

# Systematics Of The Coatis, Genus *Nasua* (Mammalia, Procyonidae)

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## SYSTEMATICS OF THE COATIS, GENUS *NASUA* (MAMMALIA: PROCYONIDAE)

Denise M. Decker

*Abstract.*—Systematics of the genus *Nasua* was examined using both qualitative and quantitative techniques. Principal component analysis was used to assess morphologic variation among the species of *Nasua*. Mann-Whitney *U* tests were used to determine whether there were any differences among the three taxa in any of the quantitative features measured and to determine whether the Cozumel coati was significantly smaller than *N. narica* of the Yucatan peninsula (including the Yucatan, Campeche, and Quintana Roo departments). Morphological features were examined to determine whether there were any qualitative features that could distinguish between any of the species of *Nasua*. Principal component analysis showed that *N. nelsoni* was not distinctly smaller in body size when compared to a series of mainland coatis. Mann-Whitney *U* tests revealed significant differences between *N. nasua* and *N. narica* ( $P < 0.01$ ) in most quantitative features measured. Significant differences ( $P < 0.05$ ) were found between Yucatan *N. narica* and *N. nelsoni* for 27 of the 32 quantitative features measured; however, when *N. nelsoni* was compared to a geographically representative sample of mainland *N. narica*, only 16 of the 32 features were significant ( $P < 0.05$ ). Eight qualitative features, including features of the anterior alveolar foramen, nasal bones, postorbital process of the jugal bone, mesopterygoid region of the palate, m2 entoconid, baculum, nose color, and hair at the nape of the neck were found to separate *N. nasua* from *N. narica* and *N. nelsoni*. Differences in the quantitative analyses between *N. nasua* and *N. narica* and between *N. nelsoni* and *N. narica* are differences commonly seen at the subspecific level and are not considered of sufficient nature to recognize any of the taxa as distinct species based on these quantitative features. The qualitative features were found useful in separating *N. nasua* from *N. narica*. No qualitative features were found to separate *N. nelsoni* from *N. narica*. Based on results of this study, *N. nelsoni* should be considered conspecific with *N. narica*. Therefore, only two species of *Nasua* (*N. nasua* and *N. narica*) are recognized.

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Historically, species-level systematics of the coatis (genus *Nasua*) has been influenced by the large range of color and size variation, much of which has been attributed to differences in sex and age (Burt & Hooper 1941, Hershkovitz 1951). Individual variation is such that Allen (1906) described different pelage colorations, previously used as subspecific designations, from

a series of specimens collected at the same time from a single locality. Individuals with different pelage coloration also have been reported in the same litter (Allen 1879). In northwestern Mexico, Burt & Hooper (1941) found that the only well-defined geographic trend is in coloration, with specimens becoming progressively darker from north to south. This variation has led to a number

of incorrect identifications, and the taxonomy of *Nasua* remains uncertain (Appendix 1).

Two (Corbet & Hill 1986, Honacki et al. 1982) or three (Ewer 1973) species of coatis are recognized currently, *Nasua narica* (white-nosed coati), *Nasua nasua* (brown-nosed coati), and *Nasua nelsoni* (Cozumel Island coati). Authors who have recognized only two species have lumped North American *N. narica* with South American *N. nasua* and considered the insular *N. nelsoni* as a distinct species. *Nasua nelsoni* generally has been accepted as a distinct species based on the original description by Merriam (1901) and its validity has not been questioned subsequently. *Nasua nasua* and *N. narica* were described originally by Linnaeus (1766), who based the description of *N. nasua* on the "coati" of Marcgrave (1648) and the "coati-mondie a queue annee" of Brisson (1756) and that of *N. narica* on the "Coati brun" of Buffon (1760). *Nasua nelsoni* was distinguished from *N. narica* primarily on the basis of its smaller size (Merriam 1901). No diagnostic qualitative features have been reported by Merriam (1901) or by later authors. Jones & Lawlor (1965) retained *N. nelsoni* as a species, believing that it was smaller than *N. narica yucatanica* of the adjacent mainland.

*Nasua narica* has been considered conspecific with *N. nasua* by several authors (Hall 1981, Honacki et al. 1982, Corbet & Hill 1986, Nowak & Paradiso 1986) despite the lack of any published data to support this conclusion. Those authors cite (directly or indirectly) a passage in Cabrera (1960: 245) concerning the color morphs of South American coatis: "Al parecer, todos los *Nasua* sudamericanos constituyen una sola especie con dos fases cromaticas, una parda y otra roja, y en algunos casos con marcada tendencia al melanismo . . ." However, Cabrera was not referring to the comparison between North and South American coatis but rather to the two color phases of South American coatis (brown phase, *Nasua na-*

*sua* Linnaeus, 1766 and red phase, *Nasua rufa* E. Geoffroy Sainte-Hilaire, 1803), each previously thought to represent separate South American species. Cabrera (1960) considered all South American forms as one species (*Nasua nasua*) and was not concerned with the North American form, *N. narica*. A detailed analysis of the *N. narica-nasua* problem has not been attempted.

Because original descriptions were based on a small number of highly variable features, the taxonomic status of *Nasua* is unclear and in need of additional investigation (Eisenberg 1989). For this study, I tested the hypothesis that *N. nasua*, *N. narica*, and *N. nelsoni* can be distinguished on either quantitative or qualitative morphological features. This was tested in two ways: (1) by examining characters that were used in the original type descriptions and in subsequent published descriptions; (2) by examining variation in additional characters (characters not used in previous studies).

### Methods

For the quantitative analysis of morphological variation, 32 measurements were recorded from 111 male and 116 female specimens (Appendix 2) with digital calipers and recorded to the nearest 0.01 mm. Measurements employed are listed in Table 1 and described in Decker (1990). Specimens (including nine holotypes) were selected from a wide geographic range (Appendix 2 and Fig. 1) to account for the great amount of variation exhibited in the genus *Nasua*. Preliminary analyses indicated sexual dimorphism in 22 of 32 skull characters for each described species, with males being consistently larger than females. Males and females were analyzed separately in each analysis. Pair-wise comparisons were made between *N. nasua* and *N. narica* and between *N. nelsoni* and *N. narica* using a Mann-Whitney *U* test to determine whether there were any differences in measured characters. A Mann-Whitney *U* test was

