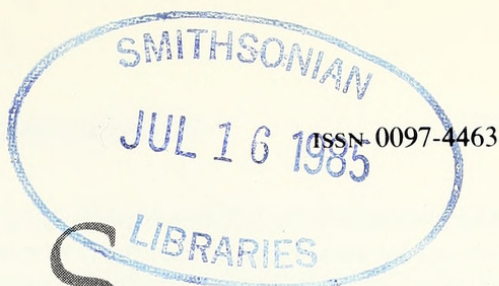


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ECOLOGY, POSTNATAL DEVELOPMENT, MORPHOMETRICS, AND TAXONOMIC STATUS OF THE SHORT-TAILED OPOSSUM, *MONODELPHIS DIMIDIATA*, AN APPARENTLY SEMELPAROUS ANNUAL MARSUPIAL

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ABSTRACT

Field data for *Monodelphis dimidiata* were collected from trapping sites near Balcarce, Buenos Aires Province, Argentina. Fallow pastures and native grasslands were live-trapped and snap-trapped as part of a rodent population dynamics study, extending from December 1968 to April 1970. The opossums represented only several percent of the total small mammal community captured each month. The greatest number were captured in the autumn (March–May), coinciding with the dispersal of the young. The animals were diurnal, with most of the activity concentrated in the late afternoon. Rarely were the opossums captured more than once. The species appears to be predominately

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insectivorous; it is not believed to be a major predator of rodents. Litters were documented for two summer months (December–January), with a high of 16 young recorded for one litter. Data on postnatal development were recorded for a limited number of young during the first five weeks after birth, close to the time of eye opening. Morphometric data from lab and field animals, and skull measurements show that the young developed rather slowly through the cooler months, whereas spring growth, especially in the males, increased drastically, with sexual maturation occurring in both sexes by summer.

Monodelphis dimidiata is shown to be an apparently semelparous and annual species. Temporal distribution of age group classes and patterns of non-geographic variation provide the primary support for this conclusion. In keeping with its apparent reproductive strategy, *M. dimidiata* shows extreme sexual dimorphism. Non-geographic variation is documented. The differences between the sexes in *M. dimidiata* and certain other *Monodelphis* have sometimes resulted in taxonomic problems, noted herein. Previously confounded with *M. henseli* (probably = *M. sorex*), *M. dimidiata* seems to be known with certainty only from Argentina and Uruguay. Although sometimes regarded as conspecific with *M. fosteri*, conspecificity has not been demonstrated.

INTRODUCTION

The New World marsupial genus *Monodelphis* Burnett contains from 14 to 18 species (genus under revision by Handley and Pine) and occurs from eastern Panamá to Argentina. Habitats range from tropical rain forest to xeric grassland. Except for *M. domestica* (Streilein, 1982a, 1982b), little else is known concerning these small, terrestrial, pouchless opossums.

Animals identified as *Monodelphis dimidiata* (Wagner) have been reported from southern Brazil, Paraguay, Uruguay, and much of the grassland of Argentina (Bertoni, 1939; Cabrera, 1958; Reig, 1964). Although several authors have contributed anecdotal notes on its natural history, only Reig (1964, 1965) added substantially to our knowledge of the species. Our report covers several aspects of the natural history, non-geographic variation, and the taxonomic history of *M. dimidiata*.

METHODS AND MATERIALS

A study area was located in the grasslands near Balcarce, Buenos Aires Province, Argentina. Dalby (1975) described the area and trapping procedures.

Over 30,000 trap nights were tallied in the Balcarce area in a period extending from December 1968 to April 1970. Sherman live traps (75 by 75 by 227 mm) were placed on two 1.2 hectare grids (10 by 10 with 12 m trap spacing). One grid was in a fallow pasture and the other was on a slope covered with native grasses. Each study plot was trapped for a three-day period every other week. Adjacent to the large grid in the fallow pasture was a smaller one (0.70 hectares, 7 by 7, 12 m spacing) which was live-trapped every three hrs, day and night, for three days (72 hrs), once a month for 13 months to determine activity patterns for small mammals. Roadside ditches were also trapped with live traps or with Museum Special snap traps in conjunction with another study. It was only in the last habitat that *Monodelphis* could be captured with any regularity, generally where the grasses and associated forbs were dense. Other areas containing *Monodelphis*

dimidiata were described by Reig (1964), Fornes and Massoia (1965), and Massoia and Fornes (1967).

Some short-tailed opossums were maintained in captivity for various periods of time. They were housed in solid-bottomed rodent cages (ca. 30 by 30 by 50 cm), provided with wood shavings, and fed mainly bird and mammal road kills and snap-trapped mice. Water was provided *ad libitum*. These captives provided the opportunity to record data on growth and postnatal development.

Skins and skulls representing 41 wild-caught individuals and deposited in The Museum, Michigan State University, were used in the analysis of non-geographic variation. These specimens from the Balcarce area were assigned to six relative age classes somewhat similar to those described by Gardner (1973) for *Didelphis*. We had no specimen of Gardner's "age class 1" (M2 not completely erupted). Our age classes were as follows: age class 2, M2 and m2 in position, M3 and m4 may be erupting but are not in position; age class 3, M3 in position and milk (deciduous) premolars not being replaced; age class 4, m4 in position, permanent PM3 erupted but not fully in place; age class 5, all permanent teeth erupted but M4 with little or no wear; age class 6, M4 with moderate wear, m4 with little or no wear; age class 7, M4 with heavy wear, m4 with moderate to heavy wear. Data from captives were pooled with those from animals killed when trapped.

External measurements were taken in the field and laboratory according to the North American system (ear to notch, hind foot including claw). All skull measurements were taken with dial calipers reading to the nearest twentieth of a millimeter. Some of the skull measurements correspond to those used by Tate (1933) for *Marmosa* and by Gardner (1973) for *Didelphis*. Measurements of tooththrows and mandibles were taken on the left side except when correct measurements were attainable only on the right side. The measurements were:

Skull length.—The greatest linear measurement attainable.

Condylolincisive length.—From the anteriormost projection of the incisors to a line through the posteriormost projections of the occipital condyles.

Palatal length.—From the anteriormost projection of the incisors to the posteriormost point on the midline of the palate.

Greatest nasal length.—Greatest length of the longer nasal.

Zygomatic breadth.—Greatest dimension from the outside (lateral) edge of one zygomatic arch to that of the other—a measurement perpendicular to the sagittal plane of the skull.

Postzygomatic braincase width.—Least width of skull taken posterior to posterior roots of zygomatic arches and anterior to lateral expansion of lambdoidal crests.

M3–M3.—The greatest distance between the most lateral point on the right upper third molar and the corresponding point on the left upper third molar.

Maxillary tooththrow.—From the anteriormost projection of an upper canine to the posteriormost projection of the fourth upper molar on the same side of the skull.

M1–M4.—From the anteriormost point on the first upper molar to the posteriormost point on the fourth upper molar on the same side of the skull.

Postorbital constriction.—Least distance between lines perpendicular to horizontal planes of skull and which touch the lateral margins of the skull in the postorbital region posterior to the lateral expansions of the frontals.

Mandibular depth.—Depth of mandibular ramus immediately behind the fourth lower molar.

Length of ramus.—Distance between anteriormost projection of first lower incisor and the posteriormost point on the mandibular condyle of ramus bearing that tooth.

Mandibular tooththrow.—From anteriormost point on first lower incisor to posteriormost point on fourth lower molar (both points on teeth of a single mandibular ramus).

Specimens examined (USNM = National Museum of Natural History, Smithsonian Institution; MSU = The Museum, Michigan State University; FMNH = Field Museum

of Natural History).—MONODELPHIS HENSELI [probably = *M. sorex* according to Handley (personal communication)]. *Brazil*: Minas Gerais: Passos (20°43'S, 46°37'W), 428 m, 1 ♂ (USNM 304594). Rio de Janeiro: "Campo Bello" = Itatiaia (=Itatiaia at 22°30'S, 44°34'W), 1 ♂ (USNM 461068—the holotype of *P[eramys]. d[imidiata]. itatiayae* A. de Miranda-Ribeiro). São Paulo: Boracéia: Casa Grande, ca. 20 k S Salesópolis (the last is at 23°32'S, 45°51'W), 1 ♂ (USNM 460504). São Paulo: Ribeirão da Lagoa (also ca. 20 k S Salesópolis), 1 ♂ (USNM 484016). MONODELPHIS DIMIDIATA. *Argentina*: Buenos Aires Prov.: Partido Balcarce: Estación Experimental del Instituto Nacional de Tecnología Agropecuaria (INTA), ca. 15 k NW Balcarce (Balcarce at 37°51'S, 58°16'W) and nearby, ca. 100–150 m: "INTA," 4 sex? (MSU 20247–20250); "INTA/ditch near buildings," 1 ♀ (MSU 17675); "INTA property in overgrown pasture," 1 ♀ (MSU 17586); "INTA, in ditch (grass tall) near buildings," 1 ♂ (MSU 17674); "INTA area, Ruta 226, ditch," 5 ♂♂ (MSU 18520–18522, 18524, 18525); "Ruta 226 ditch, 1 km west of INTA gate," 1 ♂ (MSU 18262); "near INTA, Ruta 226, Km 74, ditch," 1 ♂, 2 ♀♀ (MSU 18339, 19182, 19193); "roadside trapping near INTA entrance," 1 ♂ (MSU 17887); "Ruta 226 ditch, Km 74," 1 ♀ (MSU 18699); "ditch along INTA side along Ruta 226 Km 68," 1 ♂ (MSU 18789); "in ditch along Ruta 226, approx. Km 78," 1 ♀ (MSU 18691); "ditches along Ruta 226 between Km 65–75," 2 ♂♂, 2 ♀♀ (MSU 19227–19230); "ditch along Ruta 226," 3 ♀♀ (MSU 18579, 18698, 18699); "Hill Plot," 150 m, 1 ♀ (MSU 19834); Prov. Buenos Aires: Partido Balcarce, "Crovetto Field," ca. 6 k N Balcarce (Balcarce at 37°51'S, 58°16'W), 100 m, 6 ♂♂, 6 ♀♀, 1 sex? (MSU 17469, 17470, 17599, 17641, 18573, 18652, 18781, 19317, 19335, 19596, 19697, 19699, 20036); Pergamino (33°53'S, 60°36'W), Ruta 188, Curva de Peña, 1 ♀ (FMNH uncataloged).

