and in micromomyids (especially *Tinimomys*). Unlike P_4, the molars have a well-defined talonid notch between the trigonid and entocristid. The molar ectocingulids are poorly developed, being best expressed at the hypoflexids but virtually absent anteriorly. The talonid of M_3 has weakly crenulated enamel.

Measurements (mm) of the Holotype.—P_4 length = 1.30, breadth = 0.70; M_1 length = 1.10, breadth = 0.75; M_2 length = 1.00, breadth = 0.80; M_3 length = 1.20, breadth = 0.75; depth of dentary below M_1 = 2.70.

Discussion.—With a P_4–M_3 length of 4.5 mm, the holotype belonged to an animal much smaller than any known primate, and even smaller than the diminutive micromomyid plesiadapiforms *Tinimomys* and *Micromomys* and the microsyopid *Berruvius,* up to now the smallest known plesiadapiforms. It weighed only 9.0–10.6 g, as estimated from regressions of M_1 area on body mass in all extant primates, or in prosimians, respectively (Conroy, 1987). A somewhat higher estimate, 26 g, is obtained using the regression of Gingerich et al. (1982) but, as they note, this equation overestimates the weight of insectivorous primates. Whichever regression is used, *Picromomys* apparently was no more than one-half to two-thirds the size of *Tinimomys* (Rose et al., 1993).

Picromomys resembles plesiadapiforms in several presumably derived dental traits, including presence of a hypertrophied, procumbent incisor together with low-crowned molars having reduced paraconids and broad, basined talonids. Also like many plesiadapiforms, it is further characterized by reduction in number and size of antemolar teeth between the enlarged incisor and P_4, as well as enlargement and specialization of P_4, which has a trigonid taller than any other tooth. Although some omomyids can be similarly characterized, the combination of features in *Picromomys* conforms much more closely with that in plesiadapiforms. Thus assignment of *Picromomys* to Plesiadapiformes seems beyond doubt. The details of its dental morphology, however, indicate that *Picromomys* belongs to a clade divergent from other known plesiadapiforms. Based on the very low-crowned molars and unusual structure of P_4, the only other known member of this clade is *Alveojunctus.*

From comparisons summarized below, it will be apparent that the precise relationships and phylogenetic position of *Picromomys* and the Picromomyidae are uncertain. *Picromomys* shares numerous apparently derived dental characters, indicating potential relationship, with four known plesiadapiform clades: Paromomyidae, Picrodontidae, Micromomyidae, and uintasoricine Microsyopidae. As mentioned above, the molar trigonid arrangement in *Picromomys* is also vaguely reminiscent of that in Apatemyidae, but in the latter the accessory trigonid cusp is low and well anterior to the protoconid, forming a quadrilateral with the other trigonid cusps. There are no other compelling resemblances to apatemyids.

Phylogenetic Position of Picromomys

Cladistic analysis (using Hennig86; Farris, 1988) of 29 characters of the lower dentition in 12 plesiadapiform genera (see Appendices 1 and 2) was undertaken in an effort to resolve the relationships of *Picromomys.* The analysis yielded two equally most parsimonious trees, each with considerable homoplasy (tree length = 72, consistency index = 0.48, retention index = 0.53), one grouping picromomyids in a clade with micromomyids, and the other grouping them successively with *Niptomomys, Picrodus,* and *Ignacius* (Fig. 5). When the lanceolate incisor of microsyopids (widely considered to be an important synapomorphy of the family) was weighted 2, a single shortest tree (B) of 73 steps resulted, tree A having 74 steps under this weighting.

The two contrasting trees, and concomitant uncertain position of *Picromomys,* result in part from the very limited anatomical evidence and suggest that lower dentitions alone—at least the dental characters used in this analysis—are insufficient to establish interrelationships among plesiadapiforms with confidence. In this regard it is noteworthy that neither of the two shortest trees corroborates the widely accepted holophyly of Paromomyidae, sensu stricto (*Paromomys* and *Ignacius* in Fig. 5). Another important factor contributing to the uncertainty is the admitted ambiguity in coding several characters, usually resulting from either questionable homology (e.g., of antemolar teeth) or the inherent difficulty in coding intermediate states of continous characters. Specific ambiguities are noted in Appendix 1. The variable nature of some of the characters makes it difficult to code them consistently, and further complicates character assessment. Nonetheless, an attempt to resolve relationships on this basis is justified because the lower dentition has been the basis for much of the systematics of plesiadapiforms, and is the only evidence available for *Picromomys*; moreover, it is adequate to ascertain the uniqueness of *Picromomys.*

In both trees, *Picromomys* and *Alveojunctus* compose a monophyletic group supported by the following synapomorphies (one or both trees, indicated by A, B, or AB): P_4 larger than M_1 (10A) and with metaconid present (27B) and talonid as long as trigonid (11AB), a buccally oriented cristid obliqua on P_4 (14AB), shallow hypoflexids (16B), low, mesially canted trigonids (17B), extreme molar brachydonty (18B), weak or absent anterobuccal cingulids (19B), moderately expressed molar paraconids (21A–reversal), and molar hypoconulids close to entoconids (28A). Only character 11(1), however, is unique to picromomyids. This combination of common traits results in a closer correspondence between these two genera than either one has with any other plesiadapiform. Even so, both *Picromomys* and *Alveojunctus* are very incompletely known, and their proposed alliance remains to be tested as the record improves.

Comparisons with Other Plesiadapiformes

Paromomyidae.—Like *Picromomys,* both *Paromomys* and *Ignacius* have relatively low-crowned molars (character 18) and broad talonids on P_4 (13). *Ignacius* further resembles *Picromomys* in having a strongly procumbent medial incisor (2), reduced anterior dentition between I_1 and P_4, a buccally oriented cristid obliqua on P_4 (14), shallow hypoflexids (16), weak molar ectocingulids (19), and low and mesially canted molar trigonids (17) (Fig. 3B, 4B). Several of these traits are also shared with *Picrodus.* Both *Picromomys* and *Ignacius* also have relatively deep dentaries, but this apparent resemblance may be exaggerated because both forms are brachydont.

As already noted, holophyly of the Paromomyidae sensu stricto is not supported by either of the two shortest trees in the parsimony analysis, but this almost certainly reflects inadequacy of the characters used here rather than lack of close relationship. In fact, two important traits, a broad, basined talonid on P_4 (13) and an expanded third lobe on M_3 (25), would support that grouping. All known paromomyids except *Paromomys* are even more derived in antemolar tooth loss than *Picromomys,* and all (including *Paromomys*) tend to emphasize crests over cusps, in contrast to picromomyids. This disparity, presumably related to a difference in diet, suggests that picromomyids and paromomyids are not very closely related.

Picrodontidae.—*Picromomys* shares several derived traits with Torrejonian *Picrodus,* including very low-crowned molars (character 18) with shallow hypoflexids (16), weak ectocingulids (19), transversely compressed trigonids (20) that are low and mesially canted (17), and variably crenulated enamel (26) (Fig. 3H, 4H). In both taxa P_3 is one-rooted (9). None of these characters is uniquely shared by these two genera, however. Also intriguing is the resemblance between the unusual enlarged cheek teeth of these two genera; but the teeth are believed to be nonhomologous (P_4 in *Picromomys,* M_1 in *Picrodus*; Szalay, 1968), and close inspection shows the similarity to be far from precise. Consequently, close relationship between picromomyids and picrodontids is unlikely, and closer probable relationships are suggested by the cladistic analysis.

Uintasoricine Microsyopidae.—Tree A indicates the Wasatchian uintasoricine *Niptomomys* as the sister taxon of picromomyids, based on the shared presence of a strongly procumbent incisor (2), P_4 with a paracristid (12[1]–reversal), a metaconid (27), and a broad but unbasined talonid (13), prominent molar hypoconulids (23–reversal), and an entoconid notch (29). These characters apply equally to Bridgerian *Uintasorex* (see Szalay, 1969), which further resembles *Picromomys* (but not *Alveojunctus*) in having a low entoconid region on P_4. Uintasoricines also resemble picromomyids in having very brachydont molars with very broad talonid basins. There are other derived similarities as well which are also present in successive outgroups. However, the fundamental differences in the form of P_4, the molar trigonids (transversely broad and mesiodistally compressed, with more reduced paraconids in uintasoricines), and especially I_1, together with the improbable required reversal (regeneration of a P_4 paraconid following its loss), suggest that the observed resemblances between uintasoricines and picromomyids could well be convergent.

Micromomyidae.—Micromomyids are derived, like picromomyids, in having P_4 larger than M_1 (10), transversely compressed molar trigonids (20, *Picromomys* only), and molar hypoconulids shifted toward the entoconid (28) (see Fig. 3C, D; 4C, D; and 5B, node 3). Additional derived traits found in picromomyids and *Tinimomys* (Fig. 5B, node 4), include a strongly procumbent I_1 (2), loss of several antemolar teeth (4, 6, 8), a distinct entoconid notch on lower molars (29), and a broad, basined P_4 talonid with an enlarged entoconid (13[2], 15[2], *Alveojunctus* only). *Tinimomys* and picromomyids also have similar bunodont trigonid cusps, but this resemblance is so difficult to characterize precisely that we have not included it in the cladistic analysis. Overall, these resemblances are weakly suggestive of relationship between picromomyids and micromomyids.

Characters for *Micromomys* used in this analysis were based principally on Tiffanian *M. fremdi* (Fox, 1984), the most primitive known micromomyid. In our opinion, micromomyids have been oversplit generically, and we recognize only the genera *Micromomys* and *Tinimomys* in this report. The features originally cited to distinguish *Chalicomomys* from *Micromomys* (Beard and Houde, 1989) and *Myrmekomomys* from *Tinimomys* (Robinson, 1994) do not justify their generic separation. *Chalicomomys* closely resembles *Micromomys* in its taller P_4 with much smaller talonid basin, more acute (less bunodont) molar cusps, and several other traits cited by Beard and Houde to differentiate *Chalicomomys* from *Tinimomys*. Hence there seems little reason to separate it generically from *Micromomys*. At the same time, "*Chalicomomys*" *antelucanus* strengthens the probability of a close relationship between *Micromomys* and *Tinimomys*. The putative generic distinctions of *Myrmekomomys* compared to *Tinimomys* ("relatively greater molar trigonid relief and taller talonid. . . . hypoconulid of M_{1-2} more developed;" Robinson, 1994:86) appear to vary intraspecifically in the Willwood sample of *T. graybulliensis*. The only character that differs from known samples is the more constricted hypoconulid lobe of M_3 in the holotype of *Myrmekomomys loomisi*, a feature that could be an intraspecific variant and is unlikely to warrant generic recognition. In the present study, therefore, we consider *Micromomys* to include *Chalicomomys*, and *Tinimomys* to include *Myrmekomomys*.

DISCUSSION AND CONCLUSIONS

Picromomys is a highly distinctive new plesiadapiform, demonstrably allied closely with only one other known taxon, *Alveojunctus*. These two genera are allocated to a new family, Picromomyidae, to recognize their highly distinctive dental anatomy and their ambiguous phylogenetic position among plesiadapiforms. Picromomyids possess a number of derived characters suggesting affinity with uintasoricine microsyopids, but the combination of derived resemblances supporting a relationship between picromomyids and micromomyids, especially *Tinimomys*, seems a little less susceptible to convergence and requires fewer

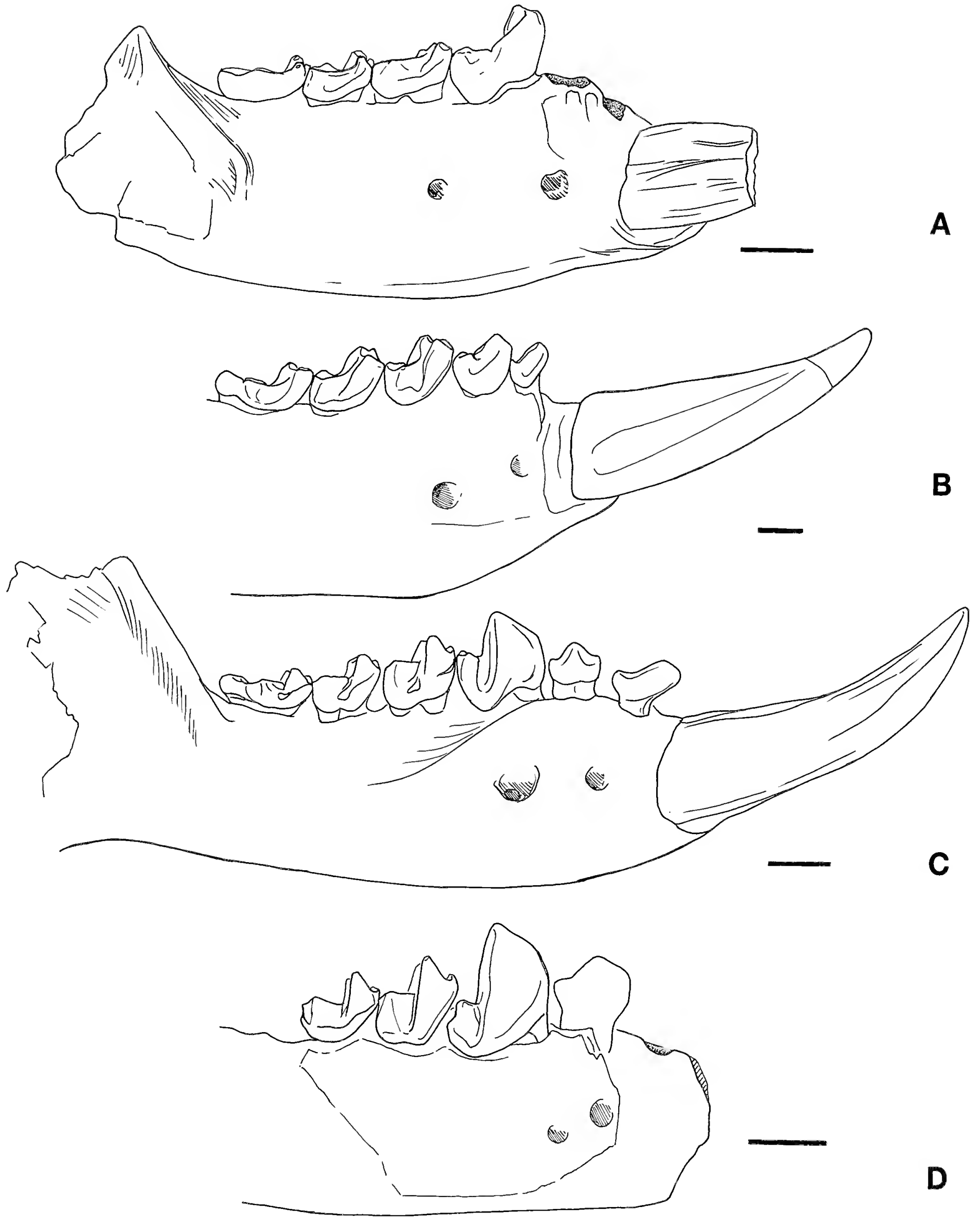


Fig. 3.—Plesiadapiform lower right dentitions in lateral view. A, *Picromomys petersonorum*, n. gen. and sp. (USNM 487900). B, *Ignacius fremontensis* (YPM-PU 14790, reversed; Paromomyidae). C, *Tinimomys graybulliensis* (after Rose et al., 1993; Micromomyidae). D, *Micromomys antelucanus* (after Beard and Houde, 1989; Micromomyidae). E, *Niptomomys doreenae* (after Rose et al., 1993; incisor restored from *N. thelmae*; Microsyopidae). F, *Navajovius kohlhaasae* (AMNH 17390, holotype, reversed; Microsyopidae). G, *Palenochtha minor* (AMNH 35451, anterior after Gunnell, 1989; Palaechthonidae?). H, *Picrodus silberlingi* (AMNH 35456, incisor after Szalay and Delson, 1979). Scales = 1 mm.

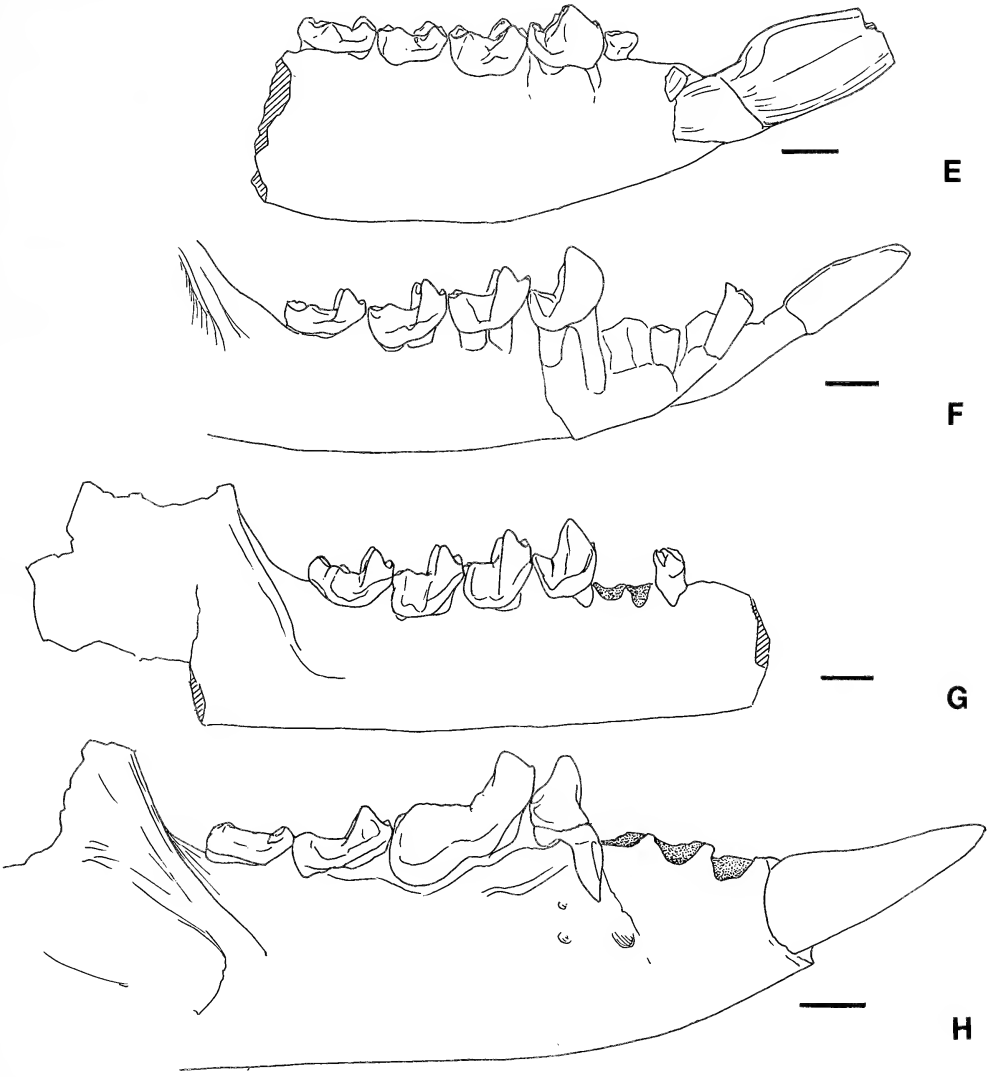


Fig. 3.—Continued.

improbable reversals or autapomorphies than other arrangements. Nonetheless, the high degree of homoplasy, including multiple convergent autapomorphies, required in both of the two shortest trees does not lend particular confidence to either one, and additional anatomical evidence is probably needed to resolve these relationships better.

When first described, *Micromomys* and *Tinimomys* were assigned to the Paromomyidae, tribe Micromomyini (Szalay, 1973, 1974). Bown and Rose (1976; Rose and Bown, 1982) used a more restricted concept of Paromomyidae, and transferred *Micromomys, Tinimomys,* and several other taxa formerly included in Paromomyidae to the Microsyopidae, an assignment followed by Fox (1984) and Gunnell (1989). More recent studies have suggested that Micromomyini diverged

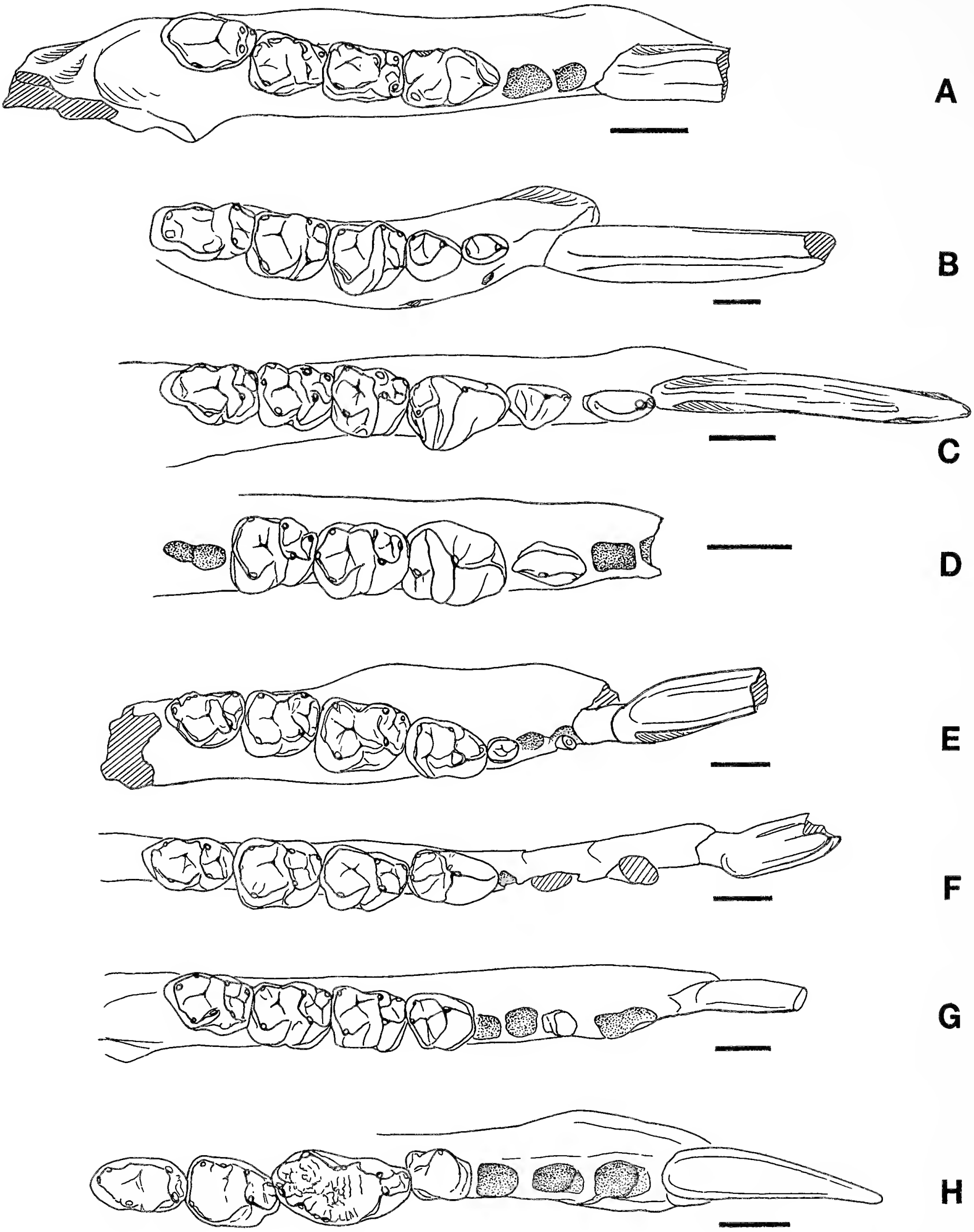


Fig. 4.—Plesiadapiform lower dentitions in occlusal view; same specimens as in Fig. 3. A, *Picromomys petersonorum,* n. gen. and sp.; B, *Ignacius fremontensis*; C, *Tinimomys graybulliensis*; D, *Micromomys antelucanus*; E, *Niptomomys doreenae*; F, *Navajovius kohlhaasae*; G, *Palenochtha minor*; H, *Picrodus silberlingi.* Scales = 1 mm.

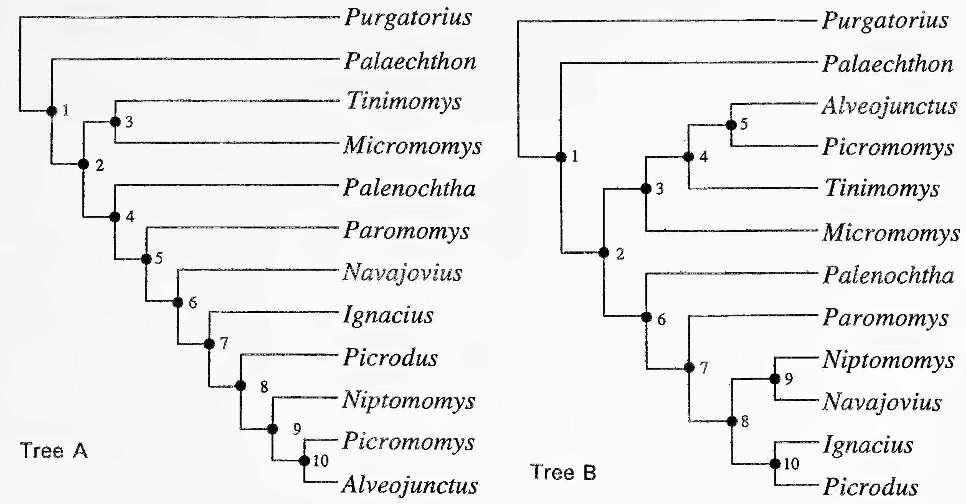


Fig. 5.—Possible relationships among picromomyids and some other plesiadapiforms: the two shortest trees based on lower dental characters given in Appendices 1 and 2, resulting from an exhaustive search using the implicit enumeration algorithm of Hennig86, which finds all trees of minimal length (Farris, 1988). Tree length = 72, consistency index = 0.48, retention index = 0.53. Ordering the characters did not change the tree topologies. Character optimization was performed using CLADOS (Nixon, 1992).

Nodes in tree A are supported by the following synapomorphies (change is from 0 to 1 for binary characters; state indicated for multistate characters): node 1—5, 7, 8(1); node 2—12(1); node 3 (Micromomyidae)—4, 10, 20, 24, 28; node 4—23; node 5—18(1), 21, 22; node 6—4, 12(2), 19; node 7—6(1), 16, 17; node 8—9, 18(2); node 9—2, 12(1–reversal), 13(1), 23 (0–reversal), 27, 29; node 10 (Picromomyidae)—10, 11, 14, 21 (0–reversal), 28. Autapomorphies required in this tree are: *Palaechthon*—21, 27; *Tinimomys*—2, 6(2), 13(2), 15(2), 18(1), 25, 28, 29; *Micromomys*—8(0–reversal); *Palenochtha*—2; *Paromomys*—8(0–reversal), 13(2), 25, 26; *Navajovius*—3, 23(0–reversal), 27; *Ignacius*—2, 6(2), 8(2), 13(2), 14, 21 (0–reversal), 25; *Picrodus*—8(2), 20, 26; *Niptomomys*—3, 4(0–reversal), 16 (0–reversal); *Picromomys*—6(2), 15(1), 20, 22(0–reversal), 26; *Alveojunctus*—12(0–reversal), 13(2), 15(2).

Nodes in tree B are supported by the following synapomorphies: nodes 1 and 2 (same as tree A); node 3—4, 10, 20, 28; node 4—2, 6(2), 13(2), 15(2), 18(1), 29; node 5 (Picromomyidae)—11, 14, 16, 17, 18(2), 19, 27; node 6—23; node 7—18(1), 21, 22; node 8—4, 12(2), 19; node 9 (Microsyopidae)—3(2), 23(0–reversal), 27; node 10—8(2), 16, 17. Taxa whose required autapomorphies differ on tree B: *Alveojunctus*—12(0–reversal), 20 (0–reversal); *Picromomys*—9, 13(1), 15(1–reversal?), 26; *Tinimomys*—24, 25; *Micromomys*—8(0–reversal), 24; *Niptomomys*—2, 4(0–reversal), 6, 9, 12(1–reversal), 13, 17, 18(2), 29; *Navajovius*—none; *Ignacius*—2, 6(2), 13(2), 14, 21 (0–reversal), 25; *Picrodus*—9, 18(2), 20, 26.

from other plesiadapiforms early in their history (Fox, 1984; Beard and Houde, 1989) and belong to a clade, the Micromomyidae, separate from other families (Beard, 1993; Rose et al., 1993). This conclusion is corroborated by the cladistic analysis presented here, but formal grouping of Micromomyidae and Picromomyidae in a higher taxon Micromomyiformes Beard, 1993, is premature from the evidence currently available (see also MacPhee et al., 1995).

Both picromomyid genera were very small plesiadapiforms, and *Picromomys* was especially diminutive (~10 g), approaching the minimum known size for mammals. Plesiadapiforms are dentally reminiscent of various extant diprotodontian marsupials such as petaurids, burramyids, and phalangerids (Cartmill, 1974). In this respect *Picromomys* and *Tinimomys* are particularly convergent on the tiny diprotodont *Acrobates*. The latter also has a hypertrophied and procumbent medial incisor, behind which are two peg-like teeth, followed by two premolariform teeth with tall trigonids and low-crowned molars with broad talonid basins. *Acrobates* is one of the smallest known marsupials, weighing only 12–14 g; it feeds on insects, larvae, and nectar (Nowak, 1991)—a diet constrained by its dental morphology and small body size. The same constraints suggest that the diet of *Picromomys* was probably very similar.

ACKNOWLEDGMENTS

We thank Drs. K. C. Beard, R. J. Emry, and P. Robinson for providing access to specimens and casts used in this study, and Dr. Robinson for supplying locality data that led to the discovery of the quarry at locality D-2035. Vivian Noble and Jay Mussell assisted with SEM photography, and Mary Silcox provided invaluable help with the cladistic analysis. The drawings were expertly prepared by Elaine Kasmer. For their insightful commentaries on the manuscript, which resulted in numerous improvements, we thank Drs. K. C. Beard and G. F. Gunnell, Mary Silcox, and an anonymous reviewer. Fossils of *Picromomys* were collected under BLM permit 183-WY-PA94. This research was supported in part by NSF grant IBN-9419776 to KDR.

LITERATURE CITED

BEARD, K. C. 1993. Phylogenetic systematics of the Primatomorpha, with special reference to Dermoptera. Pp. 129–150, *in* Mammal Phylogeny, Volume 2, Placentals (F. S. Szalay, M. J. Novacek, and M. C. McKenna, eds.). Springer-Verlag, New York.

BEARD, K. C., AND P. HOUDE. 1989. An unusual assemblage of diminutive plesiadapiforms (Mammalia, ?Primates) from the early Eocene of the Clark's Fork Basin, Wyoming. Journal of Vertebrate Paleontology, 9:388–399.

BOWN, T. M. 1982. Geology, paleontology, and correlation of Eocene volcaniclastic rocks, southeast Absaroka range, Hot Springs County, Wyoming. US Geological Survey Professional Paper, 1201-A:1–75.

BOWN, T. M., AND M. J. KRAUS. 1987. Integration of channel and floodplain suites, I. Developmental sequence and lateral relations of alluvial paleosols. Journal of Sedimentary Petrology, 57:587–601.

BOWN, T. M., AND K. D. ROSE. 1976. New early Tertiary primates and a reappraisal of some Plesiadapiformes. Folia Primatologica, 26:109–138.

BOWN, T. M., K. D. ROSE, E. L. SIMONS, AND S. L. WING. 1994. Distribution and stratigraphic correlation of upper Paleocene and lower Eocene fossil mammal and plant localities of the Fort Union, Willwood, and Tatman formations, southern Bighorn Basin, Wyoming. US Geological Survey Professional Paper, 1540:1–103.

CARTMILL, M. 1974. Rethinking primate origins. Science, 184:436–443.

CONROY, G. C. 1987. Problems of body-weight estimation in fossil primates. International Journal of Primatology, 8:115–137.

FARRIS, J. S. 1988. Hennig86 Version 1.5. Program and documentation. Port Jefferson Station, New York (privately produced).

FOX, R. C. 1984. The dentition and relationships of the Paleocene primate *Micromomys* Szalay, with description of a new species. Canadian Journal of Earth Sciences, 21:1262–1267.

GINGERICH, P. D., B. H. SMITH, AND K. ROSENBERG. 1982. Allometric scaling in the dentition of primates and prediction of body weight from tooth size in fossils. American Journal of Physical Anthropology, 58:81–100.

GUNNELL, G. F. 1989. Evolutionary history of Microsyopoidea (Mammalia, ?Primates) and the relationship between Plesiadapiformes and Primates. University of Michigan Papers on Paleontology, 27:1–157.

MACPHEE, R. D. E., K. C. BEARD, C. FLEMMING, AND P. HOUDE. 1995. Petrosal morphology of *Tinimomys graybulliensis* is plesiadapoid, not microsyopoid. Journal of Vertebrate Paleontology, 15, supplement to no. 3:42A.

NIXON, K. C. 1992. CLADOS version 1.2, IBM PC-compatible character analysis program (privately produced).

NOWAK, R. M. 1991. Walker's Mammals of the World. Fifth Edition, Volume 1. Johns Hopkins University Press, Baltimore, Maryland. 642 pp.

ROBINSON, P. 1994. *Myrmekomomys,* a new genus of micromomyine (Mammalia, ?Microsyopidae) from the lower Eocene rocks of the Powder River Basin, Wyoming. Contributions to Geology (University of Wyoming), 30:85–90.

ROSE, K. D., AND T. M. BOWN. 1982. New plesiadapiform primates from the Eocene of Wyoming and Montana. Journal of Vertebrate Paleontology, 2:63–69.

ROSE, K. D., K. C. BEARD, AND P. HOUDE. 1993. Exceptional new dentitions of the diminutive plesiadapiforms *Tinimomys* and *Niptomomys* (Mammalia), with comments on the upper incisors of Plesiadapiformes. Annals of Carnegie Museum, 62:351–361.

SZALAY, F. S. 1968. The Picrodontidae, a family of early primates. American Museum Novitates, 2329:1–55.

———. 1969. Uintasoricinae, a new subfamily of early Tertiary mammals (?Primates). American Museum Novitates, 2363:1–36.

———. 1973. New Paleocene primates and a diagnosis of the new suborder Paromomyiformes. Folia Primatologica, 19:73–87.

———. 1974. A new species and genus of early Eocene primate from North America. Folia Primatologica, 22:243–250.

SZALAY, F. S., AND E. DELSON. 1979. Evolutionary History of the Primates. Academic Press, New York. 580 pp.

WEST, R. M., AND M. R. DAWSON. 1973. Fossil mammals from the upper part of the Cathedral Bluffs tongue of the Wasatch Formation (early Bridgerian), northern Green River Basin, Wyoming. Contributions to Geology (University of Wyoming), 12:33–41.

APPENDIX 1

Description of Characters Used in Phylogenetic Analysis

Characters were polarized with respect to *Purgatorius* as the outgroup, using 0 as the primitive state and 1 or 2 for derived states. Characters 6, 8, 12, and 18 were treated as ordered; all others are unordered. Intraspecifically variable traits were coded according to the predominant character state. Autapomorphic characters known to be present in only one of the genera analyzed are excluded from the analysis.

1. I_1 small to moderate (0); hypertrophied (1). Although incisors have not been described for *Purgatorius,* alveoli suggest that its medial incisor was relatively less enlarged than in other plesiadapiforms.

2. I_1 somewhat inclined (0); strongly procumbent to horizontal (1).

3. I_1 laterally compressed (1); laterally compressed and lanceolate (2). The primitive state is unknown; both states observed could be derived, hence no taxa are scored as 0.

4. I_2 present (0); absent (1). Scoring of this character is obviously dependent on the homologies of the anterior dentition, which are equivocal in most taxa used here. See Appendix 2 for dental formulae used in this analysis.

5. I_3 present (0); absent (1). This character is subject to the same ambiguity as character 4, but relative tooth sizes support the derived state in most plesiadapiforms.

6. Canine moderately large: alveolus usually $\geq$, or crown higher, than I_2 and $P_{1 \text{ or } 2}$ (0); noticeably reduced, smaller than adjacent teeth (1); absent (2). Same ambiguity as character 4. In addition, relative size is often difficult to judge due to poor preservation.

7. P_1 present (0); absent (1). Equivocal in *Palenochtha* because of conflicting interpretations of the dental formula.

8. P_2 two-rooted (0); one-rooted (1); absent (2). Same ambiguity as character 4.

9. P_3 two-rooted (0); one-rooted (1).

10. P_4 about the size of M_1 or smaller (0); larger than M_1 (1).

11. P_4 talonid shorter than trigonid (0); about as long as trigonid (1).

12. P_4 trigonid with distinct paraconid (0); with paracristid with or without

vestigial paraconid (1); with protoconid only, no trace of paraconid or paracristid (2). Ambiguous in *Picromomys,* owing to wear and/or morphology.

13. P_4 talonid narrow (0); broad but without basin (1); broad and with basin (2).

14. P_4 cristid obliqua joins trigonid near its midline axis (0); near buccal margin of trigonid (1). Although coded "0," *Paromomys* displays a somewhat intermediate condition.

15. P_4 talonid with hypoconid and weak entoconid (0); entoconid absent (1); with enlarged entoconid (2).

16. P_4 and molar hypoflexids distinct (0); shallow to absent (1). Characters 13, 14, and 16 are often but not always correlated.

17. P_4 and molar trigonids relatively tall and erect (0); lower and strongly anteriorly inclined (1).

18. Molars relatively high crowned (0); of moderate height (1); very low crowned (2). Scoring was based on mean index of M_2 trigonid height/length, with three arbitrary divisions: ≥ 0.79 (0), 0.60–0.71 (1), ≤ 0.53 (2).

19. Anterobuccal cingulids well developed (0); weak or absent (1).

20. Molar trigonids transversely broad (0); transversely compressed (1). Intermediate condition in *Palenochtha.*

21. Molar paraconids moderately reduced (0); greatly reduced or absent (1). The utility of this character, except for extreme manifestations, is dubious because of its intraspecifically variable and continuous nature.

22. M_1 mesoconid weak (0); absent (1). Intraspecifically variable in *Tinimomys* and perhaps others.

23. M_{1-2} hypoconulids prominent (0); small or indistinct (1). Ambiguous state in *Micromomys* due to intermediate expression.

24. Molar talonid cusps and crests peripheral (0); set in from margin as a result of basal inflation (1).

25. M_3 third lobe not expanded (0); expanded (1).

26. Enamel smooth (0); crenulated to a variable degree (1).

27. P_4 trigonid without metaconid (0); with metaconid (1).

28. M_{1-2} hypoconulids central in position (0); distinctly closer to entoconid (1).

29. M_{1-2} without entoconid notch (0); with distinct notch between hypoconulid and entoconid (1). Variable in *Niptomomys* examined.