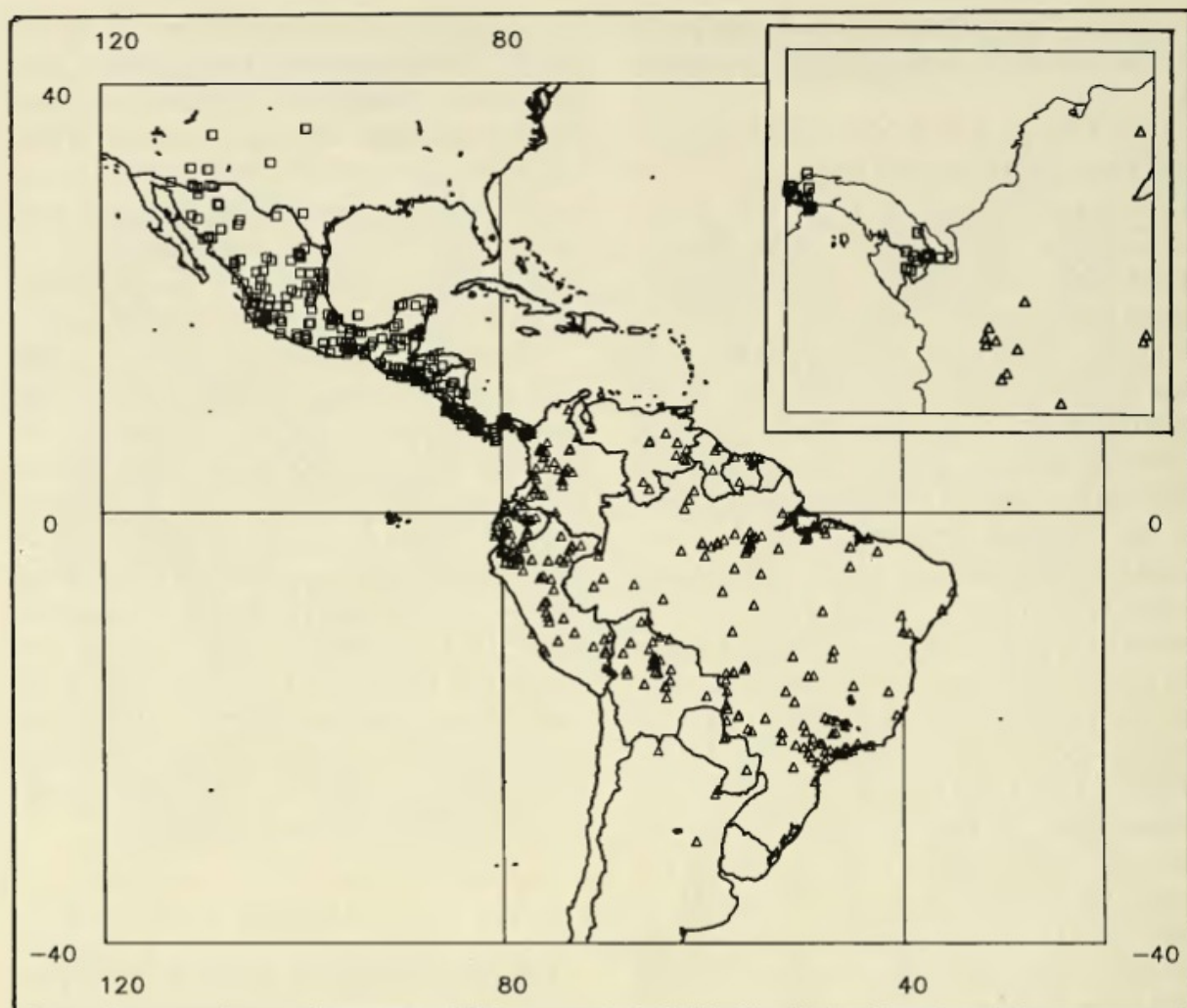


Fig. 1. The geographic range of specimens examined in this study. ( $\Delta$ ) = *N. nasua*; ( $\square$ ) = *N. narica*. Inset shows closeup of Panama/Colombia and the allopatric distribution (see text for discussion).

performed between *N. nelsoni* and *N. narica* of the Yucatan (including the Yucatan, Campeche, and Quintana Roo departments) to test Jones & Lawlor's (1965) assumption that the Cozumel Island coati is smaller than the adjacent mainland coati (*N. narica yucatanica*). Principal component analysis was used to assess morphologic variation among taxa. Because of the range of variation exhibited by individuals from the same locality, each specimen was treated as an operational taxonomic unit (OTU).

Qualitative features that have been used previously to distinguish among taxa were taken initially from the type description and from discussions in subsequent literature.

Other morphological features were added based on observations of 684 specimens (Appendix 2). Characters were scored as to presence or absence within each taxon.

#### Results and Discussion

A Mann-Whitney *U* test revealed significant differences between *N. nasua* and *N. narica* ( $P < 0.01$ ) for most characters measured (Table 1). Infraorbital foramen height was the only feature that did not differ significantly in either sex. The distance between paroccipital process and mastoid process was not significantly different in males. Premaxillary length, rostrum length, palate length, zygomatic breadth, and cranium

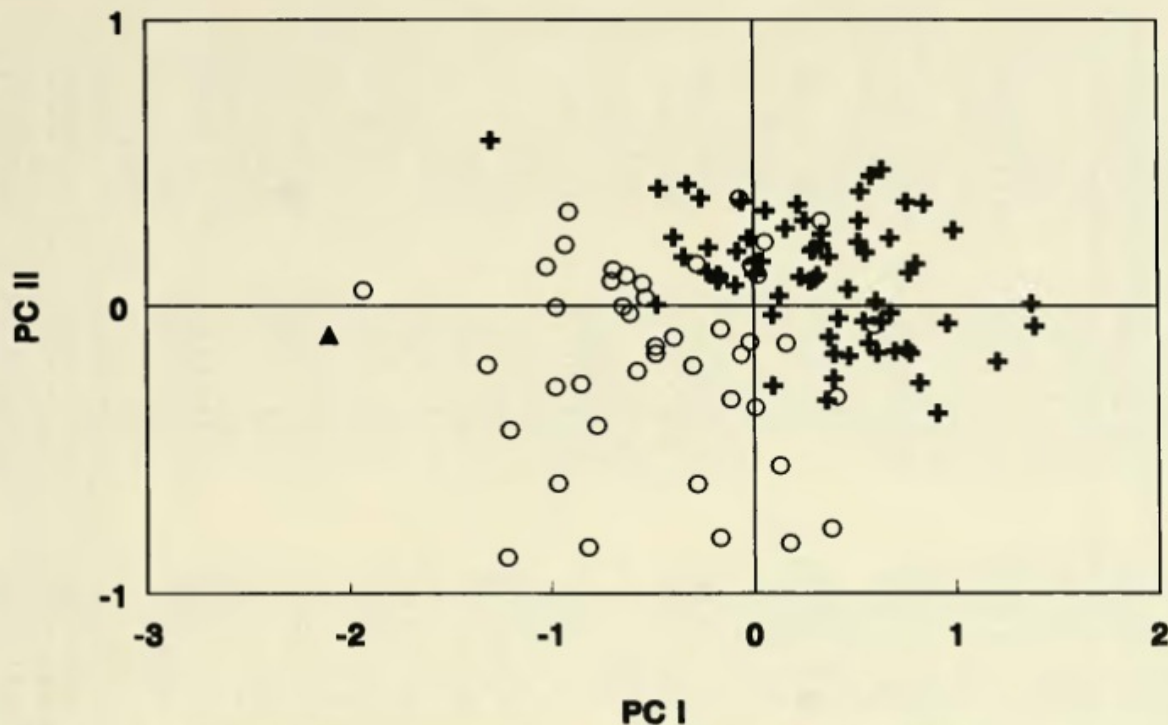


Fig. 2. Scattergram showing the results of principal component analysis of *N. nasua* (+), *N. narica nelsoni* (▲) and *N. narica* (O).

width are the characters best able to distinguish between *N. nasua* and *N. narica*; however, because there is so much overlap even in these features, these skull measurements would not be useful in identifying a single individual. Slightly less significant differences ( $P < 0.05$ ) were found in 16 of the 32 characters measured between *N. narica* and *N. nelsoni* for both males and females. Five of the six specimens of *N. nelsoni* used in this study were collected from the same locality at the same time; therefore, it is possible that most specimens from the sample of *N. nelsoni* are from one family unit. Because the Cozumel Island coatis were collected from one local population, this sample is probably not a good representation of the variation of the Cozumel coati. There probably are several local populations of mainland coatis that fall well within the range of variation of the Cozumel coati. For example, I have found a series of coatis in Estado Nuevo Leon, Mexico that do not differ in size from the Cozumel coati. Because of the lack of adequate sampling on

the island, the variation is probably much greater than represented. Despite this fact, a clear separation could not be found between *N. narica* and *N. nelsoni*. The three taxa were not easily distinguishable using principal component analysis (Fig. 2). *Nasua nasua* and *N. nelsoni* were both well within the range of variation of *N. narica*. Twenty-four of the 32 characters loaded high on principal component I (PCI), accounting for 86% of the variation. PCI has been interpreted as representing size (Kennedy & Schnell 1978, Neff & Marcus 1980, Best 1985). These results indicated that there was no apparent size difference in the quantitative features among *N. nasua*, *N. narica*, and island forms of *N. nelsoni*.

Jones & Lawlor's (1965) observation that the Cozumel coati is slightly smaller than the adjacent mainland coati, *N. narica yucatanica* was supported (Table 2). However, when the Cozumel coati is compared to a widely distributed and well sampled population of mainland coatis, the differences are not as clear (Table 1). Of the 32 char-

Table 1.—The mean, standard error, sample size ( $n$ ) and range for skull measurements of the genus *Nasika*. \*\* denotes a significant difference of *N. naska* or *nelsoni* from *N. narica* at the 0.05 level of significance. \*\*\* denotes a significant difference at the 0.01 level as revealed by a Mann-Whitney  $U$  test.