NATURAL HISTORY

Ecology and Behavior

Knowledge of *M. dimidiata* is limited, in part because the species seems to occur at low densities. Snap-trapping in a nearby *partido* (county) over a number of months in 1963 and 1964, and in a number of habitats, Reig (1965) noted that of 550 animals trapped, slightly less than 6% consisted of this species, a result comparable to ours. Of 32 (17 ♂♂, 15 ♀♀) individuals trapped from December 1968 through all of 1969, the greatest number were captured in the autumn (March–May), coinciding with the dispersal of the young. Breaking down captures by month gives: *Summers* (complete summer of 1968–69 plus December of 1969), 5 + 4 (December 1968, 3; January, 1; February, 1; December 1969, 4—one study plot designated "Activity Plot" not in operation during these times); *Autumn* of 1969, 19 (March, 7; April, 5; May, 7); *Winter* of 1969, 6 (June, 3; July, 0; August, 3); *Spring* of 1969, 9 (September, 0; October, 1; November, 8). Because some animals were captured more than once, the above figures total more than 32.

As determined through use of the Activity Plot, the animals were active from late morning to dusk, with most of the activity concentrated in the late afternoon. Seven captures (18.4%) occurred between 9:30 AM and 12:30 PM; 11 captures (36.9%) between 12:30 PM and 3:30 PM; 17 captures (44.7%) between 3:30 PM and 6:30 PM. No attempt was made to analyze possible seasonal changes in activity because no

animals were captured during five months (December–February, July, and September) and only two were captured in October and November. Autumn through early winter (March–June) provided most of the captures.

Although Talice et al. (1960) found captive Uruguayan *M. dimidiata* to be nocturnal, under field conditions at Balcarce this was not the case. Fornes and Massoia (1965) trapped for several days in August 1963 near where Reig (1964, 1965) did most of his trapping, and captured six *M. dimidiata*. Checking their trap lines continuously during the day, and twice at night, they captured one specimen at about 1:00 PM, three at about 3:00 PM, one at 5:30 PM, and one at about 7:00 PM. The last-mentioned animal was captured near dusk or shortly after. Hunsaker and Shupe (1977) treated the Didelphidae as a whole as nocturnal. That at least one species of *Monodelphis* is diurnal, in at least part of its range, is of interest. The available data, however, concern only captures made in the spring, autumn, and winter. In the same area, the rodent *Akodon azarae* is more diurnal during winter than in summer, and this might also hold for *M. dimidiata*.

Rarely were the opossums captured more than once. Out of the 32 animals captured in the study plots, 23 were captured but once, seven twice, one thrice, and one eight times. The adult female captured three times was captured on C7 of the Hill Plot study grid on 5 November, again on 20 November, then at B5 on 18 December. The opossum captured eight times was a subadult female inhabiting the Activity Plot. She was captured on 20 March at A7, 18 April at C7 and D6, 17 May at D6 and F6, 14 June at B6 (twice), and 8 August at G6. During the approximately five-month winter period, her weight fluctuated between 12–15 g.

All *M. dimidiata* reported in this study were captured in traps baited with rolled oats. Captives were fed fresh meat, and occasionally young and adult live mice (*Mus musculus*) were offered. Female *M. dimidiata*, in particular, hesitated to kill adult mice (10–25 g in weight) and some would not attack the mice at all. After some hesitancy, most females would kill young mice. The males were more aggressive and showed little or no hesitation in killing mice, although some showed hesitancy and inexperience in killing the first one or two offered. Bertoni (1914), in writing of Paraguayan animals he identified as "*Peramys brevicaudatus* (Erxl.)" stated, "*A esta especie y congeneres las observé cazando ratas más grandes que ellas*" (This species and its congeners have been observed hunting rats larger than themselves). The reader is also referred to Bertoni, 1939, and Cabrera and Yepes, 1940, but should see Azara (1801, 1802) for somewhat different observations.

Predation upon small rodents was mentioned by Walker et al. (1975) and Hunsaker (1977) for *Monodelphis*. Although some of the Balcarce

M. dimidiata ate captive mice, particularly juvenile mice, we question whether *M. dimidiata* is an important predator of rodents. Talice et al. (1960) noted, as Dalby did in the present study, that when mice (*Mus musculus*) were introduced into an opossum cage, some opossums dispatched them right away. In other cages, however, the opossum and mouse lived together, even to sharing the same nest. Talice et al. made no mention of the sex(es) of the opossums in these encounters. If under natural conditions *M. dimidiata* is a predator on rodents, then we assume that most of the predation would be by males, and probably most of that on juveniles and nestlings.

In late summer, a moth caterpillar (family Arctiidae), feeding on the umbellifer *Eryngium paniculatum*, was common in the area. In size and appearance, these caterpillars were much like the North American woolly bear caterpillar [also an arctiid, *Isia isabella* (Smith)]. Once when one of these caterpillars was given to an opossum, it grabbed the caterpillar and rolled it with its forefeet for a minute or two. After most of the hairs were off, the opossum ate it. The manipulative handling of caterpillars during the dehairing process apparently has not been reported for other opossums. This behavior is known for other mammals (for example, skunks, *Mephitis mephitis*; Knight, 1917, and Schmidt, 1936).

Darwin (in Waterhouse, 1839) wrote that his specimen from Maldonado, Uruguay "Was caught by some boys digging in a garden. Its intestines were full of the remains of insects, chiefly ants and others of the Hemipterous order."

Talice et al. (1960) mentioned that, when handled, their captive animals urinated. Dalby (present study) noted that when they were agitated, such as when an intractable individual was handled, defecation could be expected. Talice et al., and Dalby as well, heard sharp, short, repeated barking sounds, particularly when an animal was disturbed. Gaping, also characteristic of other didelphids, was frequently seen. When handled often, these opossums become quite docile. A number of animals became tame to the point where they could be handled safely. Hunsaker and Shupe (1977) reported taming in response to frequent handling in *Didelphis virginiana* and *Marmosa* sp.

Litter Size, Time of Birth, and Postnatal Development

Females with young were captured only in the roadside ditches, which were irregularly trapped. The ditches, with their more mesic conditions and denser vegetation, probably contained higher numbers of *Monodelphis* than the study plot locations.

Four females gave birth in captivity. The earliest litter (16 young) of the season was found the morning of 13 December 1969, and be-

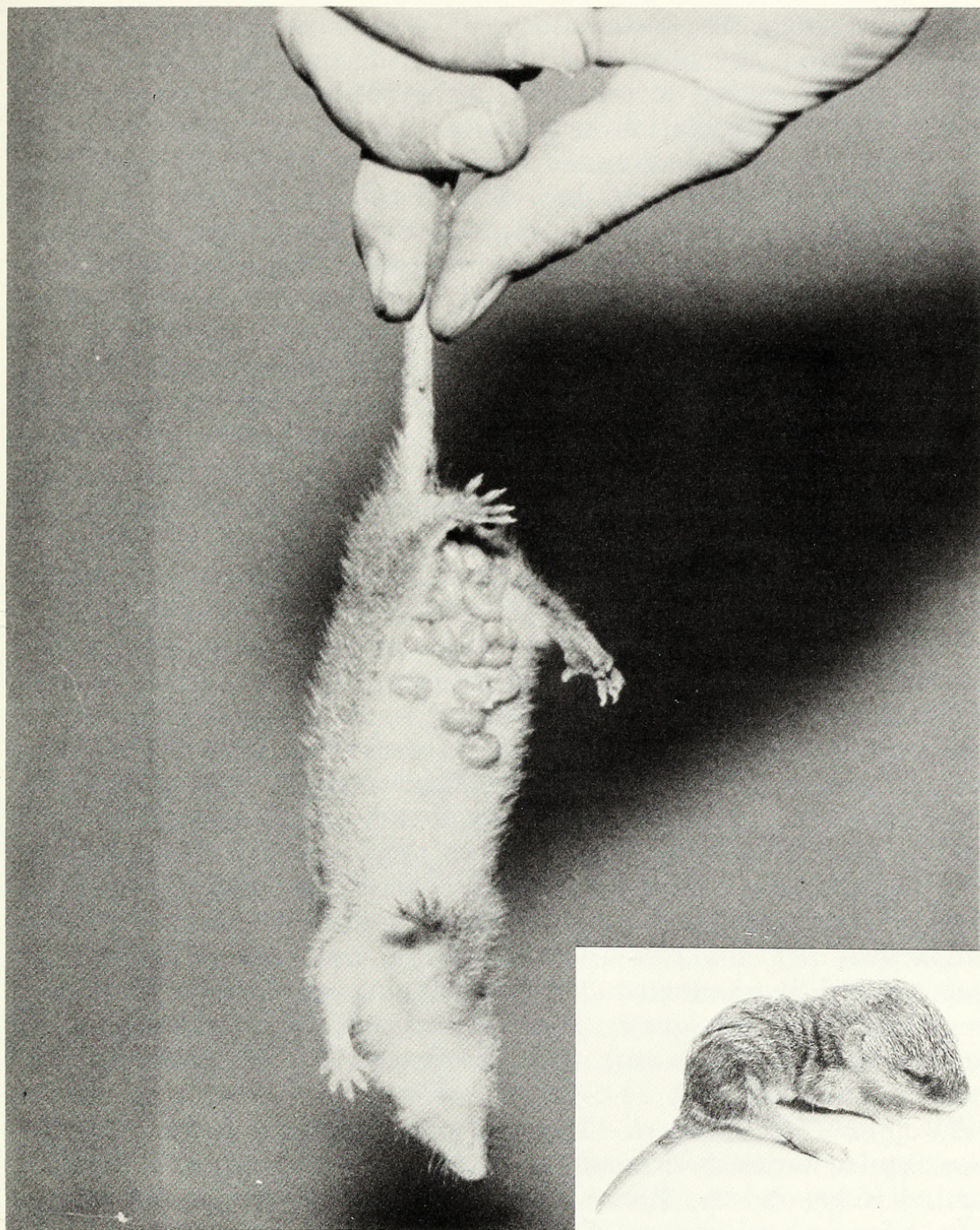


Fig. 1.—*Monodelphis dimidiata*: an adult female *M. dimidiata* with 16 newborn young attached; (inset) a young *M. dimidiata* at five weeks of age.

longed to a female (Fig. 1) that was held overnight in a trap in which she had been captured the previous afternoon. Within three days, the young had all been eaten by the mother. A female trapped several weeks earlier and caged with another female and a male was found

with eight young (the entire litter?) on 4 January 1970. This female was placed in a separate cage, where she successfully raised some of the young for a period during which postnatal observations were made. A third captive female, housed with a male for an unspecified time, was found with an undetermined number of young on 15 January 1970. The male was removed and the young disappeared after several days. The fourth female, captured 13 December and housed with a male was found with an undetermined number of newborn young on 27 January. Successful mating must have occurred in captivity. The male was removed and by the next day the young were gone.

Only one previous paper (Talice et al., 1960) has reported on newborns in this species. The date of birth was not given and apparently only a single young was seen and it soon died. Judging from information presented by Walker et al. (1975) and Hunsaker (1977) on *Monodelphis*, the litter of 16 reported here is exceptionally high for the genus, with 8 to 14 young usually reported.