APPENDIX 2

Character Matrix Used for Phylogenetic Analysis

Characters deemed too ambiguous to score are indicated by "a" and were scored as missing data ("?") for the analysis. At right is the lower dental formula assumed in this analysis. Where tooth number varies within a genus, the most primitive known formula is given.

Purgatorius	0??00	00000	00000	00000	00000	0000	3-1-4-3
Palaechthon	???01	01100	00000	00000	10000	0100	2-1-3-3
Palenochtha	11101	01100	01000	0000a	00100	0000	2-1-3-3
Picromomys	11111	21111	11111	11211	00000	1111	1-0-3-3
Alveojunctus	?????	????1	10212	11210	0?00?	?111	?
Paromomys	10?01	01000	01200	00100	11101	1000	2-1-3-3
Ignacius	11111	21200	02210	11110	01101	0000	1-0-2-3
Navajovius	10211	01100	02000	00110	11000	0100	1-1-3-3
Micromomys	10111	01001	01000	00001	00a10	0010	1-1-3-3
Tinimomys	11111	21101	01202	00101	00011	0011	1-0-3-3
Niptomomys	11211	11110	01100	01210	11000	0101	1-1-3-3
Picrodus	10??1	?1210	02000	11211	11100	1000	?-?-2-3

INSTRUCTIONS FOR AUTHORS

ANNALS OF CARNEGIE MUSEUM consist of contributions to the earth sciences, life sciences and anthropology, in 30 by 46 picas format (127 by 195 mm or 5 by 7⅝ inches). Submit all manuscripts to the Office of Scientific Publications. Authors should give particular attention to scientific content, format, and general style for the ANNALS. **Manuscripts that do not conform to the style of the ANNALS will be returned to the author immediately.** Every manuscript will be peer reviewed by at least two outside persons. Authors will be asked to subsidize, if funds are available, any or all costs of publication (approximately $100/page printed).

Manuscript style.—Articles should include the following items in this order: title page, abstract, text (with desired headings), acknowledgments, literature cited, tables, figure captions, and copies of illustrations. All manuscripts must be typed ***double-spaced*** on standard 8½ by 11 inch white bond paper, with at least one inch margins all around, and submitted ***in triplicate***—an original for the editors, and two review copies. All pages should be numbered, including tables, literature cited, and the list of figure captions. Only correspondence quality or better dot matrix printouts will be accepted; draft mode is unacceptable. A fixed-space font (e.g., Courier) is preferred.

Title Page. The title, on a separate title page should be brief, include the animal or plant group involved, and appear two to three inches below the top margin. Include the authors name(s) and the affiliations of non-CMNH authors. In the case of multiple authorship indicate the address to which proofs should be sent.

Abstracts. Abstracts should be short, double-spaced and substantive and included at the head of the first page of text.

Text. Do not right justify text or break (hyphenate) a word at the end of a line. ***Footnotes and acknowledgments as footnotes are unacceptable.*** All text is double-spaced.

Tables and figure legends. The list of figure legends and each table should be typed consecutively on individual pages separate from the text. Tables must be double-spaced throughout with **no vertical lines.**

Abbreviations. Refer to the CBE Style Manual for correct abbreviations. Mammalian dentition: use capital letters (I, C, P, M, D, for incisor, canine, premolar, molar, deciduous, respectively) and superscript/subscript numbers (M^2, P_3) to designate upper and lower teeth.

Measurements. Metric units should be used, if possible.

Literature Cited. All references in text must appear in the Literature Cited section. The data (author, date and page) in both citations must agree. ***Do not abbreviate the titles of periodicals or serials.*** The following style, double-spaced, should be used in Literature Cited:

1) Two authors in an institutional series:
    MATTHEW, W. D., AND W. GRANGER. 1923. The fauna of the Houldjin Gravels. American Museum of Natural History Novitates, no. 97: 1–6.
2) Same authors repeated—use three-em dash:
    ———. 1923. The fauna of the Ardyn Obo Formation. American Museum of Natural History Novitates, no. 98:1–5.
3) Same authors plus a third author—repeat all authors:
    MATTHEW, W. D., W. GRANGER, AND G. G. SIMPSON. 1928. Paleocene multituberculates from Mongolia. American Museum of Natural History Novitates, no. 331:1–4.
4) Chapter in an edited volume:
    RAUSCH, R. L. 1963. A review of the distribution of Holarctic mammals. Pp. 29–43, *in* Pacific Basin Biography (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.
6) Book:
    WHITE, M. J. D. 1961. The Chromosomes. Methuen and Co., Ltd., London.
7) Journal articles with usual volume and issue number:
    ANDERSON, W. I. 1969. Lower Mississippian conodonts from northern Iowa. Journal of Paleontology, 43(4):916–928.

Illustrations. All illustrations will be called figures, and are to be numbered in Arabic numerals. Three sets of illustrations are required, one (original artwork) for reproduction, two for reviewers. Xerox copies of photographs for reviewers are usually not acceptable but are adequate for line drawing review copies. Illustrations may not be larger than 72 by 102 picas (305 by 432 mm or 12 by 17 inches). All illustrations must be reducible to a maximum of 127 by 195 mm (30 by 46 picas) without loss of clarity. Line copy should be designed for reduction to ⅔ or ½ of actual size. Typewritten illustration copy will not be accepted. Photographic figures should be submitted at **actual reproduction size,** if possible.

Two or more small figures should be combined for reproduction as a unit or plate, but, if feasible, do not combine halftones and line drawings. Rectangular halftone figures should be abutted, without intervening spaces. The printer will insert narrow white spaces during the reproduction process. Halftone figures with solid black backgrounds will not be accepted unless the author agrees to pay for the printing costs. All plates must have ***minimally*** one inch borders all around. Each plate should be given a protective cover and identified on the back side.

Lettering and/or a magnification scale (linear metric scale) for rectangular halftone figures should be placed directly on the photo, not in a blank space between photos. The scale or lettering for closely cropped photos can be placed in blank areas close to the figure.

Proof.—The author should answer all queried proof marks and check the entire proof copy. Return corrected page proof with the edited manuscript ***promptly*** to the editors.

If an author chooses to make extensive alterations to a paper in proof stage the author or appropriate section will bear the cost. Original manuscripts will not be returned unless requested. Illustrations will be returned to the author.

ISSN 0097-4463

ANNALS of CARNEGIE MUSEUM

THE CARNEGIE MUSEUM OF NATURAL HISTORY
4400 FORBES AVENUE • PITTSBURGH, PENNSYLVANIA 15213

VOLUME 65 27 NOVEMBER 1996 NUMBER 4

CONTENTS

ARTICLES

Manuscripts, subscriptions, orders for individual numbers, and changes of address should be sent to:

Office of Scientific Publications
Carnegie Museum of Natural History
4400 Forbes Avenue
Pittsburgh, PA 15213-4080
Phone (412) 622-3287
Fax (412) 622-8837
E-mail: scipubs@clpgh.org

ANNALS OF CARNEGIE MUSEUM is published quarterly by The Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213-4080, by the authority of the Board of Trustees of Carnegie Institute.

THE CARNEGIE
MUSEUM OF
NATURAL HISTORY

ANNALS OF CARNEGIE MUSEUM

Vol. 65, Number 4, Pp. 323–361 27 November 1996

ARCHAEOLOGY OF TRANTS, MONTSERRAT. PART 3. CHRONOLOGICAL AND SETTLEMENT DATA

James B. Petersen[1]

Research Associate, Division of Anthropology

Abstract

Ongoing analyses of the prehistoric Amerindian Trants site in Montserrat include chronological and settlement data obtained from several episodes of field work. Artifact distributions suggest that Trants is larger than most other Saladoid period sites in the West Indies. The radiocarbon dates, artifacts, and stratigraphic associations further suggest that Trants was occupied earlier than many other Saladoid sites and over a long span, ca. 500 B.C.–A.D. 410, or later. Phosphate fractionation and other sediment data confirm the intensity and duration of occupation, and with artifact distributions discussed elsewhere suggest that the prehistoric settlement had a stable circular ring and plaza configuration. The implications of these data for research on the beginning and development of the Saladoid period in the West Indies and Lowland South America are discussed.

Introduction

Ongoing analyses of the prehistoric Trants site, located on the island of Montserrat in the northern Lesser Antilles, suggest that it is unusual in many respects. Dated as early as ca. 500 B.C., the Trants site documents regional settlement in the broad West Indies by ceramic-making populations much earlier than previously suspected, along with a few other recently studied sites. Moreover, emerging settlement pattern data from Trants document that the earliest groups known as Saladoid, with linkages to the Orinoco River drainage in Venezuela, may have been larger than commonly reconstructed, perhaps including hundreds of residents at a site like Trants. In fact, the size and character of the Amerindian deposits at Trants suggest it was a large, apparently circular village centered on a plaza from the early Saladoid period onward.

This article uses chronological and settlement data to help establish the size and configuration of the Trants site, as well as its antiquity and duration. After a brief discussion of relevant field work, radiocarbon dating, and ceramic artifacts, particular emphasis is given to the sediment analyses. Phosphate fractionation and other sediment data corroborate the very intensive and long-term use of the site during the early and later Saladoid period, ca. 500 B.C.–A.D. 410 or later, as established on the basis of radiocarbon dates and diagnostic ceramics. Although still evolving, these and other data suggest that the circular, ring-shaped Trants site is analogous to some Amerindian settlements in Lowland South America and the insular Caribbean known through the ethnographic record. These findings suggest that past perceptions about the antiquity and scale of Saladoid period developments in the Caribbean and Lowland South America may need to be reevaluated on the basis of research at Trants.

---

[1] Archaeology Research Center, University of Maine at Farmington, Farmington, Maine 04938.
Submitted 1 November 1993.

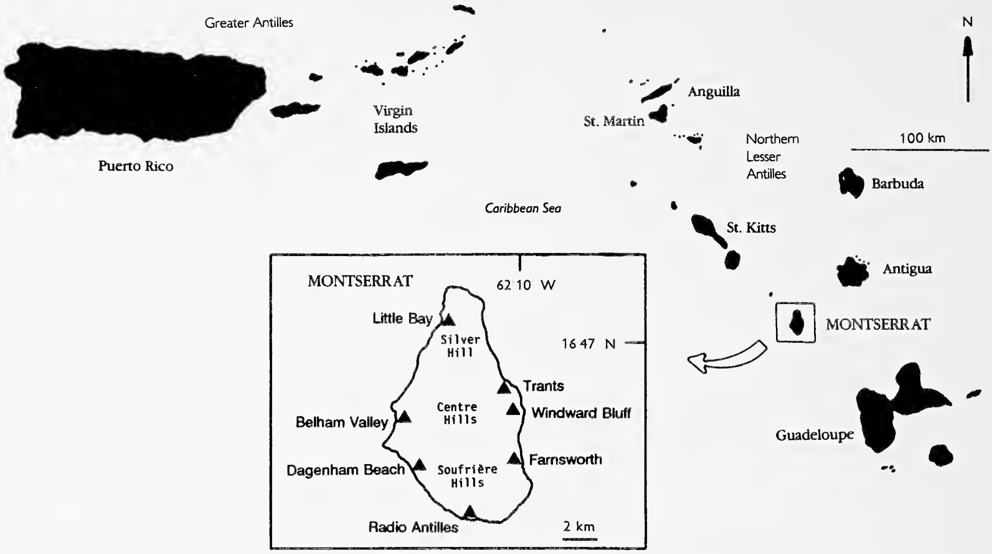


Fig. 1.—The Trants site on the eastern coast of Montserrat in the northern Lesser Antilles.

TRANTS SITE RESEARCH

The Trants site (MS-G1) is located on the eastern or windward shore of the small volcanic island of Montserrat in the northern, Leeward Islands portion of the Lesser Antilles in the insular Caribbean (Fig. 1). Montserrat lies about 670 km to the north of mainland South America and 300 km to the east of the Virgin Islands and the more distant Greater Antilles. Thus, Trants is situated in the eastern portion of the insular Caribbean. The island is relatively high for its small size, extending to about 923 m above sea level and covering an area of about 98 km^2 (Watters, 1980). Level areas are rare on the steep volcanic slopes of Montserrat and Trants occupies a portion of the only large level area on the windward coast, along with a historic estate of the same name. This landform apparently consists of ancient volcanic deposits, as described further below (Fig. 2, 3). The site lies about 9.1–18.2 m above mean sea level at present.

Long before Amerindians of the Saladoid period came to Trants, the island was born as the product of volcanic activity in the Pliocene–Pleistocene epoch (MacGregor, 1939; Martin-Kaye, 1969; Rea, 1974; Wadge and Isaacs, 1988; Maury et al., 1990). The site proper and the broader landforms on both sides of Farm River are related to early pyroclastic flows from the youngest of five volcanic centers, the Soufrière Hills. Dated to ca. 22,000–14,000 B.C. or earlier, these flow deposits were likely laid down quickly and dramatically in multiple events, whether they represent mud flows or a Pelean type *nuee ardente* ("glowing cloud"). Although most of the island's volcanoes are inactive, the Soufrière Hills remain quite active (MacGregor, 1939; Rea, 1974; Wadge and Isaacs, 1988), as seen most recently in 1995–1996.

The Trants archaeological site was first brought to the attention of archaeologists in a publication by Mark Harrington (1924). Harrington published preliminary observations about the private Howes artifact collection from Trants which had been acquired by the Museum of the American Indian (MAI), Heye Foun-

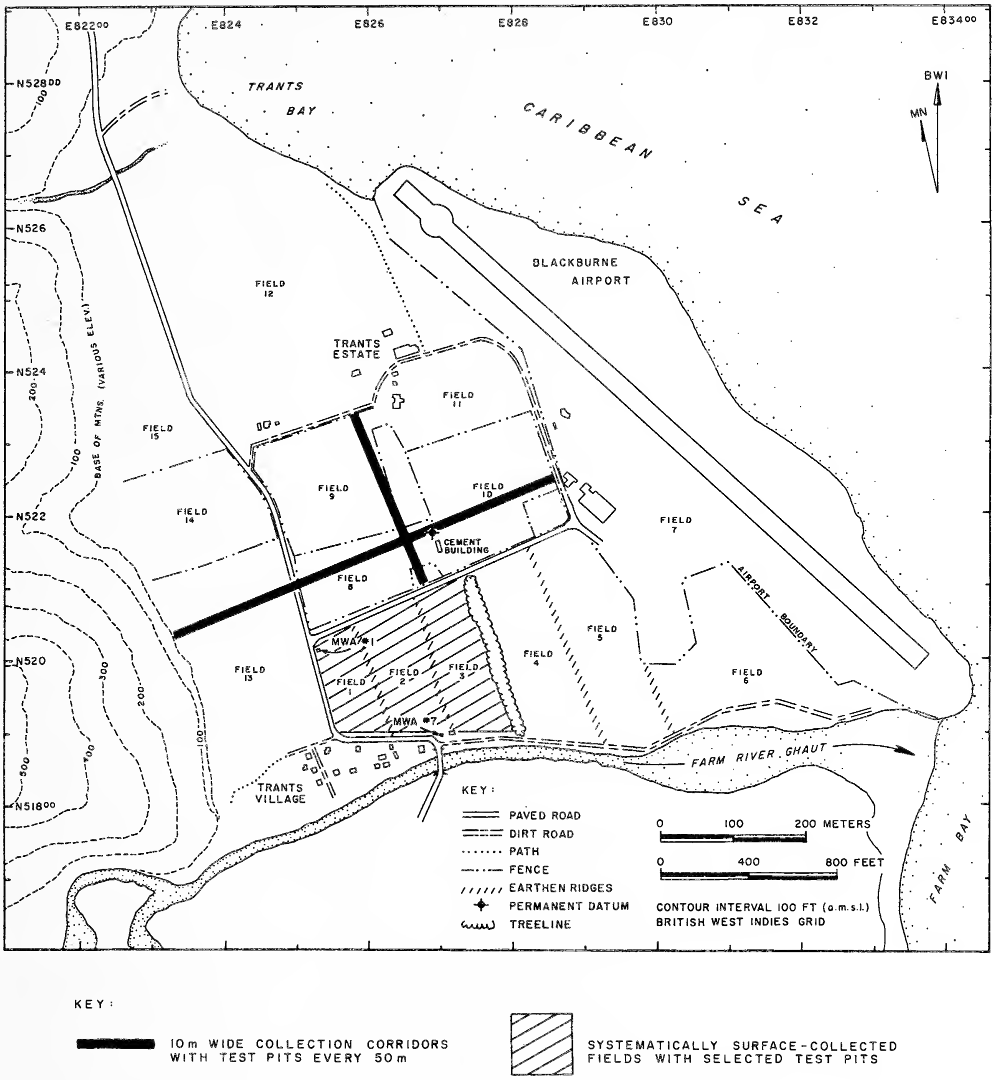


Fig. 2.—Overview map of the Trants site showing systematic collection strategies and field designations during the 1990 field work.

dation (see Watters and Scaglion, 1994). In particular, the rather substantial Howes shell and stone bead collection led Harrington to conclude that the Trants site was a "West Indian Gem Center," beginning long-term reference to the site in this light. Unfortunately, Harrington did not visit Montserrat and so he never published full details about the site.

In 1978–1979, David Watters was the first archaeologist to conduct systematic field work at Trants as part of his dissertation research (see Watters, 1980, 1994). Over ten years later, Watters and Petersen codirected more extensive testing of the Trants site in 1990 as a joint undertaking of the Carnegie Museum of Natural History (CM) and the University of Maine at Farmington (UMF) (Petersen and

Fig. 3.—General view of the Trants site and existing airport on the eastern coast of Montserrat, facing southeast.

Watters, 1991; Watters, 1994). The 1990 field work was done at the request of the Montserrat National Trust given the likelihood of site disturbance by the proposed expansion of Blackburne Airport, Montserrat's only airport (see Fig. 2, 3). A supplemental field inspection was undertaken in 1992 after backhoe "trial barrow" (or borrow) pits were excavated at the site by airport planners. Various individuals have undertaken analysis of the 1978–1979, 1990, 1992, and MAI (now Smithsonian Institution) collections (see Steadman et al., 1984; Bartone and Crock, 1991; Crock, 1993; Newsom, 1993; Reitz, 1994; Watters and Scaglion, 1994; Petersen and Watters, 1995; Reitz and Dukes, 1995). Although further field work at the site was undertaken in 1995 by CM and UMF (Petersen et al., 1995; Watters, 1995), this paper primarily addresses results of the 1978–1979 and 1990 research at the Trants site, although some of the 1995 results are cited, as appropriate.

Details about the 1978–1979 and 1990 Trants field work have been presented elsewhere (see Watters, 1980, 1994; Petersen and Watters, 1991, 1995; Watters and Petersen, 1995) and need not be repeated here, with the exception of a few specifics. Limited surface collection and a single 2.0 m × 2.0 m excavation unit were used to test the site in 1978–1979. Extensive surface collection, 29 0.5 m × 0.5 m test pits and three 1.0 m × 1.0 m test units were used to further sample Trants in 1990 (see Fig. 2). The 1978–1979 and 1990 excavations covered a combined area of only 14.25 m^2, but they have provided important artifact and sediment samples from the site.

Sediments at the Trants site are quite coarse overall, representing slightly weathered sandy deposits from pyroclastic and/or mud flows related to eruption of the Soufrière Hills on the basis of geological research (MacGregor, 1939; Rea, 1974).

Alternatively, the deposits at Trants have been designated by soil scientists as "protosols," relatively young developing soils in an "outwash" "delta" of "alluvium," or "colluvium," presumably related to the Farm and Paradise rivers (Lang, 1967:10, 13, 18, fig. II) to the south of the site (see Fig. 2). This latter attribution seems to be contradicted by the local topography, however, which shows the lowermost portion of Farm River Ghaut (near Trants village) deeply crosscutting a long, gently sloping landform extending from the base of the steep Soufrière Hills (near the modern villages of Bethel and Bramble) northeastward to the sea.

The Trants stratigraphy is quite variable across the areas sampled, including a combination of relatively fine and very coarse-grained sediments. In the archaeological excavations, the natural, noncultural strata range horizontally from sandy, rock-free zones to dense, rocky strata, as described below in the discussion of the sediment analyses (Fig. 4–9). This extreme horizontal variability is directly attributable to lateral flow variations in the volcanic deposits across the large site area. Within a defined "core" area of the site, both natural and culturally-modified strata were discerned in 1990 and 1992, as well as during the recent 1995 field work. The topography in the local area has been derived from a combination of the original volcanic deposits, later natural processes such as weathering and possible erosion, modification by the prehistoric Amerindian (and historic European and African) occupants, and one or more possible natural catastrophes during the time of the Amerindian occupation (Petersen et al., 1995).

The extensive surface collection at Trants in 1990 was conducted in two crosscutting corridors and a larger area elsewhere at this site (see Fig. 2; Watters, 1994; Watters and Petersen, 1995). The 1990 field work established an overall site size of nearly 600,000 m^2 on the basis of the full extent of observed and suspected prehistoric artifact distributions. However, the unequivocal "core" area of about 50,000 m^2, or about 5.0 hectares, was defined from the 1990 and 1992 field work; this has been revised to an area of about 62,000 m^2, or 6.2 hectares, on the basis of the 1995 research. Historic disturbance of the site in the "core" area has largely been confined to shallow hand and limited plow cultivation of sugar cane and cotton. The now abandoned Trants Estate and several existing roads to the estate buildings and Blackburne Airport also have caused localized disturbance to the prehistoric deposits. Thus, the prehistoric site is rather large and relatively little disturbed such that its original configuration can be still determined.

RADIOCARBON DATING

A total of eight radiocarbon dates were first obtained for the Trants site, two from the 1978–1979 testing and six from the 1990 testing (Table 1). These absolute dates establish that the site was minimally occupied from ca. 480 B.C. to A.D. 330; an additional 11 radiocarbon dates have recently been obtained from the 1995 research, extending the sequence to ca. A.D. 410 or later (Petersen et al., 1995). Along with another date of ca. 440 B.C. from the Radio Antilles site in Montserrat, two of the Trants dates are among the very oldest reliable published dates known for the Saladoid period anywhere in the West Indies.

In fact, only single published dates from the Fond Brûlé site in Martinique and the Hope Estate site in St. Martin are clearly older than the oldest Trants (and Radio Antilles) dates from Montserrat (Mattioni, 1982; Rouse, 1989; Haviser, 1991). In concert with recent research at Hope Estate and scattered evidence

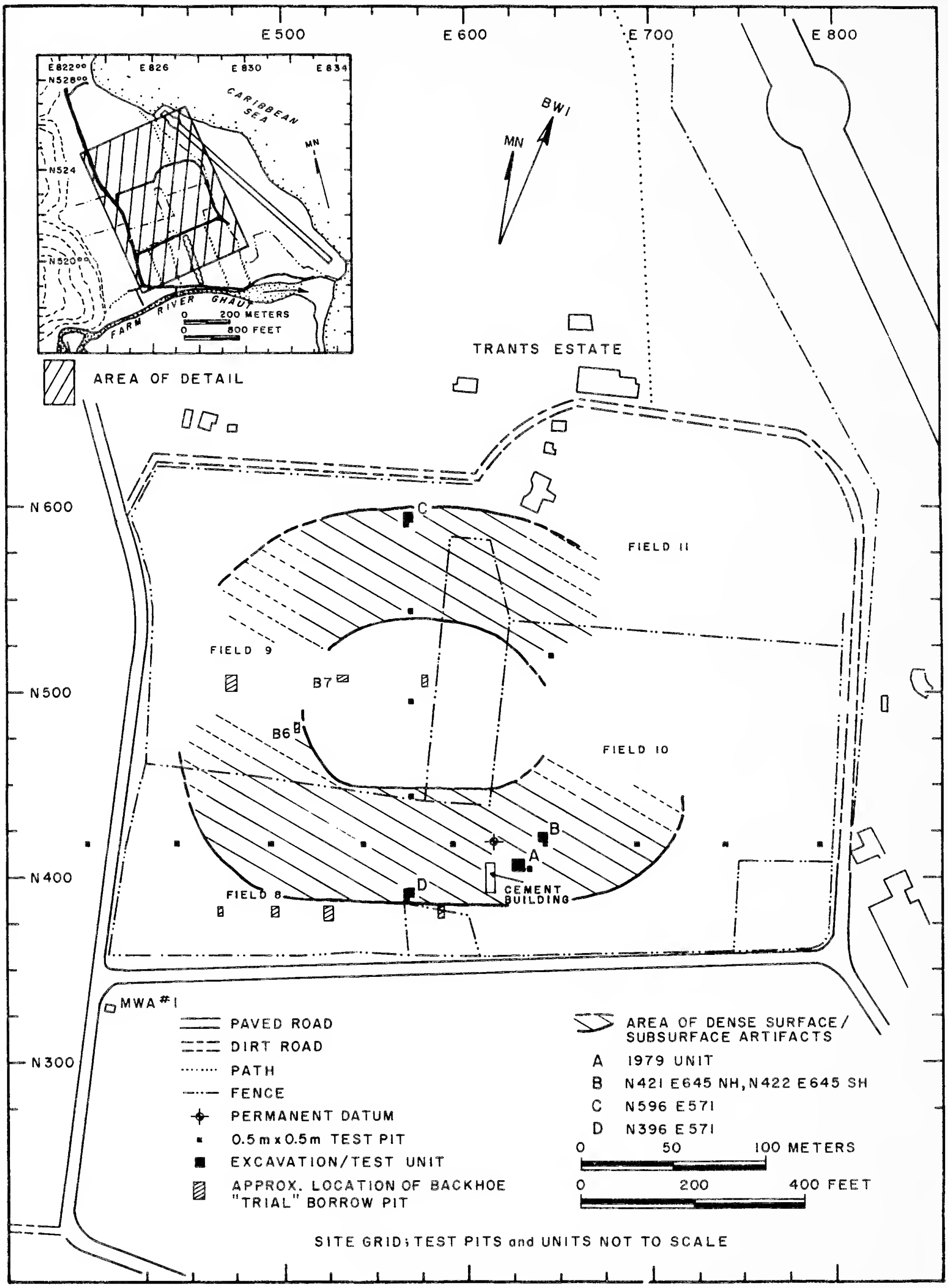


Fig. 4.—Detail map of the Trants site showing site "core" area in fields 8–11, 1990 test units and other selected excavations, and 1992 "barrow" pits. Note site grid designations along margins.

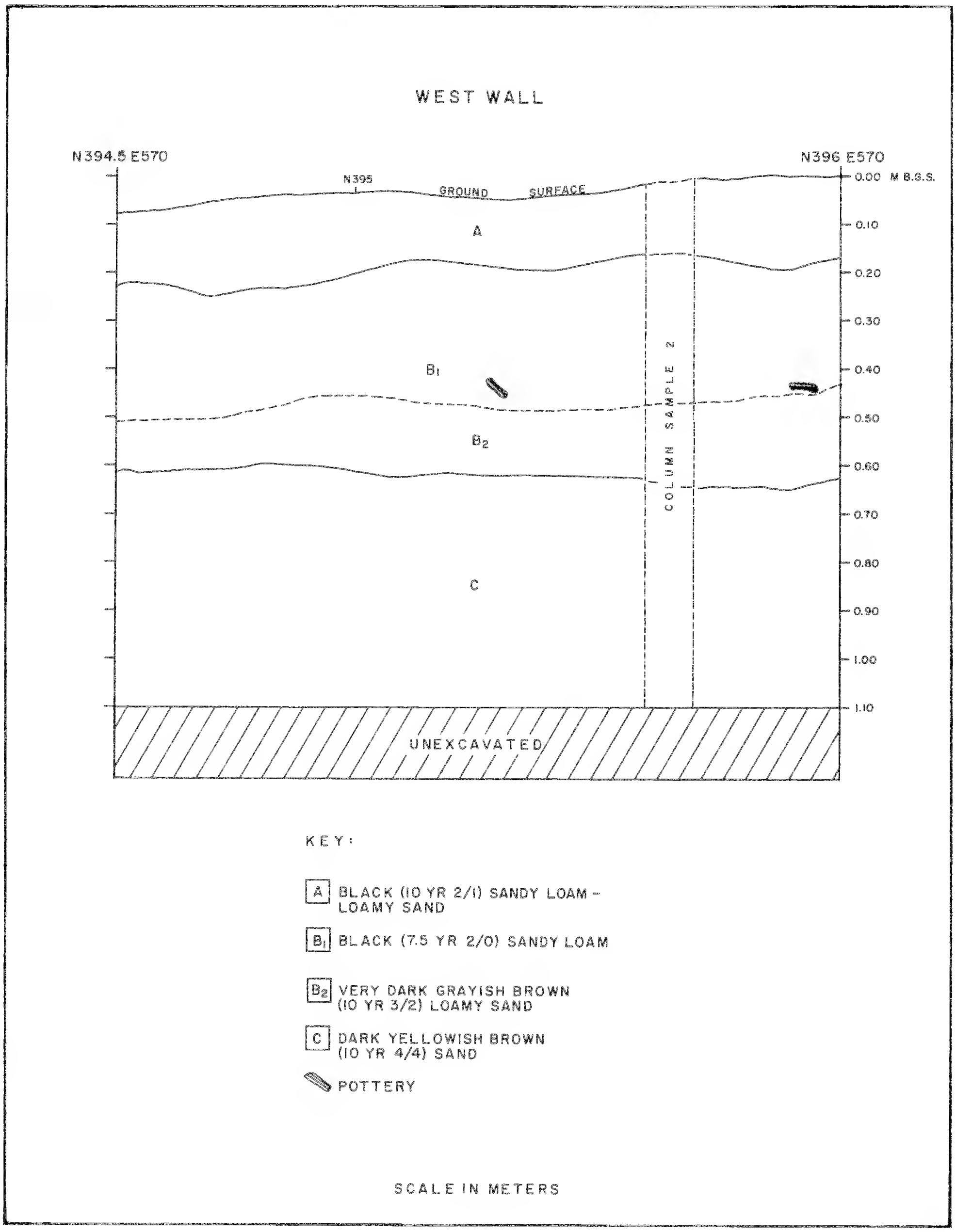


Fig. 5.—West wall profile of 1990 test unit N396 E571 in field 8 at the Trants site. Note in situ prehistoric ceramic sherds and location of sediment column 2; lower portion of field stratum B2 was radiocarbon dated to 480 B.C. ± 80.

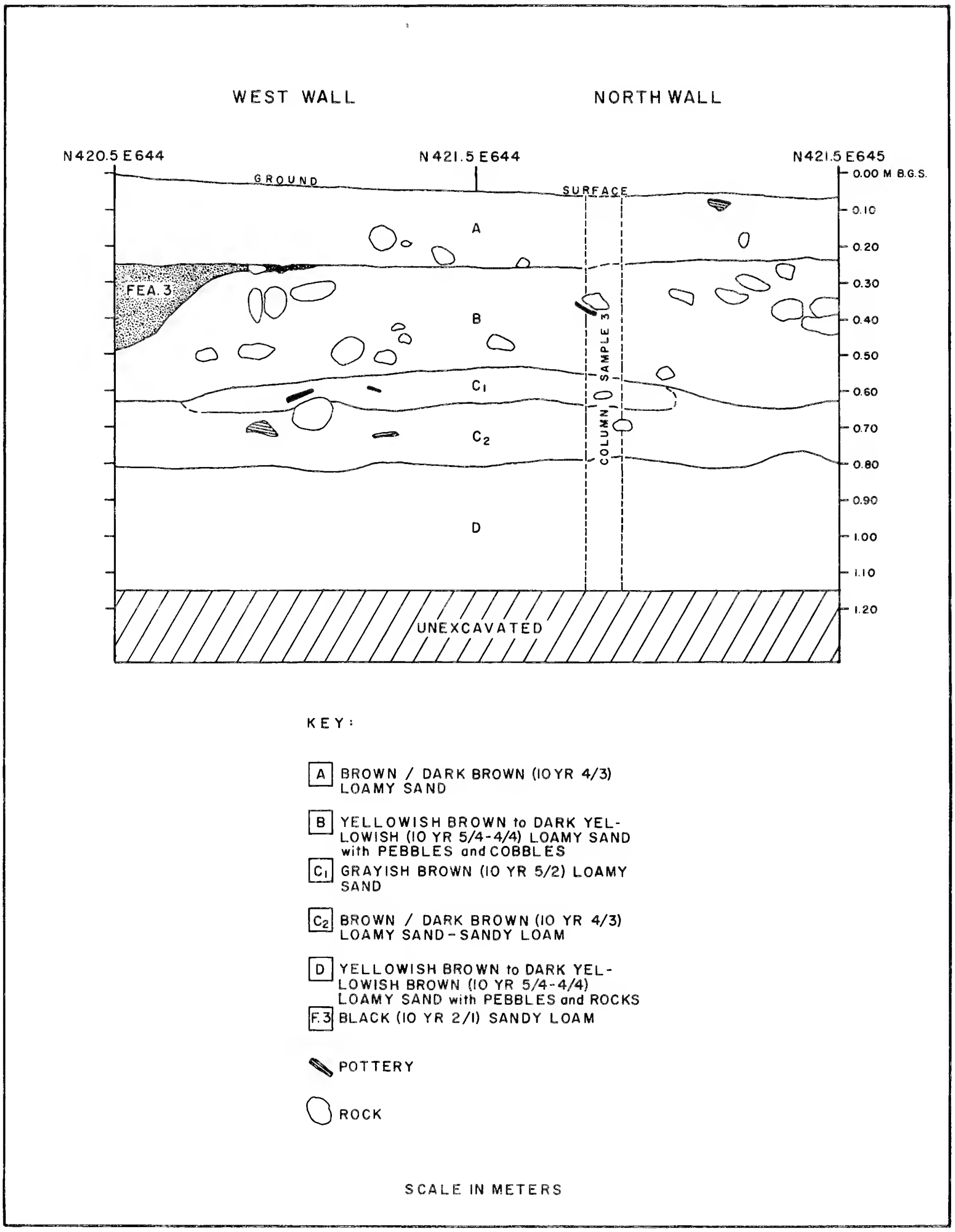


Fig. 6.—Composite west and north wall profiles of 1990 test unit N421–N422 E645 in field 10 at the Trants site. Note in situ ceramic sherds, rocks, feature 3, and location of sediment column 3; field stratum C1 was radiocarbon dated to A.D. 210 ± 90, and field stratum C2 was radiocarbon dated to 10 B.C. ± 90.

Fig. 7.—General view of west wall of 1990 test unit N421–N422 E645 in field 10 at the Trants site. Note tagged field strata and feature 3.

elsewhere in the West Indies (e.g., Rouse, 1989), the Trants radiocarbon dates suggest that various estimates of the timing of Saladoid period migration from the mainland into the insular Caribbean have been too conservative, generally thought to have occurred at about A.D. 1 or later (e.g., Willey, 1971; Rouse, 1976; Meggers and Evans, 1978; Rouse and Allaire, 1978; Goodwin, 1979:78; cf. Rouse, 1989, 1992).

Acceptance of the beginnings of Saladoid settlement as early as ca. 500 B.C. in the West Indies means that Saladoid populations may have been present for only a relatively brief period in the Orinoco River drainage prior to their colonization of the West Indies. This is especially the case if one accepts the "short" chronology for the Saladoid period in Venezuela; that is, beginning at ca. 1000 B.C., rather than 2000 B.C., as has been typically suggested (e.g., Rouse and Allaire, 1978:441–442; Roosevelt, 1980:193–196; Rouse, 1992:75; cf. Meggers and Evans, 1978; Sanoja and Vargas, 1983).

The "short" chronology for the Saladoid period and new dates from the insular Caribbean may support the hypothesis that Saladoid migration commenced in Venezuela due to climatic changes which brought increased aridity (Meggers, 1987), but this is by no means certain. Any number of factors may be responsible for Saladoid dispersal in the insular Caribbean and Lowland South America alike, and better resolution is needed for its dating and relationships all across the broad region.

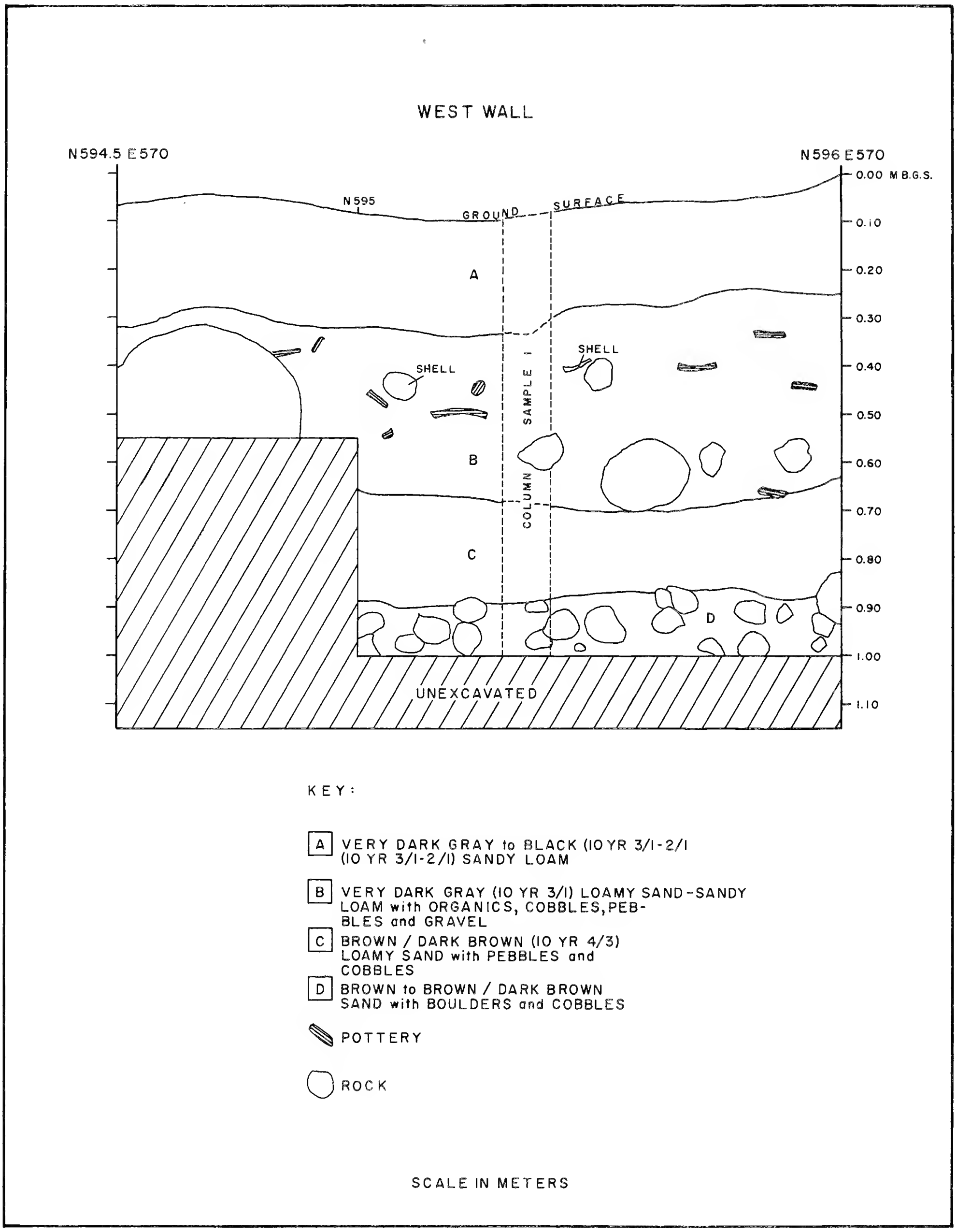


Fig. 8.—West wall profile of 1990 test unit N596 E571 in field 9 at the Trants site. Note in situ ceramic sherds, rocks, and location of sediment column 1; upper portion of field stratum B was radiocarbon dated to A.D. 60 ± 70, and the upper stratum C was radiocarbon dated to 440 B.C. ± 90.