Character	<i>N. naska</i> (66)	<i>N. naska</i> (99)	<i>N. narica</i> (68)	<i>N. narica</i> (99)	<i>N. nelsoni</i> (68)	<i>N. nelsoni</i> (99)
CBL	117.98 $n = 36$ (104.04–129.30)	108.53 $n = 26$ (99.10–121.83)	125.50 $n = 65$ (99.91–136.06)	119.36 $n = 79$ (109.14–135.70)	98.17 $n = 2$ (97.12–99.22)	97.15 $n = 2$ (93.42–100.88)
ZYB	66.42 $n = 36$ (54.07–78.21)	56.76 $n = 28$ (51.76–67.03)	70.83 $n = 69$ (50.90–82.12)	62.22 $n = 83$ (55.17–77.44)	58.11 $n = 2$ (56.56–59.66)	49.39 $n = 2$ (48.89–49.88)
PPL	85.74 $n = 27$ (78.05–93.48)	78.33 $n = 19$ (71.96–90.32)	92.01 $n = 47$ (71.79–101.18)	87.74 $n = 55$ (78.65–100.34)	71.27 $n = 1$ —	69.47 $n = 2$ (69.07–69.86)
ROS	21.49 $n = 38$ (17.04–27.55)	19.24 $n = 29$ (14.97–28.91)	23.45 $n = 69$ (17.35–27.36)	20.84 $n = 84$ (16.71–38.74)	19.01 $n = 3$ (16.44–20.74)	15.82 $n = 2$ (15.44–16.19)
IFH	4.84 $n = 38$ (3.89–5.98)	4.78 $n = 30$ (3.64–6.34)	4.84 $n = 69$ (3.44–6.66)	4.66 $n = 84$ (3.38–6.63)	5.06 $n = 3$ (4.19–5.06)	4.63 $n = 2$ (4.19–5.06)
PAL	72.90 $n = 35$ (65.07–81.68)	67.44 $n = 24$ (61.16–76.91)	78.94 $n = 63$ (62.50–86.48)	75.19 $n = 75$ (68.54–86.73)	60.18 $n = 2$ (58.01–62.35)	58.75 $n = 2$ (57.79–59.71)
POP	32.63 $n = 34$ (26.12–40.46)	29.11 $n = 28$ (24.68–33.29)	36.44 $n = 64$ (26.27–44.56)	34.15 $n = 77$ (34.15–40.84)	28.85 $n = 2$ (27.83–29.86)	26.34 $n = 1$ —
MAX	46.39 $n = 36$ (43.00–51.00)	44.24 $n = 28$ (40.00–49.00)	49.27 $n = 65$ (40.00–55.00)	47.60 $n = 82$ (43.00–52.00)	39.87 $n = 3$ (37.00–42.00)	37.77 $n = 2$ (37.00–38.00)
PMX	48.48 $n = 35$ (44.44–53.49)	45.86 $n = 29$ (41.15–52.24)	51.36 $n = 67$ (41.34–57.27)	49.51 $n = 82$ (45.43–53.97)	41.52 $n = 3$ (38.83–43.33)	39.46 $n = 2$ (39.11–39.81)
WFM	15.25 $n = 34$ (11.97–17.15)	13.34 $n = 26$ (10.82–14.55)	14.21 $n = 62$ (12.32–16.14)	13.92 $n = 72$ (12.43–15.31)	11.94 $n = 2$ (11.76–12.11)	11.95 $n = 1$ —
MAS	45.10 $n = 37$ (34.47–73.15)	40.50 $n = 28$ (23.40–48.16)	47.66 $n = 68$ (37.54–53.92)	44.74 $n = 80$ (40.41–50.88)	40.09 $n = 2$ (37.92–42.25)	35.78 $n = 2$ (34.98–36.57)

Table 1.—Continued.

Character	<i>N. nazua</i> (♂♂)	<i>N. nazua</i> (♀♀)	<i>N. narica</i> (♂♂)	<i>N. narica</i> (♀♀)	<i>N. nelsoni</i> (♂♂)	<i>N. nelsoni</i> (♀♀)
PCB	23.42 0.359** <i>n</i> = 38 (19.02–29.83)	24.88 0.367** <i>n</i> = 30 (20.31–29.29)	27.41 0.316 <i>n</i> = 67 (20.89–31.57)	29.68 0.213 <i>n</i> = 76 (26.14–34.04)	23.35 0.415 <i>n</i> = 2 (22.93–23.76)	25.24 <i>n</i> = 1
ABL	14.18 0.177** <i>n</i> = 38 (12.37–16.85)	13.71 0.213** <i>n</i> = 29 (11.98–16.41)	16.26 0.118 <i>n</i> = 68 (12.08–18.46)	15.71 0.101 <i>n</i> = 81 (12.21–17.76)	13.23 0.250* <i>n</i> = 2 (12.98–13.48)	11.68 0.425* <i>n</i> = 2 (11.25–12.10)
ABW	14.67 0.218* <i>n</i> = 38 (12.11–17.46)	13.94 0.223* <i>n</i> = 29 (11.90–16.44)	15.25 0.123 <i>n</i> = 69 (11.86–17.55)	14.54 0.112 <i>n</i> = 81 (12.31–16.86)	11.49 0.000* <i>n</i> = 2 (11.49–11.49)	10.38 0.270* <i>n</i> = 2 (10.11–10.65)
ABH	6.59 0.125** <i>n</i> = 38 (4.77–8.13)	6.29 0.179** <i>n</i> = 27 (3.68–7.84)	7.81 0.125 <i>n</i> = 63 (6.07–9.90)	7.70 0.109 <i>n</i> = 74 (5.68–10.01)	5.51 0.580* <i>n</i> = 2 (4.93–6.09)	5.95 <i>n</i> = 1
INB	25.87 0.317** <i>n</i> = 37 (22.00–29.00)	24.12 0.272** <i>n</i> = 30 (21.00–27.00)	28.18 0.384 <i>n</i> = 64 (18.00–34.00)	26.98 0.227 <i>n</i> = 75 (22.00–32.00)	17.94 3.170* <i>n</i> = 2 (15.00–21.00)	20.68 <i>n</i> = 1
ROL	56.10 0.476** <i>n</i> = 38 (50.33–60.93)	51.80 0.470** <i>n</i> = 30 (45.74–58.30)	58.83 0.407 <i>n</i> = 66 (45.09–64.18)	55.58 0.474 <i>n</i> = 79 (25.66–63.58)	45.98 1.127** <i>n</i> = 3 (44.54–48.20)	44.14 <i>n</i> = 1
MEW	15.60 0.195** <i>n</i> = 38 (12.75–17.58)	15.08 0.221** <i>n</i> = 28 (13.48–18.12)	17.22 0.128 <i>n</i> = 63 (15.35–19.94)	17.26 0.116 <i>n</i> = 75 (14.38–20.25)	13.95 0.415* <i>n</i> = 2 (13.53–14.36)	14.93 <i>n</i> = 1
MEL	18.11 0.320** <i>n</i> = 37 (14.45–22.06)	16.19 0.345** <i>n</i> = 24 (12.47–19.84)	21.56 0.243 <i>n</i> = 60 (16.16–25.93)	20.81 0.809 <i>n</i> = 70 (15.74–74.75)	14.44 0.085* <i>n</i> = 2 (14.35–14.52)	13.48 <i>n</i> = 1
PAR	13.48 0.210 <i>n</i> = 38 (10.34–16.36)	11.82 0.213* <i>n</i> = 29 (9.12–13.91)	13.76 0.162 <i>n</i> = 67 (8.20–16.21)	12.66 0.130 <i>n</i> = 82 (7.41–15.20)	10.88 0.760* <i>n</i> = 2 (10.12–11.64)	9.57 0.435* <i>n</i> = 2 (9.13–10.00)
COR	26.03 0.419** <i>n</i> = 38 (21.13–33.81)	23.22 0.495** <i>n</i> = 30 (18.86–30.19)	29.95 0.253 <i>n</i> = 66 (23.62–34.55)	28.33 0.179 <i>n</i> = 79 (23.28–32.83)	22.13 0.718* <i>n</i> = 3 (21.20–23.54)	22.62 <i>n</i> = 1
FRO	32.94 0.418** <i>n</i> = 38 (27.83–38.59)	30.46 0.604** <i>n</i> = 30 (24.94–43.66)	35.32 0.363 <i>n</i> = 64 (23.87–40.74)	32.73 0.253 <i>n</i> = 76 (28.11–41.36)	26.82 2.960* <i>n</i> = 2 (23.86–29.78)	25.13 <i>n</i> = 1

Table 1.—Continued.