The postnatal development and standard measurements and weights of the one successful litter from *M. dimidiata* are as follows.

At birth (4 January).—All pink; lenses and cranial sutures visible; no pinnae or ear openings; mouth opening a small round hole at front of snout, rest of mouth represented only by a slight groove; front feet with colorless claws (deciduous?); hind feet merely large pads with a mere hint of toes, legs poorly developed, with proximal portions of ankles seemingly attached to the body; liver visible through body wall; tail always held between legs. Each of three young measured about 10 mm in crown-rump length. Weights were 0.08, 0.08, 0.11 g. Standard measurements (in mm) of the heaviest were 17-3-1-0.

One week (11 January).—No change in overall pigmentation; front feet with lightly pigmented claws; developing toes on hind feet. Able to make a soft grunt-squeak, even when attached to nipple (sound not audible beyond 30-40 cm). One young was detached from female, measured and weighed: 24-5-2-0 = 0.45 g.

Two weeks (16 January).—Some young not attached to female, being loose under female first noted several days ago; appear to be content (and alive beyond the third week). Light pigment over entire dorsum except for first millimeter of tail; thick fuzz of less than 0.5 mm in length over entire dorsum; venter fuzzy, but fuzz less dense and shorter; cranial sutures barely visible; cleft of mouth distinct; pinnae visible; claws on front feet less pigmented than previously; little development of thigh although lower leg well-developed with flexible ankle; claws beginning to form on hind feet. Young more active, able to right themselves easily. Tail not always held between legs. One young's measurements and weight: 36-5-3-1 = 0.95 g.

Three weeks (26 January).—Dorsal pigmentation darker, hair over dorsum thicker, but still less than 0.5 mm in length; venter whitish, with no distinct line of demarcation between it and dorsum; rib cage and liver visible; fur on legs and feet, almost none on tail except at base; none on ears; vibrissae present, none longer than 2 mm; hind limbs somewhat lengthened and allowing effective locomotion. When turned over, young able to right themselves immediately. Lips completely separated. One young's measurements and weight: 47-10-4-2 = 1.6 g.

Four weeks (1 February).—Hair length on dorsum 1.0–1.5 mm, 1.0 mm on venter; brownish underfur appearing on head, underfur goes from nose to a line between ears; vibrissae 3–4 mm in length; lens no longer visible through closed pigmented eyelids; hind limbs more developed although knee joint still appears inflexible during locomotion; gum line with ridges raised by development of the as yet unerupted teeth. Measurements and weights of two are: 56-12-6-3 = 2 g; 55-13-6-3 = 2 g.

Five weeks (8 February).—Underfur of dorsum well-developed, 1–1.5 mm in length, 1 mm on venter; liver and rib cage barely visible; longest vibrissae about 5 mm; knee joint movable; scrotum about 2 mm in diameter; no evidence of ability to hear; eyelids fused; anterior teeth, including incisors, nearly all erupted. Measurements of four young were: 61-14-6-4; 62-15-6-4; 62-15-6-4; 62-15-6-4 (see Fig. 1). All weighed 2 g each. Because the mother had escaped several days before, the young were killed.

The early development of the young *Monodelphis dimidiata* roughly parallels that described for *Marmosa* sp. by Eisenberg and Maliniak (1967), and for *Marmosa mitis* (= *Marmosa robinsoni*) by Barnes and Wolf (1971). Both reports stated that the young first opened their eyes at 5 to 6 weeks and were weaned at about 8 weeks. From the fused eyelids and other body features (Fig. 1), the juvenile *M. dimidiata* were nearing the time of eye opening.

From 8 February to 26 May, no data on growth of young were recorded. On the latter date, three young individuals were captured and maintained in captivity for a three-month period. Based on the reproductive data mentioned earlier, the captured young were estimated to be approximately 4 to 5 months old. Standard measurements and weights for these individuals (1 ♂, 2 ♀♀, respectively) were as follows: *Total length.*—26 May, 122, 166, 122; 1 June, 123, 117, 122; 8 June, 122, 118, 122; 14 June, 125, 122, 126; 21 June, 125, 120, 125; 28 June, 127, 124, 127; 5 July, 130, 125, 129; 12 July, 133, 125, 130; 19 July, 136, 127, 134; 26 July, 137, 126, 132; 3 August, 140, –, 132; 9 August, 147, –, 133; 16 August, 152, –, 133; 23 August, 153, –, 133;

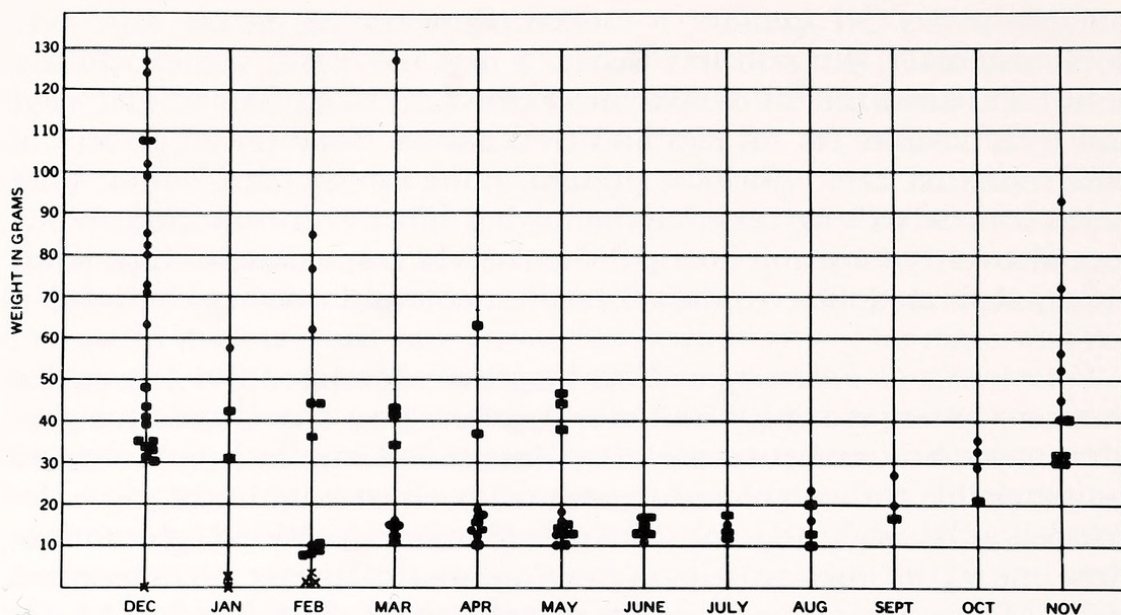


Fig. 2.—Weight distributions, shown on a monthly basis, of *M. dimidiata*. The rectangles represent females, the circles males, and the X's, very young individuals still dependent upon the females.

30 August, 155, —, 133. *Tail length*.—26 May, 37, 36, 37; 1 June, 37, 37, 37; 8 June, 36, 36, 36; 14 June, 38, 38, 38; 21 June, 38, 36, 38; 28 June, 40, 39, 39; 5 July, 41, 41, 39; 12 July, 42, 40, 38; 19 July, 42, 39, 38; 26 July, 42, 39, 37; 3 August, 42, —, 39; 9 August, 45, —, 40; 16 August, 45, —, 41; 23 August, 46, —, 41; 30 August, 48, —, 41. *Hind foot*.—26 May, 12, 11, 11; 1 June, 12, 11, 11; 8 June, 12, 11, 12; 14 June, 12, 11, 12; 21 June, 12, 11, 11; 28 June, 12, 11, 12; 5 July, 12, 11, 11; 12 July, 12, 11, 12; 19 July, 12, 11, 12; 26 July, 12, 12, 12; 3 August, 12, —, 12; 9 August, 13, —, 12; 16 August, 13, —, 12; 23 August, 13, —, 12; 30 August, 13, —, 12. *Ear*.—no growth noted—measurements fluctuated stochastically from 9 (one reading) to 10 (32 values) and 11 (7 readings). *Weight*.—26 May, 14, 12, 14; 1 June, 14, 10, 16; 8 June, 14, 10, 14; 14 June, 17, 13, 17; 21 June, 16, 13, 18; 28 June, 15, 11, 17; 5 July, 16, 12, 17; 12 July, 16, 12, 17; 19 July, 16, 13, 17; 26 July, 16, 8, 16; 3 August, 18, —, 16; 9 August, 24, —, 20; 16 August, 24, —, 20; 23 August, 27, —, 20; 30 August, 29, —, 19. The first-listed female was loose on 25 July, recaptured, showing a significant weight loss, on 26 July, and escaped permanently before 3 August. The two remaining animals were killed accidentally after 30 August.

The beginning of molt was noted in one subadult (20 g) male captured in late winter—early spring (mid-September 1969). The progress of the molt was followed in the lab. Molt was first evident only on a small dorsal area of the neck and adjacent back. By mid-October, the molt

line had moved laterally to encompass the shoulder blades and sides, and dorsally and posteriorly nearly to the hindquarters. Anteriorly, the molt line extended to the level of the eyes. By mid-November, molt was essentially completed, and the male weighed about 55 g. The new coat color was more dusky than the previous coat, lacking the reddish cast of the former.

A monthly weight profile is presented in Fig. 2. The data were taken from freshly trapped animals and also from those maintained in captivity for various lengths of time. The months of birth documented for the Balcarce area are December and January, and perhaps the first part of February (the last recorded birth occurred in the last week of January). Young animals, weighing 8–10 g, were first captured in February. Growth in the unheated lab and in the field was very slow until early spring, when weights started to increase rapidly. The young developed rather slowly through the cooler months, as documented by the laboratory, field, and morphometric data. Spring growth, especially in the males, and sexual maturation were rapid, quickly preparing these opossums for that summer's reproductive period.

All reproduction in this population appears to be dependent upon the attainment of sexual maturity by young animals, hence the late (December–January) breeding period. At the latitude of Balcarce, these young animals simply cannot reach sexual maturity before December. The evidence presented in this paper, and earlier by Reig (1964, 1965), indicates that older animals rarely, if at all, survive to the following breeding season. Thus, at least at this latitude, breeding is performed only by young of the preceding year.