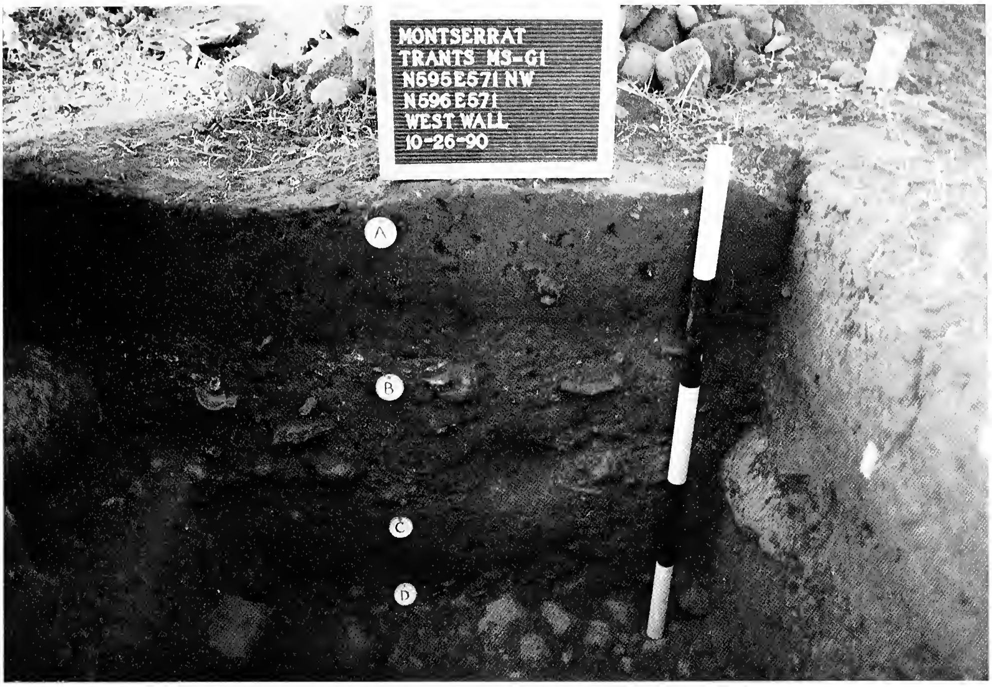


Fig. 9.—General view of west wall of 1990 test unit N596 E571 in field 9 at the Trants site. Note tagged field strata.

TRANTS AMERINDIAN CERAMICS

Diagnostic prehistoric artifacts from the Trants site, primarily Amerindian ceramics, are found in the collections curated by the MAI, from the various episodes of systematic field work, and at the Montserrat National Trust Museum. The goal of the discussion here is to further establish the early and later Saladoid period antiquity of the site, rather than to present exhaustive details about the prehistoric ceramics and other artifacts diagnostic of the Amerindian occupants. Although some of the lithic artifacts are temporally diagnostic as well, especially the lithic beads (Bartone and Crock, 1991; Watters and Scaglion, 1994), the vast majority of the diagnostic artifacts known from Trants are hand-built, open-fired Amerin-

Table 1.—*Radiocarbon dates for the Trants site.*

Radiocarbon years B.P.	Years B.C./A.D.	Sample no.	Context	Depth (in cm b.s.)
2430 ± 80	480 B.C.	Beta-44828	N396E571	50–70C
2390 ± 90	440 B.C.	Beta-41682	N596E571	70–80C
2140 ± 80	190 B.C.	Beta-18489	1979 unit	40–50
1960 ± 90	10 B.C.	Beta-41680	N422E645	70–80C
1890 ± 70	A.D. 60	Beta-41678	N596E571	30–40B
1750 ± 80	A.D. 200	Beta-41679	TP N407E634	40–60B
1740 ± 90	A.D. 210	Beta-41681	N422E645	61C
1620 ± 90	A.D. 330	Beta-18582	1979 unit	40–50

dian ceramics. More complete details about these ceramics, including stratigraphic and radiocarbon associations, among other issues, are presented elsewhere (Petersen and Watters, 1995), and a complete, exhaustive taxonomy will be presented in the future.

Cross dating of the Amerindian ceramics corroborates the available radiocarbon dates for Trants. Such local and regional comparisons generally confirm the placement of most, if not all, ceramics to Saladoid period, that is, ca. 500 B.C. to A.D. 600. The Trants ceramics are best related to Cedrosan Saladoid ceramics, as previously defined by Rouse (1992). Alternatively, these ceramics can be assigned to the Early Ceramic period or age (e.g., Haviser, 1991) and some are even attributable to the Huecan Saladoid, or Huecoid "culture" (Chanlatte Baik and Narganes Storde, 1990; Rodríguez, 1991*a*; Rouse, 1992). This discussion avoids such differentiation, however, given the close technological relationship of all ceramics at Trants (Petersen and Watters, 1995).

The available Trants ceramic samples suggest that the entire sequence for the Saladoid period in the Lesser Antilles is represented at Trants. Since most of the systematically recovered ceramics are not decorated (depending on whether solely slipped specimens are included or not, about 11–14% of the sample of 2752 sherds excavated from the three 1990 test units are decorated, for example) and are not rim sherds (Petersen and Watters, 1991, 1995), it is possible that some are, in fact, attributable to the post-Saladoid period. However, there is very little, if any, obvious evidence of post-Saladoid occupation in any of the Trants collections; reliable diagnostic artifacts of the post-Saladoid period or Late Ceramic age are not present.

The Trants Amerindian ceramics represent a diverse set of vessel forms which closely match those known from elsewhere in the region (e.g., Rouse, 1974, 1992; Petitjean Roget, 1978; Mattioni, 1982; Chanlatte Baik and Narganes Storde, 1990; Rodríguez, 1991*a*; Versteeg and Schinkel, 1992). These include, but are not limited to, effigy and noneffigy bowls of various sizes and forms (Fig. 10), cylindrical pots or jars of various sizes (Fig. 11), "incense burners," and griddles, as well as rare figurines and other forms. Both molded ceramic spindle whorls (in contrast to later post-Saladoid forms which were recycled from broken sherds), and conical and cylindrical ceramic body stamps are also known from the site.

Although most of the Trants ceramics are undecorated, some exhibit classic Saladoid types of decoration such as zone-incised crosshatched (ZIC) and white-on-red (WOR) motifs (Fig. 12–15). These two types are quite distinctive, each of which has its own vessel forms as well as distinctive decoration. Both ZIC and WOR are widespread across the site and are found together in intact subsurface deposits. Notably, the Huecan and Cedrosan Saladoid (sensu Rouse, 1992) ceramics co-occur in midden deposits at Trants, supporting the close technological similarity noted above. Thus, it is possible that these are not as different as has been suggested elsewhere (e.g., Chanlatte Baik and Narganes Storde, 1990; Chanlatte Baik, 1991; Haviser, 1991; Rouse, 1992), at least not at the Trants site. Contextual analysis of the Trants ceramic sample from the 1995 excavations should help resolve this matter, as should ongoing work at the Hope Estate site in St. Martin (Haviser, 1991; J. Haviser, C. Hoffman, and M. Hoogland, personal communications, 1993), among other sites.

Regardless of this taxonomic issue, evidence of vessel morphology, decoration per se, and rim adornos (Fig. 16) clearly establish the widespread connections between the Trants ceramics and others known from the Lesser Antilles, the Virgin

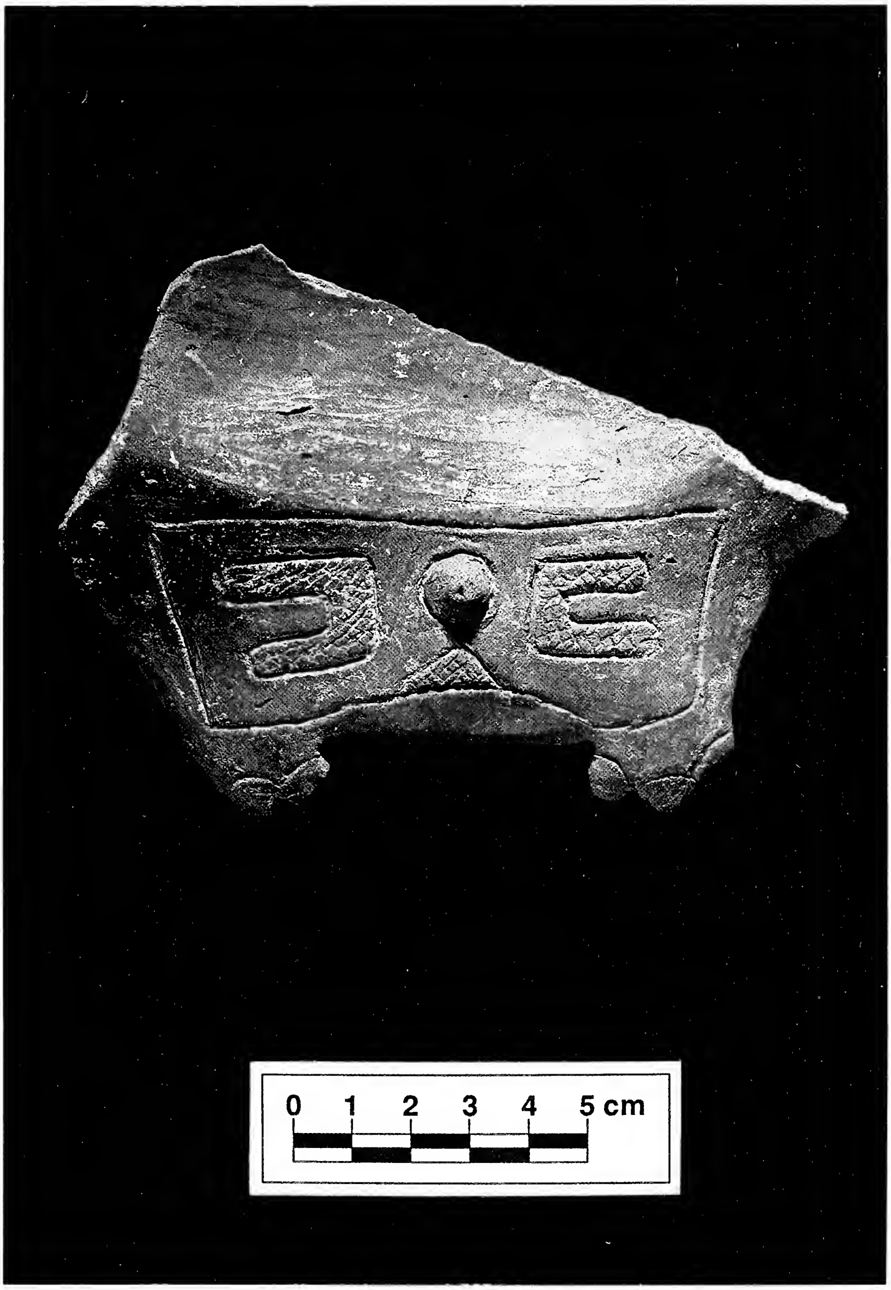


Fig. 10.—Saladoid Amerindian ceramic turtle effigy bowl rim sherd from the Trants site. Note zone-incised crosshatched and node decoration, and turtle feet.

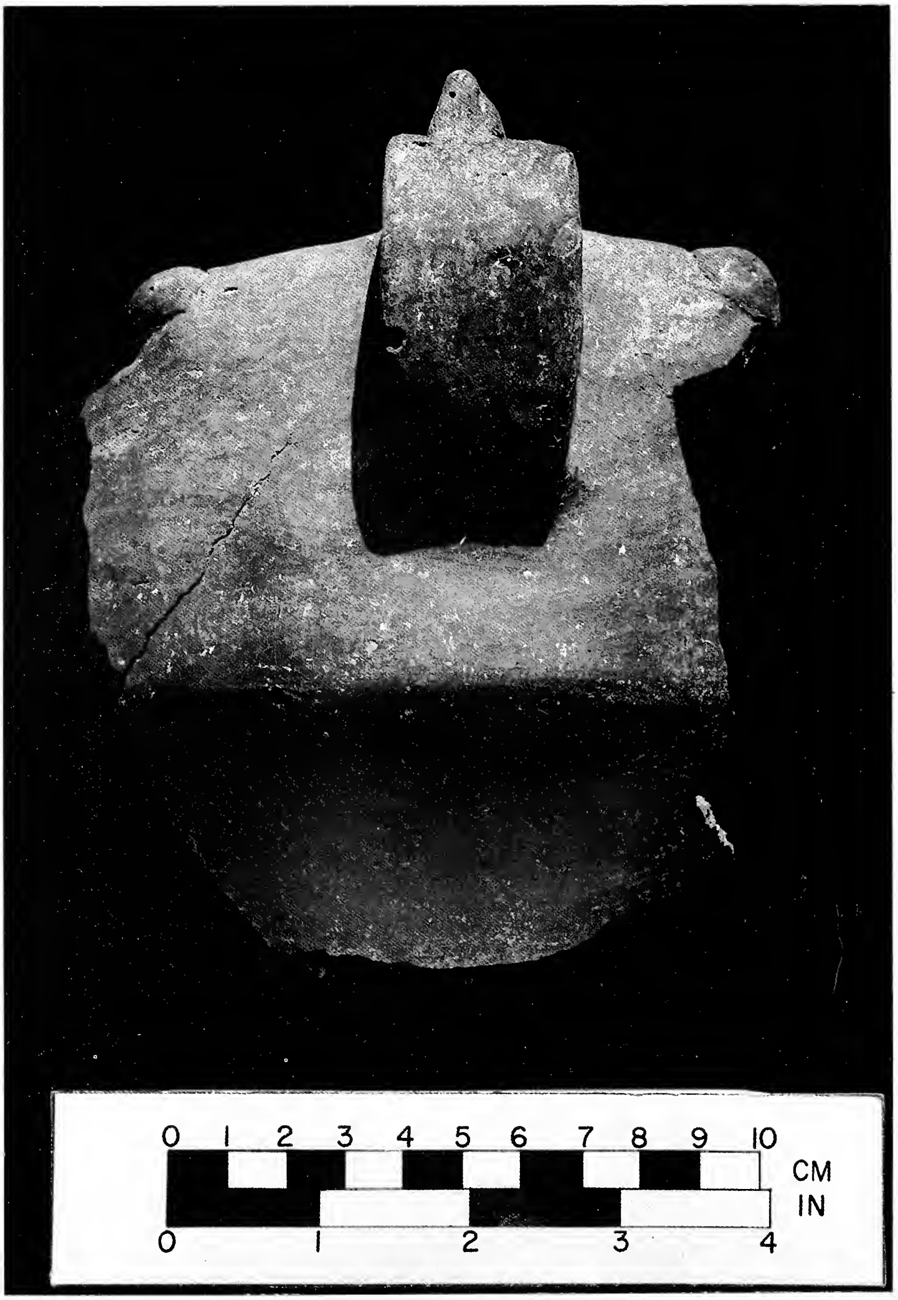


Fig. 11.—Saladoid Amerindian ceramic bowl rim sherd from the Trants site. Note node decoration and strap handle.

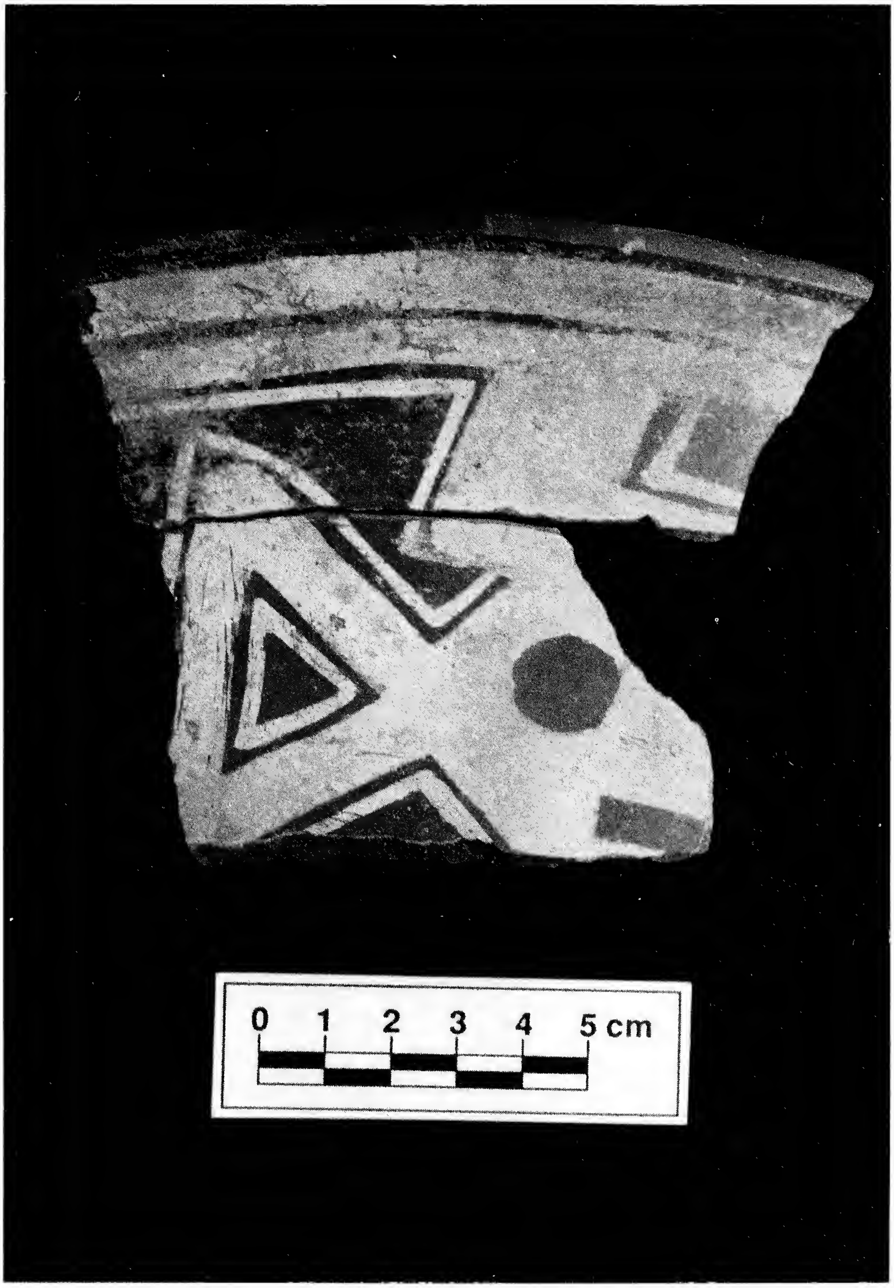


Fig. 12.—Saladoid Amerindian articulating ceramic rim and neck sherds from the Trants site. Note white-on-red decoration.

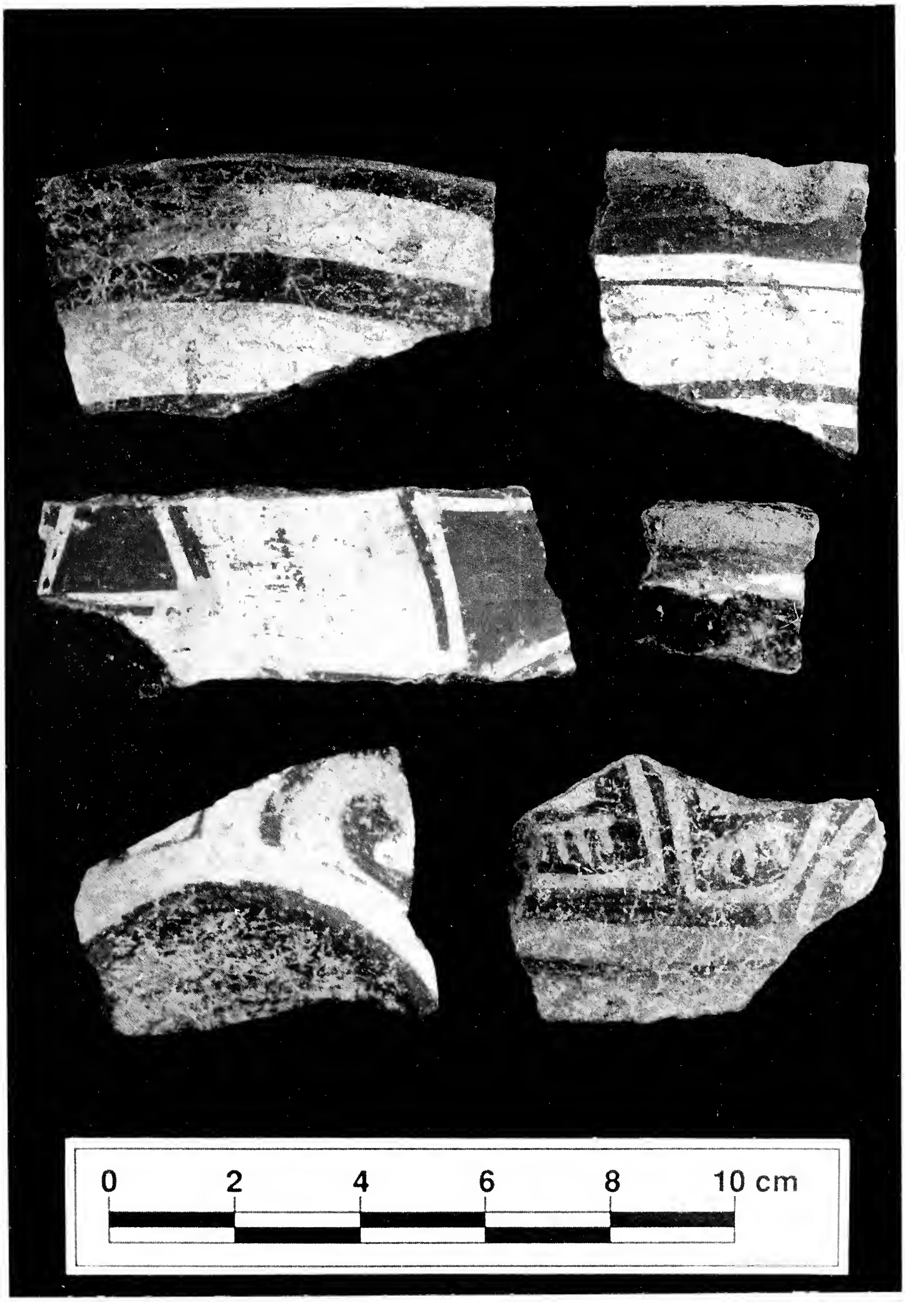


Fig. 13.—Saladoid Amerindian ceramic rim, neck, and body sherds from the Trants site. Note white-on-red decoration (all except middle right specimen) and white-and-black-on-red decoration (middle right specimen).

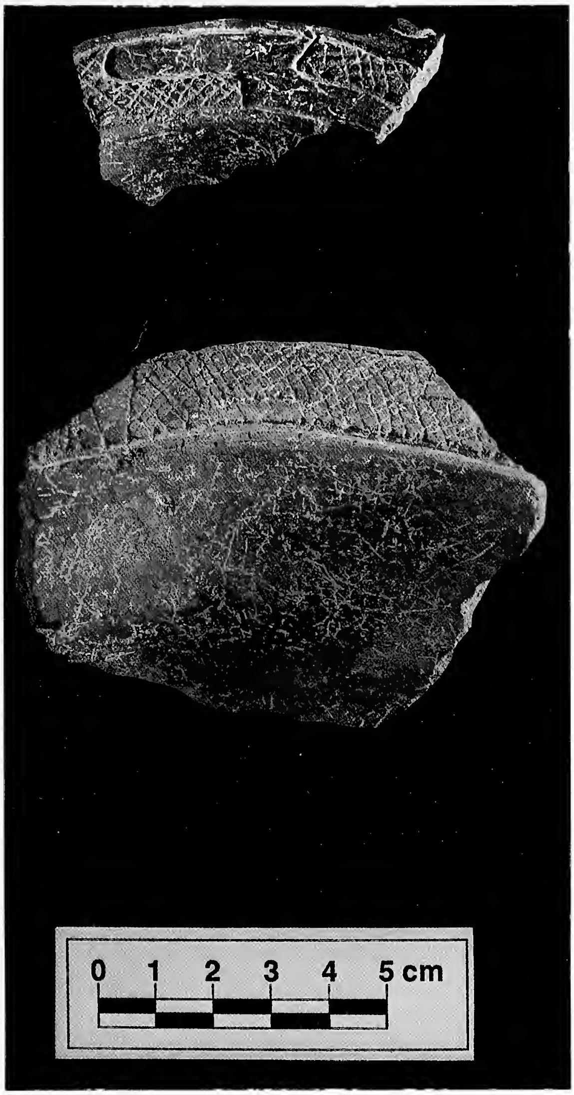


Fig. 14.—Saladoid Amerindian ceramic rim sherds from the Trants site. Note zone-incised cross-hatched decoration on rim flanges.

Islands, and Puerto Rico in the West Indies, as well as the South American mainland (Petersen and Watters, 1995). Montserratian Saladoid potters shared very similar ceramic styles with other potters over a very large area, more than 2500 km in extent, including both their mainland and insular distribution. This social interaction is further corroborated by the lithic raw materials and some of the forms represented among the copious beads known from Trants, as discussed elsewhere (e.g., Bartone and Crock, 1991; Crock, 1993; Watters and Scaglion, 1994). These likewise show connections to other Antillean islands and mainland South America.

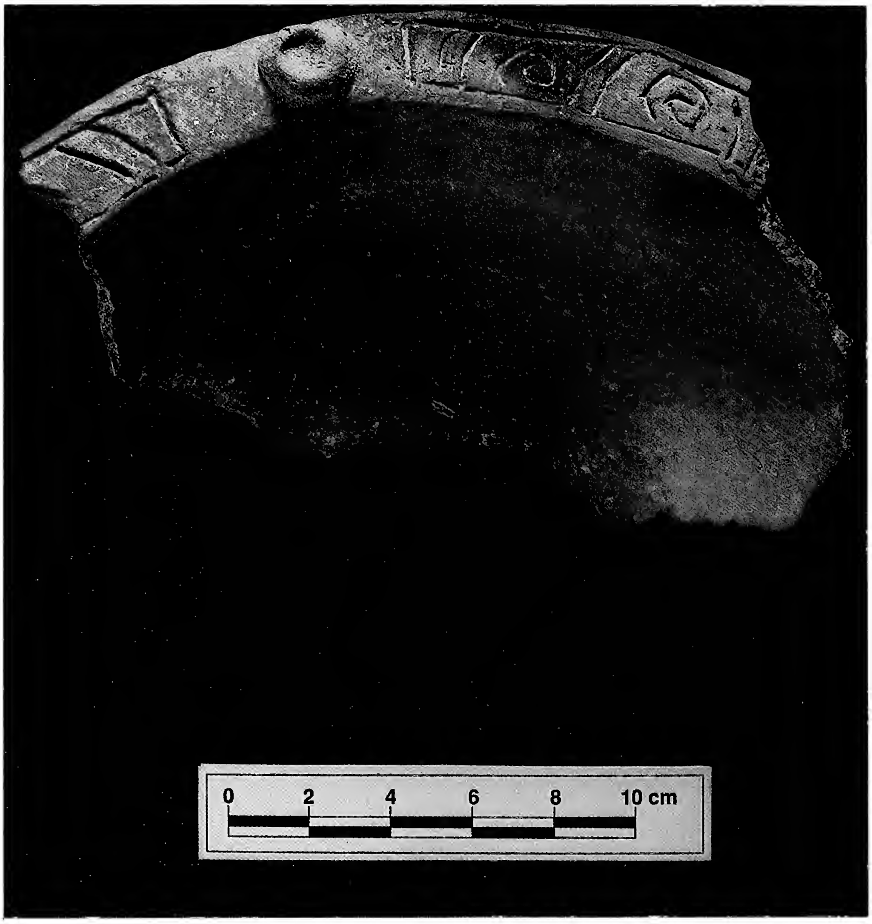


Fig. 15.—Saladoid Amerindian ceramic rim sherd from the Trants site. Note zone-incised and node punctate decoration.

TRANTS SEDIMENT DATA

Sediment analyses can be used to assess the natural and cultural processes which are responsible for the modern configuration of a given archaeological setting (Hassan, 1978). Combining analysis of sediment grain size, for example, with various chemical, pH, and organic matter determinations, among others, may allow evaluation of the natural processes of sediment origin, transport, deposition, and weathering, along with human alteration thereafter through enrichment from refuse disposal and other mechanisms. Although such analyses have been infrequently conducted in the context of Caribbean and Lowland South American archaeology, they provide an important means of studying site geomorphology and settlement structure where they have been undertaken (e.g., Smith, 1980; Eden et al., 1984; Eidt, 1984; Robinson, 1985).

Sediment samples were obtained from all of the subsurface test pits and test units excavated at Trants in 1990 as part of the overall site investigation. Incremental 10 cm × 10 cm sediment samples, maximally 10 cm deep within natural

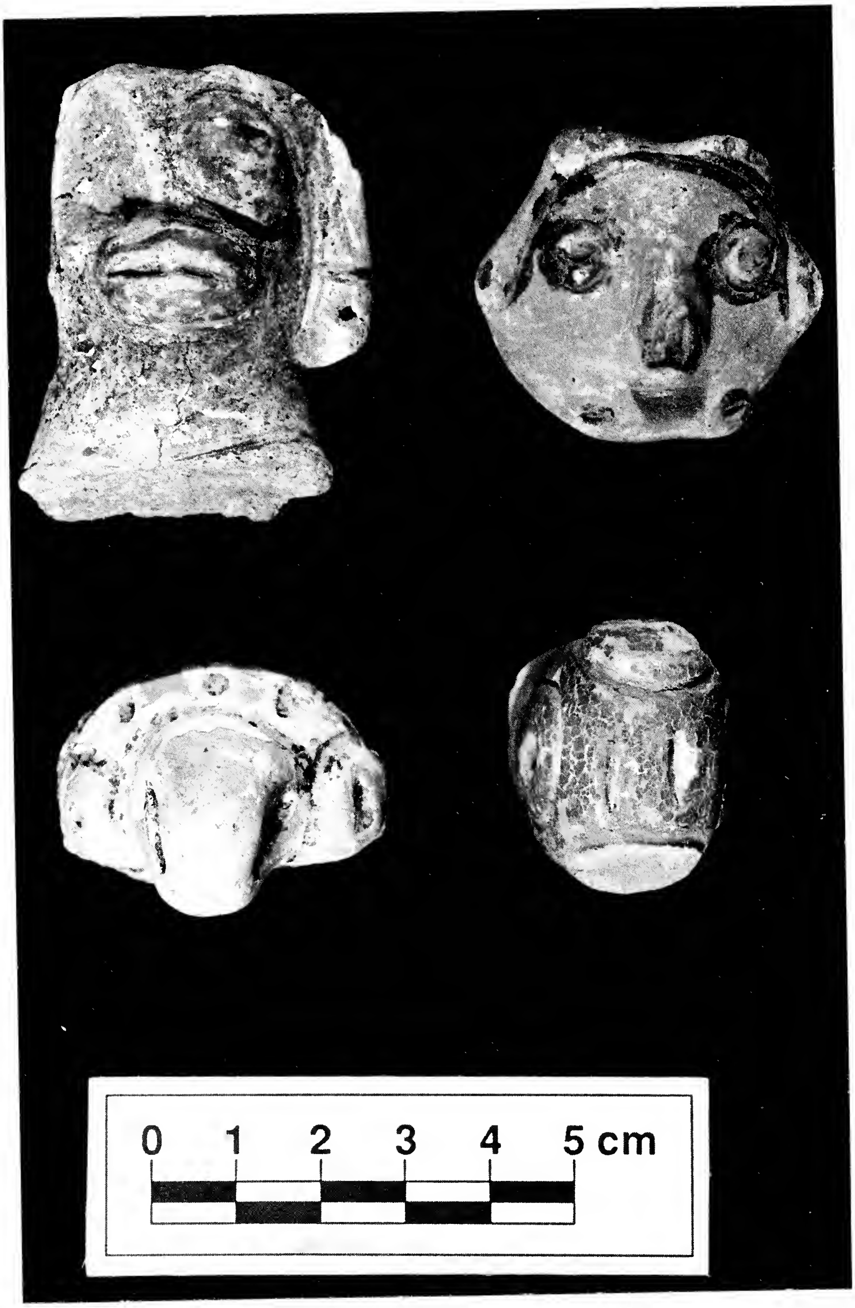


Fig. 16.—Saladoid Amerindian ceramic adornos from the Trants site. Note white-on-red, black-on-red, and white-and-black-on-red decoration.

Fig. 17.—Collection of sediment column 3 in 1990 test unit N421–N422 E645 at the Trants site. Note rocks removed largely from stratum B.

stratigraphy, were collected from the three 1990 test units, with care taken not to mix natural strata (Fig. 17). Smaller sediment grab samples were removed from the test pits to enable analysis of sediment variability across the extent of the site.

Grain size characterization, pH, organic matter, phosphate fractionation, and other chemical analyses were conducted using the professional consulting services of the University of Wisconsin–Milwaukee Sediment Laboratory and the methods of the late Robert Eidt (e.g., 1984, 1985). Of these analyses, the phosphate fractionation data were suspected to provide the most objective assessment of past land use at and near the Trants site given the long-term stability of phosphates in archaeological sediments (e.g., Sjöberg, 1976; Eidt, 1985:180–183; Lillios, 1992). Phosphate fractionation values are typically reported as a sum of three inorganic fractions, I–III, representing different combinations of aluminum, iron, and calcium; the ratio of fractions II/I can even be used as a relative dating technique, with higher ratios denoting greater antiquity (Eidt, 1984).

The three complete sediment columns from the 1990 test units at Trants were completely processed for grain size, pH, organic matter, and chemical analyses; a total of 34 samples were thus analyzed (Table 2, 3). Sediment column numbers 1 and 3 from units N596 E571 and N421–N422 E645, respectively, sampled artifact-rich stratified midden deposits, while column 2 from unit N396 E571 sampled a very notable "anthrosol" composed of dark, organic-rich soil with somewhat fewer obvious subsistence remains (see Fig. 5–9). This anthrosol in the area of unit N396 E571 is much like *terra preta,* or "black earth," as known from archaeological sites in the Lowlands of South America (e.g., Smith, 1980; Eden et al., 1984).

Phosphate fractionation analysis was undertaken for only selected increment

Table 2.—*Summary of sediment grain size data for the Trants site.*

			Grain size data		
Provenience		PN no.	% Sand	% Silt	% Clay
N596 E571, column sample 1	0–10A	2143	73.0	22.0	5.0
	10–20A	2144	73.0	22.0	5.0
	20–24A	2145	76.0	18.0	6.0
	24–30B	2146	74.0	20.0	6.0
	30–40B	2147	74.0	21.0	5.0
	40–50B	2148	76.0	20.0	4.0
	50–60B	2149	76.0	20.0	4.0
	60–65B	2150	80.0	16.7	3.3
	65–70C	2151	84.0	14.0	2.0
	70–80C	2152	85.0	12.0	3.0
	80–90D	2153	87.0	10.0	3.0
N396 E571, column sample 2	0–10A	2160	76.0	19.0	5.0
	10–20A	2161	74.0	21.0	5.0
	20–30B	2162	63.0	28.0	9.0
	30–40B	2163	61.0	29.0	10.0
	40–50B	2164	69.0	22.0	9.0
	50–60B	2165	82.0	15.0	3.0
	60–70C	2166	87.0	11.0	2.0
	70–80C	2167	89.0	11.0	0.0
	80–90C	2168	92.0	8.0	0.0
	90–100C	2169	94.0	6.0	0.0
	100–110C	2170	95.0	5.0	0.0
N422 E645, column sample 3	0–10A	2180	76.0	19.0	5.0
	10–20A	2181	76.0	19.0	5.0
	20–30B	2182	82.0	15.0	3.0
	30–40B	2183	84.0	13.0	3.0
	40–50B	2184	84.0	13.0	3.0
	50–58C	2185	74.0	23.0	3.0
	58–60C	2186	75.0	18.0	7.0
	60–70C	2187	78.0	16.0	6.0
	70–80D	2188	80.0	15.0	5.0
	80–90D	2189	84.0	13.0	3.0
	90–100D	2190	85.0	13.0	2.0
	100–105D	2191	85.0	13.0	2.0

samples from the same three Trants sediment columns and several of the 1990 test pits (Table 4). The test pit samples were selected to cover somewhat the extent of the two sampling transects, east–west and north–south, across the site area, as well as a few essentially "sterile" site margin or off-site areas to enable broad comparison. Watters (1994:table 1) provides a complete list of all excavations before the 1995 field work. Eleven phosphate fractionation samples have been analyzed to date, in all cases except two clearly from sub-cultivation zone contexts.