Character	<i>N. nasuta</i> (♂♂)	<i>N. nasuta</i> (♀♀)	<i>N. naricata</i> (♂♂)	<i>N. naricata</i> (♀♀)	<i>N. nelsoni</i> (♂♂)	<i>N. nelsoni</i> (♀♀)
WCR	43.84 0.238** <i>n</i> = 38 (40.60–46.84)	41.70 1.314** <i>n</i> = 29 (25.32–45.46)	45.51 0.185 <i>n</i> = 65 (41.62–49.38)	44.68 0.134 <i>n</i> = 73 (42.27–47.56)	38.49 0.530* <i>n</i> = 2 (37.96–39.02)	37.95 <i>n</i> = 1
PL3	5.49 0.081** <i>n</i> = 34 (4.49–6.17)	5.41 0.117* <i>n</i> = 29 (3.57–6.68)	6.06 0.049 <i>n</i> = 63 (5.23–7.01)	6.33 0.384 <i>n</i> = 78 (4.98–8.75)	4.36 0.082** <i>n</i> = 3 (4.20–4.46)	4.55 <i>n</i> = 1
PB3	3.59 0.080** <i>n</i> = 34 (2.89–4.70)	3.70 0.161** <i>n</i> = 29 (2.82–6.91)	4.10 0.050 <i>n</i> = 63 (3.16–5.26)	4.10 0.037 <i>n</i> = 78 (3.29–4.87)	3.27 0.090** <i>n</i> = 3 (3.11–3.42)	3.30 <i>n</i> = 1
PL4	6.95 0.087** <i>n</i> = 37 (5.41–8.11)	6.72 0.093** <i>n</i> = 29 (5.89–7.94)	7.46 0.064 <i>n</i> = 67 (6.02–8.73)	7.52 0.049 <i>n</i> = 84 (6.58–8.64)	5.45 0.119* <i>n</i> = 3 (5.25–5.66)	6.10 0.235* <i>n</i> = 2 (5.86–6.33)
PB4	6.88 0.096** <i>n</i> = 37 (5.26–7.85)	6.65 0.104** <i>n</i> = 29 (5.65–7.94)	7.69 0.071 <i>n</i> = 67 (5.45–8.93)	7.61 0.062 <i>n</i> = 84 (6.11–8.94)	5.52 0.131* <i>n</i> = 3 (5.28–5.73)	5.77 0.400* <i>n</i> = 2 (5.37–6.17)
ML1	7.27 0.099** <i>n</i> = 36 (5.97–8.33)	6.94 0.097** <i>n</i> = 28 (6.09–8.17)	7.78 0.060 <i>n</i> = 68 (5.96–8.94)	7.59 0.048 <i>n</i> = 83 (6.48–8.63)	6.00 0.090* <i>n</i> = 3 (5.89–6.18)	6.10 0.260* <i>n</i> = 2 (5.84–6.36)
MB1	6.56 0.092** <i>n</i> = 36 (5.35–7.82)	6.41 0.097* <i>n</i> = 28 (5.50–7.55)	7.73 0.052 <i>n</i> = 68 (6.84–8.74)	7.62 0.052 <i>n</i> = 83 (7.62–8.71)	6.08 0.171* <i>n</i> = 3 (5.77–6.36)	6.65 0.205* <i>n</i> = 2 (6.44–6.85)
ML2	6.33 0.121** <i>n</i> = 37 (4.82–7.71)	6.18 0.154** <i>n</i> = 29 (4.29–7.48)	6.94 0.082 <i>n</i> = 66 (5.15–8.25)	6.90 0.069 <i>n</i> = 84 (5.67–8.40)	4.87 0.225* <i>n</i> = 3 (4.49–5.27)	4.36 0.050* <i>n</i> = 2 (4.31–4.41)
MB2	6.63 0.108** <i>n</i> = 37 (5.19–7.90)	6.51 0.143** <i>n</i> = 28 (4.95–8.12)	7.84 0.056 <i>n</i> = 65 (6.86–8.79)	7.75 0.053 <i>n</i> = 84 (6.86–9.16)	5.93 0.261* <i>n</i> = 3 (5.42–6.27)	6.21 0.005* <i>n</i> = 2 (6.20–6.21)
BAS	32.65 0.625* <i>n</i> = 12 (28.33–36.06)	28.47 0.809* <i>n</i> = 7 (26.43–32.12)	34.50 0.476 <i>n</i> = 19 (30.64–37.67)	32.17 0.319 <i>n</i> = 24 (30.02–35.64)	25.92 <i>n</i> = 1	—



acters examined, the 16 that are significant ( $P < 0.01$ ) are related to the length of the skull and the size of the dentition. Comparisons with the skull of *N. narica* reveal an increase in the length of the skull of the Cozumel coati, while the width of the braincase remains the same. Additionally, the dentition of the Cozumel coati is also smaller in both length and width. The lengthening of the skull and the reduction of the dentition is probably associated with a shift in the diet of the Cozumel coati.

In the original description, Merriam (1901) compared Cozumel Island coatis (holotype specimen plus two males and four females) to a single specimen of *N. narica* from the Yucatan peninsula. The description of the holotype emphasized a smaller skull, zygomatic arch, auditory bullae, and dentition. Results of this study show that the variation of these features in *N. nelsoni* is within the range of variation of *N. narica* (Table 1). Based on the few specimens of mainland coatis that Merriam (1901) had to compare with the Cozumel coati, the features he emphasized as being the most important discriminators are significantly different from that of *N. narica* in this study. However, when the Cozumel coati is compared to a representative sample of *N. narica*, the differences are not as great.

Characters that were found significantly different in this study between *N. nelsoni* and *N. narica* have been shown to be of value in geographic variation studies and in delineating subspecies (e.g., Kortlücke 1973, Kennedy & Lindsay 1984). The differences among the subspecies of *N. narica* are greater than those between *N. narica* and *N. nelsoni*. Therefore, if one were to recognize *N. nelsoni* as a distinct species based on the few differences revealed at the 0.05 level of significance, it would be necessary to split the recognized subspecies of *N. narica* (see Hall 1981) into many species as well. Therefore, differences between *N. nelsoni* and *N. narica* are not of sufficient nature to warrant specific recognition.

Table 2.—Results of Mann-Whitney  $U$  test between Yucatan *N. narica* and Cozumel Island *N. nelsoni*.  $n$  = sample size (*N. narica*/*N. nelsoni*).