The sexes grew at comparable rates until early spring, at which time the growth rate of both sexes increased markedly with the males outstripping the females. A stub-tailed male captured on 20 September 1969 and weighing 20 g weighed 56 g by 17 November—a weight that placed it within the lower limits of those given for that time period in Figure 2. During one week (27 October–3 November) when an abundance of fresh meat was available, this animal went from 34 g to 43 g, a gain of 9 g, while during the next week, it lost several grams (3 November, 40 g). By the following week (10 November), the male weighed 56 g, a gain of over 2 g per day. From October to November, males went from a 32 g ($n = 3$) to a 60 g average ($n = 6$), nearly doubling their weight. Females in this same period went from approximately 21 g ($n = 1$) to an average of 33 g ($n = 5$)—about a 60% increase. Weights and measurements of mature males and females for the months of December–March were: *total length*, ♂♂, 230, 215, 216, 213, 211, 207; ♀♀, 175, 180, 188, 191, 180; *tail length*, ♂♂, 76, 50, 71, 48, 58, 63; ♀♀, 57, 56, 60, 59, 55; *hind foot* (c.u.), ♂♂, 10(?), 18, 18, 19, 18, 18; ♀♀, 13, 15, 15, 16, 15; *ear* (from notch), ♂♂, 11, 12, 12, 12, 13, 11; ♀♀, 8, 11,

11, 11, 10; *weight*, ♂♂, 99, 102, 57, 85, 77, 62; ♀♀, 31, 44, 43, 42, 34. Females weighed only 40% as much as males, but reached 85% of the males' total length. The measurements of these animals agree with those of the members of the age classes 6 and 7 (Fig. 3). According to Ralls (1976), when females are considerably smaller than males, they typically cease growth at an earlier age than males and also begin sexual activity sooner. In *M. dimidiata*, however, contemporaneous differential growth rates appear especially important. Reig's (1964, 1965) and our conclusions in regard to *M. dimidiata* are in contrast to those of Woolley (1966), Wood (1970), and others for certain dasyurid marsupials, which are somewhat similar in appearance to *Monodelphis dimidiata*. In the Australian animals, all of the males die at the end of their first (and thus only) period of sexual activity although the females are capable of surviving at least two breeding seasons.

Although an annual pattern appears clear enough in the Balcarce area, somewhat different patterns, as yet not understood, exist to the north (data largely supplied by Charles O. Handley, Jr.). The juvenile holotype of *Monodelphis fosteri* Thomas from Caleufú, Argentina (35°35'S, 64°30'W), taken on 10 April, and a series of seven juveniles taken by Oldfield Thomas at Colón, Uruguay (34°48'S, 56°14'W), would match the situation found in Balcarce, but the adult male (Thomas, 1888) holotype of *Monodelphis dimidiata* taken in June (Waterhouse, 1839) at Maldonado, Uruguay (34°54'S, 54°57'W), and the single adult females taken at Pergamino, Argentina (33°55'S, 60°32'W), on 14 August and at Río Ceballos, Argentina (31°07'S, 64°18'W), on 28 September would not.

Walker et al. (1975) and Hunsaker (1977) wrote that tropical species of *Monodelphis* apparently breed throughout the year. Certainly this appears to be the case with *M. domestica* in Brazil (Streilein, 1982a, 1982b), although *M. brevicaudata* may be seasonally polyestrous in Venezuela (O'Connell, 1979). At Balcarce, at least, year-round reproductive activity in *M. dimidiata* does not occur. We also have no evidence to suggest more than one bout of reproductive activity per female during the year. Hunsaker (1977) has written that tropical species of *Marmosa* breed throughout the year, but those in cool and temperate zones breed once. The same pattern may apply to *Monodelphis*. The lateness of breeding in *Monodelphis dimidiata* (this study), comparable to June and July in equivalent northern latitudes, is rather unusual. Because *Monodelphis dimidiata* is pouchless, perhaps a relatively late breeding season is more advantageous than an earlier one in a temperate environment, considering the altricial state of the young.

Although there is a life expectancy in *Marmosa robinsoni* of about three years in captivity, Hunsaker (1977) stated that reproductive abil-

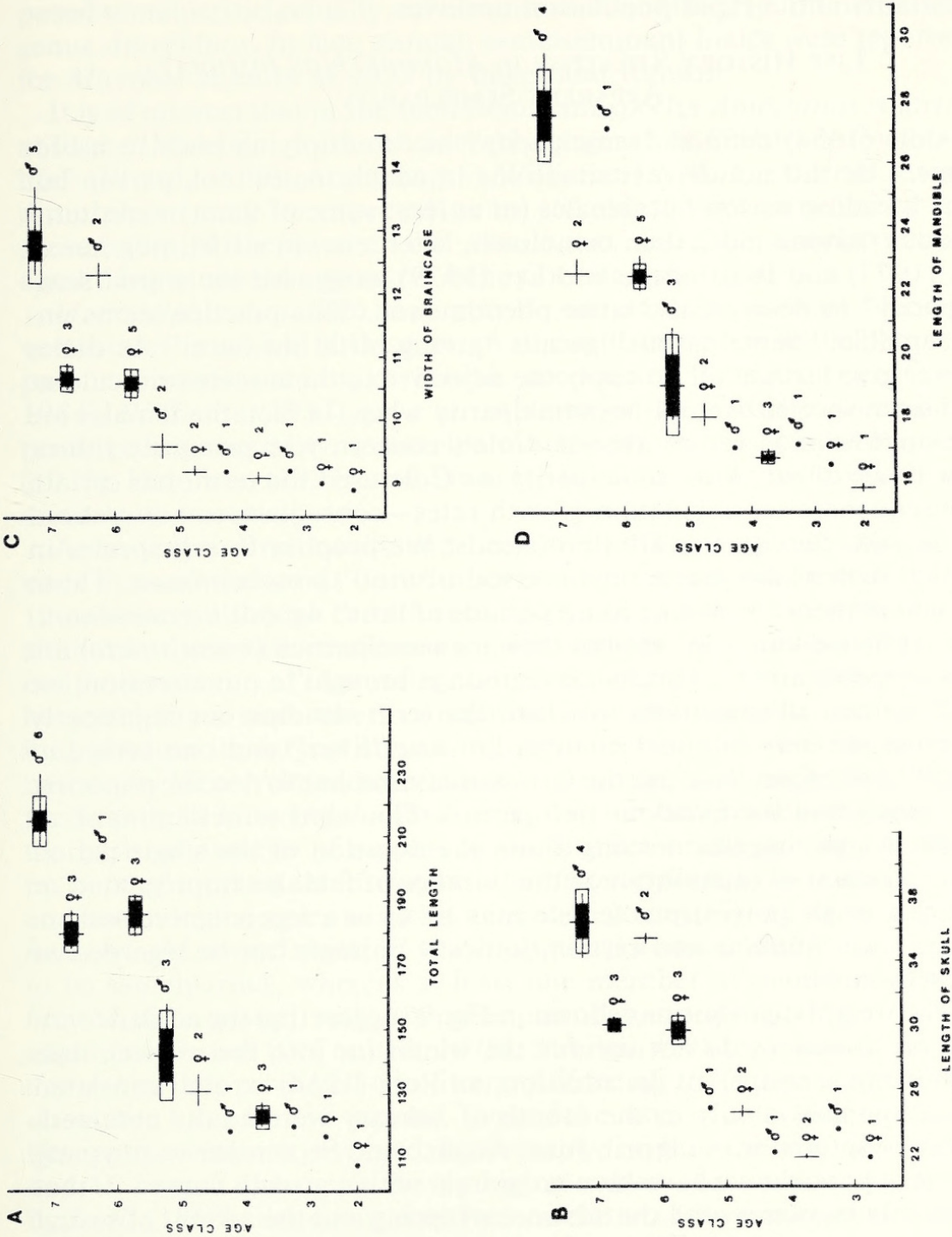


Fig. 3.—Graphs of measurements of *M. dimidiata* of both sexes and different age classes. A) total length; B) length of skull; C) width of braincase; D) length of mandible (ramus).

ity fades during the second year, and life expectancy is probably less than a year in nature. Thus, species of both *Marmosa* and *Monodelphis* apparently use a strategy of high production to compensate for high mortality and a rapid population turnover.

LIFE HISTORY STRATEGY IN *MONODELPHIS DIMIDIATA*:
APPARENT SEMELPARITY

Cole (1954) defined "semelparity" as "multiplying once in a lifetime." He did not discuss situations in which males took part in but one breeding season but females (or at least some of them) were iteroparous (having more than one clutch, litter, etc., in a lifetime). Lee et al. (1977) and Braithwaite and Lee (1979) have used the word "semelparity" to describe the latter phenomenon. This practice seems unacceptable. "Semelparous" means "giving birth but once." As males never give birth at all, to apply the adjective to them seems ridiculous. To say a species exemplifies semelparity when, in fact, the females are iteroparous also seems absurd. Cole's concern was primarily litters, not times of rut. Also, semelparity, as Cole used the term, has certain consequences on population growth rates—consequences not realized if, in fact, the females are iteroparous. We propose to call species in which males have but a single period of "rut" *semelseminant*. Those in which there are two or more periods of "rut" we call *iteroseminant*. As far as we know, all species that are semelparous (*sensu stricto*) are also semelseminant. Until an exception is brought to our attention, we will assume all organisms to which the term semelparous is properly applied are ones in which there is but one "litter" and one period of "rut." Therefore, if we use the term semelseminant to describe a species, we imply that the female is iteroparous. The word semelseminant, as defined here, implies nothing about the duration of the single period of reproductive capability nor the number of females impregnated or times a single polyestrous female may be so in a reproductive season. Thus, even humans and certain domestic animals can be regarded as semelseminant.

The weight distributions shown in Fig. 2 suggest that the adult *Monodelphis dimidiata* do not survive the winter (or into the winter), thus indicating semelparity. In addition, as Reig (1964) wrote (translated from Spanish), "only in the month of January were adults obtained. All . . . captured in . . . April, June, August, and September were young . . . It is possible we have here an animal with a growth curve . . . that suddenly increases with the advance of spring and the advent of sexual maturity—the adult individuals of large size dying at the beginning of the first autumn frost." See also Reig (1965).

Monodelphis dimidiata was the first (and remains the only) warm-blooded vertebrate for which true semelparity as defined here has been

hypothesized, notwithstanding the statement of Lee et al. (1977) that, "It has not previously been described in mammals or birds" (see also Braithwaite and Lee, 1979). These latter authors were reporting supposed semelparity (actually semelseminance) in the dasyurid marsupial genus *Antechinus*. In fact, annual, semelseminant males were reported for *Microtus* as early as 1933 by Baker and Ranson.

It is of interest that in the semelseminant species *Antechinus stuartii*, at least, "Male[s] . . . are considerably larger than females throughout life" (Wood, 1970). According to Williams (1966a), extreme sexual dimorphism may be expected to be correlated with semelparity (or presumably in the case of the *Antechinus*, with the semelseminant condition) as would aggressive behavior between males.

Monodelphis dimidiata may also be one of the few warm-blooded vertebrates in which both sexes are thought to be "annuals." Semelparous animals are not, of course, necessarily "annuals" (see Cole, 1954). Williams (1957) gave an explanation of virtually immediate postbreeding mortality in semelparous species. See Baker and Ranson (1933), Hamilton (1937), and Elton (1942) concerning voles which are annuals or essentially so.