Of all the results of the sediment analyses, perhaps most striking are those related to grain size (Fig. 18–20) and phosphate fractionation, the latter described separately below. The three full vertical sediment columns, taken in areas of obvious artifact concentrations, reveal that the macroscopically obvious anthrosol, field strata B1 and B2, in column 2 from test unit N396 E571 (see Fig. 5) has the highest percentages of fine-sized silt and clay relative to other column 2 samples and those from the other two sediment columns (see Table 2, Fig. 18). The deepest portion of the anthrosol in unit N396 E571, stratum B2, has been

Table 3.—*Summary of sediment pH, organic matter, and chemical data for the Trants site.*

			Chemical and other data						
Provenience		PN no.	pH	OM %	K ppm	Ca ppm	Mg ppm	Sol. Salts mho × 10^{-3}	P ppm
N596 E571, column sample 1	0–10A	2143	7.0	3.1	147	1476	219	0	5
	10–20A	2144	7.2	3.1	103	1350	152	0	2
	20–24A	2145	7.7	2.8	73	2154	162	0	7
	24–30B	2146	7.8	2.8	55	3144	158	0	6
	30–40B	2147	7.8	2.9	38	3684	137	0	<0.5
	40–50B	2148	7.9	3.0	1380	4182	128	0	<0.5
	50–60B	2149	7.9	2.1	1114	3732	149	0	<0.5
	60–65B	2150	8.1	1.6	1200	636	125	0	<0.5
	65–70C	2151	8.1	2.1	205	636	195	0	<0.5
	70–80C	2152	8.2	1.9	141	3246	189	0	0.5
	80–90D	2153	8.2	1.7	117	3678	293	0	13
N396 E571, column sample 2	0–10A	2160	7.8	3.0	298	1512	257	0	6
	10–20A	2161	7.8	3.3	242	1668	163	0	9
	20–30B	2162	7.8	4.6	161	2496	241	0	5
	30–40B	2163	7.8	4.2	128	2346	248	0	4
	40–50B	2164	7.9	3.1	88	1980	222	0	4
	50–60B	2165	7.9	2.0	69	1686	218	0	3
	60–70C	2166	8.0	1.8	61	1140	179	0	1
	70–80C	2167	7.9	1.9	60	906	167	0	<0.5
	80–90C	2168	8.1	1.5	48	642	128	0	1
	90–100C	2169	8.0	1.4	67	744	169	0	<0.5
	100–110C	2170	8.1	1.7	47	1320	240	0	<0.5
N422 E645, column sample 3	0–10A	2180	7.9	3.8	70	2280	326	0	5
	10–20A	2181	8.0	2.5	94	2490	137	0	2
	20–30B	2182	8.1	2.0	70	1590	121	0	1
	30–40B	2183	8.3	1.7	104	1452	108	0	2
	40–50B	2184	8.4	1.4	32	1344	67	0	<0.5
	50–58C	2185	8.2	2.5	44	3666	126	0	<0.5
	58–60C	2186	8.3	1.8	53	3912	142	0	<0.5
	60–70C	2187	8.4	2.2	1230	3384	137	0	<0.5
	70–80D	2188	8.5	1.9	1238	3234	165	0	<0.5
	80–90D	2189	8.5	1.7	67	2310	145	0	<0.5
	90–100D	2190	8.5	1.6	56	2487	190	0	<0.5
	100–105D	2191	8.5	1.6	67	2526	205	0	7

Table 4.—*Summary of sediment phosphate fractionation data for the Trants site.*

Provenience	PN no.	Fraction Ia (ppm)	Fraction Ib (ppm)	Fraction II (ppm)	Fraction III (ppm)	Total phosphate (ppm)	Ratio II/I
N596 E571, 24–30B	2146	17.0	283.0	1,264.0	1,192.0	2,756.0	4.21
N422 E645, 20–30B	2182	14.0	95.0	379.0	251.0	739.0	3.49
N422 E645, 50–58C	2185	12.0	292.0	994.0	1,390.0	2,688.0	3.39
N396 E571, 0–10A	2160	52.0	61.0	345.0	381.0	839.0	3.04
N396 E571, 20–30B	2162	37.0	45.0	245.0	323.0	650.0	2.99
T3 P1, 25–30 cm	1672	7.5	1.9	4.5	120.5	134.4	0.47
TP N421 E245, 20 cm	1897	7.3	3.5	13.5	53.9	78.2	1.25
TP N421 E495, 40 cm	1838	46.4	25.7	112.6	185.2	369.9	1.56
TP N421 E745, 30 cm	1879	17.0	7.7	22.5	82.8	130.0	0.91
TP N495 E571, 40 cm	1887	22.1	23.6	100.8	235.5	382.0	2.20
TP N521 E646, 35 cm	2009	9.2	302.4	1,954.5	978.4	3,244.5	6.27

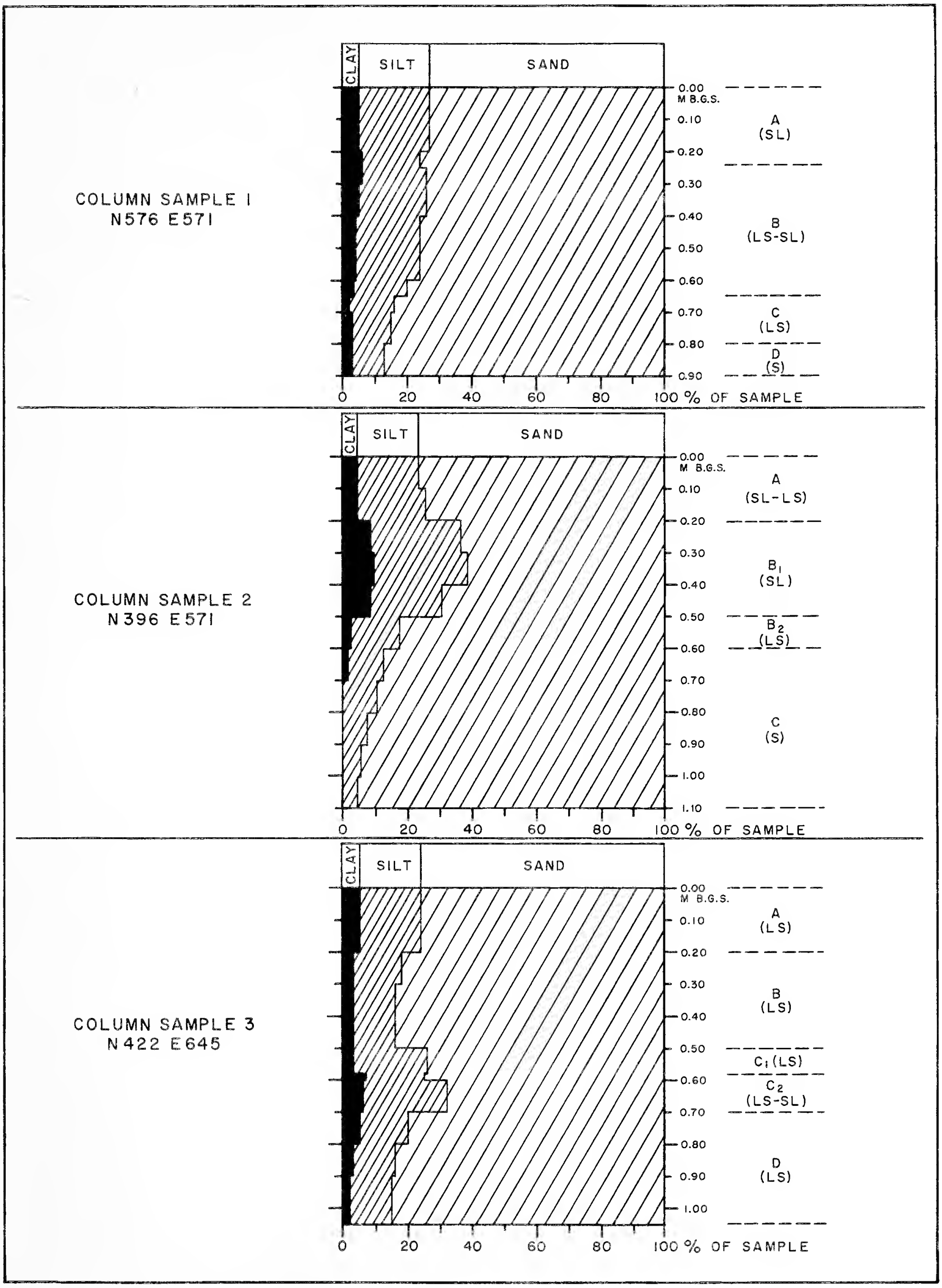


Fig. 18.—Vertical distribution of sediment grain sizes plotted against field strata at the Trants site.

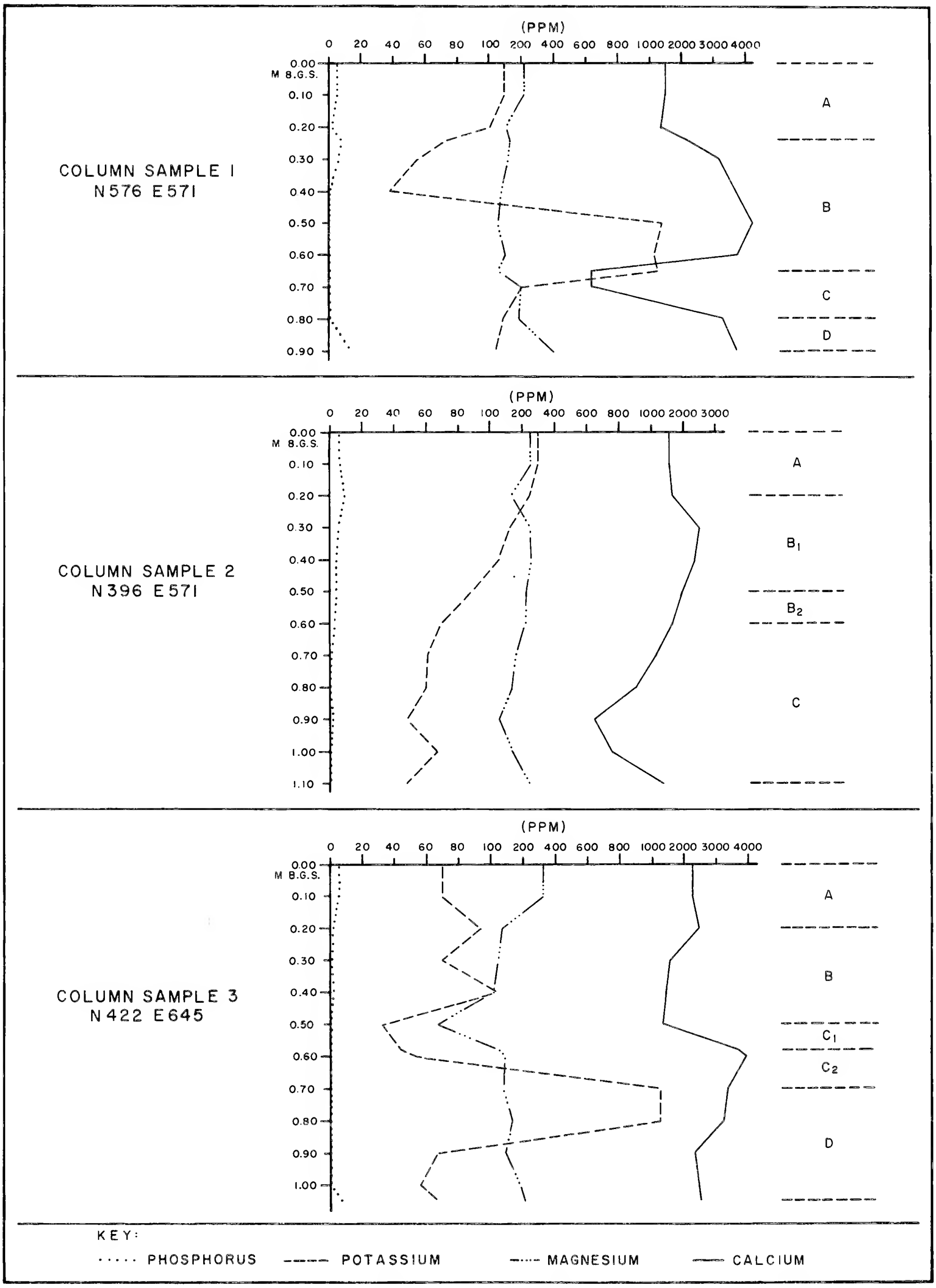


Fig. 19.—Vertical distribution of sediment chemical data plotted against field strata at the Trants site.

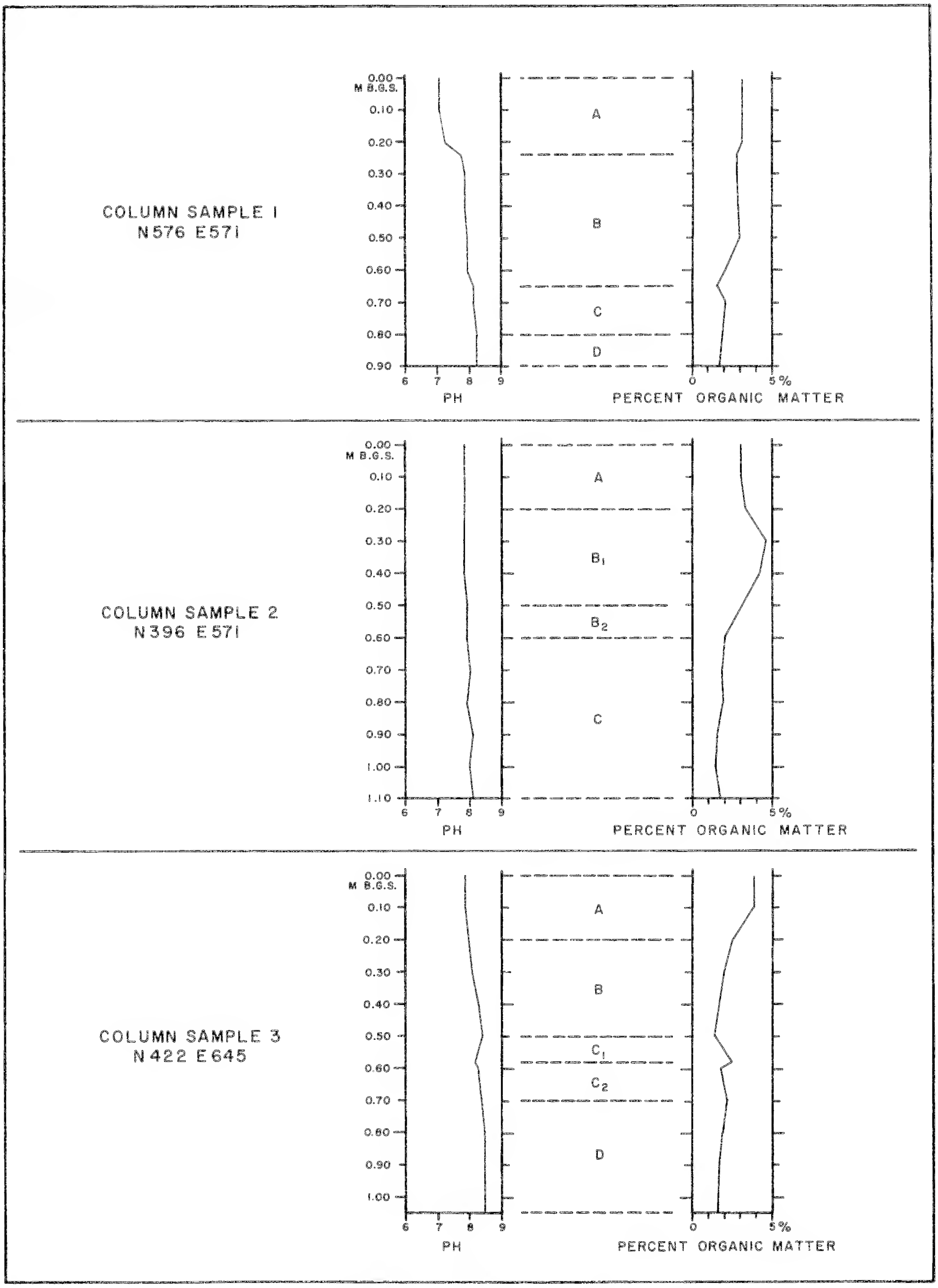


Fig. 20.—Vertical distribution of pH and organic matter data plotted against field strata at the Trants site.

dated to ca. 480 B.C. (see Table 1). The anthrosol is very dark colored and certainly represents sediment alteration caused by the Amerindian occupants. The fine-sized silt and clay fractions increase significantly in the anthrosol over the original sandier sediments, as noted in the difference between samples from a depth of ca. 20–60 cm and those both above and below them (see Fig. 18). This anthrosol area lies at the southern end of the site.

The deeper samples in Trants sediment column 2, originating below the anthrosol, or below about 60 cm, represent the original, unaltered site sediments and these are only about 5–13% silt and clay. In contrast, the preserved anthrosol proper, or sediments ca. 20–60 cm deep, includes 18–39% silt and clay, an increase of over 700% at most in terms of the percentages of the nonsand fractions (see Table 2). Even the upper 20 cm of sediments in column 2 are generally coarser than the preserved anthrosol, including about 24–26% silt and clay. Natural weathering and soil horizon formation before the Amerindian occupation and the Amerindians themselves all seemingly increased the fine sediments in sediment column 2, but historic cultivation and perhaps other mechanisms have slightly coarsened the upper portion relative to the intact anthrosol.

The other two Trants sediment columns, both of which sampled artifact-rich middens in test units N422 E645 and N596 E571 (nos. 3 and 1, respectively), also show finer-sized sediments in correlation with the prehistoric middens. However, other factors, natural and/or cultural, have affected their specific configurations to some degree (see Table 2, Fig. 18). This is most clearly the case for column 3 in unit N422 E645 which crosscuts a buried midden, field strata C1 and C2, and an upper, historically plow-disturbed midden, field stratum A (see Fig. 6, 7). These include 22–26% and 24% silt and clay for the buried midden and the upper, disturbed midden, respectively. Strata C1 and C2 in unit N422 E645 have been dated to ca. A.D. 210 and 10 B.C, respectively (see Table 1). Sediment column 3 originated towards the eastern end of the site and it is somewhat close to the original shoreline.

Stratum B overlies strata C1 and C2 in column 3 and it is a largely noncultural deposit of some sort, including a series of large, rounded cobbles, perhaps the result of a storm-surge of water due to a natural catastrophe during the time of the Saladoid occupation (see Fig. 6, 7, 17). It is also possible the strata B deposits resulted from volcanic activity during the Saladoid occupation, but their clustered distribution and proximity to the old shoreline in field 10 (and in field 9, described below) suggests that they are more likely the product of one or more storm-surge events (Petersen et al., 1995).

Underlying stratum D presumably represents the original, unaltered site sediments in column 3. The coarsest sediments in column 3 lie between the two middens and beneath the buried midden, including 16–18% silt and clay for the noncultural deposit in stratum B and 15–20% silt and clay for stratum D.

Trants sediment column 1 from unit N596 E571 was taken from an area of very dense prehistoric artifacts at the north end of the site, one of the densest midden areas discovered during the 1990 (and more recent) field work (see Fig. 8, 9). In this case, the fractions of nonsand and sand constituents in the midden sediments of column 1 remain more or less constant from the ground surface downwards to a depth of ca. 65 cm, including 20–27% silt and clay in strata A and B, the historic cultivation zone and the intact prehistoric midden, respectively. Although not isolated as a separate stratum, a series of anomalous rock deposits are present in a portion of stratum B in unit N596 E571 as sampled by column

1, sometimes including rocks weighing 75 kg or more lying directly on top of artifacts (see Fig. 8, 9). Stratum B in unit N596 E571 has been dated ca. A.D. 60 (see Table 1). Coarser sediments lie deeper still in stratum C of column 1, containing a few prehistoric artifacts and dated 440 B.C. (see Table 1), as well as in noncultural stratum D. These include a range of 13–16% silt and clay for the two combined strata.

It is difficult to interpret column 1 other than to note some degree of sediment grain size alteration in the upper portion of the column due to the Amerindian occupation, with slight fining of the midden sediments relative to the deeper sediments. The dense prehistoric occupational debris in this area seemingly reflects intensive activities which may have homogenized the cultural deposits to some degree. Alternatively, the presumed natural disturbance in stratum B reflected by the large rocks, somewhat like stratum B in unit N422 E645, may have coarsened the cultural deposits in part, or perhaps some combination of these and/or other factors pertains. The rocky deposits may be attributable to one or more storm-surge events during the Saladoid occupation given their proximity to the old shoreline in field 9, much like those in field 10, as described above (Petersen et al., 1995).

The chemical analyses also help to delineate the relative degree of sediment alteration in the sampled portions of the Trants site (Fig. 19; see Table 3). Again, this alteration is due to a combination of cultural and/or natural factors. Available (or exchangeable) calcium (Ca) values peak in all three columns in obvious correlation with the Amerindian anthrosols and middens. In the case of column 1 from unit N596 E571, the highest calcium values of 3144–4182 ppm correlate with the preserved Saladoid midden in stratum B, but the deepest and clearly noncultural samples in lower stratum C and stratum D are likewise high at 3246–3678 ppm. The cultivation-disturbed Amerindian midden in stratum A and the deposits in upper stratum C have lower combined calcium values of 636–2154 ppm. It is likely that the two calcium peaks in column 1 represent cultural enrichment to some degree in stratum B, but in lower stratum C and stratum D the high calcium concentration is perhaps due to natural, presumably geological factors. Percolation downward is negated as an explanation by the low calcium values at the top of stratum C.

Calcium data from the other two sediment columns are somewhat different than column 1 in that they each show single peaks, in both cases quite likely related to cultural enrichment. However, in column 2 from unit N396 E571 there is a tendency towards a second peak evident at the very bottom, perhaps reflecting a certain degree of calcium concentration under natural conditions (see Fig. 19). The upper, more obvious calcium peak correlates with the top of the intact stratum B anthrosol in column 2, with a peak value of 2496 ppm. Other calcium values for the intact anthrosol are 1686–2346 ppm. The cultivation zone, or stratum A, portion of the column has calcium values of 1512–1668 ppm and underlying, sterile stratum C has calcium values of 642–1140 ppm and peaks at 1320 ppm at the very bottom of column 2.

Calcium values in sediment column 3 provide the clearest case of calcium enrichment related to cultural factors. A single strong peak for calcium at 3912 ppm is correlated with the buried midden, or field stratum C2, with other high calcium values of 3384–3666 ppm for strata C1 and C2 as well (see Fig. 19). This buried midden was relatively rich in land crab subsistence remains and it is likely that these shells contributed to this peak. The cultivation-disturbed upper midden has calcium values of 2280–2490 ppm, while largely noncultural and rocky stratum B has calcium values of only 1344–1590 ppm, the lowest for the column; stratum B consists of the possible storm-surge deposits noted above. Once again there is a tentative trend towards calcium concentration at the bottom of column 3 in stratum D, where calcium values of 2310–3234 ppm may reflect percolation downward from the overlying midden and/or some natural concentration.

Available potassium (K) peaks similarly to calcium, but in this case only within the middens in columns 1 and 3 from units N596 E571 and N422 E571, respectively, and not within the anthrosol of column 2 from unit N396 E571 (see Table 3, Fig. 19). In column 1, a strong potassium peak of 1380 ppm occurs in the middle of the intact stratum B midden paralleling the calcium peak; other potassium values in stratum B range from 38–1200 ppm. The disturbed midden in overlying stratum A has potassium values of 73–147 ppm, while underlying strata C and D have combined potassium values of 117–205 ppm. The potassium concentration in stratum B is thus likely due to cultural factors, but it has seemingly percolated downward to some degree towards the bottom of the midden.

Sediment column 2, containing the anthrosol, has its highest potassium values of 242–298 ppm at the surface in the disturbed midden of stratum A, with values that drop from there steadily downward into strata B1 and B2, or the anthrosol, and underlying stratum C; potassium values for these strata combined range from 47–161 ppm. This simple distribution of potassium in column 2 is probably due to Amerindian and/or modern enrichment with relatively little percolation downward.

In sediment column 3, potassium values exhibit a single clear peak at 1230–1238 ppm at the bottom of stratum C2, the buried midden, and the top of underlying stratum D. Much lower potassium values of 70–94 ppm, 32–104 ppm, and 44–53 ppm characterize overlying stratum A, the disturbed upper midden, the largely noncultural rocky deposit in stratum B, and upper stratum C (C1 and the top of C2) respectively, while the deeper deposits of stratum D have potassium values of 56–67 ppm. This distribution suggests that it is the rich cultural deposits of the buried midden which produced the notable potassium peak in stratum C2, with its migration thereafter downward to its interface with deeper stratum D, again directly paralleling the calcium peak in the same column.

Available magnesium (Mg) values seem to vary little across the different field strata in all three sediment columns, although these values are somewhat variable through the strata in each case (see Fig. 19, Table 3). In midden-rich column 3, a peak magnesium value of 326 ppm occurs at the surface in the disturbed upper midden of stratum A and drops steadily to a low of 67 ppm at the interface of largely noncultural rocky stratum B and the underlying midden, strata C1 and C2, and then climbs slightly to 205 ppm in the deepest part of the column in stratum D. Likewise, magnesium peaks near the top and the bottom of columns 1 and 2, with a surface value of 219 ppm and a basal value of 293 ppm for column 1, and a surface value of 257 ppm and a basal value of 240 ppm for column 2. Finally, of the other chemical values, available phosphorus (P) is generally very low in all the samples, except basal peaks occur in columns 1 and 3, while soluble salts are nonexistent.

Of all three sediment columns, the highest organic matter (OM) values, 4.2–4.6%, are strongly correlated with intact stratum B1, the upper anthrosol, beneath the stratum A historic cultivation zone in column 2 from unit N396 E571 (Fig.

20; see Table 3). This dark-colored, organic-rich deposit had a notable calcium peak at the same depth, suggesting obvious organic and chemical alteration related to the Amerindian anthrosol (see Fig. 5). Other organic matter values for column 2 include 1.4–3.3% from above and below stratum B1.

In the two other sediment columns, the highest organic matter values are correlated with the historic cultivation zone at the surface (see Table 3, Fig. 20). These values, generally 2.5–3.8%, are what might be expected from the intentional (or unintentional) historic incorporation of modern vegetal crop residue and other potential organic fertilizers into the site sediments. One secondary organic matter peak of 2.5% occurs at the top of the buried midden in column 3.

Most notably, even with such historic enrichment, none of the organic matter values for columns 1 and 3 match or exceed the anthrosol values for column 2. In comparison, an earlier soils study in Montserrat recorded organic matter values of 1.01–1.72% at five localities related to the "azonal" soils around the Trants Estate, with a mean of 1.49% (Hardy et al., 1949). Of 29 *terra preta* sediment samples from the Brazilian Amazon, organic matter values range from 0.45% to 4.70%, with most values less than 2.0% (Smith, 1980:table 1), further reflecting the high relative value of some of the Trants samples.

Uniformly high pH values, 7.0–8.5, characterize all three Trants sediment columns and in all cases the values increase downward from the surface (see Table 3, Fig. 20). Historic cultivation may have lowered the pH in the uppermost stratum in each case. Curiously, there is a small decrease in pH from largely noncultural rocky stratum B downward to the buried stratum C1 midden in column 3, perhaps again reflecting cultural alteration of some sort. In any case, all of these pH values are neutral to basic and they help account for the superb preservation of faunal remains at the Trants site, at least within the midden areas (Steadman et al., 1984; Reitz, 1994; Reitz and Dukes, 1995).

The Trants pH values are likely high because of a combination of cultural modification due to Amerindian refuse disposal and the natural mildly acidic to basic conditions of the volcanic sediments in Montserrat. Refuse disposal made the sediments even less acidic, building on the favorable conditions naturally inherent in the sediments. In fact, previous soil analyses on the island have established naturally occurring average pH values of about 6.0–6.3 to 7.1 islandwide, with an overall average of 6.5 (Hardy et al., 1949; Lang, 1967). Such relatively nonacidic conditions have been caused by the generally basic character of the bedrock types (Lang, 1967; Rea, 1974). Earlier soil studies have specifically recorded a pH range of 6.6 to 7.2 for five determinations around the Trants Estate, with an average pH value of 6.9 (Hardy et al., 1949).

The results of the phosphate fractionation analyses are the most interesting of all the available sediment data (Fig. 21; see Table 4). The 11 values derived from nine different excavations, including test units and test pits across the site and the site margins, generally confirm the circular ring configuration of the prehistoric artifact distributions (see Fig. 4). Although only a limited number of samples have been analyzed thus far for phosphate fractionation, they document a single peak in intensity along the east–west sampling transect and two peaks along the north–south transect, directly paralleling the Amerindian artifact distributions (Watters, 1994:fig. 8–10; Watters and Petersen, 1995:fig. 4–7).

Moreover, the phosphate fractionation data establish a dramatic variation across the site and nearby areas, with low values of 78 ppm and 130 ppm near or beyond the site limits in fields 13 and 10 on the west and east, respectively (see Table 4,

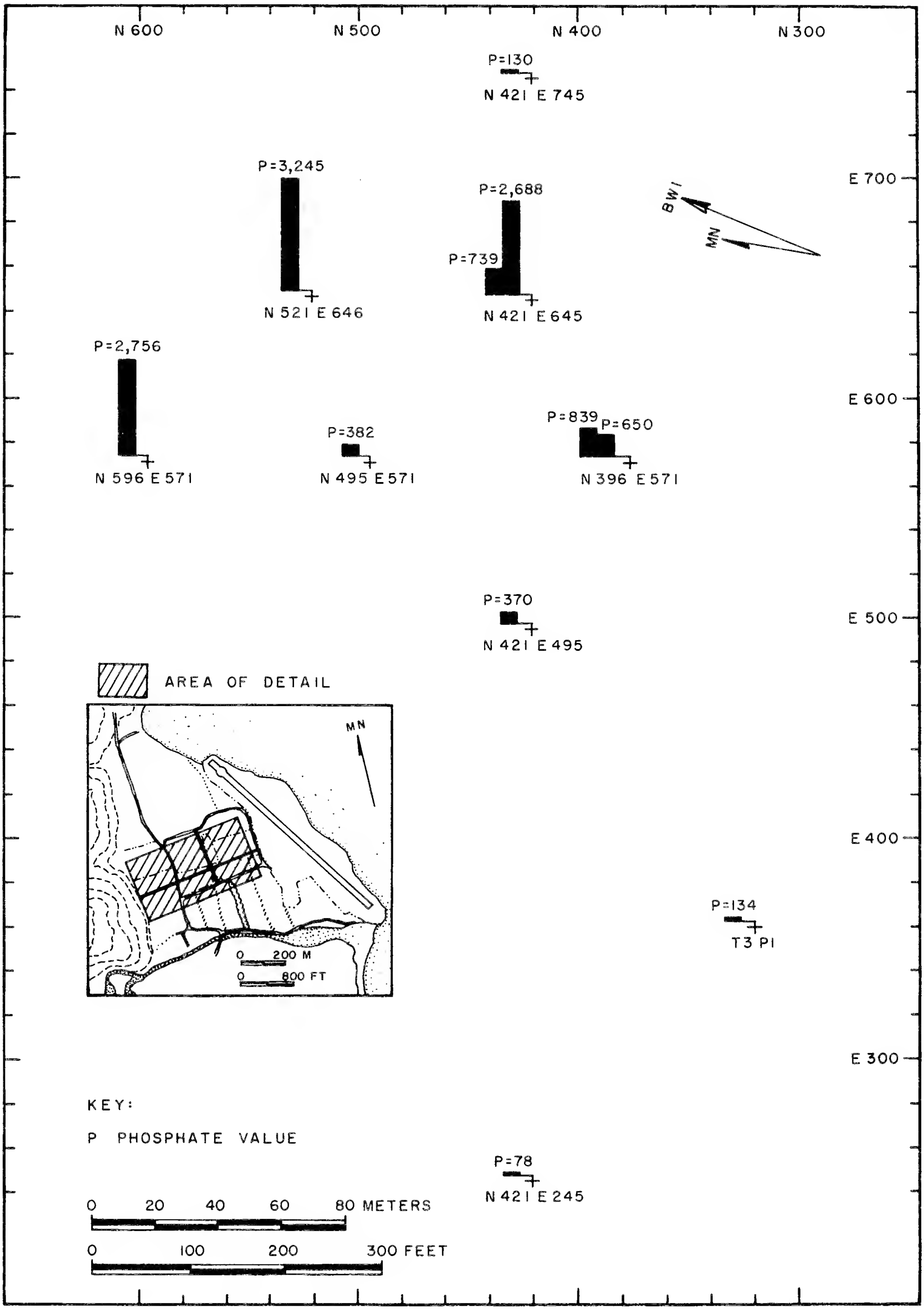


Fig. 21.—Horizontal distribution of phosphate fractionation data plotted on the metric grid at the Trants site.

Fig. 4, 21). Another low value of 134 ppm is documented for field 2 to the south of the "core" site area towards Farm River Ghaut. Intermediate values of 370, 382, 650, 739, and 839 ppm characterize the site "core" area (see Fig. 4, 21).

Very high phosphate fractionation values of 2756 ppm in sediment column 1 in field 9, 2688 ppm in sediment column 3, and 3245 ppm in a test pit in field 10 document intensive soil alteration by the Amerindian occupants, clearly marking the ring configuration on three sides. Eidt (1984:43) has characterized phosphate values of 10–200 ppm as representing "a range of economic activities such as those from ranching to hack farming," while values above 200 ppm are indicative of "more intensive activities such as dwelling areas, intensive gardening, manufacturing, etc." He goes on to say "extremely high" values "above 2,000 ppm, for example" are representative of "burials, garbage pits, slaughter areas, urbanized zones, etc." Elsewhere, Eidt (1984:95) notes that such high values are indicative of "intensive residential activities of the type found in Middle East tells or in urbanized zones." In direct comparison with the values reported here, given use of the same techniques by the same laboratory, the highest of the Trants values also exceed those recently reported for control and archaeological sediments from Bronze Age and Medieval deposits in Portugal (Lillios, 1992:table 1, 2).

Another important aspect of the phosphate fractionation data is relative age estimation through comparison of two of the three constituent fractions. Although not very useful at this stage in differentiating the age of the prehistoric Saladoid period deposits from one another, the ratio of phosphate fractions II/I is reflective of gross time differences across the areas sampled. The highest Trants ratio values, 2.99–6.27, are all attributable to the obvious prehistoric midden and anthrosol deposits, with a central plaza ratio of 2.20 (see Table 4). In contrast, the ratios for the samples outside of the "core" area are as low as 0.47 for test pit T3 P1 beyond the "core" in field 2 to as high as 1.56 for test pit N421 E495 near (but outside) the ring midden. These latter ratios may be reflective of modern phosphate enrichment (and relatively low phosphate values) produced primarily through historic farming, while the higher ratios clearly reflect the greater age (and much higher phosphate values) of the prehistoric Saladoid deposits.

Thus, the phosphate fractionation data confirm the general site configuration first noted on the basis of Amerindian artifacts. They also provide an absolute means of establishing the intensity of occupation across the site area. It seemingly represents a circular or elliptical midden, approximately 250 m × 200 m in size on the basis of the 1995 field work, with a more or less open central plaza, or "common ground." Unidentified house structures likely lie between the central area and the midden, perhaps like those known from the Golden Rock site in St. Eustatius (Versteeg and Schinkel, 1992). Tentative evidence of a structure may have been identified during the 1995 field work at Trants (Petersen et al., 1995).

The chronological data, including matching early radiocarbon dates and ceramic styles, establish that at least the northern and southern portions of the Trants site were occupied contemporaneously. Moreover, the radiocarbon dates and the dense cultural deposits establish a relatively long span of occupation at Trants, at least 800–900 years in duration and possibly longer. It is still unclear if the site represents a continuous Saladoid occupation or various episodes of occupation, but if it was not continuously occupied, one would expect at least partial obliteration of the ring midden from one occupation to another, unless the later occupants took great care to align their settlements with those that came before. Even with continuous occupation, it might be expected that the ring pattern would have been effaced by reconfiguration of the settlement over time, with house replacement, for example, disturbing the circular settlement and open plaza plan.

The long time span of occupation and the strong likelihood that the Amerindian occupants modified the site topography (Petersen and Watters, 1991; Petersen et al., 1995) make the clarity of the preserved ring configuration at Trants all the more remarkable, regardless of whether there was one or more occupations there during the Saladoid period. The Amerindian occupants must have had a very strong cultural imperative which led them to preserve their circular settlement and plaza plan over this long period. Moreover, it seems likely that this imperative was related to maintenance of the open plaza, rather than to the precise positioning of houses and other structures around it.

RESEARCH IMPLICATIONS OF ARCHAEOLOGICAL AND ETHNOGRAPHIC ANALOGUES

Habitation sites in the South American Lowlands can be both large and representative of long-term occupation on the basis of archaeological and ethnographic examples (e.g., Myers, 1973; Smith, 1980; Posey, 1987; Roosevelt, 1991). Among the four major types of ethnographic settlements in the South American Lowlands, as recognized in a typology developed by Myers (1973:243–246), the circular village and plaza configuration with multiple house structures is particularly germane to Trants; the other three types in this typology include single-family and multiple-family single-structure settlements, and multiple-structure settlements arranged in a linear or irregular fashion. Alternatively, there are three forms of lowland settlements in another similar classification developed by Roe (1987): the "Linear Riverine" type, the "Oval Upper Tributaries" type, and the "Round Interfluvial" type, correlating with the three gross environmental categories referred to in their designations.

The archaeological implications of these ethnographic settlement plans have been hotly debated among regional researchers in the Lowlands in terms of settlement size, form, and duration, as well as resident population. Not all scholars are willing to recognize extensive, long-term occupations at some lowland sites, choosing instead to see them as aggregate deposits resulting from repeated small-scale occupations (e.g., Meggers and Evans, 1957, 1978; Evans and Meggers, 1960). In general, archaeological sites in the South American Lowlands are very poorly known in terms of their sizes and spatial configurations. Most lowland sites have been recognized as being smaller than 0.5–1.0 hectare in extent, although larger sites of up to 8.0–9.0 hectares are known (Myers, 1973:tables 2–4, 7–10; Roosevelt, 1980:tables 16–18). At least a few sites in the Central Amazon region are even larger than 10 hectares in size, and at least one is apparently as large as 80 hectares (Myers, 1973:table 7).

The ethnographic circular village and plaza configuration, or "Round Interfluvial" type, seems more characteristic of certain environments in any case. The savannah grassland environments of central and eastern Brazil are pertinent, for example, where various Gê-speaking and closely related groups, different cultures in the Upper Xingu region, and the Tupinamba along the Atlantic coast, among others, have had circular plaza-oriented settlements. Seemingly less common in densely forested areas, circular settlements with multiple separate houses are typically divided into secular domestic and public political/ceremonial zones, corresponding to outer house ring and plaza spaces, respectively; middens and house gardens lie behind the houses on the outer margin of the house ring in most cases (Myers, 1973; Maybury-Lewis, 1979; Novaes, 1983; Costa and Malhano, 1987).

This tentative environmental linkage may be biased by the incomplete nature of the ethnographic record, however, and the poorly known prehistoric cultures of the Lowlands may have used this configuration over a much broader area. Certainly, circular single-family and circular multiple-family single structures, with open plazas in some of the latter cases, are known in forested areas (Myers, 1973). Moreover, Roe (1987) has suggested that all of the various lowland settlement configurations, including the circular village and plaza plan, are linked by a common cosmological model of concentric space related to a basic sexual duality or opposition among the Amerindians.