Character	$n$	$df$	$Z$	$P$
CBL	10/5	14	-2.33	0.020
ZYB	10/5	14	-1.71	0.086
PPL	11/4	13	-2.61	0.009
ROS	11/6	15	-1.81	0.070
IFH	11/6	15	-0.60	0.547
PAL	9/5	13	-3.00	0.003
POP	8/4	11	-1.36	0.174
MAX	11/6	14	-3.22	0.001
PMX	11/6	15	-3.02	0.003
WFM	8/3	10	-2.45	0.014
MAS	10/5	14	-2.45	0.014
PCB	10/4	13	-2.40	0.016
ABL	11/5	14	-3.12	0.002
ABW	11/5	14	-2.89	0.004
ABH	9/3	10	-2.50	0.013
INB	8/3	10	-2.45	0.014
ROL	9/4	11	-2.78	0.006
MEW	8/3	10	-2.45	0.014
MEL	7/3	9	-2.39	0.017
PAR	11/5	14	-2.44	0.015
COR	9/4	11	-2.78	0.006
FRO	8/3	10	-2.25	0.025
WCR	8/3	10	-2.45	0.014
PL3	9/4	10	-2.78	0.006
PB3	9/4	10	-2.78	0.006
PL4	11/6	14	-3.32	0.001
PB4	11/6	14	-2.82	0.005
ML1	11/6	14	-3.02	0.003
MB1	11/6	14	-2.31	0.021
ML2	11/6	14	-3.22	0.001
MB2	11/6	14	-2.81	0.005
BAS	3/1	2	-1.34	0.180

There is no question that the Cozumel coatis are typically small, but the variation overlaps with the mainland coati for most characters measured. This tendency to be slightly smaller may be related to island dwarfism. Factors that may cause body size to increase or decrease in insular populations include metabolic considerations, resource availability, predation, and competition (Case 1978, Heaney 1978) and probably have different roles in different species. Lawlor (1982) proposed that mammals which specialize on a diet of particulate nature decrease in size on islands, whereas generalists that feed on nonparticu-



Fig. 3. A ventral view of *N. nasua* (left) and *N. narica* (right) demonstrating a feature of the palate; (b) Bacula of *N. narica* (left) and *N. nasua* (right).

late foods increase in size. Although the mainland coatis are generalists, the Cozumel coati may not be. This study suggests that the Cozumel coati is specializing on smaller prey items, but additional study of its ecology and behavior is necessary.

Size does not appear to discriminate populations. *Nasua nelsoni* cannot be clearly differentiated from *N. narica* based on the original size-related features used in the type description or on subsequent measured variables if a representative sample of *N. narica* from a wide geographic range is used in the comparison.

Of 100 qualitative features examined, eight separate *N. nasua* from *N. narica* and none separate *N. nelsoni* from *N. narica* (Table 3). Of the eight, five are features of the skull and dentition, one of the postcranial skeleton, and two of the pelage. Of the five skull features, the most easily discernible is a feature of the palate (Fig. 3a) first recognized by Alston (1879). The mesopterygoid region of the palate is flat in *N. nasua*, whereas in *N. narica* (and *N. nelsoni*) it is depressed along the midline resulting in a relatively small distance between the presphenoid and palate (ca. 2.20 mm in *N. narica* versus 4.70 mm in *N. nasua*). In *N. narica*, the vomer extends beyond and at-

taches to the posterior portion of the palate and can be easily seen in ventral view. The distance between the presphenoid and palate of *N. nasua* is much greater than in *N. narica* (and *N. nelsoni*) and the vomer does not reach the posterior edge.

Additional skull features that distinguish *N. nasua* from *N. narica* (and *N. nelsoni*) include features of the rostrum. In *N. nasua*, the anterior alveolar foramen (as used by Wahlert 1974, Cooper & Schiller 1975, Shoshani 1986) is situated anterior to the infraorbital canal, whereas in *N. narica* (and *N. nelsoni*), it is medial to the infraorbital canal and cannot be seen in lateral view. The alveolar foramen serves as a passageway for the anterior superior alveolar nerve along with a small artery and vein (Shoshani, pers. comm.). The sides of the nasal bones are parallel in *N. narica* (and *N. nelsoni*) so that the posterior width is about equal to the anterior width. In *N. nasua*, the nasal bones converge posteriorly so that the most posterior width is less than the most anterior width. The postorbital process of the jugal bone is present in *N. nasua* and absent in *N. narica* (and *N. nelsoni*). In the dentition, the entoconid of the second lower molar is present and very distinctive in *N. narica* (and *N. nelsoni*), causing the molar to

have a well defined talonid. The entoconid is absent in *N. nasua* and the talonid is indistinct.

In the postcranial skeleton, only one feature of the baculum was found that discriminated among OTUs. The distal tip of the baculum (Fig. 3b) of *N. narica* (and *N. nelsoni*) is distinctly bilobed with a vestigial third lobe on the ventral surface. The baculum of *N. nasua* is spatulate dorsally with a prominent central lobe on the ventral surface. Pocock (1921) noted that the bacula of *N. nasua* and *N. narica* differ significantly in length and commented that this difference may be diagnostic. I examined seven bacula and there seems to be a size difference. However, the utility of size as a diagnostic character remains uncertain, as the variability in baculum size over the whole geographic range has not been examined.

Differences among the many described forms of coatis have usually centered on external pelage. The color of the nose adjacent to the rhinarium distinguishes *N. narica* (and *N. nelsoni*) from *N. nasua* and was used commonly by early authors (Linnaeus 1766, Allen 1879, Alston 1879). *Nasua narica* (and *N. nelsoni*) have a white rhinarial patch and in *N. nasua* it varies from gray to brown (i.e., absent), but is never white. My observations confirm those of A. Gardner (pers. comm.) who recognized that the hair at the nape of the neck is reversed in *N. nasua*, but not in *N. narica* (and *N. nelsoni*).

The eight characters of the skull, postcranial, and skin, discussed above, are diagnostic and justify recognition of *N. narica* as a species distinct from *N. nasua*. Nose color and presence or absence of the postorbital process do not vary in any part of the species' range. Other skull features, such as the position of the rostral foramen and concavity of the palate, were found to vary slightly at the extreme ends (in Mexico for *N. narica* and in southern Brazil for *N. nasua*) of the species' range, however, where

Table 3.—Qualitative features used to separate species of the genus *Nasua*. The plus (+) denotes the presence of the character and the dash (–) denotes the absence of the character. NAS = *Nasua nasua*; NAR = *N. narica*; and NEL = *N. nelsoni*.

Character	NAS	NAR	NEL
Anterior alveolar foramen			
medial to infraorbital foramen	+	–	–
Nasal bones converge			
posteriorly	+	–	–
Mesopterygoid depression	–	+	+
Preorbital process	+	–	–
m2 entoconid	+	–	–
Baculum bilobate	–	+	+
Muzzle white	–	+	+
Nape hair reversed	+	–	–

the ranges are contiguous, these features are always discrete. For identification, the following key should be used together with locality.

#### Key to Species of *Nasua*

1. Palate flat (not concave along midline); nasal bones converging posteriorly; anterior alveolar foramen anterior to infraorbital canal; postorbital process (of jugal) present; M2 entoconid absent; spatulate baculum; brown muzzle . . . . . *N. nasua*
2. Palate depressed along midline; nasal bones near parallel; anterior alveolar foramen medial to infraorbital canal; postorbital process (of jugal) absent; M2 entoconid absent; baculum not spatulate; white muzzle . . . *N. narica* (including *N. n. nelsoni*)

The geographic range of *N. narica* extends from southern Arizona and southwestern New Mexico southward throughout Mexico and Central America with three specimens reported from northern Colombia, Gulf of Uraba (FMNH 69599, 69600, 69601). The range of *N. nasua* extends throughout most of northern South America to northern Argentina and northern Uruguay (Fig. 1). The

apparent lack of parapatry of the two species in northern Colombia may be a collecting artifact.

### Conclusion

Eight qualitative features were found to separate *Nasua nasua* from *N. narica* (including *N. n. nelsoni*). No qualitative features were found to distinguish *N. n. nelsoni* from *N. narica*, and *Nasua n. nelsoni* is not distinctly smaller in body size when compared to a geographically representative sample of mainland coatis. Consequently, I propose that *N. nelsoni* be considered conspecific with *N. narica* and recognize only two species, *Nasua nasua* and *N. narica*.

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Appendix 1.—Synonymys of the genus *Nasua*.

- Viverra* Linnaeus, 1766:64 (part).  
*Ursus* G. Cuvier, 1798:113 (part).  
*Nasua* Storr, 1780:35; type species *Viverra nasua* Linnaeus, 1766, by absolute tautonymy.  
*Coati* Lacepede, 1799:7; type species *Coati nasua* Lacepede, 1799 (= *Viverra nasua* Linnaeus, 1766) by monotypy.  
*Cuati* Liais, 1872:427; incorrect subsequent spelling of *Coati* Lacepede, 1799.