According to Braithwaite and Lee (1979), "The largest known litter sizes in small dasyurids occur in species with semelparous males (10–12 neonates), although certain species with this strategy have litter sizes similar to those with iteroparous males (eight or less, occasionally nine or 10 neonates . . .)." Assuming that some species of *Monodelphis* may be semelparous and others iteroparous, and that semelparous species may produce the largest number of neonates, and that number of neonates may be correlated with number of nipples, one might be able to predict which *Monodelphis* (and other didelphids?) are semelparous on the basis of number of nipples in the females (male marsupials have no trace of nipples). *Monodelphis dimidiata* appears to be semelparous and has enough nipples to suckle at least 16 young (Fig. 1). *Monodelphis henseli* (= *M. sorex*?) with 17 to 27 nipples (Thomas, 1888), may prove to be semelparous, whereas at least one member of the *Monodelphis brevicaudata* group, with a smaller number of nipples (Pine, 1980), apparently is not (O'Connell, 1979). Streilein (1982b) reported an *M. domestica* that produced two litters. According to Thomas (1923), *M. domestica* has 11 or 13 nipples. Even if the issue of semelparity versus iteroparity were not involved, however, we might expect *M. dimidiata* and *M. henseli* to have relatively high numbers of mammae. As noted by Lord (1960), there is a positive correlation between litter size and latitude, and the two species in question are among the southernmost *Monodelphis* (see also Cody, 1966; Pianka, 1970). MacArthur and Wilson (1967) wrote, "where climates are rigorously seasonal and winter survivors recolonize each spring, in the presence of a bloom of foliage

and food, we expect *r* selection favoring large productivity." Both *M. dimidiata* and *M. henseli*, however, show extreme sexual dimorphism as compared to most other *Monodelphis*, and this characteristic has been noted in non-mammalian vertebrate semelparous annuals (Myers, 1952; Storey, 1940).

M. dimidiata would seem to be producing far more neonates than can later be weaned. This appears to be the usual case in didelphids, but *M. dimidiata* is an extreme instance. According to Low (1978), "When the time of risk for offspring falls early within the period of parental effort and is predictable, even if unavoidable by increased PI [=parental investment, the portion of parental effort (PE) received by each offspring such that $\sum \text{PI} = \text{PE}$ for any period under consideration], parents may be able to profit by starting more offspring than they could otherwise raise, investing minimally until the high-risk period is past and then investing maximally." Perhaps this situation occurs in *Monodelphis dimidiata*, although potential risks suffered by attached neonates are unknown. Low also noted, "In some cases the PE invested in offspring which later die may be partly recovered . . . when the parent or surviving offspring eat the . . . carcasses of dead juveniles." The cannibalizing reported here of young *M. dimidiata* by their mothers is of interest in this regard. Might free-living *M. dimidiata* females cannibalize some of their young (even if alive) during times of stress? During a "good year" more young might be safe from being eaten than during a "bad year." The female could adapt her maternal behavior to changing conditions. Eating *all* her young has no selective advantage in a semelparous animal unless termination of lactation could allow a female to escape the physiological exhaustion following weaning and thus perhaps survive into a new breeding season.

NON-GEOGRAPHIC VARIATION

Variation with Age

As the sample sizes representing most age classes were small, we did not test for differences. Fig. 3 shows the general trends of increasing dimensions in four selected characters for both sexes in going from younger to older age classes. Detailed data are presented in Table 1. In general, there were no apparent differences between males and females in the same age class until age class 5, at which stage males began to be larger than females. Gardner (1973) found a similar situation in *Didelphis*, in which genus the differences between males and females began at his age class 4. In *Monodelphis dimidiata* from Balcarce, males are substantially larger by age class 6 for all measurements except tail length, M1-M4 length, and width of postorbital constriction.

The development of the lambdoidal and sagittal crests also follows

a characteristic general growth pattern. Each age-sex class was scored, as to development of a crest, as follows: 1) no indication of a crest; 2) a slight ridge present; 3) a definite ridge present; and 4) a highly developed ridge present. In the specimens of *M. dimidiata* from Balcarce, a female of age class 2 showed no indication of either crest. All individuals (both male and female) of age classes 3 through 5 were scored as 2 and 1, respectively, as to lambdoidal and sagittal crests. All females of age classes 6 and 7 showed a definite lambdoidal crest and a slight sagittal crest—whereas most males of age classes 6 and 7 had both crests well-developed. One male of age class 7 had both crests highly developed. These comparisons were based upon proportional development of the crests and not on absolute size. As adult males are larger than females, the absolute size of the crests would be expected to be greater in males, but the sexual difference goes beyond that and would appear to be allometric in nature.

The most marked development of cranial crests occurs between age classes 5 and 6. Because little change was evident in this and other characters between age classes 6 and 7, members of both age classes are treated here as adults. We also noted that for each sex there was no overlap in size between individuals of age classes 5 and 6 for most characters.

Individual and Secondary Sexual Variation

One male showed fusion of the first and second left lower premolars (see Fig. 4). Torre and Dysart (1966) reported fused incisors in *Didelphis* and summarized the literature on fused teeth in mammals.

Basic statistics for adults are presented in Table 2. Individual variation is most clearly expressed by the coefficients of variation (CV). Among external characters, males had higher CV's than females for total length and tail length, whereas females were more variable in length of hind foot and ear. The extremely high CV's for tail and ear lengths may be artifacts of either measuring techniques or small sample size. However, in most mammals, external characters have been shown to be generally more variable than cranial characters (Long, 1968, 1969; Yablokov, 1974). Males were more variable in 12 of the 13 cranial characters studied. Females were more variable only in M1–M4, and these CV's were of the same magnitude. The CV's for cranial characters averaged more than half again as large in males as in females (the mean CV for males was 4.65, and for females, 2.87). Long (1969) considered cranial measurement CV's between 2.5 and 5.3 to be normal for mammals in general. Male *M. dimidiata* had CV's higher than 5 in nasal length, postorbital constriction, and mandibular depth. Only mandibular depth had a CV sufficiently high (8.45) as to bring into question

Table 1.—Summary statistics on age variation in *Monodelphis dimidiata* from Balcarce area, Argentina. Under each age and sex class, for each measurement, the first line is the mean with sample size in parentheses; the second line is the range; the third line is the standard deviation with the coefficient of variation in parentheses.

Measurement	Sex	Age class						
		2	3	4	5	6	7	
Total length	Females	108 (1)	117 (1)	123.00 (3) 120-127	131.00 (2) 126-136	186.00 (3) 179-191	180.67 (3) 175-187	
	Males	—	120 (1)	3.61 (2.93) 119 (1)	— 142.00 (3) 132-158	6.24 (3.36) 204 (1)	6.03 (3.34) 215.33 (6) 207-230	
Tail length	Females	30 (1)	38 (1)	35.67 (3) 35-37	41.00 (2) 38-44	58.67 (3) 57-60	55.33 (3) 54-57	
	Males	—	40 (1)	1.15 (3.24) 34 (1)	— 41.67 (3) 37-48	1.53 (2.60) 58 (1)	1.53 (2.76) 61.00 (6) 48-76	
Hind foot (c.u.)	Females	11 (1)	12 (1)	11.67 (3) 11-12	12.00 (2) 12-12	15.33 (3) 15-16	14.33 (3) 13-15	
	Males	—	12 (1)	0.56 (4.95) 12 (1)	— 14.00 (2) 13-15	0.58 (3.76) 19 (1)	1.15 (8.02) 18.33 (6) 18-19	
Ear (from notch)	Females	8 (1)	10 (1)	9.00 (3) 9-9	9.50 (2) 9-10	10.67 (3) 10-11	0.52 (2.84) 9.00 (2) 8-10	
	Males	—	10 (1)	0.00 (0.00) 10 (1)	— 10.00 (3) 10-10	0.58 (5.41) 13 (1)	— 11.83 (6) 11-13	
Skull length	Females	—	22.8 (1)	22.85 (2) 22.8-22.9	0.00 (0.00) 24.65 (2) 24.4-24.9	— 29.70 (3) 29.0-30.7	0.75 (6.34) 30.07 (3) 29.8-30.5	
						0.89 (2.99)	0.38 (1.26)	

Table 1.—Continued.

Measurement	Sex	Age class					
		2	3	4	5	6	7
Condylolincisive length	Males	—	23.5 (1)	23.1 (1)	24.9 (1)	35.55 (2)	36.48 (4) 34.2–38.2 1.95 (5.35)
	Females	—	22.4 (1)	22.40 (2) 22.3–22.5	24.20 (2) 23.8–24.6	29.30 (4) 28.5–30.2 0.70 (2.38)	29.45 (2) 29.3–29.6
	Males	—	23.1 (1)	22.9 (1)	25.95 (2) 24.4–27.5	35.20 (2) 35.2–35.2	36.33 (3) 33.7–37.9 2.29 (6.31)
	Females	11.5 (1)	11.9 (1)	12.17 (3) 12.1–12.2	13.15 (2) 13.0–13.3	15.18 (5) 14.9–15.7	15.85 (2) 15.3–16.4
	Males	—	12.3 (1)	12.1 (1)	13.70 (3) 13.0–15.0 1.13 (8.22)	17.80 (4) 17.3–18.1 0.36 (2.00)	18.04 (5) 17.1–19.2 0.96 (5.32)
Greatest nasal length	Females	9.1 (1)	9.3 (1)	9.53 (3) 9.3–9.9	11.10 (2) 10.9–11.3	12.22 (4) 11.8–12.6	12.43 (3) 12.2–12.6
	Males	—	9.7 (1)	0.32 (3.37) 9.9 (1)	10.70 (2) 10.6–10.8	0.35 (2.86) 14.95 (4) 14.5–15.4	0.21 (1.67) 15.13 (7) 14.0–16.4
	Females	10.7 (1)	11.2 (1)	11.60 (2) 11.5–11.7	11.9 (1)	0.37 (2.47) 15.75 (4) 15.5–16.0	0.97 (6.42) 16.15 (2) 16.0–16.3
Zygomatic breadth	Females	—	—	—	—	0.21 (1.32) 20.35 (2) 20.2–20.5	— 21.03 (3) 19.8–22.3
	Males	—	11.9 (1)	11.4 (1)	12.3 (1)	—	1.25 (5.94)

Table 1.—Continued.