In the West Indian archipelago, the ethnographic record is even more poorly known or nonexistent for settlement size, form, and duration across much of the region (Robinson, 1985:G1–G2; Curet, 1992; Keegan, 1992:167). Rouse (1992: 9) notes that Classic Taino houses in Hispaniola known through ethnohistory "were irregularly arranged around a central plaza" and the permanent villages "contained an average of one thousand to two thousand people and ranged in size from a single building to twenty to fifty houses, all made of wood and thatch." To the east in the Lesser Antilles, Rouse (1992:17–18) suggests that the very poorly known villages of the Eastern Taino were probably like those of the Western Taino; that is, they may have "contained only an estimated 120–225 people, divided among twelve to fifteen houses."

The West Indian archaeological record is not much better for such concerns given the general paucity of broad-scale sampling and large block excavations (but see a few recent exceptions, e.g., Mattioni, 1982; Drewitt, 1991; Rodríguez, 1991*a*; Siegel, 1991; Curet, 1992; Versteeg and Schinkel, 1992). However, where horizontal excavations have been extensive and/or sampling has been designed to address this issue, the majority of known Lesser Antillean sites are a few hundred to a few thousand square meters in size, with nearly all sites less than 10,000 m^2 or 1.0 hectare in extent (e.g., Rouse, 1976; Watters, 1980; Wilson, 1989; Haviser, 1991; Watters and Petersen, 1992).

A few notable Saladoid period sites larger than 1.0 hectare can be specified for the Lesser Antilles, such as Pearls in Grenada, Indian Creek in Antigua, and Golden Rock in St. Eustatius (Rouse, 1974; Cody, 1991; Versteeg and Schinkel, 1992). Likewise, other Saladoid sites in Puerto Rico (e.g., Siegel 1989, 1991, 1992; Rodríguez, 1991*a*) are also large, but none of these are clearly larger than Trants. In fact, Trants is larger than most post-Saladoid sites in the region, although a few sites may approach or exceed its size on the basis of available information (e.g., Wilson, 1989; Rodríguez, 1992).

Thus, several factors about the Trants site at first seem anomalous or unique in the local record, especially for the earliest settlement by ceramic-making Saladoid groups. These include multiple early dates for Trants, its large size, upwards of 5–6 hectares or more for the "core" area and upwards of 50–60 hectares for the full scatter of artifacts, its configuration as an apparently stable, circular or oval midden (and corresponding unexposed structures) around an open plaza, and the phosphate fractionation and other sediment data which suggest both intensive and long-term occupation.

At this point, it is obviously premature to put much stock in precise population estimates for Trants, but it seems quite likely that as many as 200–300 individuals may have occupied the site at any one time. Considerably more or perhaps fewer individuals may have been resident at Trants, depending on the size and number of the houses. Although quite large for typical reconstructions of Saladoid groups, an estimate of 200–300 people is reasonable on the basis of ethnographic information drawn from the South American Lowlands where circular settlements of similar size are known, as discussed above, along with rare examples of still larger circular sites (e.g., Myers, 1973; Novaes, 1983; Costa and Malhano, 1987; Posey, 1987; Frechione, 1990).

In ethnographic examples, the midden almost always lies outside of the circular village consisting of multiple houses, with the central plaza left largely empty. A ceremonial structure, often a men's house, may occupy the very center of the plaza (e.g., J. Crocker, 1985; Costa and Malhano, 1987; Roe, 1987; W. Crocker, 1990; Heckenberger and Petersen, 1995). A more complicated picture may pertain to West Indian archaeological sites and other, noncircular settlement forms were likely used too. Nonetheless, circular settlement configurations are locally known or posited for Saladoid period sites in Antigua, St. Eustatius, and Puerto Rico (e.g., Rouse, 1974; Siegel, 1989, 1991; Rodríguez, 1991*a,* 1992; Versteeg and Schinkel, 1992).

The stable configuration and character of the Trants deposits, including both anthrosols and middens, and the phosphate fractionation data suggest that the site was occupied more or less continuously, as do the chronological data including radiocarbon dates and diagnostic artifacts. Quite obviously, if one assumes such an occupation at the Trants site, no analogues can be posited for the local ethnographic record, but comparably long or longer occupations are known at other archaeological sites in the insular Caribbean (e.g., Rouse, 1976; Siegel, 1991; Rodríguez, 1992). Additional excavation, artifact analyses, sediment analyses, and radiocarbon dating will be necessary to verify the inferences about Trants offered here.

SUMMARY AND CONCLUSIONS

Several conclusions are based on the available data from the Trants site and attendant interpretations. The first is that recent research at Trants, along with a few other Saladoid period sites in the region, requires reconsideration of the timing and scale of Saladoid settlement of the West Indies. Saladoid groups seem to have come to the Caribbean islands considerably earlier than previously suspected; that is, by ca. 500 B.C. or so, on the basis of evidence from Martinique, Montserrat, and St. Martin.

Secondly, Saladoid groups established variably-sized settlements, with some such as Trants being quite large early on and presumably occupied by correspondingly large groups of perhaps as many as 200–300 people or more. It is possible that different sizes among the Saladoid sites reflect early establishment of settlement hierarchies in the region, but this matter awaits detailed consideration elsewhere. In any case, not only did the Saladoid settlers occasionally establish large sites, but some were occupied for long periods, over many centuries in various cases. Intensive occupation is documented by dense cultural deposits at different sites, along with newly obtained results of sediment analyses as reported here for Trants. The Trants data suggest a stable settlement configuration, even if the site was not continuously occupied. The remarkable clarity of the ring midden and interior plaza even after 800–900 years or more of Saladoid occupation at Trants suggests that a very strong cultural imperative was operative; the central plaza endured more or less intact in spite of undoubted house reconstruction and other potentially disruptive activities at Trants.

Thirdly, recently obtained settlement data from sites such as Trants, Golden Rock, and Maisabel, among others, tentatively establish that Saladoid groups brought more than their Lowland South American material culture and aspects of their subsistence practices with them to the West Indies. They also apparently brought traditional settlement patterns and a corresponding cosmology (Heckenberger and Petersen, 1995). Saladoid settlements almost certainly reflect clear conceptions of secular and public political/ceremonial space, as previously posited for the later Saladoid period Golden Rock and Maisabel sites (Siegel, 1989, 1992; Versteeg and Schinkel, 1992; see also Roe, 1987). Trants suggests that this pattern was present among the earliest Saladoid settlers too.

In summary, a full understanding of Saladoid period sites including site structure and related settlement data, among other topics, will only be possible through broad-based research. Refinement of past notions of social structure and complexity in West Indian prehistory should be possible very soon. Evidence of repeated and continuous widespread social interaction, as expressed in common diagnostic artifacts over time, is obvious for the Saladoid period, with linkages from Puerto Rico southward through the Lesser Antilles to mainland South America.

Likewise, the available evidence suggests very extensive trade over much the span of the West Indian archipelago and a portion of the South American Lowlands during the Saladoid period (e.g., Boomert, 1987; Cody, 1991; Rodríguez, 1991*b*; Watters and Scaglion, 1994). This evidence supports the inference that Saladoid social complexity, along with its antiquity, may have been underestimated in the past. In fact, much of the social complexity that was to become characteristic of ethnohistoric cultures in the West Indies may well have been brought there by the first Saladoid settlers.

ACKNOWLEDGMENTS

The author extends thanks first and foremost to David Watters who provided an introduction to West Indian prehistory as free of bias as humanly possible. David's approach can be simply stated: "Here's all of the literature you want; we don't know enough to say much about many issues; draw your own conclusions!" I will be always thankful for this wise and appropriate introduction to a very complicated and still understudied field of inquiry. David also introduced me to the Trants site and that's another reason to give him thanks.

The UMF Archaeology Research Center and the Carnegie Museum of Natural History jointly funded recent (pre-1995) field work at the Trants site, visits before and after that time, as well as analyses of previous and recent site collections. At UMF, Belinda Cox prepared the drafted graphics, Bill Crandall and Shirley Thompson helped with manuscript preparation, and Laurie Kidd helped with sediment sample preparation. Fred Dearnley of the UMF Media Center kindly printed the photographs from the author's negatives and he also printed copies of the drafted graphics. The 1990 field work was conducted by Robert Bartone, Ellen Cowie, John Crock, Elizabeth Subin, David and Cathy Watters, and the author. Bob Bartone made a particularly significant contribution in serving as the project coordinator for UMF.

All the sediment samples were analyzed at the University of Wisconsin–Milwaukee (UW–M) Soils and Physical Geography Laboratory by Bob Brinkman and his staff. As with all their work, the services of the UW–M lab are greatly appreciated and any success gained from this aspect of the overall research is largely due to their expertise. Irving Rouse and two anonymous reviewers, Mary Ann Schmidt, and David Watters all provided useful help and advice during the preparation of this article. An earlier version of this paper was presented in the symposium, "Early Saladoid Period Settlement of the Lesser Antilles: Implications from the Trants Site, Montserrat," at the 58th annual meeting of the Society for American Archaeology held in St. Louis in 1993.

In Montserrat, the kind assistance and sponsorship of the Montserrat National Trust were critical to the conduct of the 1990 (and 1995) field work and facilitation of related analyses. Their responsible

stewardship of historic and prehistoric resources in Montserrat sets a high standard to which other West Indian islands and governments should aspire.

LITERATURE CITED

BARTONE, R. N., AND J. G. CROCK. 1991. Flaked stone industries at the early Saladoid Trants site, Montserrat, West Indies. Pp. 124–146, *in* Proceedings of the Fourteenth International Congress for Caribbean Archaeology (A. Cummins and P. King, eds.). Barbados Museum and Historical Society, Barbados.

BOOMERT, A. 1987. Gifts of the Amazons: "Green stone" pendants and beads as items of ceremonial exchange in Amazonia and the Caribbean. Anthropológica, 67:33–54.

CHANLATTE BAIK, L. 1991. El inciso entrecruzado y las primeras migraciones agroalfareras antillanas. Pp. 187–203, *in* Proceedings of the Fourteenth International Congress for Caribbean Archaeology (A. Cummins and P. King, eds.). Barbados Museum and Historical Society, Barbados.

CHANLATTE BAIK, L. A., AND Y. M. NARGANES STORDE. 1990. La Nueva Arqueologia de Puerto Rico (su Proyección en Las Antillas). Taller, Santo Domingo, Dominican Republic.

CODY, A. 1991. From the site of Pearls, Grenada: Exotic lithics and radiocarbon dates. Pp. 589–604, *in* Proceedings of the Thirteenth International Congress for Caribbean Archaeology (E. N. Ayubi and J. B. Haviser, eds.). Reports of the Archaeological–Anthropological Institute of the Netherlands Antilles (Curaçao), 9.

COSTA, M. H. F., AND H. B. MALHANO. 1987. Habitação indígena Brasileira. Pp. 27–94, *in* Tecnologica Indígena (B. G. Ribeiro, coord.), SUMA Etnológica Brasileira, Volume 2 (D. Ribeiro, ed.). Financiadora de Estudos e Projetos, Petrópolis, Brazil.

CROCK, J. G. 1993. Saladoid period lithic technology as seen from the Trants site, Montserrat, West Indies. Paper presented at the 58th annual meeting of the Society for American Archaeology, St. Louis, Missouri.

CROCKER, J. C. 1985. Vital Souls: Bororo Cosmology, Natural Symbolism, and Shamanism. University of Arizona Press, Tucson, Arizona.

CROCKER, W. H. 1990. The Canela (Eastern Timbira), I: An Ethnographic Introduction. Smithsonian Contributions to Anthropology, 33.

CURET, A. L. 1992. House structure and cultural change in the Caribbean: Three case studies from Puerto Rico. Latin American Antiquity, 3:160–174.

DREWETT, P. L. 1991. Prehistoric Barbados. Institute of Archaeology, London, United Kingdom.

EDEN, M. J., W. BRAY, L. HERRERA, AND C. MCEWAN. 1984. *Terra preta* soils and their archaeological context in the Caquetá basin of southeast Colombia. American Antiquity, 49:125–140.

EIDT, R. C. 1984. Advances in Abandoned Settlement Analysis: Application to Prehistoric Anthrosols in Colombia, South America. Center for Latin America, University of Wisconsin–Milwaukee, Milwaukee, Wisconsin.

———. 1985. Theoretical and practical considerations in the analysis of anthrosols. Pp. 155–190, *in* Archaeological Geology (G. Rapp and J. A. Gifford, eds.). Yale University Press, New Haven, Connecticut.

EVANS, C., AND B. J. MEGGERS. 1960. Archeological Investigations in British Guiana. Smithsonian Institution BAE Bulletin, 177.

FRECHIONE, J. 1990. Supervillage formation in the Amazonian terra firme: The case of Asenöña. Ethnology, 24:117–133.

GOODWIN, R. C. 1979. The Prehistoric Cultural Ecology of St. Kitts West Indies: A Case Study in Island Archaeology. Unpublished Ph.D. Dissert., Arizona State University, Tempe, Arizona.

HARDY, F. G., G. RODRIGUES, AND W. R. E. NANTON. 1949. The agricultural soils of Montserrat. Studies in West Indian Soils 2. Imperial College of Tropical Agriculture, Trinidad.

HARRINGTON, M. R. 1924. A West Indian gem center. Indian Notes (Museum of the American Indian, Heye Foundation, New York, New York), 1:184–189.

HASSAN, F. A. 1978. Sediments in archaeology: Methods and implications for paleoenvironmental and cultural analysis. Journal of Field Archaeology, 5:197–213.

HAVISER, J. B. 1991. Preliminary results from test excavations at the Hope Estate site (SM-026), St. Martin. Pp. 647–666, *in* Proceedings of the Thirteenth International Congress for Caribbean Archaeology (E. N. Ayubi and J. B. Haviser, eds.). Reports of the Archaeological–Anthropological Institute of the Netherlands Antilles (Curaçao), 9.

HECKENBERGER, M. J., AND J. B. PETERSEN. 1995. Concentric circular village patterns in the Caribbean: Comparisons from Amazonia. Paper presented at the Sixteenth International Congress for Caribbean Archaeology, Basse Terre, Guadeloupe.

KEEGAN, W. F. 1992. The People Who Discovered Columbus: The Prehistory of the Bahamas. University Press of Florida, Gainesville, Florida.

LANG, D. M. 1967. Montserrat. Soil and Land-use Surveys 22. Regional Research Centre, University of the West Indies, Trinidad.

LILLIOS, K. T. 1992. Phosphate fractionation of soils at Agroal, Portugal. American Antiquity, 57: 495–506.

MACGREGOR, A. G. 1939. The Royal Society expedition to Montserrat, B.W.I.: The volcanic history and petrology of Montserrat, with observations on Mt. Pelé, in Martinique. Philosophical Transactions of the Royal Society of London, 229(B557):1–90.

MARTIN-KAYE, P. H. A. 1969. A summary of the geology of the Lesser Antilles. Overseas Geology and Mineral Resources, 10:172–206.

MATTIONI, M. 1982. Salvage Excavations at the Fond-Brûlé Site, Martinique, Final Report. University of Manitoba Anthropology Papers (Winnipeg, Manitoba), 27.

MAURY, R. C., G. K. WESTBROOK, P. E. BAKER, P. BOUYSSE, AND D. WESTERCAMP. 1990. Geology of the Lesser Antilles. Pp. 141–166, *in* The Caribbean Region (G. Dengo and J. E. Case, eds.). The Geology of North America, Volume H. Geological Society of America, Boulder, Colorado.

MAYBURY-LEWIS, D., ED. 1979. Dialectical Societies: The Gê and Bororo of Central Brazil. Harvard University Press, Cambridge, Massachusetts.

MEGGERS, B. J. 1987. Oscilacion climatica y cronologia cultural en el Caribe. Pp. 23–54, *in* Actas del Tercer Simposio de la Fundacion de Arqueologia del Caribe (M. Sanoja, ed.). Washington, D.C.

MEGGERS, B. J., AND C. EVANS. 1957. Archeological Investigations at the Mouth of the Amazon. Smithsonian Institution BAE Bulletin, 167.

———. 1978. Lowland South America and the Antilles. Pp. 543–591, *in* Ancient Native Americans, (J. D. Jennings, ed.). W. H. Freeman and Company, San Francisco, California.

MYERS, T. P. 1973. Toward the reconstruction of prehistoric community patterns in the Amazon Basin. Pp. 233–252, *in* Variation in Anthropology: Essays in Honor of John C. McGregor (D. W. Lathrap and J. Douglas, eds.). Illinois Archaeological Survey, Urbana, Illinois.

NEWSOM, L. 1993. Paleoethnobotanical investigation of the Saladoid Trants site, Montserrat: Preliminary results. Paper presented at the 58th annual meeting of the Society for American Archaeology, St. Louis, Missouri.

NOVAES, S. C. (ED.). 1983. Habitações Indígenas. Livraria Nobel, Editora da Universidade de Sao Paulo, Saõ Paulo, Brazil.

PETERSEN, J. B., AND D. R. WATTERS. 1991. Archaeological testing at the early Saladoid Trants site, Montserrat, West Indies. Pp. 286–305, *in* Proceedings of the Fourteenth International Congress for Caribbean Archaeology (A. Cummins and P. King, eds.). Barbados Museum and Historical Society, Barbados.

———. 1995. A preliminary analysis of Amerindian ceramics from the Trants site, Montserrat. Pp. 131–140, *in* Proceedings of the Fifteenth International Congress for Caribbean Archaeology (R. E. Alegria and M. Rodríguez, eds.). Centro de Estudios Avanzados de Puerto Rico y el Caribe.

PETERSEN, J. B., R. N. BARTONE, AND D. R. WATTERS. 1995. Pyroclastic, storm-surge and Saladoid villager deposits: The archaeological and geological stratigraphy of the Trants site, Montserrat. Paper presented at the Sixteenth International Congress for Caribbean Archaeology, Basse Terre, Guadeloupe.

PETITJEAN ROGET, H. 1978. L'art des Arawak et des Caraibes des Petites Antilles: Analyse de la decoration des ceramiques. Centre d'études Régionales Antilles–Guyane.

POSEY, D. A. 1987. Contact before contact: Typology of post-Columbian interaction with northern Kayapó of the Amazon Basin. Boletin Museu Paraense Emílio Goeldi, 3:135–154.

REA, W. J. 1974. The volcanic geology and petrology of Montserrat, West Indies. Journal of the Geological Society of London, 130:341–366.

REITZ, E. J. 1994. Archaeology of Trants, Montserrat. Part 2. Vertebrate fauna. Annals of Carnegie Museum, 63:297–317.

REITZ, E. J., AND J. A. DUKES. 1995. Use of vertebrate resources at Trants, a Saladoid site on Montserrat. Pp. 201–208, *in* Proceedings of the Fifteenth International Congress for Caribbean Archaeology (R. E. Alegria and M. Rodríguez, eds.). Centro de Estudios Avanzados de Puerto Rico y el Caribe.

ROBINSON, L. S. 1985. Structural remains at El Bronce archaeological site: Decoding the soil record. Pp. G1–G39, *in* Archaeological Data Recovery at El Bronce, Puerto Rico: Final Report, Phase 2 (L. S. Robinson, E. R. Lundberg, and J. B. Walker) Archaeological Services, Inc., Ft. Myers, Florida.

RODRÍGUEZ, M. 1991*a*. Arquelogia de Punta Candelero, Puerto Rico. Pp. 609–627, *in* Proceedings of the Thirteenth International Congress for Caribbean Archaeology (E. N. Ayubi and J. B. Haviser, eds.). Reports of the Archaeological–Anthropological Institute of the Netherlands Antilles (Curaçao), 9.

———. 1991*b*. Early trade networks in the Caribbean. Pp. 306–314, *in* Proceedings of the Fourteenth International Congress for Caribbean Archaeology (A. Cummins and P. King, eds.). Barbados Museum and Historical Society, Barbados.

———. 1992. Late Ceramic age diversity in eastern Puerto Rico. Paper presented at the 57th annual meeting of the Society for American Archaeology, Pittsburgh, Pennsylvania.

ROE, P. G. 1987. Village spatial organization in the South American Lowlands: Evidence from ethnoarchaeology. Paper presented at the 52nd annual meeting of the Society for American Archaeology, Toronto, Ontario.

ROOSEVELT, A. C. 1980. Parmana: Prehistoric Maize and Manioc Subsistence along the Amazon and Orinoco. Academic Press, New York, New York.

———. 1991. Mound Builders of the Amazon: Geophysical Archaeology on Marajo Island, Brazil. Academic Press, San Diego, California.

ROUSE, I. 1974. The Indian Creek excavations. Pp. 166–176, *in* Proceedings of the Fifth International Congress for the Study of Pre-Columbian Cultures of the Lesser Antilles (R. P. Bullen, ed.). Florida State Museum, Gainesville, Florida.

———. 1976. The Saladoid sequence on Antigua and its aftermath. Pp. 35–41, *in* Proceedings of the Sixth International Congress for the Study of Pre-Columbian Cultures of the Lesser Antilles (R. P. Bullen, ed.). Florida State Museum, Gainesville, Florida.

———. 1989. Peoples and cultures of the Saladoid frontier in the Greater Antilles. Pp. 383–403, *in* Early Ceramic Population Lifeways and Adaptive Strategies in the Caribbean (P. Siegel, ed.). BAR International Series 506, Oxford, United Kingdom.

———. 1992. The Tainos: Rise and Decline of the People Who Greeted Columbus. Yale University Press, New Haven, Connecticut.

ROUSE, I., AND L. ALLAIRE. 1978. Caribbean. Pp. 431–481, *in* Chronologies in New World Archaeology (R. E. Taylor and C. Meighan, eds.). Academic Press, New York, New York.

SANOJA, M., AND I. VARGAS. 1983. New light on the prehistory of eastern Venezuela. Pp. 205–244, *in* Advances in World Archaeology (F. Wendorf and A. Close, eds.). Academic Press, New York, New York.

SIEGEL, P. E. 1989. Site structure, demography, and social complexity in the early Ceramic age of the Caribbean. Pp. 193–245, *in* Early Ceramic Population Lifeways and Adaptive Strategies in the Caribbean (P. E. Siegel, ed.). BAR International Series 506, Oxford, United Kingdom.

———. 1991. Occupational history of the Maisabel site: A progress report. Florida Journal of Anthropology, 16:65–79.

———. 1992. Ideology, power, and social complexity in prehistoric Puerto Rico. Unpublished Ph.D. Dissert., Department of Anthropology, State University of New York, Binghamton, New York.

SJÖBERG, A. 1976. Phosphate analysis of anthropic soils. Journal of Field Archaeology, 3:447–454.

SMITH, N. J. H. 1980. Anthrosols and human carrying capacity in Amazonia. Annals of the Association of American Geographers, 70:553–566.

STEADMAN, D. W., D. R. WATTERS, E. J. REITZ, AND G. K. PREGILL. 1984. Vertebrates from archaeological sites on Montserrat, West Indies. Annals of Carnegie Museum, 53:1–29.

VERSTEEG, A. H., AND K. SCHINKEL (EDS.). 1992. The Archaeology of St. Eustatius: The Golden Rock Site. Saint Eustatius Historical Foundation Publication (Saint Eustatius), 2.

WADGE, G., AND M. C. ISSACS. 1988. Mapping the volcanic hazards from Soufriere Hills Volcano, Montserrat, West Indies using an image processor. Journal of the Geological Society, 145:541–551.

WATTERS, D. R. 1980. Transect Surveying and Prehistoric Site Locations on Barbuda and Montserrat, Leeward Islands, West Indies. Unpublished Ph.D. Dissert., Department of Anthropology, University of Pittsburgh, Pittsburgh, Pennsylvania.

———. 1994. Archaeology of Trants, Montserrat. Part 1. Field methods and artifact density distributions. Annals of Carnegie Museum, 63:265–295.

———. 1995. Trants, Montserrat: The 1995 field season. Paper presented at the Sixteenth International Congress for Caribbean Archaeology, Basse Terre, Guadeloupe.

WATTERS, D. R., AND J. B. PETERSEN. 1992. Inter-island settlement pattern variability in post-Saladoid Barbuda and Montserrat, northern Lesser Antilles. Paper presented at the 57th annual meeting of the Society for American Archaeology, Pittsburgh, Pennsylvania.

———. 1995. Spatial analysis at Trants, Montserrat. Pp. 15–25, *in* Proceedings of the Fifteenth International Congress for Caribbean Archaeology (R. E. Alegria and M. Rodríguez, eds.). Centro de Estudios Avanzados de Puerto Rico y el Caribe.

WATTERS, D. R., AND R. SCAGLION. 1994. Beads and pendants from Trants, Montserrat: Implications for the prehistoric lapidary industry of the Caribbean. Annals of Carnegie Museum, 63:215–237.

WILLEY, G. R. 1971. South America, an Introduction to American Archaeology, Volume 2. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

WILSON, S. M. 1989. The prehistoric settlement pattern of Nevis, West Indies. Journal of Field Archaeology, 16:427–450.

ANNALS OF CARNEGIE MUSEUM

VOL. 65, NUMBER 4, PP. 363–381 27 NOVEMBER 1996

PIPUNCULIDAE (INSECTA: DIPTERA) OF THE DOMINICAN REPUBLIC: NEW RECORDS AND DESCRIPTION OF NEW SPECIES

J. A. RAFAEL[1,2]

ABSTRACT

The Pipunculidae of the Dominican Republic are reviewed. Keys to genera, subgenera, and species of West Indies Pipunculidae are presented with notes on geographical distribution. Seventeen species in seven genera of Pipunculidae are reported from the Dominican Republic. Eight new species are described and illustrated: *Cephalosphaera insularis, Cephalops pedernalensis, Eudorylas curvicaudatus, E. dominicanensis, Metadorylas antillensis, M. cornutus, M. pilosus,* and *M. youngi.* All Neotropical species of the *Cephalops latifrons* (Hardy) group are transferred to the genus *Microcephalops* De Meyer as new combinations: *M. inermus* (Hardy), *M. latifrons* (Hardy), *M. ravilateralis* (Hardy), *M. transversalis* (Rafael), and *M. williamsi* (Hardy). Eight species are recorded from the Dominican Republic for the first time: *Basileunculus aliceae* Rafael, *Cephalops varius stygius* (Hardy), *Metadorylas cressoni* Johnson, *M. dominicensis* Scarbrough and Knutson, *Microcephalops latifrons* (Hardy), *M. williamsi* (Hardy), *Tomosvaryella mexicanensis* Ale-Rocha and Rafael, and *T. tuberculata* Hardy. The previously unknown male of *Cephalosphaera mocaensis* Hardy and *Microcephalops latifrons* (Hardy) are described for the first time.

INTRODUCTION

Pipunculidae is a poorly represented family in the Dominican Republic fauna. The only previously recorded species is *Cephalosphaera mocaensis* Hardy, based on a single female specimen (Rafael, 1992). The opportunity to study recently collected material in the collections of the Carnegie Museum of Natural History (CMNH) revealed eight undescribed species, and new distribution records for eight species for that country. It is hoped that this contribution will stimulate interest in collecting and studying this fascinating, though poorly collected, family from the Dominican Republic and elsewhere.

Most of the available studied specimens were collected in July, with a few from October and December. Those collected late in the season represented taxa different from those collected in July. It is inevitable that additional species and records will be found when more collections are made in other seasons.

The material studied was taken from intercept traps, light traps, and sweep samples. Genitalia were studied by removing the abdomen, after which it was placed in a microvial with glycerin and pinned along with the specimen. Taxonomic keys including geographical distribution records for the New World were compiled for all the species studied from the West Indies. Primary types are deposited in the collections of CMNH, and representative paratypes and other specimens have been deposited at the Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (INPA).

The generic classifications adopted here follows Rafael and De Meyer (1992). Since the pipunculid fauna of the Dominican Republic and of other islands in the West Indies is still largely unknown, it is premature to conduct a zoogeographic

---

[1] Instituto Nacional de Pesquisas da Amazônia (INPA), Caixa Postal 478, 69011-970, Manaus, Amazonas, Brazil.

[2] Fellow of the Conselho Nacional de Desenvolvimento Científico e Tecnológico.

Submitted 24 March 1995.

and phylogenetic study at the present time. The following is primarily a taxonomic study and should provide a foundation for future systematic research.

KEY TO GENERA AND SUBGENERA OF PIPUNCULIDAE FROM THE WEST INDIES

(Genera not recorded, but of probable occurrence in the West Indies, are also included)

1	Ocellar bristles present; head hemispherical; postcranium narrow; veins M and dm–cu absent	*Chalarus* Walker
1′	Ocellar bristles absent; head nearly spherical; postcranium swollen; wing venation complete	2
2(1′)	Proepisternum with fan-like tuft of hairs	3
2′	Proepisternum without fan-like tuft of hairs	9
3(2)	Scutum with conspicuous pilosity anteriorly, dorsocentral hairs not differentiated	4
3′	Scutum without pilosity between rows of dorsocentral hairs	5
4(3)	Vein M_2 absent	*Pipunculus* Latreille
4′	Vein M_2 present	*Parapipunculus* Rafael
5(3′)	Vein M_2 present	*Cephalosphaera* Enderlein 6
5′	Vein M_2 absent	7
6(5)	Male abdominal syntergosternite VIII with membranous area reaching epandrium	*C.* (*Neocephalosphaera*) Enderlein
6′	Male abdominal syntergosternite VIII with membranous area not reaching epandrium	*C.* (*Cephalosphera*) De Meyer
7(5′)	Face equal or subequal in width to lower portion of frons; frons not inflated; flagellum distinctly larger than pedicel	*Cephalops* Fallén 8
7′	Face narrower than lower portion of frons; frons inflated; flagellum small, slightly larger than pedicel	*Microcephalops* De Meyer
8(7)	Male abdominal syntergosternite VIII with membranous area reaching epandrium; abdomen broad and shortened	*C.* (*Semicephalops*) De Meyer
8′	Male abdominal syntergosternite VIII with membranous area apical; abdomen elongate	*C.* (*Cephalops*) Fallén
9(2′)	Pterostigma absent; third section of costa shorter or equal in length to fourth section of costa	10
9′	Pterostigma present; third section of costa longer than fourth section of costa	11
10(9)	Crossvein r–m located near base of cell dm; abdomen clavate	*Dorylomorpha* Aczél
10′	Crossvein r–m located near middle of cell dm; abdomen cylindrical	*Tomosvaryella* Aczél
11(9′)	Tergite VI visible dorsally in males	12
11′	Tergite VI not visible dorsally in males	13
12(11)	Apex of flagellum obtuse below; ventral ctenidia present on mesofemur only; tergites with oblique gray pruinose spot posterolaterally	*Elmohardyia* Rafael
12′	Apex of flagellum acuminate to subfiliform; ventral ctenidia present on profemur and mesofemur; tergites without gray pruinose spots	*Metadorylas* Rafael
13(11′)	Pedicel with many long hairs; abdomen with conspicuous hairs laterally	14
13′	Pedicel with a few short hairs; abdomen with small inconspicuous hairs	*Eudorylas* Aczél
14(13)	Distal section of vein M_1 straight; aedeagus trifid	*Allomethus* Hardy
14′	Distal section of vein M_1 curved; aedeagus simple and heavily sclerotized	*Basileunculus* Rafael

SYSTEMACTIC ACCOUNTS

Genus *Chalarus* Walker

This genus is cosmopolitan in distribution but has not been recorded from the Dominican Republic. Two species of *Chalarus* have previously been recorded from Trinidad (Rafael, 1990*a*). A third species, *C. spurius* (Fallén) was recorded from Dominica by Scarbrough and Knutson (1989) based on a female specimen. Further studies (Rafael, 1988*a*, 1990*a*; Jervis, 1992) indicated that *C. spurius* represents a species complex of six species, and is restricted to Europe in distribution. Records from the New World and other regions (Afrotropical, Palaearctic, Oriental, and Australian) are questionable and therefore this species was not included in the following key.

Key to Species of *Chalarus* from the West Indies

1. Cell r_1 closed (Trinidad, Brazil) . . . . *C. connexus* Rafael
1′ Cell r_1 open (Trinidad, Brazil) . . . . *C. amazonensis* Rafael

Genus *Cephalosphaera* Enderlein

Cephalosphaera is cosmopolitan in distribution. Recently it was divided by De Meyer (1994) into two subgenera: *Cephalosphaera* sensu stricto Enderlein and *Neocephalosphaera* De Meyer. Both are widespread from Canada to Chile in the New World.

Key to Species of *Cephalosphaera* from the West Indies

1 Femora yellow to chestnut, sometimes with brown discoloration (Jamaica, Dominican Republic) . . . . *C. insularis*, new species
1′ Femora dark brown to black, with bases and apices yellow 2
2(1′) Flagellum yellow, pedicel brown; syntergosternite VIII not divided by membranous area; aedeagus short (Dominican Republic) . . . . *C. mocaensis* (Hardy)
2′ Flagellum and pedicel brown to black; syntergosternite VIII divided by membranous area on the dorsum and the venter; aedeagus long, spiraled (Jamaica) . . . *C. jamaicensis* (Johnson)

Cephalosphaera (*Cephalosphaera*) *mocaensis* (Hardy)
(Fig. 1–6)

Dorilas (*Cephalosphaera*) *mocaensis* Hardy, 1948*b*:127, fig. 4a, b.

Description.—Male: frons and face silvery gray pruinose. Antennae with scape and pedicel dark brown to black; flagellum yellow, long and acute (Fig. 1). Thorax dark brown to black, gray-brown pruinose on the dorsum and gray pruinose on sides. Postpronotal lobe brownish yellow on margins. Propleural fan well developed. Legs with coxae black, trochanters yellow, femora black with base and apex yellow, tibiae and tarsi yellow, except metatarsomeres brown. Wings with third costal section twice as long as fourth and equal in length to fifth. Crossvein r–m located between basal third and basal two-fifths of cell dm. Halteres yellow. Abdomen dark brown to black, brown pruinose, velvety black on bases of tergites III–V and gray pruinose in dorsal view on tergite I and posterolaterally on tergites II–V; gray pruinosity larger on tergite V. Terminalia with apical membranous area on syntergosternite VIII. Surstyli symmetrical (Fig. 2). Parameres and aedeagus as in Fig. 3, 4.

Specimens Examined.—DOMINICAN REPUBLIC: Pedernales, 26 km N Cabo Rojo, 18–06N 71–38W, 730 m, 13–25 July 1990, L. Masner, J. Rawlins, C. Young, deciduous forest, intercept trap (two males, two females, one female without vein M_2); 13–20 July 1990 (one male, one female, INPA); Pedernales, 7 km NE Los Arroyos, 1870 m, 18–16N 71–44W, 15 July 1990, L. Masner, J. Rawlins, C. Young, intercept trap (four females, two females without vein M_2); Pedernales, 23.5 km N Cabo Rojo, 18–06N 71–38W, 540 m, 19–25 July 1990, L. Masner, J. Rawlins, C. Young, deciduous forest, intercept trap (one male); 19–21 July 1990 (two males, two females); Pedernales, 26 km N Cabo Rojo, 18–06N 71–38W, 730 m, 26–27 September 1991, R. Davidson, C. Young, S. Thompson, J. Rawlins, wet deciduous forest (one female, INPA, without vein M_2); Pedernales, 5 km NE Los Arroyos, 18–15N 71–45W, 1680 m, 17–18 July 1990, C. Young, J. Rawlins, S. Thompson (one male, INPA); Pedernales, La Abeja, 38 km NNW Cabo Rojo, 18–09N 71–38W, 1250 m, 15 July 1987, J. Rawlins, R. Davidson (one male, INPA); Independencia, 32 km NW La Descubierta, Sierra de Neiba, 1850 m, 1–5 Dec. 1991, L. Masner, S. Peck, mountain forest, Malaise trap (one male, INPA); Bara-

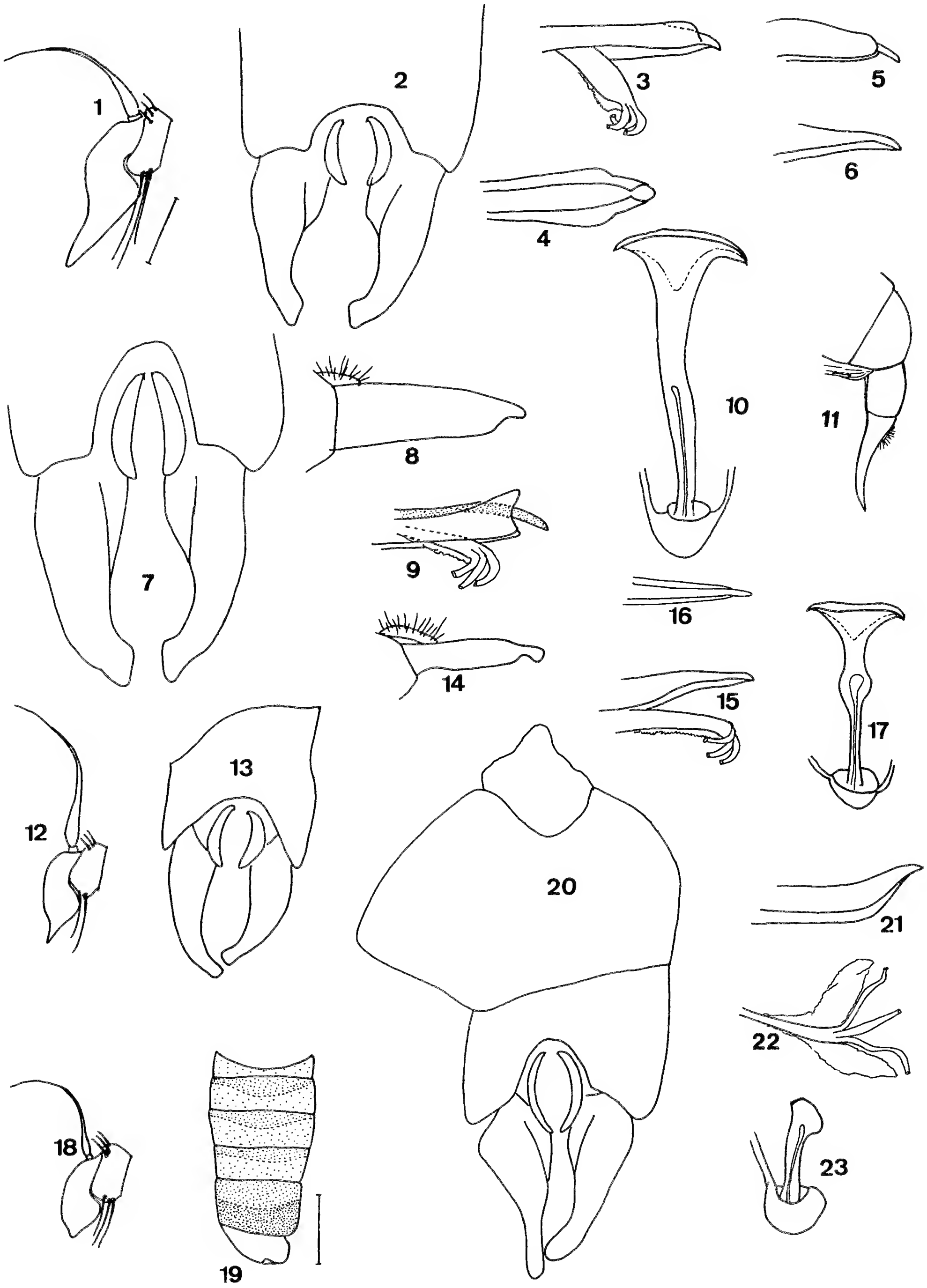


Fig. 1–23.—Pipunculidae from the Dominican Republic. 1–6. *Cephalosphaera mocaensis,* male: 1, antenna; 2, surstyli; 3, parameres and aedeagus; 4, parameres, ventral view; 5–6, parameres (variation). 7–11. *Cephalosphaera insularis,* 7, surstyli; 8, inner surstylus, lateral view; 9, parameres and aedeagus; 10, ejaculatory apodeme; 11, ovipositor. 12–17. *Cephalops pedernalensis,* male: 12, antenna; 13,

hona, 5 km SE Polo, slopes of Loma La Torre, 18–03N 71–16W, 16 July 1992, disturbed forest with coffee, C. Young, R. Davidson, S. Thompson, J. Rawlins (one male).