*Nasua narica* (Linnaeus, 1766)

## White-nosed coati

- [*Viverra*] *narica* Linnaeus, 1766:64; type locality "America." Subsequently restricted to "Veracruz, Mexico" by Allen (1879) and further restricted to Achotal, Isthmus of Tehuantepec, Veracruz by Hershkovitz (1951:560).  
 [*Viverra*] *vulpecula* Erxleben, 1777:490 (part); type locality "in Mexico."  
*Ursus narica*: G. Cuvier, 1798:113; name combination.  
*Coati narica*: Daudin, 1799:154; name combination.  
*Nasua narica*: E. Geoffroy St.-Hilaire, 1803:86; name combination.  
*Nasua nasica* Winge, 1895:35; unjustified emendation of *Viverra narica* Linnaeus, 1766. Alston (1879:74) also insisted that Linnaeus intended the name to be *nasica*, meaning "with a long or pointed nose," but misspelled it.  
*Nasua solitaria mexicana* Weinland, 1860:191; type locality "mexico."  
*Nasua nelsoni* Merriam, 1901:100; type locality "Cozumel Island, Yucatan," Mexico.  
*Nasua narica molaris* Merriam, 1902:68; type locality "Manzanillo, Colima, Mexico."  
*Nasua narica bullata* Allen, 1904:48; type locality "Pozo Azul, Pirris Province, Costa Rica."  
*Nasua narica panamensis* Allen, 1904:51; type locality "Boqueron, Chiriqui," Panama.  
*Nasua narica yucatanica* Allen, 1904:52; type locality "Chichenitza, Yucatan," Mexico.  
*Nasua narica pallida* Allen, 1904:53; type locality "Sierra Nevada (vicinity of Guadalupe y Calva), Chiuhuahua, Mexico."  
*Nasua narica richmondi* Goldman, 1932:312; type locality "Escondido River, 50 miles above Bluefields, Nicaragua."  
*Nasua narica tamaulipensis* Goldman, 1942:80; type locality "Cerro de la Silla, near Monterrey, Nuevo Leon, Mexico (altitude 2,600 feet)."  
*Nasua narica isthmicus* Goldman, 1942:81; type locality "Santa Efigenia, an hacienda about eight miles northwest of Tapanatepec, southeastern Oaxaca, Mexico (altitude 1,200 feet)."

## Appendix 1.—Continued.

*Nasua nasua* (Linnaeus, 1766)

## Brown-nosed coati

- [*Viverra*] *nasua* Linnaeus, 1766:64; type locality "America."  
 [*Nasua*] *nasua* Storr, 1780: 35; first use of current name combination, generic description.  
 [*Viverra*] *quasje* Gmelin, 1788:87 (part); type locality "Surinami."  
*Ursus nasua*: G. Cuvier, 1798:113; name combination.  
*Nasua rufa* E. Geoffroy St.-Hilaire, 1803:85; type locality "L'Amerique."  
*Nasua quasje*: E. Geoffroy St.-Hilaire, 1803:85; name combination.  
*Nasua pusillus* E. Geoffroy St.-Hilaire, 1803:87; type locality "L'Amerique meridionale," restricted to French Guiana by Desmarest (1820:15).  
 [*Nasua*] *rufa* Fischer von Waldheim, 1814:175; type locality "in regionibus calidis Americae." Synonym and homonym of *N. rufa*, E. Geoffroy St.-Hilaire, 1803.  
 [*Nasua*] *fusca* Fischer von Waldheim, 1814:176; type locality "in regionibus calidis Americae."  
*N* [*asua*]. *obfuscata* Olfers, 1818: 227; type locality "Brasilien."  
*N* [*asua*]. *mondie* Olfers, 1818:227; type locality "Brasilien."  
*Nasua rufa* Desmarest, 1820:170; type locality "L'Amerique meridionale"; synonym and homonym of *N. rufa* E. Geoffroy St.-Hilaire, 1803.  
*Nasua fusca* Desmarest, 1820:170; type locality "L'Amerique meridionale"; synonym and homonym of *N. fusca* Fischer, 1814.  
*Nasua sociabilis* Schinz, 1821:199; type locality "in Brasilien."  
*Nasua solitaria* Schinz, 1821:199; type locality "in Brasilien." Restricted to "Morro d'Arara, Rio Mucuri, state of Bahia, Brazil," by Avila-Pires (1965).  
*N* [*asua*]. *socialis* Weid-Neuwied, 1826:283; type locality restricted to "Morro d'Arara, Rio Mucuri, state of Bahia, Brazil," by Avila-Pires (1965).  
 [*Nasua socialis*] *Rufa*: Fischer, 1829:148; name combination.  
 [*Nasua socialis*] *Fusca*: Fischer, 1829:148; name combination.  
 [*Nasua socialis*] *aurea* Lesson, 1842:77; type locality not mentioned, based on "coati brun" of F. Cuvier, Pl. I.  
*Nasua monticola* Schinz, 1844:310; type locality "Peru."  
*Nasua nasuta* Tschudi, 1845:99; incorrect subsequent spelling of *N. nasua* Linnaeus, 1766.  
*Nasua rufina* Tschudi, 1845:99; incorrect subsequent spelling of *N. rufa* Desmarest, 1820.  
*Nasua leucorhynchus* Tschudi, 1845:100; type locality

## Appendix I.—Continued.

- not known. "It is often brought by travellers from the interior of Brazil, but there is apparently good reason for questioning the correctness of the locality" (Allen, 1879).
- Nasua vittata* Tschudi, 1845:100; type locality "Innern von Guyana."
- N[asua]. montana* Tschudi, 1845:102; type locality Umanpuquio, "Cejaregion," Peru.
- Nasua dorsalis* Gray, 1866:169; type locality "South America."
- Nasua leucorhyncha* Gray, 1869:36; incorrect subsequent spelling of *Nasua leucorhynchus* Tschudi, 1845.
- Nasua quichua* Thomas, 1901:248; type locality "Jima, Central region of Cordilleras, Province of Azuay, Ecuador."
- Nasua phaeocephala* Allen, 1904:334; type locality "Suapure, Caura district, Venezuela."
- Nasua socialis mexiana* Hagmann, 1908:12; type locality "Insel Mexiana," Para, Brazil.
- Nasua narica juruana* Ihering, 1911:239; type locality "Rio Jurua," Brazil.
- Nasua candace* Thomas, 1912:228; type locality "Medellin, Antioquia, Colombia."
- Nasua manium* Thomas, 1912:229; type locality "Balzar Mts., N.W. of Guayaquil, western Ecuador."
- Nasua quichua jivaro* Thomas, 1914:58; type locality "Gualaquiza, Oriente [Morrone-Santiago] Ecuador; alt. 2500 feet.
- Nasua judex* Thomas, 1914:57; type locality "Bogota, Colombia."
- Nasua nasua manium*: Allen, 1916:121; name combination.
- Nasua nasua candace*: Allen, 1916:221; name combination.
- Nasua nasua quichua*: Allen, 1916:122; name combination.
- Nasua nasua soderstromii* Lonnberg, 1921:98; type locality "near Baeza, road to Napo, Ecuador."
- Nasua nasua soederstroemmii* Lonnberg, 1921:98; (Cabrera, 1958:246); mandatory change in spelling of *N. n. soderstromii* Lonnberg, 1921.
- Nasua gualeae* Lonnberg, 1921:30; type locality "Guala, Ecuador."