Measurement	Sex	Age class					
		2	3	4	5	6	7
Postzygomatic braincase width	Females	8.9 (1)	9.0 (1)	9.10 (2) 9.0-9.2	9.20 (2) 9.1-9.3	10.58 (5) 10.3-10.8	10.67 (3) 10.5-10.9
	Males	—	9.2 (1)	9.2 (1)	9.60 (2) 9.4-9.8	0.22 (2.05) 12.30 (2) 12.1-12.5	0.21 (1.97) 12.78 (5) 12.3-13.7
	Females	—	7.3 (1)	7.37 (3) 7.2-7.5	7.60 (2) 7.5-7.7	8.86 (5) 8.8-8.9	9.05 (2) 9.0-9.1
	Males	—	7.3 (1)	0.15 (2.07) 7.1 (1)	7.77 (3) 7.4-8.0 0.32 (4.14)	0.05 (0.62) 9.75 (4) 9.5-10.0 0.24 (2.44)	— 10.03 (7) 9.6-10.8 0.47 (4.70)
Maxillary toothrow	Females	—	—	9.45 (2) 9.4-9.5	9.95 (2) 9.9-10.0	11.04 (5) 10.9-11.2	10.95 (2) 10.8-11.1
	Males	—	—	—	10.50 (2) 10.0-11.0	0.11 (1.03) 12.10 (2) 12.0-12.2	— 12.48 (5) 11.8-13.0 0.46 (3.68)
	Females	—	—	5.30 (2) 5.3-5.3	5.65 (2) 5.6-5.7	5.46 (5) 5.4-5.5	5.33 (3) 5.1-5.6
	Males	—	—	—	5.50 (3) 5.4-5.6 0.10 (1.82)	0.05 (1.00) 5.52 (4) 5.3-5.7 0.17 (3.09)	0.25 (4.69) 5.50 (7) 5.2-5.6 0.14 (2.54)
Postorbital constriction	Females	4.85 (2) 4.8-4.9	5.1 (1)	5.05 (2) 4.9-5.2	5.15 (2) 5.1-5.2	5.10 (5) 5.0-5.4 0.17 (3.40)	5.13 (3) 5.1-5.2 0.06 (1.13)
		—	—	—	—	—	—
		—	—	—	—	—	—

Table 1.—Continued.

Measurement	Sex	Age class						
		2	3	4	5	6	7	
Mandibular depth	Males	—	5.1 (1)	5.2 (1)	5.10 (3) 4.9–5.3 0.20 (3.92)	5.00 (4) 4.5–5.3 0.42 (8.48)	4.96 (7) 4.6–5.2 0.21 (4.23)	
	Females	—	—	1.8 (1)	1.95 (2) 1.8–2.1 —	2.68 (5) 2.6–2.8 0.08 (3.12)	2.67 (3) 2.6–2.7 0.06 (2.10)	
	Males	—	—	—	2.20 (3) 2.0–2.4 0.20 (9.09)	3.47 (3) 3.4–3.6 0.12 (3.33)	3.67 (7) 3.3–4.2 0.36 (9.81)	
Length of ramus	Females	15.75 (2) 15.6–15.9	16.5 (1)	16.73 (3) 16.5–16.9 0.21 (1.24)	18.05 (2) 17.7–18.4 —	22.46 (5) 22.0–23.1 0.42 (1.88)	22.55 (2) 22.2–22.9 —	
	Males	—	17.1 (1)	17.0 (1)	18.97 (3) 17.9–20.8 1.59 (8.41)	27.1 (1) —	27.55 (4) 26.2–29.5 1.39 (5.04)	
	Females	—	11.8 (1)	11.73 (3) 11.5–11.9 0.21 (1.77)	12.20 (2) 12.2–12.2 —	13.38 (5) 13.1–13.5 0.16 (1.23)	13.10 (2) 12.9–13.3 —	
Mandibular toothrow	Males	—	12.0 (1)	11.8 (1)	12.57 (3) 11.8–13.4 0.80 (6.38)	14.7 (1) —	14.90 (4) 14.3–15.8 0.70 (4.70)	

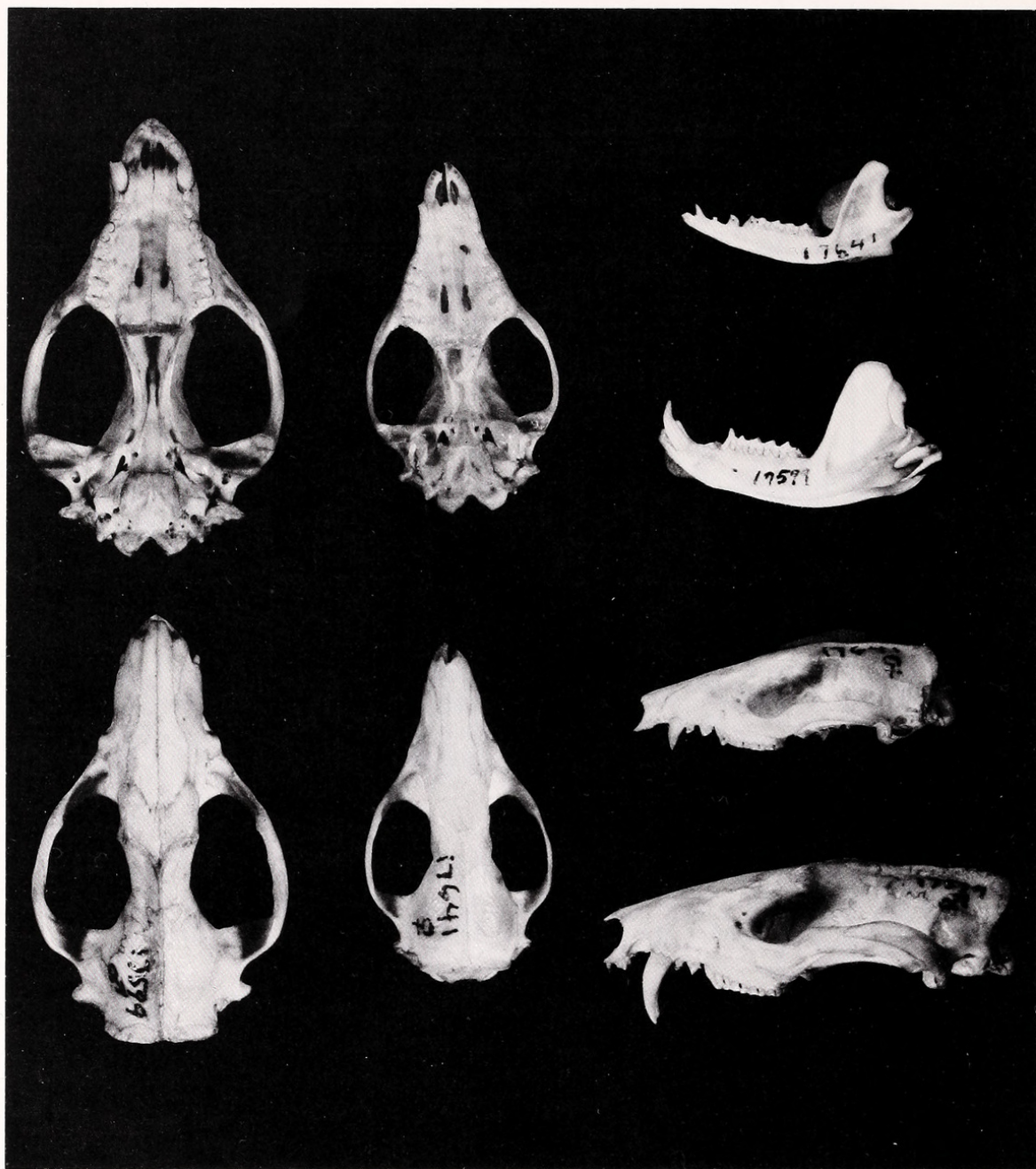


Fig. 4.—Skulls of adult (age class 7) male and female *M. dimidiata*. The male is to the left or is the lower in each pair. Note larger, more robust skull with stronger crests in male—also longer canines. In left mandibular ramus of male, the first two premolars are fused (an abnormality). Note cutting edge of third lower premolar, which forms a carnassial-like pair of shearing teeth with upper third premolar. Photograph is $1.2\times$.

its utility in systematic studies. Females had no CV's over 5 and most were below 2.0. A possible explanation for the differences between male and female variability may be related to the reproductive energetics hypothesis of Gardner (1973) for the genus *Didelphis*. Adult

females thus show less variability owing to a virtual cessation of growth after attainment of a certain size, whereas males are more variable because they continue growing throughout life.

The results of analyses of variance between adult males and females for each character are given in Table 2. Of the 17 characters, 14 were significantly different, with males being larger in each case. In the three characters that were not significantly different, males averaged slightly larger in tail length and in M1–M4, whereas females were slightly larger in postorbital constriction. Overlap in measurements occurred in tail length, ear length, M1–M4, and postorbital constriction.

The extreme sexual dimorphism (Fig. 4) in absolute size and in relative variability necessitates treating the sexes separately in systematic work. Although similar to the situation described by Gardner (1973), the magnitude of sexual dimorphism in *M. dimidiata* is much greater, and the variability within the population studied considerably less, than that in populations of *Didelphis*. Ralls (1977) listed the Marsupialia as one of the orders that contain "extreme cases of sexual dimorphism favoring males, defined as a ratio of average male to female weights greater than 1.6." The condition in marsupials was known to Ralls only in the Macropodidae. On the basis of our studies of *M. dimidiata*, the Didelphidae will have to be added to the "extreme sexual dimorphism favoring males" category. Ralls' statement, "In the Marsupialia and the Chiroptera the extremely dimorphic species are found in the families which have the largest modal species size in their orders" will also now need to be modified.

One specimen (MSU 17887) was excluded from the study of non-geographic variation. Placed in age class 6, it was labelled as a male but the development of the cranial crests matched that in females of the same age class. Perhaps the sex was incorrectly recorded for this specimen. On the other hand, Gardner (1973) found occasional reversal of the usually sexually dimorphic skull characters in *Didelphis*, and MSU 17887 may be an example of the same sort of phenomenon in *Monodelphis dimidiata*.

The usual size and proportional differences between the skulls of adult *Monodelphis dimidiata* of different sexes are quite extreme. The differences are sufficiently great that a taxonomist examining a small sample might easily be led to treat females and young males as one species, and adult males as another. The molars are of about the same size, however, and this factor is useful when making comparisons of what are apparently similar species of opossums that differ in size.