Remarks.—Cephalosphaera mocaensis is the only pipunculid species previously recorded from the Dominican Republic (Hardy, 1966), and the present study shows that it is a frequently collected species. The original description was based on one female specimen, and the following is the first description of the male. This species was previously classified in the subgenus *Neocephalosphaera* by De Meyer (1994). However, based on the male characters pointed out by De Meyer (1994), this species belongs to the subgenus *Cephalosphaera. Cephalosphaera mocaensis* is most closely related to *C. incomitata* (Hardy) from Argentina on the basis of characteristics of the male terminalia. It differs from the latter species by the yellow flagellum and by the postpronotal lobe (humeri) being concolorous with scutum. Further study with more specimens from the northern part of South America will likely reveal that *C. incomitata* is a junior synonym of *C. mocaensis.* The male specimens collected from the Dominican Republic show variations in the parameres (Fig. 5, 6). Variation also occurs in wing venation. Vein M_2 is absent from the left wing of one male and from both wings of three females. These three female specimens key to the genus *Cephalops,* but they match the description of *Cephalosphaera mocaensis* in all respects, except the absence of vein M_2.

Cephalosphaera (*Cephalosphaera*) *insularis* Rafael, **new species**
(Fig. 7–11)

Diagnosis.—This species differs from all other *Cephalosphaera* species by the following combination of characters: antennae yellow, scutellum with yellow margin, tergites III–V with narrow velvety black bands across the bases, surstyli symmetrical, forcipate, and parameres with a distinct projection at apex.

Description.—Male: body length 4.0 mm; wings 4.7 mm. Antennae yellow; flagellum acutum. Eyes joined on the frons for a distance slightly greater than the length of frontal triangle. Front and face silvery gray pruinose. Thorax dark brown to black, brown pruinose dorsally, gray pruinose laterally. Postpronotal lobes yellow. Scutellum yellow at margin, with long bristles. Propleural fan with long, pale bristles. Legs yellow, except coxae brown, metafemor brown on distal half, and all fifth tarsomeres light brown. All femora with ventral ctenidia. Wings slightly infuscated; pterostigma brown. Third costal section about as long as fourth. Crossvein r–m located near basal one-third of cell dm. Section between cell dm and vein M_2 longer than vein dm–cu. Halteres light yellow. Abdomen dark brown to black, brown pruinose, with gray pruinosity on tergite I and laterally on tergites II–V. When illuminated at a certain angle tergites III–V with narrow interrupted velvety black bands across the bases. Tergite I with 6–8 bristles laterally. Terminalia with syntergosternite VIII about equal length as tergite V and with distal membranous area. Surstyli (Fig. 7, 8) symmetrical, forcipate. Parameres (Fig. 9) with a distinct projection at apex. Ejaculatory apodeme as in Fig. 10. Female: body length 3.6–4.0 mm; wings 4.2–4.5 mm. Frons and face silvery gray pruinose, except frons black near ocellar triangle. Antennae yellow, long, and acute. All coxae brownish yellow. Abdomen brown pruinose, except tergites I and II gray pruinose, the latter with narrow band brown pruinose across posterior margin; tergites III–VI with narrow velvety black band across the bases and gray pruinose on the sides. Other aspects as in male. Terminalia (Fig. 11) with syntergosternite VII + VIII concolorous with abdomen,

---

←

epandrium and surstyli; 14, inner surstylus, lateral view; 15, parameres and aedeagus; 16, parameres, ventral view; 17, ejaculatory apodeme. 18–23. *Microcephalops latifrons,* male: 18, antenna; 19, abdomen; 20, terminalia; 21, parameres; 22, aedeagus; 23 ejaculatory apodeme. All figures to same scale as Fig. 1 (= 0.1 mm), except Fig. 11 and 19 (scale = 0.5 mm).

rather cylindrical dorsally, flattened ventrally; ovipositor bright yellow, curved outward and longer than syntergosternite VII + VIII.

Type Material.—Holotype: male (CMNH). Verbatim text of three pin labels: "DOMINICAN REPUBLIC: Pedernales, 26 km N Cabo Rojo, 18–06N 71–38W, 730 m" / "13–25 July 1990, L. Masner, J. Rawlins, C. Young, wet deciduous forest, intercept trap" / "HOLOTYPE *Cephalosphaera insularis* Rafael [red paper]". Paratype: eight males seven females, topotypic, (two males, three females, INPA); JAMAICA: Portland, just east of Hardwar Gap, 22 Aug. 1980, 1100 m, A. Norrbom (one male).

Etymology.—The specific name refers to the island locality where the type series was collected (from Latin *insularis* = of an island).

Remarks.—*Cephalosphaera insularis* is closely related to *C. panamaensis* (Hardy). It differs by the smaller size, yellow antennae, and scutellum yellow at margin. In the terminalia, it differs by the shape of the parameres (which possess a distinct projection at apex in *insularis* and it is bifid in *panamaensis*) and by the aedeagus (which is short in *insularis* and elongated and with a bifid dorsal projection in *panamaensis*).

Cephalosphaera spp.

Remarks.—Four female specimens cannot be identified to species and were not associated with any males. Two females have ovipositors curved outward and longer than those of *C. panamaensis*; the other two female specimens have straight ovipositors. It is clear that more *Cephalosphaera* species remain to be described from the Dominican Republic.

Specimens Examined.—DOMINICAN REPUBLIC: Pedernales, 23.5 km N Cabo Rojo, 18–06N 71–38W, 540 m, 19–25 July 1990, L. Masner, J. Rawlins, C. Young, deciduous forest, intercept trap (three females); Pedernales, La Abeja, 38 km NNW Cabo Rojo, 18–09N 71–38W, 1250 m, 15 July 1987, J. Rawlins, R. Davidson (one female).

Genus *Cephalops* Fallén

Cephalops is a cosmopolitan genus and has a wide distribution in the New World, ranging from Canada to Chile. Recently the genus *Cephalops* was separated by De Meyer (1994) into four subgenera: *Cephalops* sensu stricto Fallén, *Semicephalops* De Meyer, *Parabeckerias* De Meyer, and *Beckerias* Aczél. The last two subgenera are not recorded in the New World.

Key to Species of *Cephalops* from the West Indies

1 Flagellum dark brown to black; crossvein r–m located at basal third of cell dm; third section of costa twice as long as fourth; surstyli equal to or longer than epandrium (Dominican Republic) . . . . *C. pedernalensis,* new species

1′ Flagellum yellow; crossvein r–m located near middle of cell dm; third section of costa subequal to fourth; surstyli shorter than epandrium (Jamaica, Dominican Republic) . . . . *C. varius stygius* (Hardy)

Cephalops (*Cephalops*) *pedernalensis* Rafael, **new species**
(Fig. 12–17)

Diagnosis.—This species differs from other described species of *Cephalops* by the predominantly brown to black antennae and legs, short acute flagellum, and crossvein r–m at basal third of cell dm. Surstyli are forcipate, subsymmetrical, both curved inward, with the outer one slightly shorter than inner one.

Description.—(Male only, female unknown.) Body length 3.1 mm; wings 3.5 mm. Frons brown pruinose. Face gray pruinose. Antennae dark brown; flagellum acute (Fig. 12), light brown at margin. Thorax dark brown to black, brown pruinose dorsally, gray pruinose laterally. Propleural fan with five white bristles. Legs predominantly black with trochanters, apex of femora, base and apex of tibiae, and basal tarsomeres yellow. All femora with ventral ctenidia. Wings slightly infuscated; pterostigma brown. Third costal section two times longer than fourth and as long as fifth section. Halteres white, slightly yellow at apex. Abdomen dark brown to black, brown pruinose, with gray pruinosity posterolaterally; when illuminated at a certain angle, tergites II–V show velvety black bands across bases. Terminalia: syntergosternite VIII with apical membranous area. Surstyli subsymmetrical, curved inward (Fig. 13, 14). Parameres and aedeagus as in Fig. 15, 16. Ejaculatory apodeme as in Fig. 17.

Type Material.—Holotype: male (CMNH). Verbatim text of three pin labels: "DOMINICAN REPUBLIC: Pedernales. 23.5 km N Cabo Rojo, 18–06N 71–38W" / "26–27 September 1991 J. Rawlins, R. Davidson, C. Young, S. Thompson, Wet deciduous forest" / "HOLOTYPE *Cephalops pedernalensis* Rafael [red paper]." Paratype: one male, Pedernales, La Abeja, 38 km NNW Cabo Rojo, 18–09N 71–38W, 1250m, 15 July 1987, J. Rawlins, R. Davidson (INPA).

Etymology.—The species name refers to the locality Pedernales where the type series was collected.

Remarks.—This species is being treated in the subgenus *C.* (*Cephalops*) Fallén by the presence of one or more erected spines on the metatibiae median anteriorly and with membranous area not reaching the epandrium. Following the key of Rafael (1991), specimens of this species will run to couplet 16 for *C. pauculus* and *C. penepauculus,* described from Brazil and Argentina respectively. The new species clearly shows characteristics of *Cephalosphaera* species in the terminalia and it could well belong to this genus instead of *Cephalops.* Both of these genera are morphologically very closely related sister groups within the same monophyletic lineage (Rafael and De Meyer, 1992), and the character vein M_2 has been considered as the only character to separate the two genera. Since this character is invalidated to date, *pedernalensis* is being treated in the genus *Cephalops.* This should be further studied to clarify the status of these two genera.

Cephalops (*Semicephalops*) *varius stygius* (Hardy)

Dorilas (*Dorilas*) *stygius* Hardy, 1948*a*:5, fig. 4a–c.

Remarks.—*Cephalops varius stygius* possesses the apomorphic characteristic, the membranous area reaching the epandrium, stated by De Meyer (1994) for the subgenus *Semicephalops* De Meyer. *Cephalops stygius* was treated as a subspecies of *varius* with the observation that it might be only a synonym of that species (Rafael, 1991). This is the first record subsequent to its original description from Jamaica.

Specimens Examined.—DOMINICAN REPUBLIC: Pedernales, 37 km N Cabo Rojo, 18–09N 71–35W, 1500 m, 11 July 1987, R. Davidson, J. Rawlins (one female); Pedernales, La Abeja, 38 km NNW Cabo Rojo, 18–09N 71–38W, 1250 m, 15 July 1987, J. Rawlins, R. Davidson (one female, INPA); Pedernales, 9.7 km NE Los Arroyos, 18–16N 71–44W, 2070 m, 15–16 July 1990, J. Rawlins, C. Young, L. Masner (one male); Pedernales, 23.5 km N Cabo Rojo, 18–06N 71–38W, 510 m, 19–25 July 1990, L. Masner, J. Rawlins, C. Young, deciduous forest, intercept trap (one female, INPA); Pedernales, 1 km S Los Arroyos, 1125 m, 18–14N 71–45W, 18 Oct. 1991, R. Davidson, C. Young, S. Thompson, J. Rawlins, second growth forest (one female).

Cephalops sp.

Remarks.—Three female specimens with antennae and legs entirely yellow and abdomen partially yellow cannot be identified to species. No male association can be established with these females.

Specimens Examined.—DOMINICAN REPUBLIC: Pedernales, 26 km N Cabo Rojo, 730 m, 18–06N 71–38W, 26–27 Sept. 1991, R. Davidson, C. Young, S. Thompson, J. Rawlins, wet deciduous forest (one female, INPA); Hato Mayor, Parque Los Haitises, 3 km W Cueva de Arena, 19–04N 69–29W, 20 m, 7–9 July 1992, R. Davidson, J. Rawlins, S. Thompson, C. Young, mesic lowland forest (two females).

Genus *Microcephalops* De Meyer

This genus was established recently by De Meyer (1989) to encompass four Nearctic and one Palaearctic species of small size, face distinctly narrower than the lower portion of the frons, and the flagellum only slightly larger than pedicel. This genus also contains the following Neotropical species treated in the *Cephalops latifrons* group by Rafael (1991).

Microcephalops inermus (Hardy), **new combination**
= *Dorilas* (*Eudorylas*) *inermus* Hardy, 1954:26
Microcephalops latifrons (Hardy), **new combination**
= *Dorilas* (*Dorilas*) *latifrons* Hardy, 1948*a*:1
Microcephalops ravilateralis (Hardy), **new combination**
= *Pipunculus* (*Pipunculus*) *ravilateralis* Hardy, 1965*a*:234
Microcephalops transversalis (Rafael), **new combination**
= *Pipunculus* (*Pipunculus*) *transversalis* Hardy, 1965*b*:22
Microcephalops williamsi (Hardy), **new combination**
= *Dorilas* (*Dorilas*) *williamsi* Hardy, 1954:54

Key to Species of *Microcephalops* from the West Indies

1 Tergites II–IV velvety dark brown to black, without bands of pruinosity; both surstyli curved inward at apex (Brazil, Colombia, Dominica, Dominican Republic) . . . . *M. williamsi* (Hardy)
1′ Tergites II–IV brown pruinose across posterior margin; outer surstylus slightly curved inward at apex (Dominican Republic, Jamaica) . . . . *M. latifrons* (Hardy)

Microcephalops latifrons (Hardy), **new combination**
(Fig. 18–23)

Dorilas (*Dorilas*) *latifrons* Hardy, 1948*a*:1, fig. 1a, b.

Remarks.—This species is known from the female and has previously been recorded only from Jamaica. It was recharacterized by Rafael (1991). One male fitting the female description apparently belongs here, and is described below.

Description.—Male: body length 3.2 mm; wings 3.7 mm. Frons black, brown pruinose, with a small shining black point medially. Face narrower than frons, slightly gray pruinose. Antennae (Fig. 18) with flagellum short, acute. Abdomen (Fig. 19) dark brown to black, velvety black pruinose across bases of tergites II–V; metallic brown pruinose on tergite I and across posterior margin of tergites II–IV; tergite V sub-shining black on posterior half. In other respects as in female description. Terminalia: syntergosternite VIII with apical membranous area. Surstyli asymmetrical (Fig. 20), outer surstyli curved inward distally. Parameres simple (Fig. 21). Aedeagus trifid (Fig. 22) with pair of membranous projections. Ejaculatory apodeme as in Fig. 23.

Specimens Examined.—DOMINICAN REPUBLIC: Pedernales, 37 km N Cabo Rojo, 4 km E La Abeja, 18–10N 71–37W, 1440 m, 13–16 July 1987, R. L. Davidson, J. E. Rawlins (one male); Pedernales, 23.5 km N Cabo Rojo, 18–06N 71–38W, 540 m, 20 July 1990, C. W. Young, J. E. Rawlins, S. Thompson (one female).

Microcephalops williamsi (Hardy), **new combination**

Dorilas (*Dorilas*) *williamsi* Hardy, 1954:54, fig. 27a–c.

Remarks.—This species is widespread across southern Brazil. It is also recorded from Colombia (Rafael, 1991) and Dominica (Scarbrough and Knutson, 1989).

Specimens Examined.—DOMINICAN REPUBLIC: Pedernales, La Abeja, 38 km NNW Cabo Rojo, 18–09N 71–38W, 1250 m, 15 July 1987, J. Rawlins, R. Davidson (one male); Barahona, 9.2 km NW Paraiso, confluence of Rio Nizao and Rio Coltico, 18–03N 71–12W, 230 m, 9–10 Aug. 1990, J. Rawlins, S. Thompson (one male, INPA).

Genus *Basileunculus* Rafael

Basileunculus is a Neotropical genus previously recorded from Brazil, El Salvador, Guyana, Panama, and now the West Indies.

Basileunculus aliceae Rafael

Basileunculus aliceae Rafael, 1987:630, fig. 11–13.

Remarks.—This species was described by Rafael (1987) from the states of Rio de Janeiro and Paraná in Brazil. The Dominican Republic specimens represent the first record of the species subsequent to its original description. This is also the only species of the genus *Basileunculus* from the material examined. The specimens present differ in the following ways from the original description: frons, face, and mesopleuron rather gray pruinose; tibiae predominantly black with only base and apex yellow.

Specimens Examined.—DOMINICAN REPUBLIC: Pedernales, 37 km N Cabo Rojo, 4 km E La Abeja, 18–10N 71–37W, 1440 m, 13–16 July 1987, R. Davidson, J. Rawlins (one male); Pedernales, 26 km N Cabo Rojo, 18–06N 71–38W, 13–25 July 1990, L. Masner, J. Rawlins, C. Young, wet deciduous forest, intercept trap (two males, two females, INPA); Pedernales, 5 km NE Los Arroyos, 18–15N 71–45W, 1680 m, 28 July 1990, C. W. Young, J. E. Rawlins, S. Thompson (one female); Elias Pina, Sierra de Neiba at crest, 5.5 km NNW Angel Feliz, 1800 m, 18–41N 71–47W, 15 Oct. 1991, R. Davidson, C. Young, S. Thompson, J. Rawlins, cloud forest (two males); Independencia, 32 km NW La Descubierta, Sierra de Neiba, 1850 m, 01–05 Dec. 1991, L. Masner, S. Peck, mountain forest, Malaise trap (one male, one female).

Genus *Metadorylas* Rafael

Metadorylas is limited to the New World. It is best known in the Neotropical region (Rafael, 1990*b*), and revisionary studies are needed for the Nearctic region.

Key to Species of *Metadorylas* from the West Indies

1 Abdomen predominantly yellow to rufous (Bahamas, Dominican Republic, Jamaica) .... *M. cressoni* (Johnson)
1′ Abdomen dark brown to black 2

2(1′) Legs predominantly yellow 3
2′ At least femora predominantly dark brown to black 6

3(2) Antennae predominantly yellow to chestnut-brown 4
3′ Antennae with scape and pedicel chestnut-brown to black, flagellum yellow 5

4(3) Parameres with distinct hairs before the recurved processes located near middle; female syntergosternite globose (Dominican Republic) .... *M. youngi,* new species

4′ Parameres without hairs and with processes located at apex not recurved; female syntergosternite VII + VIII with deep median groove (Dominican Republic, Dominica) .... *M. dominicensis* Scarbrough and Knutson

5(3′) Abdomen opaque brown to black, brown pruinose; male with a median tubercle on the inflated sternite VI; parameres with two apical recurved processes (Dominican Republic) .... *M. cornutus,* new species.

5′ At least tergites III–V shining black, without pruinosity; male sternite VI less inflated and without median tubercle (Mexico, Costa Rica, Grenada, Trinidad, Colombia, Ecuador, Brazil, Argentina) .... *M. spinosus* (Hardy)

6(2′) Scape and pedicel brown to black, flagellum yellow; parameres without dorsal recurved processes, only with small subapical spines; outer gonopod not developed (Dominican Republic) .... *M. antillensis,* new species

6′ Antennae predominantly dark brown to black; parameres simple with outer gonopod well developed and densely haired (Dominican Republic) .... *M. pilosus,* new species

Metadorylas youngi Rafael, **new species**
(Fig. 24–29)

Diagnosis.—This species differs from all other described *Metadorylas* species by the following: yellow antennae, postpronotal lobes, halteres, legs, epandrium, and surstyli; profemora and mesofemora with ventral ctenidia; protibiae and mesotibiae with posteroventral apical bristle; and parameres simple, long bristled with two subapical, recurved processes dorsally.

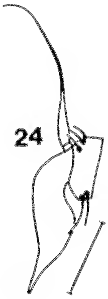
Description.—Male: body length 3.1 mm; wings 3.7 mm. Antennae yellow, flagellum long, acuminate (Fig. 24). Frons and face gray pruinose. Thorax dark brown to black, brown pruinose dorsally and gray pruinose laterally (mesopleuron and postnotum). Postpronotal lobe yellow. Legs yellow, except fifth tarsomeres brown. Profemora and mesofemora with short ventral ctenidia. Protibiae and mesotibiae with posteroventral bristle. Wings hyaline, except for brown pterostigma; crossvein r–m located near basal one-third of the cell dm; last section of vein M_1 almost straight. Halteres yellow. Abdomen dark brown to black, brown pruinose, except tergite I dorsally and laterally and tergites II–V posterolaterally with gray pruinosity. Terminalia with large membranous area apically on syntergosternite VIII; surstyli (Fig. 25) asymmetrical; parameres and aedeagus as in Fig. 26, 27. Female: body length 3.1 mm; wings 3.6 mm. Frons silvery gray pruinose near antennae, becoming white pruinose dorsally and with a shiny black median ridge extended from ocellar triangle to area of larger eye facets. Posteroventral apical bristles of protibiae and mesotibiae longer than in male. Tergites II–V more dense gray pruinose posterolaterally than in male. Terminalia (Fig. 29) with ovipositor yellow, straight, shorter than syntergosternite VII + VIII.

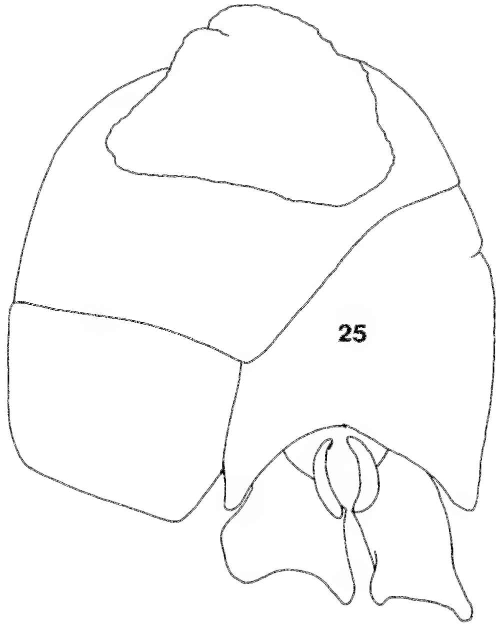
Type Material.—Holotype: male (CMNH). Verbatim text of three pin labels: "DOMINICAN REPUBLIC: Pedernales. 26 km N Cabo Rojo. 18–06N 71–38W. 730 m" / "13–25 July 1990 L. Masner, J. Rawlins, C. Young, Wet deciduous forest; intercept trap" / "HOLOTYPE *Metadorylas youngi* Rafael [red paper]." Paratypes: Thirteen males and four females, topotypic, 15 July 1987, J. Rawlins, R. Davidson (three males, one female, INPA); 21 July 1990, L. Masner; 19–25 July 1990, L. Masner, J. Rawlins, C. Young.

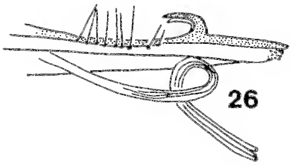
Etymology.—This species is named in honor of one of the collectors, Dr. Chen W. Young, Carnegie Museum of Natural History.

→

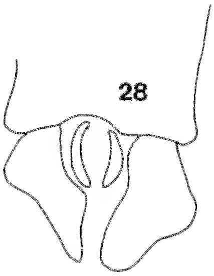
Fig. 24–33.—*Metadorylas* from the Dominican Republic. 24–29. *Metadorylas youngi,* male: 24, antenna; 25, terminalia; 26, parameres and aedeagus; 27, parameres, ventral view; 28, surstyli, variation in a paratype; 29, female terminalia. 30–33. *Metadorylas cornutus,* male: 30, terminalia; 31, parameres and aedeagus; 32, parameres, ventral view; 33, ejaculatory apodeme. All figures to same scale as Fig. 24 (= 0.1 mm), except Fig. 29 (scale = 0.5 mm).

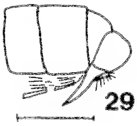

24

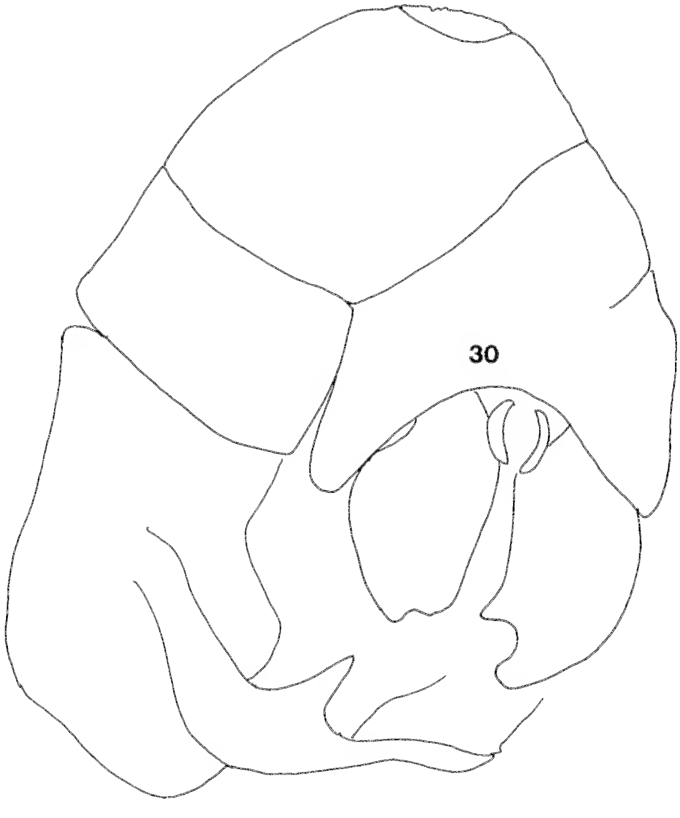

25

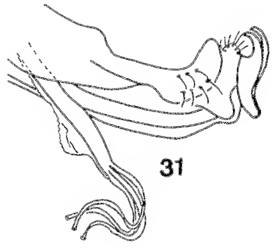

26

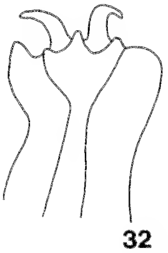

27

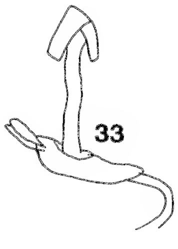

28


29


30


31


32


33

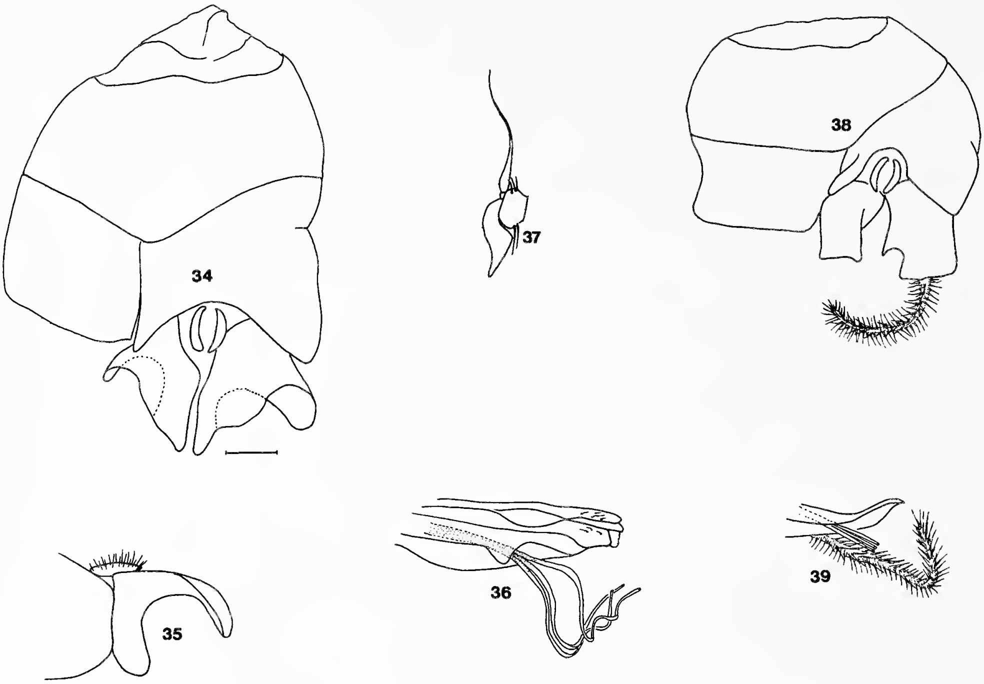


Fig. 34–39.—*Metadorylas* from the Dominican Republic. 34–36. *Metadorylas antillensis,* male: 34, terminalia; 35, inner surstylus, lateral view; 36, parameres and aedeagus. 37–39. *Metadorylas pilosus,* male: 37, antenna; 38, terminalia; 39, parameres and aedeagus, showing outer gonopod. All figures to same scale as Fig. 34 (= 0.1 mm).

Remarks.— *Metadorylas youngi* resembles in most respects the description of *M. dominicensis* Scarbrough and Knutson, recently described from Dominica. It can be easily separated from *M. dominicensis* by characters of the terminalia. One male with different surstyli (Fig. 28), one of the most variable characters in pipunculids, belongs here because it has identical aedeagus and parameres.

Metadorylas cornutus Rafael, **new species**
(Fig. 30–33)

Diagnosis.—This species differs from all other *Metadorylas* species by its extremely large sternite VI inflated with a median tubercle, and by its complex parameres, short bristles with two apical recurved processes.

Description.—(Male only, female unknown.) Male: Body length 3.8 mm; wings 4.4 mm. Antennae yellow, with scape and pedicel black; flagellum long, acuminate. Frons and face gray pruinose. Thorax dark brown to black, brown pruinose dorsally and gray pruinose laterally (mesopleuron and postnotum). Postpronotal lobe yellow. Legs yellow, except fifth tarsomeres brown. Profemora and mesofemora with short ventral ctenidia. Protibiae and mesotibiae with posteroventral bristle. Wings hyaline, except for brown pterostigma; crossvein r-m located near basal one-third of the cell dm. Halteres yellow. Abdomen dark brown to black, brown pruinose, except tergite I dorsally and laterally and tergites II–V posterolaterally with gray pruinosity. Terminalia (Fig. 30) with sternite VI inflated with median tubercle; syntergosternite VIII with small membranous area; surstyli asymmetrical, the outer with an apical sinus. Parameres and aedeagus as in Fig. 31, 32. Parameres with two recurved processes distally. Ejaculatory apodeme as in Fig. 33.

Type Material.—Holotype: male (CMNH). Verbatim text of three pin labels: "DOMINICAN REPUBLIC: Pedernales. 3.3 km NE Los Arroyos. 18–15N 71–45W 1450m" / "16–18 July 1990, L. Masner, J. Rawlins, C. Young, Wet mountain forest, sweep samples" / "HOLOTYPE *Metadorylas cornutus* Rafael [red paper]."

Etymology.—The specific name refers to the two recurved processes at the apex of the parameres in male terminalia (from Latin *cornus* = horn).

Remarks.—*Metadorylas cornutus* is closely related to the new species *M. youngi* described above. The distinct black scape and pedicel will instantly separate the two species. The male genitalia also provide reliable specific characters. The male of *M. cornutus* has peculiar terminalia with sternite VI inflated with a median tubercle, the outer surstyli with an apical sinus, and the parameres with two recurved apical processes.

Metadorylas antillensis Rafael, **new species**

(Fig. 34–36)

Diagnosis.—This species differs from all other *Metadorylas* species by its black coxae, trochanters, and femora, by the extremely large bases of the surstyli, and by parameres being almost straight dorsally with small subapical spines.

Description.—(Male only, female unknown.) Body length 3.0 mm; wings 3.6 mm. Antennal scape and pedicel brown, flagellum yellow. Frons with a narrow, dark median ridge. Thorax dark brown to black, brown pruinose dorsally and gray pruinose laterally on mesopleuron and postnotum. Postpronotal lobe yellow. Legs with coxae, trochanters black; femora black with base and apex yellow; tibiae and tarsi yellow, except fifth tarsomeres brown. Profemora and mesofemora with short ventral ctenidia. Protibiae and mesotibiae with posteroventral bristle. Wings hyaline, except for brown pterostigma; crossvein r–m located near basal one-third of the cell dm; last section of vein M_1 almost straight. Halteres yellow. Abdomen dark brown to black, brown pruinose, except tergite I dorsally and laterally and tergites II–V posterolaterally with gray pruinosity. Terminalia (Fig. 34) with large membranous area apically on syntergosternite VIII; surstyli asymmetrical, in lateral view as in Fig. 35; parameres and aedeagus as in Fig. 36. Parameres without dorsal processes but with small subapical spines.

Type Material.—Holotype: male (CMNH). Verbatim text of three pin labels: "DOMINICAN REPUBLIC: Pedernales. 23.5 km N Cabo Rojo, 18–06N 71–38W 540 m" / "19–25 July 1990, L. Masner, deciduous forest, intercept trap" / "HOLOTYPE *Metadorylas antillensis* Rafael [red paper]." Paratype: one male, topotypic, 19–21 July 1990 (INPA).

Etymology.—The species name refers to the Antilles.

Remarks.—The male surstyli of *Metadorylas antillensis* are superficially similar to *M. spinosus* (Hardy). It can be separated from that species by the key characters presented above and by the parameres which possess small dorsal subapical spines instead of the dorsal processes present in *M. spinosus*.

Metadorylas cressoni (Johnson)

Pipunculus cressoni Johnson, 1919:433.

Remarks.—Three specimens (two in poor condition, sex undetermined) may be referred to *M. cressoni*. The male terminalia are identical to those figured of the holotype (Rafael, 1990*b*). This species has been recorded previously only from the Bahamas (New Providence) and Jamaica.

Specimens Examined.—DOMINICAN REPUBLIC: Dajabón, Mariano Cestero, 13 Aug. 1980, 650 m, A. Norrbom (one specimen); 14 Aug. 1980 (one male); Azua, Padre la Casa, 500 m, 18 Aug. 1980, A. Norrbom (one specimen).

Metadorylas dominicensis Scarbrough and Knutson

Metadorylas dominicensis Scarbrough and Knutson, 1989:531, fig. 11–15

Remarks.—One female with deep median groove on syntergosternite VII + VIII agrees with the description of *M. dominicensis* from Dominica. This is the first record of this species subsequent to its original description.

Specimens Examined.—DOMINICAN REPUBLIC: Pedernales, 1 km S Los Arroyos, 1125 m, 18–14N 71–45W, 18 Oct. 1991, R. Davidson, C. Young, S. Thompson, J. Rawlins, second growth forest (one female).

Metadorylas pilosus Rafael, **new species**
(Fig. 37–39)

Diagnosis.—This species differs from all other described *Metadorylas* species by its well-developed and densely haired outer gonopod, and by the outer surstylus being larger than the inner surstylus and having an apical sinus.

Description.—(Male only, female unknown.) Body length 2.9 mm; wings 3.2 mm. Antennae (Fig. 37) brown to black, flagellum acuminate. Thorax dark brown to black, brown pruinose on dorsum, gray on the sides. Postpronotal lobes and halteres yellow. Femora predominantly black, profemur without ventral ctenidia; tibiae yellow with small posteroventral bristle on protibiae and mesotibiae. Wings hyaline with brown pterostigma; last section of vein M_1 slightly curved; vein CuA_1 as long as vein dm–cu. Abdomen dark brown to black, brown pruinose, except tergites II–V laterally and posterolaterally with gray pruinosity. Terminalia: syntergosternite VIII with apical membranous area (Fig. 38); outer surstylus with apical sinus and larger than inner surstylus. Parameres and aedeagus as in Fig. 39. Parameres simple; outer gonopod curved, long, thin, and densely haired.

Type Material.—Holotype: male (CMNH). Verbatim text of three pin labels: "DOMINICAN REPUBLIC: Pedernales. 23.5 km N Cabo Rojo. 18–06N 71–38W 540 m" / "19–21 July 1990, L. Masner, J. Rawlins, C. Young, Deciduous forest, intercept trap" / "HOLOTYPE *Metadorylas pilosus* Rafael [red paper]." Paratype: one male, topotypic, 19–25 July 1990 (INPA).

Etymology.—The specific name refers to the densely haired gonopod in male terminalia (from Latin *pilus* = hair).

Remarks.—*Metadorylas pilosus* is the third known species with outer gonopod densely haired. The other two species are *M. disgregus* (Hardy) described from Argentina and *M. gratiosus* (Kertész) described from Paraguay. *Metadorylas pilosus* can be separated from both species by the following characters of the terminalia: outer surstylus larger than inner one; parameres simple; outer gonopod thinner.

Genus *Eudorylas* Aczél

Eudorylas is a cosmopolitan genus, and it occurs from Canada to Chile in the New World.

Key to Species of *Eudorylas* from the West Indies

1 Postpronotal lobes dark brown to black, concolorous with scutum 2
1′ Postpronotal lobes yellow, scutum dark brown to black 3

2(1) Legs predominantly yellow, except coxae and distal tarsomeres black and brown respectively; crossvein r–m placed at basal fourth of cell dm (Mexico, Costa Rica, St. Vincent) . . . . *E. willistoni* (Kertész)

2′ Legs predominantly black; crossvein r–m placed near middle of cell dm (Dominican Republic) . . . . *E. curvicaudatus*, new species

3(1′) Combined length of third and fourth costal section longer than fifth; crossvein r–m placed near middle of cell dm; last section of vein M_1 slightly curved; membranous area of the male terminalia extended (Fig. 46) (Dominican Republic) . . . *E. dominicanensis*, new species

3′ Combined length of third and fourth costal section shorter than fifth; crossvein r–m placed near basal third of cell dm; last section of vein M_1 straight; membranous area of the male terminalia not extended (Puerto Rico, Peru, Brazil) . . . . *E. regalis* (Curran)

Eudorylas dominicanensis Rafael, **new species**
(Fig. 40–43)

Diagnosis.—Antennae dark brown to black; flagellum long and acuminate; legs predominantly black; mesopleuron gray pruinose; crossvein r–m placed near middle of cell dm; membranous area of the male terminalia extended.