## Appendix I.—Continued.

- Nasua henselii* Lonnberg, 1921:102; type locality "Sta Catharina, S. Brazil."
- Nasua henselii cinerascens* Lonnberg, 1921:103; type locality "Rio de Oro, a small tributary to Rio Paraguay, near mouth of Rio Bermejo, Chaco Austral, Argentina."
- Nasua nasua mephisto* Thomas, 1927:367; type locality "Yurac Yacu, Peru, 2500'."
- Nasua candace dichromatica* Tate, 1939:200; type locality "plateau of Mt. Auyantepui, S. Venezuela, at approximately 6000 feet."
- [*Nasua*] *juruana*: Tate, 1939:200; name combination.
- [*Nasua*] *jivaro*: Tate, 1939:200; name combination.
- Nasua nasua aricana* Vieira, 1945:404; type locality "Faz. Arica, Rio Arica, sul de Cuiaba," Mato Grosso, Brazil.
- Nasua nasua mexianae* Vieira, 1945:410; name combination.
- Nasua nasua solitaria*: Vieira, 1945:410; name combination.
- Nasua nasua boliviensis* Cabrera, 1956:2; type locality "provincia de Chapare, departamento de Cochabamba, Bolivia, a 1.500 m de altitud."
- Nasua nasua cinerascens*: Cabrera, 1958:246; name combination.
- Nasua nasua dorsalis*: Cabrera, 1958:246; name combination.
- Nasua nasua montana*: Cabrera, 1958:247; name combination.
- Nasua nasua quichua*: Cabrera, 1958:247; name combination.
- Nasua nasua vittata*: Cabrera, 1958:248; name combination.
- Nasua nasua molaris*: Hall and Kelson, 1959:976; name combination.
- Nasua nasua yucatanica*: Hall and Kelson, 1959:976; name combination.
- Remarks: The following species names have been incorrectly applied and are invalid: *monde*, *squash*, *spadicea*, *quasje*, *minor*, *canina* (Illiger, 1815:109); *nocturna* (Wied, 1826:298); *olivacea* (Gray, 1843:195).



Appendix 2.—Specimens Examined.—Specimens denoted with “\*\*\*” were used in both the quantitative and qualitative analyses. Specimens denoted with “\*” were used only in the qualitative analyses. Locality data are given in Decker (1990). Museum acronyms for museums in the United States follow Yates et al. (1987), other acronyms are as follows: BMNH = British Museum of Natural History.

*N. nasua*.—AMNH 333\*, 15091\*, 15296\*, 16051\*, 16304\*, 16717\*, 16776\*, 17557\*, 24420\*, 21626\*, 26400\*, 26522\*, 28498\*, 29256\*, 30203\*, 31167\*, 32357\*, 33040\*\*, 33042\*\*, 33043\*\*, 33044\*\*, 33247\*, 34348\*, 33899\*\*, 36461\*, 36480\*\*, 36585\*, 36586\*, 36587\*, 36588\*, 36964\*, 36974\*, 38801\*, 38802\*, 38803\*, 39989\*, 40832\*, 41943\*, 42449\*, 46516\*, 46517\*, 46518\*, 46521\*, 61437\*, 61438\*, 61603\*, 61872\*, 62854\*, 64043\*, 67100\*, 67705\*, 67714\*, 68313\*, 68314\*, 71361\*\*, 71841\*, 73764\*, 74459\*, 76036\*, 76642\*, 77694\*, 78594\*, 81487\*, 83294\*, 88202\*, 88204\*, 91788\*, 91792\*, 93668\*, 94152\*, 95096\*, 95293\*, 95297\*, 96296\*, 96298\*, 96300\*, 98493\*, 98496\*, 98499\*, 98502\*, 98503\*, 99257\*, 131166H\*, 133979\*, 133981\*, 133990\*, 133991\*, 133993\*, 134000\*, 134030\*, 147504\*, 147505\*, 176366\*, 181487\*, 181490\*, 181491\*\*, 181492\*, 182958\*, 209129\*, 209130\*, 214713\*, 214714\*, 214717\*, 214719\*, 214724\*, 215130\*, 246973\*, 247709\*, 255871\*, 260323\*, 261315\*, 261316\*, 261317\*, 261321\*, ANSP 2540\*, 2541\*, 2542\*, 4678\*, 4679\*, 4680\*, 4681\*, 4682\*, 4683\*, 4684\*, 4685\*, 4686\*, 4687\*, 4688\*, 4689\*, 4690\*, 4691\*, 4692\*, 4693\*, 4694\*, 4695\*, 4696\*, 4697\*, 4698\*, 4699\*, 4700\*, 4701\*, 4702\*, 4703\*, 4704\*, 4705\*, 4706\*, 4707\*, 4708\*, 4709\*, 4710\*, 4711\*, 4712\*, 13961\*, 14266\*, 14302\*, 17125\*, 17126\*, 19147\*, 19410\*, 19411\*, BMNH 77435\*, 271169\*, 734235\*, 805678\*, 4411813\*, FMNH 18911\*, 20199\*\*, 20846\*, 20847\*, 21399\*, 21400\*, 21401\*, 21402\*, 21592\*, 21676\*, 28318\*, 28319\*, 28320\*, 28321\*, 28322, 28323\*, 28324\*, 28325\*, 28326\*, 34330\*, 34681\*, 34682\*, 34683\*, 34684\*, 34685\*, 34686\*, 34687\*, 34688\*, 41194\*, 41195\*, 41196\*, 41197\*, 41198\*, 41199\*, 41200\*, 41201\*\*, 41202\*\*, 41203\*, 41225\*, 41238\*, 50887\*, 50888\*, 52335\*, 54328\*, 58757\*, 64291\*, 69602\*\*, 69603\*, 69604\*, 69605\*\*, 70728\*\*, 70729\*\*, 70730\*, 70731\*\*, 70732\*\*, 70733\*\*, 70734\*, 70735\*\*, 70736\*, 70737\*, 70738\*, 70739\*, 70740\*, 78403\*, 79869\*, 79870\*, 79871\*, 79872\*, 79873\*, 79874\*, 84210\*\*, 84241\*, 86764\*\*, 86747\*\*, 86749\*\*, 86750\*\*, 86849\*\*, 86910\*, 86911\*, 86912\*, 86913\*, 87853\*, 87854\*, 87855\*\*, 88875\*, 88876\*, 88877\*, 88878\*, 88879\*, 88880\*, 88881\*, 89232\*, 89233\*\*, 89234\*, 89235\*\*, 92206\*, 92207\*, 92208\*, 92209\*, 92210\*, 92211\*, 92212\*, 93170\*, 93171\*, 93172\*\*, 93663\*, 93664\*, 94221\*, 94322\*, 94323\*, 94325\*, 94326\*,

Appendix 2.—Continued.

94327\*, 94328\*, 96002\*, 98082\*, 119373\*, 119374\*, 119375\*, 119376\*, 119377\*, FSM 20658\*, LACM 27367\*, 27368\*, 27370\*, 54507\*, 56765\*, 56766\*, MCZ 999\*, 1000\*, 1001\*, 8017\*, 28094\*, 29615\*, 30975\*, 30976\*, 30978\*, 30979\*, 30981\*, 30982\*, 32046\*, 32047\*, 32048\*, 52579\*, 52580\*, 52581\*, 52586\*, 52604\*, 52606\*, MSUM 8575\*\*, 8576\*\*, 8577\*\*, 9346\*\*, 9347\*\*, 9348\*\*, 9349\*\*, 9350\*\*, 10692\*\*, 11920\*\*, 11921\*\*, 11937\*\*, 14369\*\*, 14370\*\*, 14371\*\*, 14372\*\*, MVZ 62688\*, 121211\*, 135822\*, 153639\*, 153640\*, 153641\*, 153642\*, 155209\*, 155210\*, 155211\*, USNM 526\*, 4657\*, 149000\*, 172992\*\*, 172991\*\*, 172993\*, 238671\*, 241335\*\*, 241336\*, 241337\*, 241338\*, 255127\*, 255128\*, 255129\*, 255130\*\*, 255131\*, 259480\*, 270365\*, 270366\*\*, 281513\*, 283471\*\*, 309084\*, 362119\*\*, 374835\*, 374836\*\*, 374837\*, 374838\*, 388316\*, 388236\*\*, 406823\*, 406824\*, 406825\*\*, 460075\*, 544416\*, 544417\*, 544418\*\*, 544419\*, 546101\*\*, 546102\*, 546103\*.