Compared to those of the females, the skulls of males are not only much larger, but more massive with proportionately larger crests. They have enlarged postorbital processes of the frontals, or at least heavy ridges in that area, more flaring zygomatic arches, sabre-like canines,

Table 2.—*Basic statistics for and results of analyses of variance between male and female Monodelphis dimidiata (age classes 6 and 7 combined) from Balcarce area, Argentina. In each column are presented the mean \pm 1 standard deviation followed by the range and the coefficient of variation for each measurement. F-values with *, **, and *** represent significance levels of $P \leq 0.05$, 0.01 , and 0.001 , respectively.*

Measurement	Males		Females		F-value
	N	$\bar{X} \pm 1$ SD	N	$\bar{X} \pm 1$ SD	
Total length	7	213.71 \pm 8.36 204–230 3.91	6	183.33 \pm 6.22 175–191 3.39	53.53***
Tail length	7	60.57 \pm 10.29 48–76 16.99	6	57.00 \pm 2.28 54–60 4.00	0.68 ns
Hind foot (c.u.)	7	18.43 \pm 0.53 18–19 2.90	6	14.83 \pm 0.98 13–16 6.63	70.34***
Ear (from notch)	7	12.00 \pm 0.82 11–13 6.80	5	10.00 \pm 1.22 8–11 12.00	11.67**
Skull length	6	36.17 \pm 1.58 34.2–38.2 4.38	6	29.88 \pm 0.64 29.0–30.7 2.15	81.06***
Condylolincisive length	5	35.88 \pm 1.74 33.7–37.9 4.84	6	29.35 \pm 0.55 28.5–30.2 1.89	76.94***
Palatal length	9	17.93 \pm 0.72 17.1–19.2 4.04	7	15.37 \pm 0.52 14.9–15.7 3.40	61.93***
Greatest nasal length	11	15.06 \pm 0.78 14.0–16.4 5.21	7	12.31 \pm 0.30 11.8–12.6 2.41	77.34***
Zygomatic breadth	5	20.70 \pm 0.99 19.8–22.3 4.81	6	15.88 \pm 0.28 15.5–16.3 1.75	131.14***
Postzygomatic braincase width	7	12.64 \pm 0.54 12.1–13.7 4.28	8	10.61 \pm 0.20 10.3–10.9 1.91	97.74***
M3–M3	11	9.93 \pm 0.41 9.5–10.8 4.16	7	8.91 \pm 0.11 8.8–9.1 1.20	40.22***
Maxillary toothrow	7	12.37 \pm 0.43 11.8–13.0 3.45	7	11.01 \pm 0.13 10.8–11.2 1.22	64.57***
M1–M4	11	5.51 \pm 0.14 5.2–5.7 2.62	8	5.41 \pm 0.16 5.1–5.6 2.87	2.08 ns

Table 2.—*Continued.*

Measurement	Males		Females		F-value
	N	$\bar{X} \pm 1 \text{ SD}$	N	$\bar{X} \pm 1 \text{ SD}$	
Postorbital constriction	11	4.97 \pm 0.28 4.5–5.4 5.69	8	5.11 \pm 0.14 5.0–5.4 2.65	1.66 ns
Mandibular depth	9	3.60 \pm 0.30 3.3–4.2 8.45	8	2.68 \pm 0.07 2.6–2.8 2.64	69.38***
Length of ramus	5	27.46 \pm 1.22 26.2–29.5 4.45	7	22.49 \pm 0.40 22.0–23.1 1.79	103.80***
Mandibular tooththrow	5	14.86 \pm 0.61 14.3–15.8 4.12	7	13.30 \pm 0.22 12.9–13.5 1.68	39.61***

the anterior end of the lower jaw bent upwards, proportionately deeper lower jaws, a strongly-developed postorbital constriction, and a larger notch in the maxilla to receive the lower canine. A number of these male characteristics were used in Cabrera's (1919) diagnosis of *Minuania* (regarded by him as a genus in 1919, a subgenus in 1958) from which we can assume that Cabrera was unfamiliar with the characteristics of adult females.

Although fairly extreme sexual differences in size have been found in both North American *Didelphis* (Gardner, 1973), *Marmosa* (Tate, 1933), and in *Monodelphis*, it does not exist in all species of didelphids—not being found, for example, in *Marmosa parvidens* Tate (Pine, 1981). Gardner (1973) cited Lowrance (1949) in noting that bone growth continues throughout the life of the individual in at least some species of opossums. According to Gardner, "size differences between sexes become accentuated following the attainment of reproductive maturity . . . suggesting that the nutritional load placed on pregnant and lactating females diverts energy sources that would otherwise contribute to increased growth." Assuming these considerations apply to some extent to *M. dimidiata*, then gestation, and not lactation, would have to be the more responsible for the sexual dimorphism in size. By the time the young are born, the adult males have already achieved large size. The gestation period is unknown in *M. dimidiata* but is fairly long (26–35 days) in *Antechinus stuartii* (Woolley, 1966 *vide* Lee et al., 1977). Examination of Fig. 2 seems to indicate that in *M. dimidiata*, the males may begin to outstrip the females in size before sexual maturity is attained, unless sexual maturity is reached considerably before growth

stops and the gestation period is exceedingly long (parturition occurred in captives from the middle of December until late January).

According to Williams (1966*b*), strong sexual dimorphism is indicative of high reproductive effort. In those didelphids that show it, this correlation may be owing to very direct causation—the actual investment being responsible for the dimorphism rather than its being brought about by such common means as the difference in the sex chromosome complement.

Whatever its cause, the extreme dimorphism in *Monodelphis dimidiata* may result in a certain amount of ecological role separation—a result that might be beneficial to survival of individuals and the species. Such role separation may be hinted at by the differential tendency we noted in the two sexes to attack and eat mice. Downhower's (1976) observation that "Agonistic encounters are likely to reduce the time available for foraging and thus larger size may provide males with the physiological reserves necessary to hold a territory" may have relevance for *M. dimidiata*. As presumed semelseminant annuals, the males may find it to their "advantage" virtually to abandon foraging during the mating season. Downhower's observation that when food is abundant, smaller individuals can replenish their stored energy reserves faster than larger individuals can may also have relevance for female *M. dimidiata*. Selander (1958) found a positive relationship between polygamous or promiscuous mating relationships and degree of size difference by sex in icterids. Orians (1969) discussed this sort of relationship in other animals, including mammals. Male *Monodelphis dimidiata* presumably are promiscuous.

ABBREVIATED HISTORY RELATING TO THE NAME
MONODELPHIS DIMIDIATA

- 1838. Waterhouse first mentioned the animal now known as *Monodelphis dimidiata* (Wagner) under the name "Didelphis brachyura. Gmel." This and later references by Waterhouse (1839, 1841, 1843, 1846) were based on a specimen brought back by Darwin from Maldonado, Uruguay.
- 1847. Wagner named Darwin's animal *D[idelphys]. dimidiata*.
- 1854. Burmeister called Darwin's animal *Didelphys brachyura*.
- 1855. Schreber included it in "*D[idelphys]. brachyura* SCHREB."
- 1856. Burmeister referred Darwin's animal to *Microdelphys brachyura*.
- 1873. Hensel used the name *Microdelphys brachyura* for a Brazilian animal.
- 1882, 1887. Arechavaleta (*fide* Ximénez et al., 1972) discussed the Uruguayan distribution of *Monodelphis dimidiata* under the name *Didelphis brachyura*.

1888. Beddard described the sternal gland of *Didelphys dimidiata*. Thomas used this same name for specimens from Taquara and San Lorenzo (=São Lourenço do Sul), Rio Grande do Sul, Brazil. All of the specimens available to Thomas were males as his redescription clearly indicates (see discussion on sexual dimorphism in this paper).
1892. Ihering used the name *Peramys dimidiatus* for animals from Rio Grande do Sul.
1894. Figueira used the name "*Didelphys brevicaudata* Erxl." for Uruguayan *Monodelphis*.
1896. Lydekker wrote about *Didelphys dimidiata*.
1898. Holmberg recorded *Monodelphis dimidiata* from "La Tinta," Argentina, using the name "*?Didelphys brachyura*" (p. 478). Trouessart wrote about the geographic range of [*Peramys*] *dimidiata*.
1899. Lahille referred to *Peramys dimidiata* (Wagn.) as "El Colicorto de Azara.—Mesopotámica-orientalis.—Pampeana."
1900. Thomas reported *Peramys dimidiata* Wagn. from Palmeira, Paraná, Brazil.
1914. Bertoni used the name *P [eramys]. dimidiatus*, stating that it was not "el <<Colicorto>> de Azara."
1916. Matschie used the name combination "[*Didelphis (Monodelphis)*] *dimidiata* WAGN."
1919. Cabrera described the nominal genus *Minuania* with [*Minuania dimidiata* Wagner as the type and only species. The distinguishing characters were largely those found (only?) in adult males.
1923. Larrañaga (1771–1848, published in 1923) referred to *D. Brachyura*, giving a description of external characteristics and some natural history notes. He considered it to be Azara's "*Colicorto*."
1924. Thomas named *Monodelphis fosteri* from Caleufú, La Pampa, Argentina. Thomas compared *M. fosteri* with *M. dimidiata*.
1929. Sanborn recorded a specimen identified as *M. dimidiata* from Montevideo, Uruguay.
1932. Marelli used the combination *Minuania dimidiata*.
1935. Devincenzi used the combination *Minuania dimidiata* and put Azara's "*Colicorto*" in its synonymy.
1936. Miranda-Ribeiro described *P [eramys]. d [imidiata]. itatiayae* from Itatiaia, Rio de Janeiro, Brazil, and named *Minuania umbristriata* on page 422. On page 419, he included a key with the words: "[Coloração] ruiva, aparentemente uniforme . . . *M. goyana*." *Minuania goyana* was mentioned only in the key. The description of *M. umbristriata* agrees with that of *M. goyana* in the key. Clearly, *M. goyana* and *M. umbristriata* were intended

- to apply to one and the same animal. In the key, two species were included in the subgenus *Minuania* (*M. dimidiata* and *M. goyana*). However, in the remainder of the paper, Miranda-Ribeiro recognized only *M. dimidiata* and *M. umbristriata* (see also Cabrera, 1958, below).
1939. Bertoni reported "*Peramys dimidiatus* (Wagn.)" from Puerto Bertoni, Alto Parana, Paraguay, and repeated that it is not "el <<Colocorto>> de Azara."
1940. Cabrera and Yepes gave the geographic range of *Minuania dimidiata* as Uruguay and Rio Grande do Sul to Rio de Janeiro, Brazil. They stated that this animal is not "el colicorto" of Azara, and recognized *Minuania umbristriata* Miranda-Ribeiro and *M. fosteri* (Thomas) as full species.
1941. Gilmore treated *Minuania* as a subgenus of *Monodelphis*, using color pattern as the criterion (but see Pine, 1976).
1955. Vieira wrote about *Monodelphis dimidiatus* (Wagner) and *Monodelphis umbristriata*, submerging *Minuania* in the synonymy of *Monodelphis*.
1958. Cabrera considered *Minuania goyana* Miranda-Ribeiro a *nomen nudum* and placed it in synonymy with *Monodelphis dimidiata*. He placed *Minuania umbristriata* in synonymy with *Monodelphis americana*, and treated *Minuania* as a subgenus of *Monodelphis*, containing *M. dimidiata* (Wagner) and *M. fosteri* Thomas.
1959. Lyne discussed the vibrissae in "*Peramys dimidiatus* Wagner," recording a specimen from "Palmeira, Parana, Brazil."
1960. Talice et al. wrote about the coloration and natural history of *Monodelphis dimidiata* in Uruguay. On pages 149 and 150, they seemed to think it likely that the "Colicorto" of Azara represented *M. dimidiata* but later (p. 152) contradicted this position.
1963. Godoy wrote that *M. fosteri* occurred in Buenos Aires and La Pampa in Argentina.
1964. Crespo reported on an animal identified by him as *Monodelphis* (*Minuania*) *fosteri* from Argentina. Reig felt that knowledge of the genus *Monodelphis* was not sufficient to justify recognition of the subgenus *Minuania*. He reported *M. dimidiata* from several localities in Argentina. He also stated that immature specimens of *M. dimidiata* have a coloration similar to that described by Thomas for *M. fosteri*. Reig suggested that *M. fosteri* Thomas may be a synonym of *M. dimidiata*.
1965. Reig wrote about the natural history of *M. dimidiata*. Fornes and Massoia compared specimens of Argentine *M. dimidiata* with those of typical Uruguayan *dimidiata* and found no differences (see also Massoia and Fornes, 1967).