Description.—(Male only, female unknown.) Body length 4.1 mm; wings 4.7 mm. Frons and face silvery gray pruinose. Antennae (Fig. 40) brown to black with flagellum long and acuminate. Thorax brown to black, brown pruinose dorsally, gray pruinose laterally. Postpronotal lobe yellow. Legs predominantly black with base and apex of the femora narrowly yellow, base and apex of the tibiae widely yellow and basal two to three tarsomeres yellow. All femora with short ventral ctenidia. Wings slightly infuscated; pterostigma brown; third costal section as long as fourth, both longer than fifth; crossvein r–m placed near middle of cell dm; last section of vein M_1 slightly curved. Abdomen dark brown to black, brown pruinose dorsally, gray pruinose on tergite I and laterally on tergites II–V. Terminalia with syntergosternite about equal in length to tergite V and with extended down-curved membranous area. Surstyli asymmetrical (Fig. 41). Epandrium narrow. Parameres and aedeagus as in Fig. 42. Ejaculatory apodeme as in Fig. 43.

Type Material.—Holotype: male (CMNH). Verbatim text of three pin labels: "DOMINICAN REPUBLIC: Pedernales. 7 km NE Los Arroyos. 1870 m, 18–16N 71–44W" / "15 July 1990 L. Masner, C. Young, J. Rawlins, intercept trap" / "HOLOTYPE *Eudorylas dominicanensis* Rafael [red paper]."

Etymology.—The species names refers to the country Dominican Republic.

Remarks.—*Eudorylas dominicanensis* closely resembles *E. curvicaudatus* in the appearance of the male terminalia. It can be differentiated by the longer flagellum and by the less symmetrical surstyli in *E. dominicanensis.*

Eudorylas curvicaudatus Rafael, **new species**
(Fig. 44–48)

Diagnosis.—Antennae dark brown to black; flagellum short and acute; legs black; mesopleuron brown pruinose; crossvein r–m placed near middle of cell dm; membranous area of the male terminalia extended and down-curved distally.

Description.—(Male only, female unknown.) Body length 3.2 mm; wings 3.7 mm. Frons brown pruinose; face silvery gray pruinose. Antennae (Fig. 44) brown to black with flagellum short, acute, and yellowish under strong illumination. Thorax brown to black, dusted with brown pruinosity. Legs black, except apex of the femora and base of the tibiae narrowly yellow. All femora with short inconspicuous ventral ctenidia. Wings slightly infuscated; pterostigma brown; third costal section slightly longer than fourth; third and fourth sections combined slightly longer than the fifth section; crossvein r–m placed near middle of cell dm; last section of vein M_1 curved. Abdomen (Fig. 45) dark brown to black, brown pruinose dorsally, light brown pruinose on tergite I and gray pruinose laterally on tergites II–V. Terminalia with syntergosternite about two-thirds length of the tergite V, with extended down-curved membranous area. Surstyli subsymmetrical (Fig. 46). Epandrium narrow. Parameres and aedeagus as in Fig. 47. Ejaculatory apodeme as in Fig. 48.

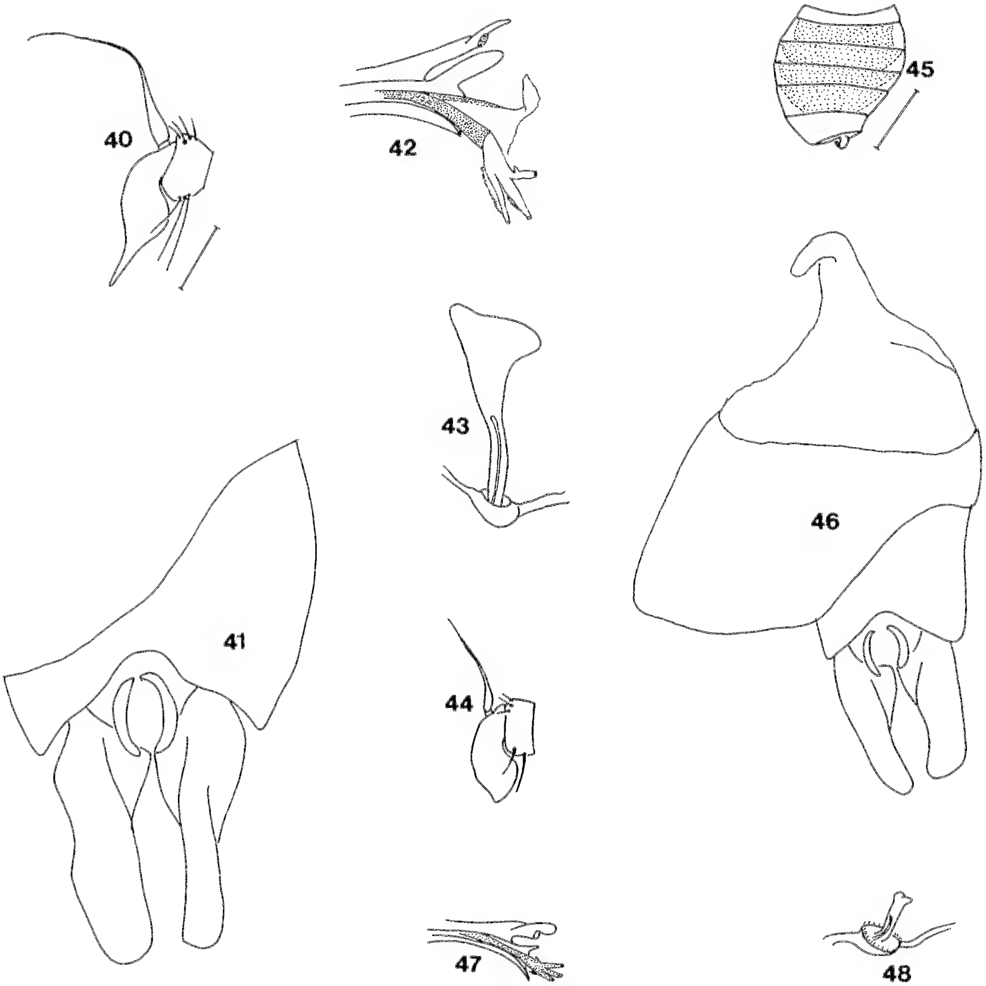


Fig. 40–48.—*Eudorylas* from the Dominican Republic. 40–43. *Eudorylas dominicanensis,* male: 40, antenna; 41, epandrium and surstyli; 42, parameres and aedeagus; 43, ejaculatory apodeme. 44–48. *Eudorylas curvicaudatus,* male: 44, antenna; 45, abdomen; 46, terminalia; 47, parameres and aedeagus; 48, ejaculatory apodeme. All figures to same scale as Fig. 40 (= 0.1 mm), except Fig. 45 (scale = 0.5 mm).

Type Material.—Holotype: male (CMNH). Verbatim text of three pin labels: "DOMINICAN REPUBLIC: Hato Mayor. Parque Los Haitises, 3 km W Cueva de Arena, 19–04N 69–29W" / "20 m, 7–9 July 1992 R. Davidson, J. Rawlins, S. Thompson, C. Young, mesic lowland forest" / "HOLOTYPE *Eudorylas curvicaudatus* Rafael [red paper]."

Etymology.—The specific name refers to the extended down-curved membranous area in male terminalia (from Latin *curvus* = curve, *caudatus* = having tail).

Remarks.—*Eudorylas curvicaudatus* differs from other Neotropical species by the terminalia with an extended, down-curved membranous area and by the subsymmetrical surstyli.

Eudorylas spp.

Remarks.—Four female specimens representing three different species cannot be identified and were not associated with males.

Specimens Examined.—DOMINICAN REPUBLIC: Peravia, Arroyo Cañas, 650 m, 08 Aug. 1980, A. Norrbom (one female); Pedernales, 37 km N Cabo Rojo, 4 km E La Abeja, 18–10N 71–37W. 1440 m, 13–15 July 1987, R. Davidson, J. Rawlins (one female); Pedernales, 23.5 km N Cabo Rojo, 18–06N 71–38W, 540 m, 19–25 July 1990, L. Masner, J. Rawlins, C. Young, deciduous forest, intercept trap (one female); Pedernales, La Abeja, 38 km NNW Cabo Rojo, 18–09N 71–38W, 1250 m, 15 July 1987, J. Rawlins, R. Davidson (one female)

Genus *Tomosvaryella* Aczél

Tomosvaryella is a cosmopolitan genus and it has been recorded from Canada to Chile. Seven species have been reported from the West Indies, and six species were observed in this study. The excluded species is *T. polita* (Williston) described from St. Vincent. The original description was very brief and generalized and it fits all the described species from the West Indies. Since the type has been lost, no comparison can be conducted to verify the status of this species, therefore it has been excluded from the present study.

Key to Species of *Tomosvaryella* from the West Indies

1 Syntergosternite VIII symmetrical, subhemispherical; metatrochanters with short square-topped process densely white pubescent (USA, Mexico, Belize, Nicaragua, Costa Rica, Panama, Bahamas, Cuba, Puerto Rico, Jamaica, Colombia, Peru, Brazil, Chile) . . . . *T. subvirescens* (Loew)
1′ Syntergosternite VIII asymmetrical in dorsal view, compressed to right; metatrochanters not as above 2

2(1′) Metatrochanters with two spiniform ventral processes (USA, Mexico, Bahamas, Brazil) . . . . . . *T. bidens* (Cresson)
2′ Metatrochanters with only one ventral process 3

3(2′) Metatrochanters with long process, about as long as width of trochanters; surstyli with apex wider than base; parameres without dorsal spine (Mexico, Costa Rica, Cuba, Haiti, Dominican Republic, "Hispaniola," Jamaica, Dominica, St. Lucia) . . . . *T. tuberculata* Hardy
3′ Metatrochanters with short obtuse process or small inconspicuous ridge 4

4(3′) Metafemur with sparse long and slender bristles on posterior face; surstyli with apex as wide as base; parameres with one dorsal spine and with one branch of the aedeagus serrate (Mexico, Dominican Republic) . . . . . . *T. mexicanensis* Ale-Rocha and Rafael
4′ Metafemur with short bristles 5

5(4′) Surstyli rather simple with bristles on dorsal protuberance, more distinct in lateral view (Mexico, Cuba, Dominica, Colombia) . . . . . . *T. scopulata* Hardy
5′ Surstyli forcipate, distinctly larger at base, without bristles on dorsal protuberance (Puerto Rico, Dominica) . . . . . . *T. spangleri* Scarbrough and Knutson

Tomosvaryella tuberculata Hardy

Tomosvaryella tuberculata Hardy, 1948*a*:11, fig. 7a–d.

Remarks.—This species is widespread across Central America and the West Indies, being recorded in Mexico, Costa Rica, Cuba, Dominica, Bahamas, Haiti, Jamaica (Scarbrough and Knutson, 1989; Ale-Rocha and Rafael, 1995) and now Dominican Republic and St. Lucia.

Specimens Examined.—DOMINICAN REPUBLIC: Azua, Padre la Casas, 500 m, 18 Aug. 1980, A. Norrbom (one male); Pedernales, 37 km N Cabo Rojo, 18–09N 71–35W, 1500 m, 11 July 1987,

R. Davidson, J. Rawlins (one female); Pedernales, 23.5 km N Cabo Rojo, 18–06N 71–38W, 540 m, 19–25 July 1990, L. Masner, J. Rawlins, C. Young, deciduous forest, intercept trap (one male, INPA). ST. LUCIA: Anse La Raye, Anse Galet, 1 km SSW Anse La Raye, 13–56N 61–03W, 50 m, 21–30 June 1991, J. E. Rawlins, S. A. Thompson (one male).

Tomosvaryella mexicanensis Ale-Rocha and Rafael

Tomosvaryella mexicanensis Ale-Rocha and Rafael, 1995:416, fig. 29–35.

Remarks.—This is the first record of this species subsequent to its original description from Mexico.

Specimens Examined.—DOMINICAN REPUBLIC: Azua, Padre la Casas, 500 m, 18 Aug. 1980, A. Norrbom (two males, CMNH; two males, INPA).

Genus *Elmohardyia* Rafael

Elmohardyia is a New World genus, better known in the Neotropical region through recent studies (Rafael, 1988*b*). This genus has not been recorded from the Dominican Republic, but two species have been previously recorded from Jamaica and Trinidad (Rafael, 1988*b*).

Key to Species of *Elmohardyia* from the West Indies

1 Tergite II predominantly gray pruinose; tergites III–V with gray pruinose spots visible in dorsal view; inner surstylus about four times longer than outer one (Jamaica, Costa Rica, Guyana) . . . . *E. gowdeyi* (Curran)

1′ Tergite II brown pruinose; only tergite V with gray pruinose spot visible on dorsal view; inner surstylus slightly longer than outer one (Trinidad, Brazil) . . . . *E. trinidadensis* (Hardy)

ACKNOWLEDGMENTS

I thank Dr. Chen W. Young, Section of Invertebrate Zoology, Carnegie Museum of Natural History, for the loan of the specimens and for reviewing an early draft of the manuscript. I also thank two anonymous reviewers for their comments.

LITERATURE CITED

ALE-RACHA, R., AND J. A. RAFAEL. 1995. *Tomosvaryella* Aczél, do México, América Central e Antilhas (Diptera: Pipunculidae). Revista Brasileira de Zoologia, 12:405–430.

DE MEYER, M. 1989. Systematics of the Nearctic species of the genus *Cephalops* Fallén (Diptera, Pipunculidae). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie, 59: 99–130.

———. 1994. Phylogenetic relationships within the Cephalopsini (Diptera, Pipunculidae). Bulletin et Annales de la Société Royale Belge d'Entomologie, 130:7–18.

HARDY, D. E. 1948*a*. Neotropical Dorilaidae (Pipunculidae) studies; Part 1 (Diptera). Psyche, 55:1–15.

———. 1948*b*. New and little known Neotropical Dorilaidae (Pipunculidae–Diptera). Journal of the Kansas Entomological Society, 21:124–133.

———. 1954. Neotropical Dorilaidae studies, part III. Brazilian species and key to the known species of *Dorilas sens. lat.* Boletim do Museu Nacional Zoologia, 123:1–60.

———. 1965*a*. The Pipunculidae of Argentina. Acta Zoologica Lilloana, 19:187–241.

———. 1965*b*. Neotropical Pipunculidae (Diptera) studies, part IV. Further studies of Brazilian species. Arquivos de Zoologia 4:1–68.

———. 1966. Family Pipunculidae (Dorilaidae). 45:1–15, *in* A Catalogue of the Diptera of the Americas South of the United States (N. Papavero, ed.). Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil.

JERVIS, M. A. 1992. A taxonomic revision of the pipunculid fly genus *Chalarus* Walker, with particular reference to the European fauna. Zoological Journal of the Linnean Society (London), 105:243–352.

JOHNSON, C. W. 1919. A revised list of the Diptera of Jamaica. Bulletin of the American Museum of Natural History, 41:421–449.

RAFAEL, J. A. 1987. *Basileunculus,* um gênero novo de Pipunculidae (Diptera) da região neotropical, com chave para as espécies. Acta Amazonica, 16/17:627–634.

———. 1988*a*. Pipunculidae (Diptera) neotropicais da região Neotropical. I. Redescrição de *Chalarus chilensis* Collin, comb. n. e descrição de duas espécies novas da Amazônia. Revista Braxileira de Zoologia, 5:1–9.

———. 1988*b*. Pipunculidae (Diptera) neotropicais do gênero *Elmohardyia.* Acta Amazonica 18: 223–264.

———. 1990*a*. Revisão das espécies neotropicais do gênero *Chalarus* Walker, 1834 (Diptera, Pipunculidae). Iheringia, Série Zoologia, 70:45–53.

———. 1990*b*. As espécies neotropicais de *Metadorylas* Rafael (Diptera: Pipunculidae). Boletim do Museu Paraense Emilio Goeldi, Série Zoologia, 6:127–164.

———. 1991. Revisão das espécies neotropicais do gênero *Cephalops* Fallén (Diptera: Pipunculidae). Acta Amazonica, 20:353–390.

———. 1992. A review of the Neotropical species of big-headed flies, genus *Cephalosphaera* (Diptera, Pipunculidae). Pp 631–646, *in* Insects of Panama and Mesoamerica: Selected Studies (D. Quintero and A. Aiello, eds.). Oxford University Press, Oxford, United Kingdom.

RAFAEL, J. A., AND M. DE MEYER. 1992. Generic classification of the family Pipunculidae (Diptera): A cladistic analysis. Journal of Natural History, 26:637–658.

SCARBROUGH, A. G., AND L. V. KNUTSON. 1989. Asilidae, Bombyliidae, Conopidae, and Pipunculidae (Diptera) of Dominica, West Indies. Florida Entomologist, 72:519–537.

ANNALS OF CARNEGIE MUSEUM
Vol. 65, Number 4, Pp. 383–391 27 November 1996

NEW GENERA AND NEW SPECIES OF COLPURINI (INSECTA: HETEROPTERA: COREIDAE) FROM PHILIPPINES, BORNEO, AND MALAYA

Harry Brailovsky[1]
Research Associate, Section of Invertebrate Zoology

Abstract

Three new genera of Colpurini (Coreidae) are described, each containing a single undescribed species: *Kinabaluhygia sabah* from Sabah (Borneo), *Eludohygia parvioculata* from Malaya, and *Baumannhygia insulata* from Mindanao (Philippines). Adult dorsal habitus for each are illustrated, and drawings of the male genital capsule are provided.

Introduction

The tribe Colpurini is represented in the South Pacific Islands by a number of species that show various bizarre morphological specialization. The most striking features of these genera are the remarkable reduction of the hemelytra, the development of the head including the eyes, and the high degree of endemicity. The three genera described at this time complement a series of papers prepared by the author to clarify the systematics of the tribe (Brailovsky 1990, 1993*a*, 1993*b*, 1993*c*; Brailovsky et al., 1992; Brailovsky and Ortega Leon, 1994).

The following abbreviations are used for the institutions cited in this paper: BMNH, The Natural History Museum, London, United Kingdom; FMNH, Field Museum of Natural History, Chicago, Illinois; QMBA, Queensland Museum, Brisbane, Australia; UNAM, Colección Entomológica del Instituto de Biología, Universidad Nacional Autónoma de México, México D. F., Mexico.

Systematic Entomology

Kinabaluhygia, new genus
(Fig. 1–4)

Diagnosis.—*Kinabaluhygia,* n. gen., is the only genus within the tribe Colpurini that exhibits a conspicuous globosity on the side of the head in front of and close to the eyes, with the apex truncated.

This new genus closely resembles *Wygohygia* Brailovsky (1993) in having the eyes small and protruding on short stalks, head quadrate, ocelli present, buccula with short anterior projection, postocular tubercle protuberant, tylus unarmed, scutellum flattened, and plica and fissura on abdominal sternite VII of the female.

It differs from other Colpurini in a number of important characteristics: sides of head in front of and close to eyes conspicuously globose, raised above eyes and apically truncated; hemelytra brachypterous, with hemelytral membrane reduced; posterior lobe of metathoracic peritreme small and globose; callar region uniformly and slightly convex; posterior pronotal lobe near middle third flat; and antenniferous tubercle unarmed. In *Wygohygia,* the sides of head in front of eyes

---

[1] Instituto de Biología, UNAM, Depto. de Zoología, Apdo. Postal 70153, México 04510 D. F. México.
Submitted 31 March 1995.

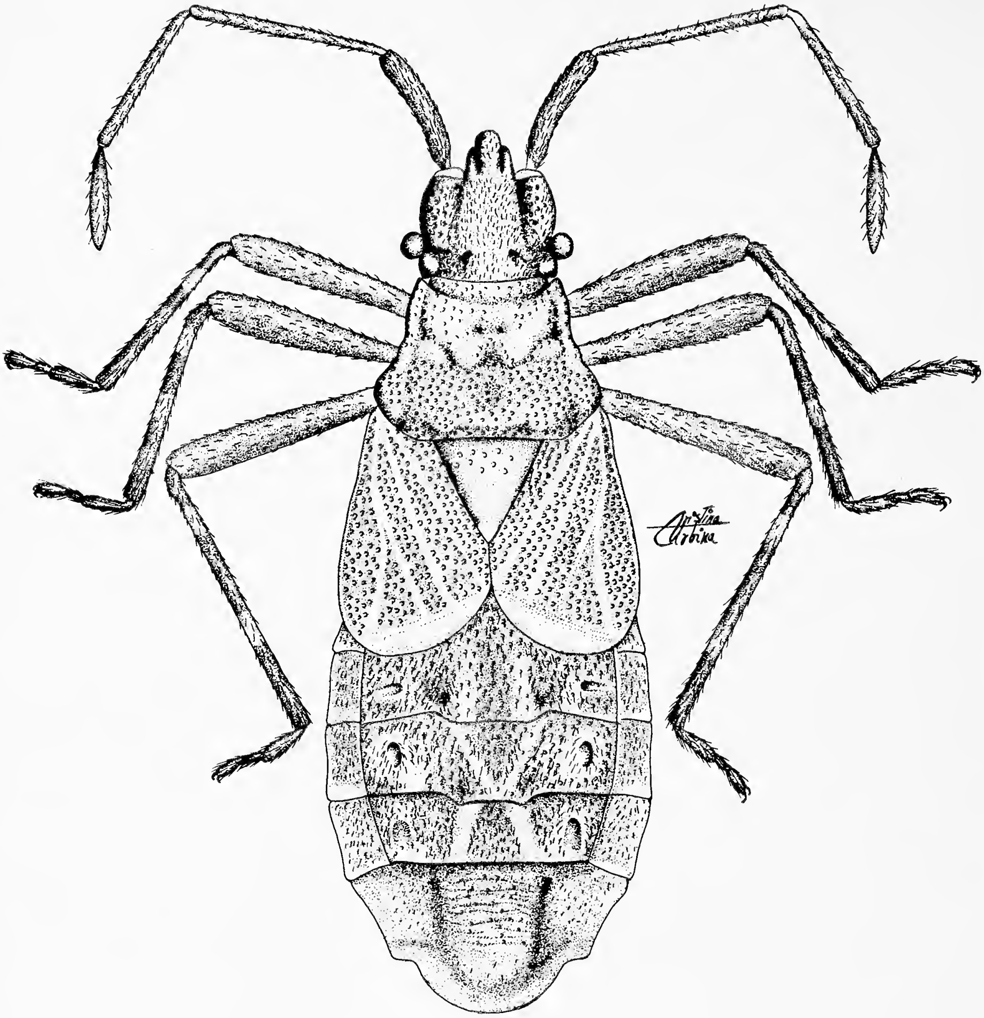
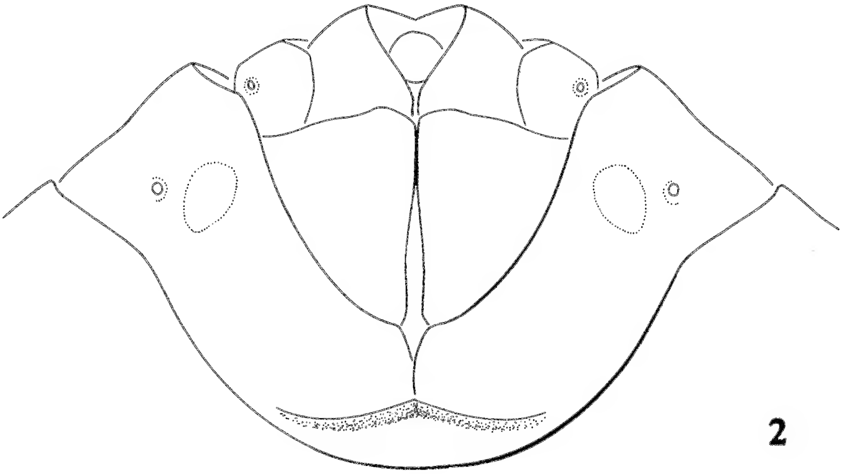


Fig. 1.—*Kinabaluhygia sabah* Brailovsky, male.

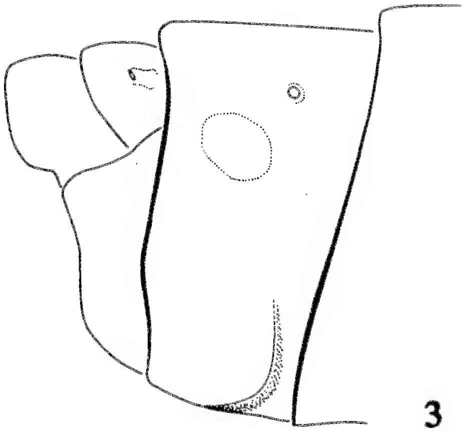
are laterally globose, never raised above eyes, and apically projected on a long and robust lobe; the hemelytra are submacropterous with the hemelytral membrane well developed with few veins furcate; posterior lobe of the metathoracic peritreme small and sharp, callar region transversely convex and separated along midline by slightly longitudinal depression; posterior pronotal lobe near middle third with two lateral and irregular convexities separated by longitudinal depression; antenniferous tubercle armed with a long robust spine.

→

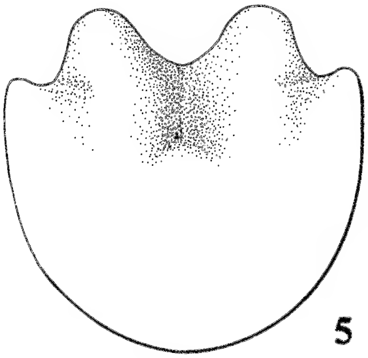
Fig. 2–6.—Colpurini. Fig. 2–4, *Kinabaluhygia sabah* Brailovsky; 2, female genital plates, caudal view; 3, female genital plates, lateral view; 4, male genital capsule, caudal view; 5, *Baumannhygia insulata* Brailovsky, male genital capsule, caudal view; 6, *Eludohygia parvioculata* Brailovsky, male genital capsule, caudal view.



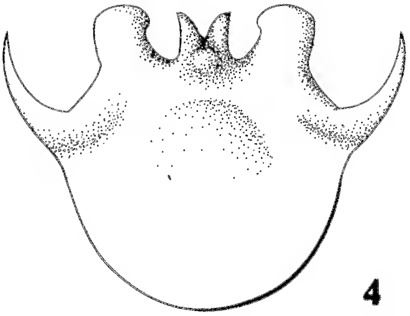
2



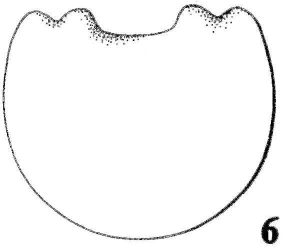
3



5



4



6

Wygohygia, known only from New Guinea, is much more robust and longer than 12 mm (female; male unknown) and *Kinabaluhygia,* recorded from Borneo, is shorter, less than 10.50 mm.

Description.—Head: quadrate, wider than long, sunken between lateral lobes; tylus unarmed, apically globose, extending anteriorly to the jugae and more raised in lateral view; jugae unarmed; sides of head in front of and close to eyes globose, elevated, conspicuously convex, and raised above eyes; antennal segment I robust, thickest, slightly curved outward, and shorter than head; segments II and III cylindrical and slender; segment IV fusiform; segment II longest; segment IV the shorter; segment I longer than III (male) or shorter than III (female); ocelli reduced, not elevated, and difficult to see; preocellar pit weakly deep; eyes small, pimple-like, protruding on short stalks; postocular tubercles protuberant; vertex and frons sunken and flattened; buccula rounded, short, elevated, not projecting beyond antenniferous tubercle, with a short anterior projection; rostrum long, reaching posterior third of abdominal sternite V (male) or anterior third of VI (female); rostral segment I reaching posterior gular region; mandibular plate absent.

Thorax: pronotum wider than long, trapeziform, nondeclivent; collar wide; frontal angles projecting forward as rounded thickened lobes; humeral angles rounded, not exposed and slightly elevated; anterolateral borders weak and obliquely straight; posterolateral and posterior borders straight; callar region slightly convex; posterior margin with two lateral convexities. Anterior lobe of metathoracic peritreme reniform, posterior lobe small, subglobose.

Legs: femora unarmed; tibiae sulcate.

Scutellum: longer than wide (female) or as long as wide (male); triangular, with subacute apex; disc flat.

Hemelytra: brachypterous, reaching median third of abdominal segment IV; clavus and corium fused into a coriaceous pad, and the wings meeting each other along the midline; hemelytral membrane reduced.

Abdomen: connexival segments strongly elevated, higher than abdominal segments; angle of connexival complete; abdominal sternites with the medial furrow extending to posterior border of sternite V.

Integument: body surface mostly shining, with short decumbent, silvery bristle-like setae, intermixed with long, erect setae located on the abdominal sterna. Head, pronotum, scutellum, hemelytra, thorax, abdomen, and exposed parts of genital segments punctate. Head with frons and vertex and connexival segments practically smooth; antennal segments and legs covered by long and short setae.

Male genitalia: genital capsule: posteroventral border with lateral diverging spine-like projections, medial process bilobed, and with submedian truncated lobes (Fig. 4).

Female genitalia: abdominal sternite VII with plica and fissura; plica triangular reaching median third of sternite VII; gonocoxae I squarish, large; paratergite VIII short, subtriangular, with spiracle visible; paratergite IX square, longer than paratergite VIII (Fig. 2, 3).

Distribution.—Known only from Borneo.

Etymology.—Named for its occurrence on Mt. Kinabalu (Borneo). Gender feminine.

Type Species.—*Kinabaluhygia sabah,* n. sp.

Kinabaluhygia sabah, **new species**
(Fig. 1–4)

Description.—Dorsal coloration, male: head, pronotum, and scutellum bright black with pale yellow antenniferous tubercle and apex of scutellum; antennal segment I black, segments II and III dark red with basal and apical joint yellow, and IV yellow-orange with basal joint dark red; clavus, corium, connexival segments, and abdominal segments bright orange-chestnut tinged with red, except the posterior margin of the connexival II to VII ocher; hemelytral membrane dirty chestnut-orange. Ventral coloration, male: head and thorax bright black tinged with red on acetabulae; rostral segments I to IV, and anterior and posterior lobes of metathoracic peritreme bright pale orange with chestnut reflections; coxae dark chestnut-orange; trochanters yellow; femora bright dark red with basal joint yellow; tibiae bright dark red with one or two pale yellow-orange rings; tarsi bright yellow-orange; abdominal sternites and pleural margins bright brownish red except the posterior angle of pleural margins III to VII ocher; genital capsule black with bright brownish red reflections.

Color, female: similar to male. Legs: tarsal segments I and III dark red with chestnut-orange reflections; segment II mostly bright yellow-orange. Genital plates: gonocoxae I black with red reflections except the external upper angle creamy yellow; paratergite VIII and IX black with red reflections.

Measurements.—Male, female (mm). Head length 1.72, 1.72; width across eyes 1.88, 1.88; interocular space 1.32, 1.32; interocellar space 0.48, 0.48; preocular distance 1.30, 1.34; length antennal segments: I, 1.52, 1.41; II, 2.16, 2.20; III, 1.48, 1.44; IV, 1.32, 1.30. Pronotum: total length 1.72, 1.92; width across frontal angles 1.68, 1.64; width across humeral angles 2.64, 2.60. Scutellar length 1.04, 1.02; width 1.04, 1.00. Total body length 10.10, 10.40.

Type Specimens.—Holotype, male (QMBA): BORNEO, SABAH, Park Headquarters, Mt. Kinabalu, 5000 ft, 24–26 December 1975, G. B. and S. R. Monteith. Paratype, one female (UNAM): same data as holotype.

Etymology.—Named after the type locality.

Eludohygia, new genus
(Fig. 6, 7)

Diagnosis.—Eludohygia, n. gen., is a medium-sized striking insect easily distinguished from all other Colpurini by the pronounced dorsal convexity of the head, the minute eyes occupying only a small portion of the head surface (Fig. 7), tylus conspicuously enlarged, postocular tubercle weakly developed, buccula entirely without external teeth and femora armed with two rows of spines.

Description.—Male. Head: pentagonal, longer than wide across eyes, remarkably convex dorsally; tylus conspicuously enlarged, unarmed, apically globose, extending anteriorly to the jugae, and more raised in lateral view; jugae unarmed, thickened and extended to middle third of tylus; antenniferous tubercle unarmed; sides of head in front of eyes unarmed and straight; antennal segment I robust, thickened, slightly curved outward and shorter than head; segments II to IV mutilated; ocelli absent; preocellar pit deep; eyes minute, occupying only a small portion of the head surface; postocular tubercles developed but not protuberant; buccula rounded, short, elevated, not projecting beyond antenniferous tubercles, without teeth; rostrum long, reaching posterior third of abdominal sternite VI; mandibular plate absent.

Thorax: pronotum trapeziform, wider than long, nondeclivent; collar wide; frontal angles produced forward as rounded and globosus lobes; humeral angles rounded, not exposed; anterolateral borders obliquely straight, emarginated, and raised above pronotal disc; posterolateral border straight and posterior border slightly concave; pronotal disc with anterior half slightly concave and posterior half flat. Anterior lobe of metathoracic peritreme reniform, posterior lobe sharp, small.

Legs: femora armed with two rows of robust spines along ventral surface; tibiae with sulcus difficult to see.

Scutellum: wider than long, triangular, with sharp apex; disc flat.

Hemelytra: brachypterous, reaching posterior third of abdominal segment III; clavus and corium fused into a coriaceous pad and the wings meeting each other along the midline; hemelytral membrane reduced.

Abdomen: connexival segments strongly elevated, with posterior angle complete, not produced into spines; abdominal sternites with the medial furrow extending to posterior third of sternite V.

Integument: body surface mostly dull, with head, anterior third of pronotum, thorax, and abdomen shining. Head, thorax, abdomen, and genital capsule strongly punctate; pronotum, scutellum, hemelytra, dorsal abdominal segments, and connexival with scattered punctures. Body with short decumbent silvery bristle-like setae, intermixed with long erect setae located on the abdominal sterna and legs.

Male genitalia: genital capsule: posteroventral border complete, laterally enclosed by two medium-sized lobes (Fig. 6).

Female. Unknown.

Distribution.—Known only from Malaya.

Etymology.—From the latin *eludo* = escape, avoid, or elude. Gender feminine.

Type Species.—Eludohygia parvioculata, n. sp.

Eludohygia parvioculata, new species
(Fig. 6, 7)

Description.—Male. Dorsal coloration: head bright black; antennal segment I pale chestnut-orange; pronotum with anterior half shining black and posterior half dull black with dark red reflections;

anterolateral margin chestnut-orange; scutellum, hemelytra, connexival segments and dorsal abdominal segments dark red with posterior border of connexival ocher-yellow; hemelytral membrane dark chestnut-orange. Ventral coloration: head bright black with dark red reflections; buccula (except basal third dark red) and rostral segments I to IV pale chestnut-orange-yellow; thorax and abdominal sternite bright orange-red with following areas pale chestnut-yellow-orange: anterior and posterior lobe of metathoracic peritreme, posterior margin of metapleura, acetabulae, posterior border of pleural segments III to VII, and legs.

Measurements.—Male (mm). Head length 1.84; width across eyes 1.68; interocular space 1.20; preocular distance 1.36; length antennal segment: I, 1.28 (segments II–IV mutilated). Pronotum: total length 1.60, width across frontal angles 1.76; width across humeral angles 2.76. Scutellar length 1.00; width 1.32. Total body length 10.00.

Type Specimen.—Holotype, male (BMNH): MALAYA, BUKIT PALAS, Cameron Highlands, 5400 ft, 5 May 1939, N. C. E. Miller.

Etymology.—Referring to the appearance of the eyes in lateral view.

Baumannhygia, **new genus**
(Fig. 5, 8)

Diagnosis.—The reduction of wings, the membrane absent, the prominent postocular tubercle, the ocelli absent, the unarmed legs, and tibial sulcus difficult to see might suggest a relationship with *Grosshygioides* Brailovsky (1993). In *Baumannhygia*, n. gen., known only from Philippine Republic, the antenniferous tubercles are armed, the head slightly convex dorsally, mandibular plate unarmed, scutellar disc and hemelytra weakly punctate, hemelytra micropterous, and the pronotal disc flat. In *Grosshygioides*, described from Australia, the antenniferous tubercles are unarmed, the dorsal head flat, mandibular plate armed, scutellar disc and hemelytra strongly punctate, hemelytra staphylinoid, and the pronotal disc never flat.

Grosshygia Brailovsky (1993) like *Baumannhygia*, has the antenniferous tubercle armed, the mandibular plate unarmed, the eyes small and globular, postocular tubercle protuberant, pronotal disc nondeclivent, legs unarmed, tibiae with sulcus difficult to see, hemelytra micropterous, and the membrane absent. The two genera can be separated by the following combination of characters. In *Baumannhygia*, the head in dorsal view is slightly convex, buccula with small and blunt anterior projection, and callar region, including the pronotal and scutellar disc, flat. In *Grosshygia*, known from Australia, the head in dorsal view is conspicuously convex and raised above eyes, buccula rounded without teeth, callar region nodulose, and scutellar disc raised and convexly rounded.

Description.—Male. Head: quadrangular, wider than long, and dorsally slightly convex; tylus unarmed, apically globose, extending anteriorly to the jugae, and more raised in lateral view; jugae unarmed, thickened, and shorter than tylus; antenniferous tubercle armed with long robust spine; side of head in front of eyes unarmed and apically divergent; antennal segment I robust, thickest, slightly curved outward and shorter than head; segments II and III cylindrical and slender; segment IV fusiform; segment II longest; segment I longer than III; segment III subequal to IV; ocelli absent; preocellar pit deep; eyes small, globular; postocular tubercle protuberant; buccula rounded, short, not projecting beyond antenniferous tubercle, with small and blunt anterior projection; rostrum long, reaching posterior third of abdominal sternite V; mandibular plate absent.

Thorax: pronotum trapeziform, wider than long, nondeclivent; collar wide; frontal angles produced forward as rounded and globosus lobes; humeral angles rounded, not expanded; anterolateral borders obliquely straight and raised above pronotal disc; posterolateral borders straight, and posterior border slightly concave; pronotal disc flat. Anterior lobe of metathoracic peritreme reniform, posterior lobe sharp, small.

Legs: femora unarmed; tibiae with a vague longitudinal sulcus.

Scutellum: wider than long, triangular, with sharp apex; disc flat.