*N. narica*.—AMNH 1424\*, 6676\*, 7124\*, 7125\*, 12037\*\*, 14330\*, 14332\*, 17256\*, 18901\*\*, 19210\*\*, 23278, 24001\*, 24639\*, 24644\*, 25191\*, 25199\*, 25201\*, 25202\*, 25207\*, 25255\*, 25841\*, 25842\*, 25843\*, 26182\*, 27251\*, 28433\*, 28434\*, 28489\*, 29438\*, 29439\*, 29599\*, 29600\*, 29830\*, 30880\*, 37626\*, 38097\*, 38100\*, 38187\*, 68525\*\*, 70110\*, 72195\*, 123276\*\*, 123277\*\*, 123278\*\*, 126182\*\*, 126183\*\*, 135970\*\*, 139317\*, 141854\*\*, 141855\*\*, 141977\*\*, 143968\*\*, 145151\*\*, 145152\*\*, 145153\*\*, 145157\*\*, 145200\*\*, 145650\*\*, 145651\*\*, 145652\*\*, 145653\*, 145932\*\*, 145933\*\*, 145935\*, 145936\*\*, 145940\*\*, 145942\*\*, 145943\*\*, 145944\*, 145946\*\*, 145947\*\*, 145960\*\*, 149144\*\*, 165973\*\*, 171905\*, 172191\*\*, 172192\*\*, 172194\*\*, 173530\*\*, 176653\*, 176657\*, 206832\*, ANSP 13631\*\*, 17902\*, 17903\*\*, 18856\*, 18857\*, 18916\*, 18917\*, 18918\*, 18919\*, 19791\*, 19792\*, 20009\*, BMNH 2702\*, CAS 6429\*, 7233\*\*, 14824\*\*, 15087\*, 15088\*, FMNH 253\*, 11700\*, 13252\*, 13253\*, 13254\*, 13255\*, 13256\*, 13257\*, 13258\*, 13260\*, 13261\*, 14011\*, 14012\*, 14013\*, 14014\*, 14471\*, 15543\*, 30736\*, 51101\*, 58561\*, 63904\*\*, 63905\*, 64445\*, 66963\*, 66964\*, 66965\*, 66966\*, 66967\*, 69599\*\*, 69600\*\*, 69610\*\*, 106849\*, 14178\*, 14404\*, 14826\*, 15985\*, 30737\*, 35169\*\*, FSM 6792\*, 6858\*, 12303\*, KU 876\*, 11989\*\*, 11990\*\*, 19256\*, 24873\*, 26954\*\*, 29985\*\*, 29986\*\*, 33421\*, 39187\*, 63118\*\*, 65928\*\*, 65932\*, 68056\*, 68614\*, 68616\*, 71925\*, 81537\*, 83381\*, 89904\*, 92566\*, 92676\*, 104496\*, 115604\*, LACM 8823\*, 9112\*, 14350\*, 24826\*, 24835\*, 29312\*, 30099\*, 30340\*, 33251\*, 33252\*, 36056\*, 56410\*, 59442\*, 59443\*, 59444\*, 59445\*, 59446\*, 59447\*, 59448\*, LSUMZ 2757\*\*, 2758\*, 2760\*\*, 7286\*\*.

## Appendix 2.—Continued.

13381\*; MCZ 5723\*\*, 6418\*\*, 7020\*\*, 9090\*\*,  
 10123\*\*, 10124\*\*, 10125\*\*, 12456\*\*, 29042\*\*,  
 34338\*\*, 41313\*\*, 42788\*; MSUM 3564\*, 5679\*,  
 9203\*\*, 16374\*, 16536\*\*, 20618\*, 23043\*,  
 23044\*; MVZ 23840\*, 95049\*, 98257\*, 98258\*,  
 98259\*\*, 98260\*\*, 98261\*, 98262\*, 98263\*, 98264\*,  
 98265\*, 106048\*, 106049\*, 106050\*, 109604\*,  
 116822\*, 118877\*, 132107\*, 132108\*, 132109\*\*,  
 132110\*\*, 132111\*\*, 132112\*\*, 132113\*, 132114\*\*,  
 132115\*, 132116\*; TTU 13505\*, 17488\*; UANL 3721;  
 USNM 983\*, 6213\*, 6214\*, 6215\*, 6821\*\*, 7228\*,  
 7230\*, 8976\*\*, 9069\*, 9375\*, 11405\*, 12193\*, 12194\*,  
 12195\*, 12757\*, 12878\*, 14194\*\*, 15942\*, 15970\*\*,  
 16088\*, 19506\*, 20918\*, 20919\*, 32628\*, 32629\*,  
 32630\*, 32631\*, 32632\*, 32651\*, 32652\*, 32653\*,  
 33032\*, 33270\*, 33271\*, 33272\*, 33273\*, 33274\*,  
 33275\*, 33276\*, 33277\*, 33278\*, 33520\*, 33521\*,  
 33522\*, 33523\*, 33524\*, 33525\*, 33797\*, 33798\*,  
 34337\*, 34408\*, 34409\*, 34923\*, 37282\*\*, 37284\*\*,  
 37287\*\*, 38137\*\*, 44553\*\*, 45276\*, 45277\*\*, 45278\*\*,  
 45279\*\*, 45280\*\*, 45281\*\*, 45283\*\*, 45567\*\*,  
 45568\*\*, 45570\*\*, 46428\*\*, 51331\*\*, 54983\*\*,  
 60366\*\*, 61204\*, 61259\*\*, 61260\*\*, 61261\*, 61262\*,  
 61263\*, 61264\*, 68168\*, 68194\*, 73324\*, 73325\*,  
 74680\*\*, 74681\*\*, 88144\*\*, 88145\*, 88146\*, 96214\*\*,  
 96828\*, 96829\*\*, 96830\*, 96831\*, 96832\*, 96833\*\*,  
 98075\*\*, 100412\*\*, 100413\*\*, 100414\*\*, 100415\*,  
 100528\*\*, 108308\*, 108309\*\*, 108310\*\*, 108311\*,  
 108312\*\*, 108313\*\*, 108315\*\*, 108519\*\*, 108525\*\*,  
 108537\*\*, 116753\*\*, 116754\*\*, 126146\*, 126147\*\*,  
 126148\*\*, 126149\*\*, 126151\*\*, 126152\*, 126153\*,  
 126154\*, 126155\*, 126705\*\*, 127531\*\*, 127532\*\*,  
 127533\*\*, 170894\*, 171671\*\*, 173071\*\*, 179975\*\*,  
 239116\*\*, 239348\*\*, 239349\*\*, 239350\*\*, 244896\*\*,  
 244897\*\*, 244898\*, 244899\*, 244900\*, 245424\*\*,  
 257314\*\*, 257353\*, 261435\*, 261661\*\*, 265662\*,  
 265936\*, 265937\*, 268902\*, 271095\*\*, 271136\*\*,  
 275666\*\*, 284936\*, 287488\*, 287489\*, 287490\*,  
 290671\*\*, 290672\*\*, 296339\*\*, 296340\*\*, 304659\*\*,  
 304660\*, 307015\*, 307016\*\*, 307017\*\*, 307018\*\*,  
 307019\*\*, 307020\*\*, 307021\*\*, 307022\*, 309224\*\*,  
 309225\*\*, 310658\*\*, 310659\*\*, 310660\*, 310661\*\*,  
 314547\*\*, 316212\*, 316213\*\*, 318178\*, 324284\*\*,  
 324285\*\*, 324286\*\*, 324287\*\*, 324288\*\*, 324289\*\*,  
 334544\*, 334545\*\*, 334546\*, 334547\*, 334548\*,  
 334549\*, 334550\*, 334666\*, 336217\*\*, 336218\*\*,  
 337817\*, 337818\*, 337819\*\*, 338347\*, 340742\*,  
 340743\*\*, 340744\*\*, 360453\*\*, 503822\*, 511711\*,  
 520614\*\*, 520615\*, 541322\*, 541394\*.

*N. nelsoni*.—KU 876\*\*, 92570\*\*, MCZ 55722\*\*,  
 USNM 14808\*, 14809\*, 108520\*\*, 108521\*, 108522\*\*,  
 108523\*\*, 108524\*, 108615\*.