1968. Avila Pires noted that the holotype of *P. [eramys]. d [imidiata]. itatiayae* Miranda-Ribeiro was, at that time, supposed to be prepared as a skin and skull. In the original description, the holotype was stated to be in alcohol. Avila Pires could not find the holotype in the Museu Nacional, Rio de Janeiro. He wrote that specimens from Itatiaia and Rio Grande do Sul could not be distinguished subspecifically. He followed Cabrera (1958) in treating *M. goyana* Miranda-Ribeiro as a synonym of *M. dimidiata*, also noting that he could not find the type (not realizing that *M. goyana* and *M. umbristriata* Miranda-Ribeiro are one and the same).
1969. Reig and Bianchi reported the karyotype of *M. dimidiata* from Argentina.
1972. Wainberg reported information concerning the karyotype of *M. dimidiata* from other localities in Argentina. Ximénez et al. gave information on the distribution of *M. dimidiata* in Uruguay. They also reported that Ximénez had examined the holotype of *M. d. itatiayae* and found no differences sufficient to justify subspecific distinction from *M. dimidiata* of Uruguay.
1974. Vaz-Ferreira and Palerm gave information on the natural history of *M. dimidiata* in Uruguay.
1975. Solari and Bianchi discussed the X and Y chromosomes of *M. dimidiata*.
1976. Pine treated *Minuania* as a valid subgenus containing *M. dimidiata* and *M. umbristriata*.
1977. Kirsch and Calaby did not recognize the subgenus *Minuania* and did not include *Monodelphis umbristriata* in their classification. They did, however, place *M. fosteri* in synonymy with *M. dimidiata*, based on the remarks made by Reig (1964).
1980. Pine compared the holotype of *P. [eramys]. d [imidiata]. itatiayae* Miranda-Ribeiro with specimens of *M. henseli* from Brazil, and concluded that the former probably does not deserve subspecific recognition.

STATUS OF NAMED FORMS RELATED TO OR
CONFOUNDED WITH *MONODELPHIS DIMIDIATA*

Monodelphis dimidiata (Wagner)

We have seen specimens of what C. O. Handley, Jr. (personal communication) regards as true *M. dimidiata* only from Argentina. This is unfortunate as the type locality is in Uruguay. Although we have not been able to make direct comparisons of the Brazilian specimens Handley identifies as *M. henseli* (probably a junior synonym of *M. sorex*) with the Argentine *M. dimidiata*, our recollections and notes indicate

that the Brazilian specimens are more brightly colored on the flanks and belly, and darker dorsally than the Argentine ones. Bertoni (1914) also found what he regarded as northern (Paraguayan) *M. dimidiata* to be brighter than southern ones. Similarly, Cabrera and Yepes (1940, 1960) reported that specimens from the state of Rio de Janeiro, Brazil, were especially bright, and that for this reason they had been regarded as a separate subspecies. Reig (1964) noted that coastal Argentine *dimidiata* agreed in color with the type of *M. dimidiata*, and Massoia and Fornes (1967) also found them to essentially agree in color with Uruguayan specimens. However, Ximénez et al. (1972) reported that Ximénez had examined the holotype of *P [eramys]. d [imidiata]. itatiayae* (an *M. henseli* according to Handley) and found no differences justifying its separation at the subspecific level from topotypic *M. dimidiata*. They claimed that *M. dimidiata* shows variable coloration even at a single locality, which, by implication, could account for the external differences between the holotype of *itatiayae* and *M. dimidiata*.

As *M. dimidiata* has been confused with *M. henseli* (probably = *M. sorex*), the actual distributions of the two species and identities of some published specimens are problematical.

***Monodelphis dimidiata itatiayae* (Miranda-Ribeiro)**

See *M. henseli*.

***Monodelphis fosteri* Thomas**

This name was based on a single immature female from "Caleufú . . . about 64°30'W and 35°35'S . . . La Pampa, Argentina." Thomas (1924) wrote, "This specimen is just about the same age as a number of *M. dimidiata* which I collected in 1896 near Montevideo, and is conspicuously different in colour from any of them," describing *M. fosteri* as "of a very much paler grey colour above, near 'deep mouse-grey,' the sides scarcely more buffy than the back, the belly only faintly tinged with buffy, as is also the case with the cheeks, instead of these parts being in each case strong prominent buffy. Tail bicolor, black above, whitish below. Skull and teeth as in *dimidiata*."

Reig (1964) stated that his immature *M. dimidiata* from Argentina had the coloration Thomas gave for *fosteri*, being paler than Reig's adults and the holotype of *M. dimidiata*. This seems odd because the specimens from Balcarce, which is not far from Reig's localities, show the reverse, the young being darker than the adults, as was also reported by Crespo (1964) for his Argentine *Monodelphis*. Our notes taken on one of three essentially identical immature male specimens from Balcarce (MSU 17469), with total length equals 120 mm, skull equals 23.5 mm ("age group 3"), are as follows: "belly fur . . . with gray bases

tipped with buff [;] belly much darker than in adults which have more or less monochromatic orangish or yellowish bellies. Lateral orangish color on flanks not nearly as well-developed as in adults. Side of head and neck fairly orange however." These immatures are darker and browner overall than the adults. One point apparently missed by Reig is that Thomas (1924) compared the (pale) type of *M. fosteri* with what he regarded as typical (dark) *M. dimidiata* of approximately the same age. Assuming Thomas' *M. fosteri* shows a growth pattern similar to that of *M. dimidiata* from near Balcarce, its holotype would, judging from its measurements, fall in our "age group 5," at which time adult pelage should be developed (as Thomas no doubt knew). Reig, however, concluded that *M. fosteri* Thomas is probably a synonym of *M. dimidiata*, with *M. fosteri*'s characters being merely those typical of juvenile *dimidiata*. He made no definite decision on this, however, and stated that his supposition ought to be checked out by comparison of types and study of specific characters in the genus. According to Kirsch and Calaby (1977), however, "Reig (1964) showed that *M. fosteri* specimens were simply juveniles of *M. dimidiata*, and *fosteri* is accordingly omitted [from their list of species]." Although they have not themselves made the studies recommended by Reig, Kirsch and Calaby have treated the conspecificity of *M. dimidiata* and *M. fosteri* as proved and they were the first to place the names in synonymy. We believe that the conservative course is to treat *M. fosteri* as a full species pending further direct comparisons with other specimens.

***Monodelphis goyana* (A. de Miranda-Ribeiro)**

See *M. umbristriata*.

***Monodelphis henseli* (Thomas)**

This name is a junior synonym of *Monodelphis sorex* (Hensel) according to C. O. Handley, Jr. (personal communication). Handley has convinced us that the holotype of *P [eramys]. d [imidiata]. itatiayae* Miranda-Ribeiro is a junior synonym of *M. henseli* (see Pine, 1980).

***Monodelphis sorex* (Hensel)**

See *M. henseli*.

***Monodelphis umbristriata* (Miranda-Ribeiro)**

In the same paper (p. 422) as the description of "*Monodelphis dimidiata itatiayae*," Miranda-Ribeiro (1936) named *Minuania umbristriata*. On page 419 in a key, he wrote, "[Coloração] ruiva, aparentemente uniforme . . . *M. goyana*." Cabrera (1958) tentatively placed *Minuania umbristriata* in the synonymy of *Monodelphis americana*

Müller. In regard to *M. goyana*, Cabrera wrote "mencionada solamente en una clave, sin indicación de localidad ni más caracteres diferenciales que . . . [quotes Miranda-Ribeiro], apenas puede ser considerada más como un *nomen nudum*. En todo caso, es por ahora una forma nominal muy dudosa, tal vez simplemente una variante erítica de *dimidiata*." Brief as Miranda-Ribeiro's remarks are, they constitute a description, and whatever *M. goyana*'s status, it is not a *nomen nudum*. Although this did not occur to Cabrera, it is clear that *Minuania goyana* and *Minuania umbristriata* were intended to apply to one and the same animal. In his key, Miranda-Ribeiro recognized two species in the subgenus *Minuania* (*M. dimidiata* and *M. goyana*). In the rest of the text, he also recognized two species (*M. dimidiata* and *M. umbristriata*). The description of *M. goyana* in the key agrees with the description of *M. umbristriata* in the main text. The specific name *goyana* in Brazilian Portuguese means a (female) inhabitant of the Brazilian state Goiás, and both of Miranda-Ribeiro's specimens of *M. umbristriata* are from that state. Obviously, he initially intended to call his new form by one name and then changed his mind but failed to make all the necessary changes in his manuscript. As first revisers, we select the name *Minuania umbristriata* Miranda-Ribeiro 1936 to have priority over *Minuania goyana* Miranda-Ribeiro 1936.

Pine (1976) reported a specimen of *Monodelphis umbristriata* from Minas Gerais, and treated *Minuania* as a valid subgenus containing *M. umbristriata* and *dimidiata*. A character used by Miranda-Ribeiro (1936) and Pine (1976) to distinguish *M. umbristriata* (as adults) from other striped-backed *Monodelphis* was the extremely faint dorsal stripes in *M. umbristriata*. Thomas (1888) noted this color pattern in animals he called *M. americana* and remarked that it may be seasonal because he had seen a specimen in Paris that was rufous-striped anteriorly and black-striped posteriorly. When Miranda-Ribeiro (1936) and Pine (1976) were writing about *M. umbristriata*, the extreme sexual dimorphism in at least some *Monodelphis* was unappreciated. The status of the name *M. umbristriata* may be in need of reassessment because both reported adult specimens are males.

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