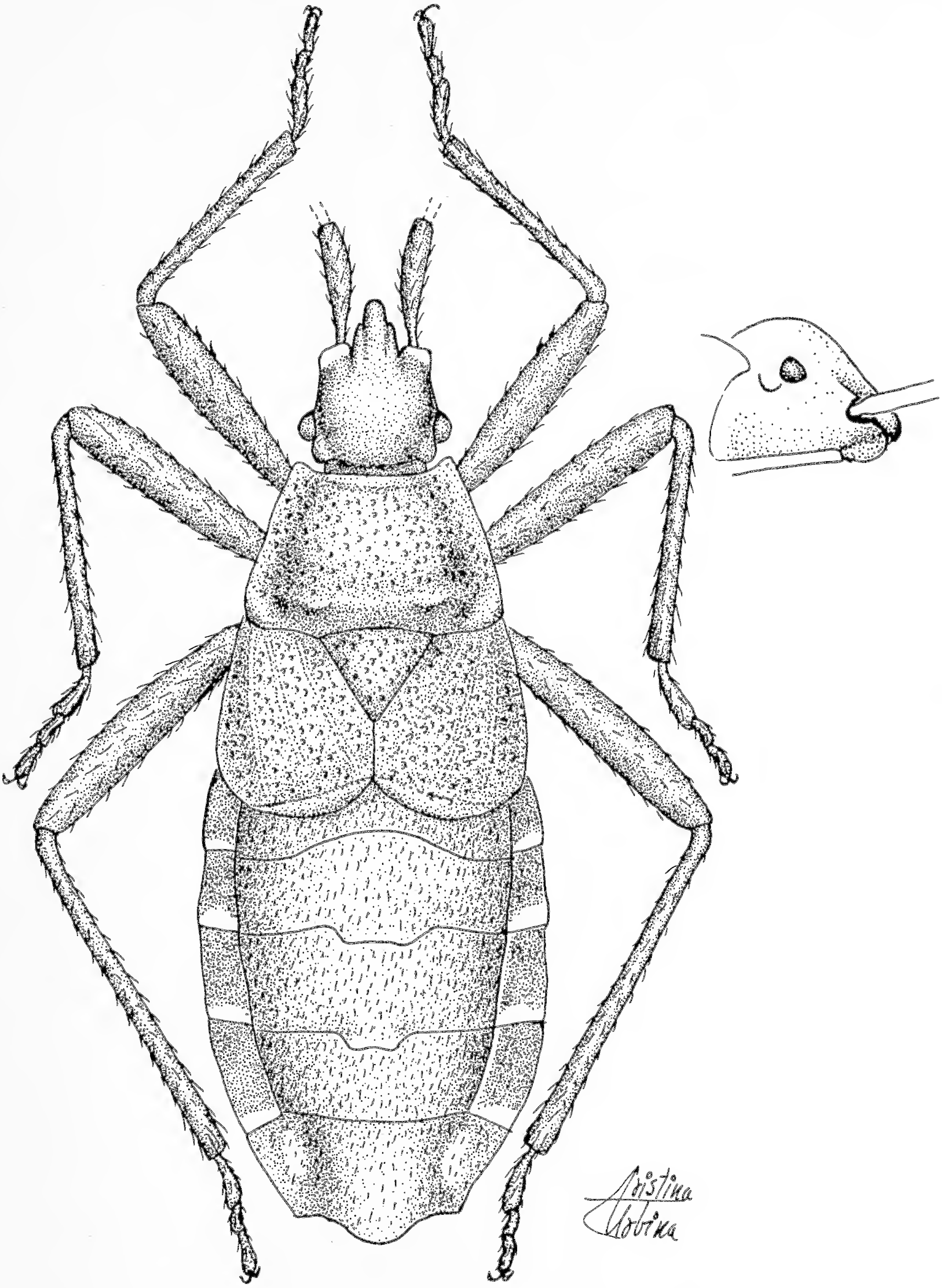


Fig. 7.—*Eludohygia parvioculata* Brailovsky, male.

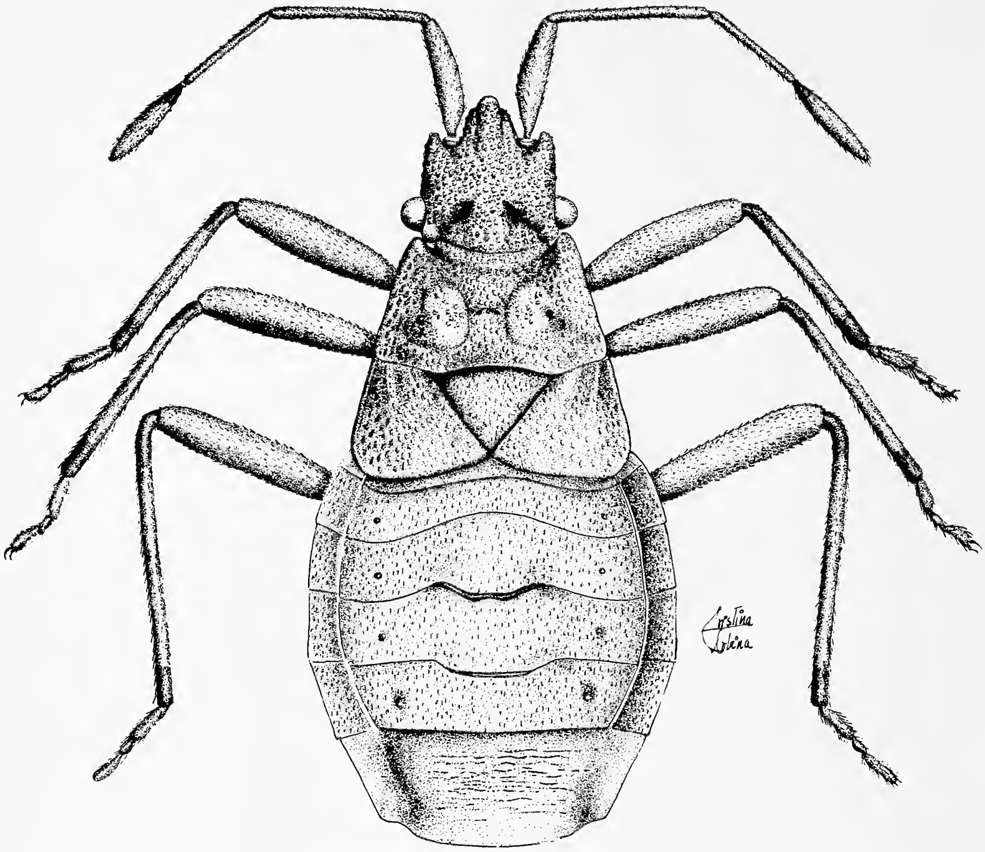


Fig. 8.—*Baumannhygia insulata* Brailovsky, male.

Hemelytra: micropterous reaching posterior third of abdominal segment II; wings reduced to small pads, separated from each other; clavus and corium fused; membrane absent.

Abdomen: connexival segments strongly elevated, higher than abdominal segments; angle of connexival complete; abdominal sternites with the medial furrow extending to middle third of sternite V.

Integument: mostly shining, with hemelytra, connexival segments, and dorsal abdominal segments dull. Head, thorax, abdomen, and exposed parts of genital segments strongly punctate; pronotum, scutellum, hemelytra, and connexival segments weakly punctate. Body with short decumbent silvery bristle-like hairs, intermixed with long erect setae located on the abdominal sternites, legs, and antennal segments.

Male genitalia: genital capsule: posteroventral edge with two large and robust lobes, with deep V-shaped notch (Fig. 5).

Female. Unknown.

Distribution.—Known only from the Philippine Republic.

Etymology.—I am please to name this new genus for Dr. Richard W. Baumann, distinguished American plecopterist. Gender feminine.

Type Species.—*Baumannhygia insulata,* n. sp.

Baumannhygia insulata, **new species**
(Fig. 5, 8)

Description.—Male. Dorsal coloration: head bright black; antennal segment I black, II and III dark red, and IV yellow-ocher with basal joint dark red; pronotum, scutellum, and hemelytra bright black with dark red reflections; connexival segments dull black with dark red reflections, except the posterior margin, and dorsal abdominal segments dark red. Ventral coloration: bright black with following areas bright brownish red: acetabulae, metapleura, abdominal sternite III to VII, and genital capsule; rostral segments I to IV bright orange-yellow; coxae bright red-brown; trochanters bright orange-yellow; femora dark red with basal joint bright orange-yellow; tibiae yellow with basal and apical joint dark red; tarsi pale chestnut-orange; anterior and posterior lobe of metathoracic peritreme dirty orange-yellow; pleural margin of abdominal sternite III to VII dark red with posterior border ocher-yellow.

Measurements.—Male (mm). Head length 1.78; width across eyes 1.96; interocular space 1.30; interocellar space 0.76; preocular distance 1.32; length antennal segments: I, 1.48; II, 204; III, 1.42; IV, 1.42. Pronotum: total length 1.48; width across frontal angle 1.80 mm; width across humeral angle 2.64. Scutellar length 0.92; width 1.08. Total body length 9.50.

Type Specimens.—Holotype, male (FMNH): PHILIPPINE REPUBLIC, DAVAO PROVINCE, Mindanao (Calian), 31 December (without year), C. S. Clagg. Paratype, one male (UNAM): PHILIPPINE REPUBLIC, DAVAO PROVINCE, Mindanao (Calian), 11 July (without year), C. S. Clagg.

Etymology.—This species is named for its island distribution.

ACKNOWLEDGMENTS

I thank the following colleagues and institutions for the loan of specimens and other assistance relevant to this study: Gordon M. Nishida (Bernice P. Bishop Museum, Honolulu, Hawaii); Janet Margerison (The Natural History Museum, London, United Kingdom); P. P. Parrillo (Field Museum of Natural History, Chicago, Illinois); G. B. Monteith (Queensland Museum, Brisbane, Australia). Ernesto Barrera and Cristina Urbina from Instituto de Biología, UNAM, prepared the illustrations. Special thanks to the Consejo Nacional de Ciencia y Technología (CONACyT) for financial assistance.

Comments on the manuscript from the anonymous reviewers are greatly appreciated.

LITERATURE CITED

BRAILOVSKY, H. 1990. Three new species of Indo-Pacific Colpurini (Hemiptera: Heteroptera: Coreidae). Pan-Pacific Entomologist, 66:292–300.

———. 1993*a*. New genera and new species of Colpurini (Heteroptera: Coreidae) from the Fiji Islands and New Guinea). Proceedings of the Entomological Society of Washington, 95:435–448.

———. 1993*b*. New genera and new species of micropterous Colpurini from Buru Islands and New Guinea (Heteroptera: Coreidae). Pan-Pacific Entomologist, 69:281–289.

———. 1993*c*. A revision of the tribe Colpurini from Australia (Hemiptera–Heteroptera–Coreidae). Memoirs of the Queensland Museum, 34:35–60.

BRAILOVSKY, H., AND G. ORTEGA LEON. 1994. Three new genera and six new species of Colpurini (Heteroptera: Coreidae) from New Guinea. Proceedings of the Entomological Society of Washington, 95:500–515.

BRAILOVSKY, H., E. BARRERA, AND W. LOPEZ-FORMENT. 1992. Revision of the genus *Tachycolpura* Breddin (Hemiptera: Heteroptera: Coreidae: Colpurini). Pan-Pacific Entomologist, 68:122–132.

ANNALS OF CARNEGIE MUSEUM

VOL. 65, NUMBER 4, PP. 393–399 27 NOVEMBER 1996

ON THE GENUS *ACANTHOLYBAS* BREDDIN (INSECTA: HETEROPTERA: COREIDAE: COLPURINI), WITH DESCRIPTION OF ONE NEW SPECIES FROM JAVA

HARRY BRAILOVSKY[1]
Research Associate, Section of Invertebrate Zoology

ABSTRACT

Acantholybas steinbaueri, a brachypterous new species, is described and illustrated from Java (Bali Island and Dammerman). The genus *Acantholybas* is redescribed, and a key to the four known species is provided.

INTRODUCTION

The genus *Acantholybas* was proposed by Breddin (1899) to include the species *A. longulus* collected from Lombok Island and later recorded from Sumbawa (Blöte, 1936). Subsequently Breddin (1900*b*) described the genus *Acanthocolpura* with one species, *A. brunneus,* from New South Wales, Australia, and in the same year (Breddin, 1900*a*) synonymized *Acanthocolpura* with *Acantholybas* and transferred *A. brunneus* to *Acantholybas.* Bergroth (1909) described *A. kirkaldyi* from Tasmania (Semmens et al., 1992).

Acantholybas belongs to the group of Colpurini with the abdominal sternite VII of the female complete, without plica or fissura, and has not been previously reviewed or revised. There are no keys or modern descriptions for any of the species except *A. brunneus* (Woodward, 1951, 1953, 1961; Wise, 1958*a,* 1958*b*; Brailovsky, 1993).

An examination of material representing *Acantholybas* spp. indicates that the critical differences between species are found in the development of the callar region, tylus, hemelytra, proportions of the antennal segments, and relative body size. This paper presents a summary of these comparisons.

The following abbreviations identify the institutions where types are deposited: BPBM, Bernice P. Bishop Museum, Honolulu, Hawaii; UNAM, Colección Entomológica del Instituto de Biología, Universidad Nacional Autónoma de México; ZIL, Zoological Institute, St. Petersburg, Russia.

SYSTEMATIC ENTOMOLOGY

Acantholybas Breddin
(Fig. 1–10)

Acantholybas Breddin, 1899:169–170.

Diagnosis.—*Acantholybas* Breddin is distinguished by the globose, apically truncated or bifid tylus, the armed antenniferous tubercle, the armed buccula with an obvious spine near the middle third, the unarmed femora and the abdominal sternite VII of female without plica or fissura. *Pachycolpuroides* Brailovsky

---

[1] Instituto de Biología, UNAM, Depto. de Zoología, Apdo. Postal 70153, México 04510 D. F. México. Submitted 31 March 1995.

(1993), the most closely related genus, may be recognized by its smaller size, rounded buccula without teeth or spiny projection, and shorter rostrum not extending beyond the anterior margin of the metasternum.

Redescription.—Head: pentagonal, wider than long (across eyes) and dorsally slightly convex; tylus unarmed, apically globose or bifid, extending anteriorly to the jugae and more raised in lateral view; jugae unarmed, thickened, and shorter than tylus; antenniferous tubercle armed, lobes raised, diverging anteriorly, and apically subacute; side of head in front of eye short, unarmed, and obliquely straight; antennal segment I robust, thickest or more or less slender, slightly curved outward and shorter than head; segments II and III cylindrical and slender; segment IV fusiform; segment II longest; segment I shorter; segment IV longer or shorter than III (Fig. 2–4); ocelli tuberculate, well developed; preocellar pit deep; eyes large, hemispherical, sessile; postocular tubercle protuberant; buccula rounded, short, not projecting beyond antenniferous tubercle, with sharp spiny projection; rostrum reaching posterior third of abdominal sternite IV or anterior third of V; mandibular plate absent.

Thorax: pronotum wider than long, nearly trapeziform, slightly bilobed, and nondeclivent; anterior lobe shorter than posterior lobe, both with lateral margins convexly rounded, not elevated, and slightly reflexed; collar wide; frontal angles produced forward as conical lobes; humeral angles rounded; posterolateral border straight and posterior border slightly concave; callar region transversely convex with or without median longitudinal depression. Anterior lobe of metathoracic peritreme reniform, posterior lobe sharp, small.

Legs: femora unarmed; tibiae sulcate.

Scutellum: longer than wide, wider than long, or equilateral; triangular, with the apex rounded or subacute and raised or not above disc; disc nearly flat.

Hemelytra: macropterous forms with hemelytral membrane well developed, extending to the apex of abdomen or beyond. Brachypterous forms with clavus and corium distinctly separate; hemelytral membrane reduced, reaching the third abdominal segment; wings widely separated from each other, leaving the abdomen exposed mesally.

Abdomen: connexival segments higher than abdominal segments, with posterior angle not produced into spines; abdominal sternites with medial furrow extending to anterior third of sternite V.

Integument: body surface mostly dull, with head, thorax, and abdomen slightly shining. Pronotum, scutellum, clavus, corium, dorsal abdominal segments, ventral surface of head, thorax, abdominal sterna, and genital capsule strongly punctate. Dorsal surface of head with scattered punctures and connexival segments practically smooth. Body with short, decumbent, silvery bristle-like setae, intermixed with long erect setae located on the abdominal sterna, legs, and antennal segments.

Male genitalia: genital capsule: posteroventral border broadly rounded, with a large internal emargination (Fig. 5). Parameres: body robust, with anterior lobe convex, and posterior lobe long (Fig. 6–7, variation for the different view).

Female genitalia: abdominal sternite VII complete, without plica or fissura. Genital plates: gonocoxa I oblique, with a convex and protruding external margin, slightly emarginate; paratergite VIII short, square, with visible spiracle; paratergite IX squarish, larger than paratergite VIII (Fig. 8–9).

Distribution.—*Acantholybas* species have been collected from Lombok Island (Indonesia), Australia, Tasmania, New Zealand, and now recorded from Java.

Type Species.—*Acantholybas longulus* Breddin.

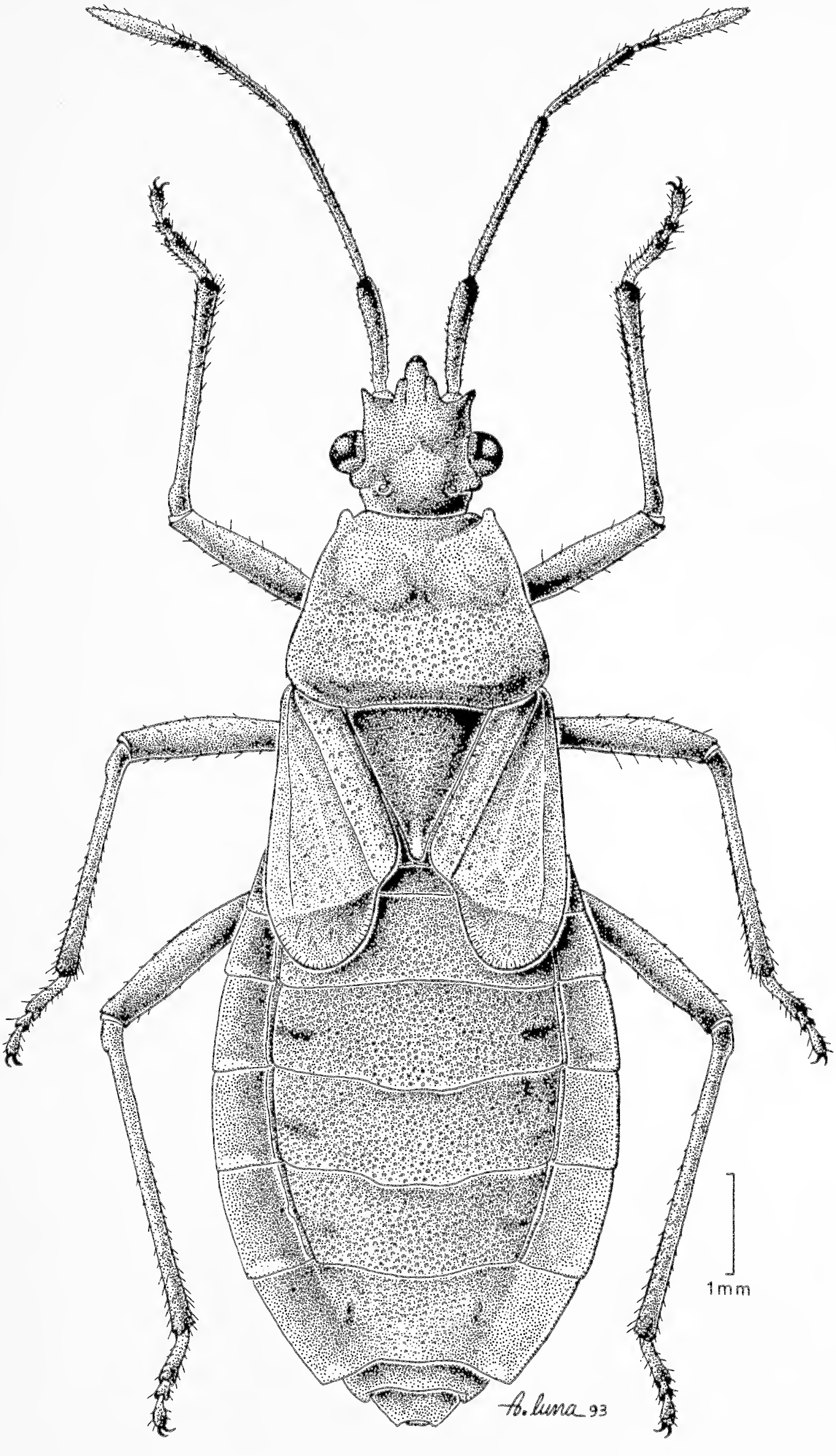
Acantholybas steinbaueri, **new species**
(Fig. 1–2, 5, 8–9)

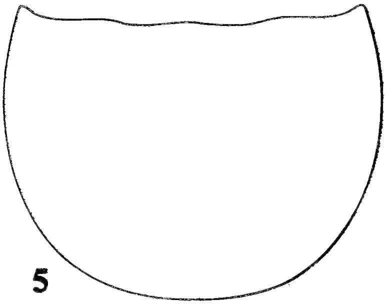
Description.—Color, male. Head: anterior lobe of the pronotum, scutellum, connexival segments, dorsal abdominal segments, thorax, and abdominal sterna bright to dark red-brown with dark orange reflections; apex of scutellum and anterior and posterior lobe of metathoracic peritreme yellowish white to pale yellow; antennal segments I–III dark orange-brown with reddish brown reflections; segment IV pale yellow with proximal end dark orange-brown; posterior lobe of pronotum, clavus, and corium dark to pale orange-yellow; rostral segments dark orange-brown with basal segment paler; superior area of the postocular tubercle, posterior edge of connexival segments IV–VI, and posterior

---

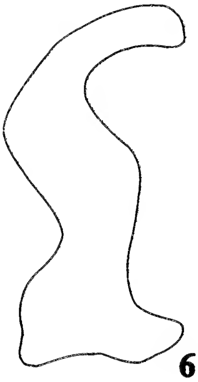
→

Fig. 1.—*Acantholybas steinbaueri* Brailovsky, new genus, new species; female.

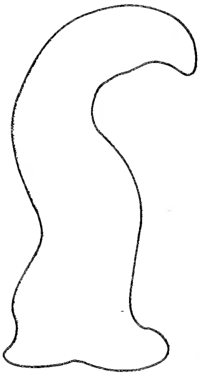

1mm
A. luna 93



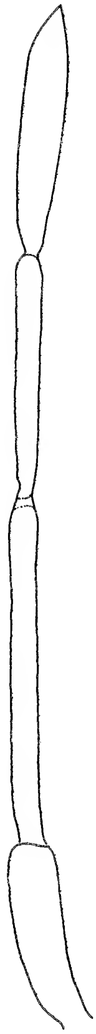
5



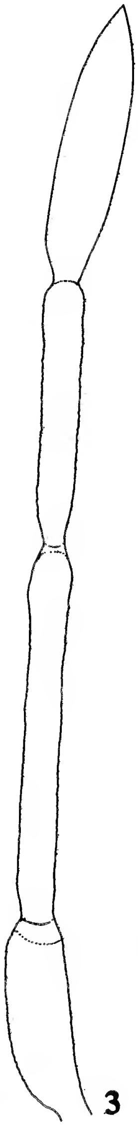
6



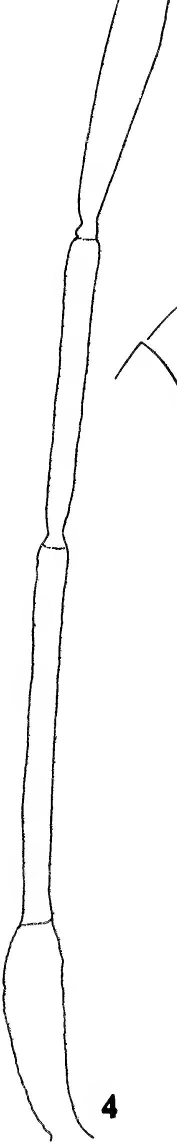
7



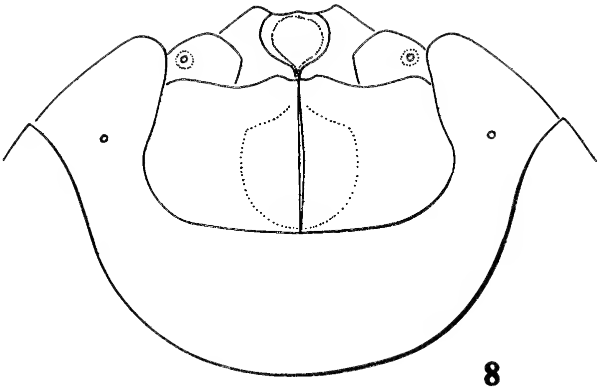
2



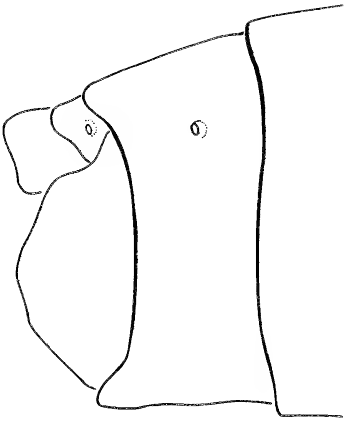
3



4



8



9

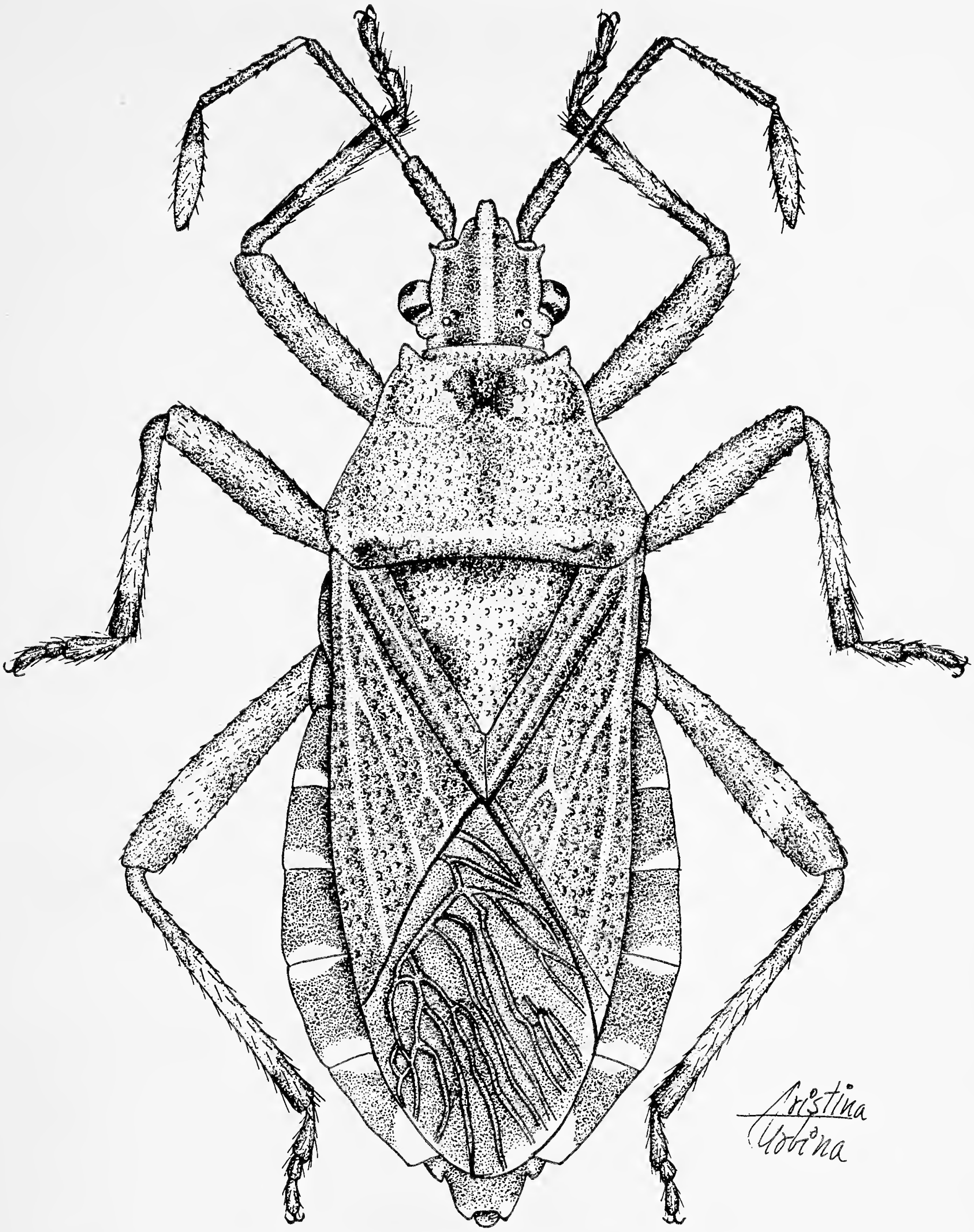


Fig. 10.—*Acantholybas brunneus* (Breddin); female.

←

Fig. 2–9.—Antennae and genitalia of *Acantholybas*. 2, antennal segments of *A. steinbaueri* Brailovsky; 3, antennal segments of *A. kirkaldyi* Bergroth; 4, antennal segments of *A. brunneus* (Breddin); 5, male genital capsule of *A. steinbaueri* Brailovsky; 6–7, parameres of *A. brunneus* (Breddin); 8–9, female genital plates of *A. steinbaueri* Brailovsky; 8, caudal view; 9, lateral view.

edge of pleural sterna IV–VI yellow; coxae dark reddish brown with orange reflections; trochanters dark orange-brown with dorsal face pale yellow; anterior and middle femora dark orange-brown; posterior femora dark orange-brown with a wide yellow ring located on the middle third; tibiae dark orange-brown; tarsi with dorsal surface dark orange-brown, and ventral surface pale yellow.

Color, female. Similar to male.

Structure. Head: tylus apically globose; antennal segment III shorter than IV. Pronotum: callar region transversely convex, with or without a vague, difficult-to-see, median longitudinal depression. Scutellum: wider than long (male) and longer than wide (female). Hemelytra: brachypterous, with the membrane reaching the third abdominal segment.

Measurements.—Male, female (mm). Head length 1.32, 1.46; width across eyes 1.48, 1.60; interocular space 0.90, 0.96; interocellar space 0.46, 0.51; preocular distance 0.86, 0.94; length antennal segments: I, 0.88, 1.04; II, 1.44, 1.56; III, 1.00, 1.08; IV, 1.08, 1.16. Pronotum: total length 1.52, 1.84; width across frontal angles 1.56, 1.48; width across humeral angles 2.40, 2.56. Scutellar length 1.04, 1.32; width 1.08, 1.24. Total body length 8.40, 9.90.

Type Specimens.—Holotype, male (BPBM): JAVA, Bali I., Dadjan Danu, 29 March 1956, J. Winkler. Paratypes: one female (UNAM), data as for holotype; one male (ZIL), Dammerman, Idjen Kendeng, 1400 m, 15 June 1924 (no. 68-III).

Etymology.—Named for Martin James Steinbauer in recognition of his recent rediscovery of *Acantholybas kirkaldyi* Bergroth.

KEY TO THE KNOWN SPECIES OF *ACANTHOLYBAS*

1 Brachypterous, with the wings widely separated from each other, leaving the abdomen exposed mesally; hemelytral membrane reduced, reaching the third abdominal segment (Fig. 1) (Java) . . . . *A. steinbaueri,* new species
1′ Macropterous; hemelytral membrane well developed, reaching the apex of the abdomen (Fig. 10) 2

2 Antennal segment I longer than 1.00 mm; antennal segment II longer than 1.90 mm. (Lombok Island) . . . . *A. longulus* Breddin
2′ Antennal segment I shorter than 0.90 mm; antennal segment II shorter than 1.60 mm. (Fig. 3, 4) 3

3 Antennal segment I robust; body robust and longer than 10.20 mm; scutellum wider than long or equilateral (Tasmania) . . . . *A. kirkaldy* Bergroth
3′ Antennal segment I slender; body slender and shorter than 10.00 mm; scutellum longer than wide (Fig. 10) (Australia and New Zealand) . . . . *A. brunneus* (Breddin)

ACKNOWLEDGMENTS

I am grateful to the following individuals and institutions for the loan of specimens and other assistance: Gordon M. Nishida (BPBM); Tamas Vasarhelyi (Hungarian Natural History Museum); G. B. Monteith (Queensland Museum, Brisbane, Australia); Margaret Schneider (University of Queensland, Brisbane, Australia); I. M. Kerzhner (ZIL). Ernesto Barrera, Albino Luna, and Cristina Urbina (UNAM) prepared the illustrations. Special thanks to the Consejo Nacional de Ciencia y Tecnología (CONACyT) for financial assistance.

Comments on the manuscript from the anonymous reviewers are greatly appreciated.

LITERATURE CITED

BERGROTH, E. 1909. Hemiptera Nova Orientalia. Annales de la Société Entomologique de Belgique, 53:184–190.

BLÖTE, H. C. 1936. Catalogue of the Coreidae in the Rijksmuseum van Natuurlijke Historie. Part III. Coreinae, Second part. Zoologische Mededeelingen, 19:23–66.

BRAILOVSKY, H. 1993. A revision of the tribe Colpurini from Australia (Hemiptera–Heteroptera–Coreidae). Memoirs of the Queensland Museum, 34:35–60.

BREDDIN, G. 1899. Hemiptera Insulae Lombok in Museo Hamburgensi asservata adiectis speciebus nonnullis, quas continet collectio auctoris. Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten, 16:155–194.

———. 1900*a*. Materiae ad cognitionem subfamiliae Pachycephalini (Lybantini Olim) ex Hemipteris–Heteropteris, Fam. Coreidae. Revue d'Entomologie, Caen, 19:194–217.

———. 1900*b*. Hemiptera nonnulla regionis Australicae (figuris duodecim illustrata). Entomologische Nachrichten (Berlin), 26:33–46.

SEMMENS, T. D., P. B. MCQUILLAN, AND G. HAYHURST. 1992. Catalogue of the Insects of Tasmania. Department of Primary Industry, Hobart, Tasmania.

WISE, K. A. J. 1958*a*. Notes on insects pests, 1956–57. New Zealand Entomologist, 2:26–28.

———. 1958*b*. Notes on insects pests, 1957–58. New Zealand Entomologist, 2:12–14.

WOODWARD, T. E. 1951. The occurrence of *Acantholybas brunneus* Breddin in New Zealand (Heteroptera: Coreidae). Transactions of the Royal Society of New Zealand, 79:206–209.

———. 1953. Notes on *Acantholybas brunneus* Breddin (Heteroptera: Coreidae). New Zealand Entomologist, 1:8–9.

———. 1961. The Heteroptera of New Zealand. Part III. Coreidae, Berytidae, Tingidae, Cimicidae. Transactions of the Royal Society of New Zealand, 1:145–158.

INDEX TO VOLUME 65

CONTENTS

ARTICLES

REVIEW

NEW TAXA

NEW FAMILIES, GENERA, AND SPECIES

† Fossil taxa

AUTHOR INDEX

INSTRUCTIONS FOR AUTHORS

ANNALS OF CARNEGIE MUSEUM consist of contributions to the earth sciences (including paleontology), life sciences, and anthropology, in 30 by 46 picas format (127 by 195 mm or 5 by 7⅝ inches). Submit all manuscripts to the Office of Scientific Publications. Authors should give particular attention to scientific content, format, and general style for the ANNALS. **Manuscripts that do not conform to the style of the ANNALS will be returned to the author immediately.** Every manuscript will be subjected to external peer review. Authors should submit the names, addresses, phone and fax numbers, and e-mail addresses of at least four qualified potential reviewers for each manuscript. Authors will be asked to subsidize, if funds are available, any or all costs of publication (approximately $100/page printed). A detailed set of instructions to authors may be requested from the Office of Scientific Publications.

Manuscript Style.—Articles should include the following items in this order: title page, abstract, text (with desired headings), acknowledgments, literature cited, tables, figure captions, and copies of illustrations. All manuscripts must be typed ***double-spaced*** on standard 8½ by 11-inch white bond paper, with at least one-inch margins all around, and submitted ***in quadruplicate***—an original for the editors, and three review copies. All pages should be numbered, including tables, literature cited, and the list of figure captions. Only correspondence quality or better dot matrix printouts will be accepted; draft mode is unacceptable. A monospaced font, (e.g., Courier) is required. A disk in WordPerfect x.x or ASCII is helpful.

Title Page. The title should be brief, include the animal or plant group involved, be placed on a separate page, and appear two to three inches below the top margin. Include the author's name(s) and the affiliations of non-CMNH authors. In the case of multiple authorship, indicate the address to which proofs should be sent.

Abstracts. Abstracts should be short, but substantive, and included at the head of the first page of text.

Text. Do not right justify text or break (hyphenate) a word at the end of a line. ***Footnotes and acknowledgments as footnotes are unacceptable.*** All text is double-spaced in a monospaced font (e.g., Courier).

Tables and Figure Legends. The list of figure legends and each table should be typed consecutively on individual pages separate from the text. Tables must be double-spaced throughout with **no vertical lines**.

Measurements. Metric units should be used, if possible.

Literature Cited. All references to literature in text must appear in the Literature Cited section. The data (author, date, and page) in both citations must agree. ***Do not abbreviate the titles of periodicals or serials.*** The following style, double-spaced, should be used in Literature Cited:

1) Two authors in a journal series:
   SOLTIS, D. E., AND P. S. SOLTIS. 1992. The distribution of selfing rates in homosporous ferns. American Journal of Botany, 79:97–100.
2) Same authors repeated—use three-em dash:
   ———. 1923. The fauna of the Ardyn Obo Formation. American Museum of Natural History Novitates, 98:1–5.
3) Same authors plus a third author—repeat all authors:
   KNUTSON, L. V., R. E. ORTH, AND W. L. MURPHY. 1986. Catalog of Sciomyzidae (Diptera) of America north of Mexico. Entomography, 4:1–53.
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. Metheuen and Co., Ltd., London, United Kingdom.
7) Journal articles with usual volume and issue number:
   ANDERSON, W. I. 1969. Lower Mississippian conodonts from northern Iowa. Journal of Paleontology, 43:916–928.

Figures. Including all illustrative materials (line art, halftones, photographs), figures are to be numbered in Arabic numerals. Four sets of figures are required, one (original artwork) for reproduction, three for reviewers. Photocopies of photographs for reviewers are usually not acceptable but are adequate for line drawing review copies. Figures may not be larger than 17 by 12 inches. Reducing figures is the responsibility of the author. All figures must be reducible to a maximum of 127 by 195 mm (30 by 46 picas) without loss of clarity. Line copy should be designed for reduction to ⅔ or ½ or actual size. Typewritten figure copy will not be accepted. Photographic figures should be submitted at **actual reproduction size**, if possible.

Rectangular halftone figures should be abutted, without intervening spaces. The printer will insert narrow white spaces during the reproduction process. All figures must have **minimally** one-inch borders all around. Each figure should be given a protective cover and identified on the back side.

Lettering and/or a magnification scale (linear metric scale) for rectangular halftone figures should be placed directly on the photo, not in a blank space between photos. The scale or lettering for closely cropped photos can be placed in blank areas close to the figure.

Proof.—The author should answer all queried proof marks and check the entire proof copy. Return corrected page proof with the edited manuscript ***promptly*** to the Office of Scientific Publications.

If an author chooses to make extensive alterations to a paper in proof stage, the author will bear the cost. Original manuscripts will not be returned unless requested. Figures will be returned to the author only if requested prior to publication.