

Rousettus egyptiacus. By Gary G. Kwiecinski and Thomas A. Griffiths

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Rousettus Gray, 1821

- Rousettus* Gray, 1821:299. Type species *Pteropus Egyptiacus* É. Geoffroy St.-Hilaire, 1810, by original designation.
Cercopteropus Burnett, 1829:269. Type species *Pteropus aegyptiacus*, by subsequent designation (Andersen, 1912).
Xantharpyia Gray, 1843:37. Type species *Pteropus amplexicaudatus*, by subsequent designation (Andersen, 1912).
Eleutherura Gray, 1844:29. Type species *Pteropus leachi*, by monotypy.
Cynonycteris Peters, 1852:25. Type species *Pteropus leachi*, by monotypy.
Senonycteris Gray, 1870:115. Type species *Xantharpyia seminda*, by monotypy.
Stenonycteris Andersen, 1912:23 (proposed as a subgenus originally, but used occasionally as a genus—valid as subgenus). Type species *Rousettus lanosus*, by monotypy.

CONTEXT AND CONTENT. Order Chiroptera, Suborder Megachiroptera, Family Pteropodidae, Subfamily Pteropodinae, Tribe Pteropodini, Subtribe Rousettina. *Rousettus* contains eight living species arranged in two subgenera, not including *Lissonycteris angolensis*, which had been included as a ninth species in a third subgenus of *Rousettus* (Koopman, 1993, 1994), but has recently been shown to merit full generic status (Juste et al., 1997).

DIAGNOSIS. Tympanic bone not extending into auditory meatus (Fig. 1). Palate usually clearly broader posteriorly than between canines. Length of rostrum always at least somewhat greater than width across lacrimals. Front of orbit vertically above middle or posterior half of M1. Basicranial deflection variable. Premaxillaries in contact or fused in front. Dental formula is i 2/2, c 1/1, p 3/3, m 2/3, total 34. First upper premolar (in cross section) much reduced (equal to or smaller than upper incisor). First lower molar shorter than other two molars combined. All species in the genus are medium sized; forearm 65–102 mm (Koopman, 1994). The genus is distributed in sub-Saharan Africa, Egypt, around the eastern Mediterranean to Cyprus and southern Turkey, on Comoros and Madagascar, across southern Asia to southern China and Malaya, and through the East Indies including the Philippines to New Guinea, the Bismarck Archipelago, and Solomon Islands (Koopman, 1994).

Key to species of *Rousettus* (with *Lissonycteris*, which has often been placed in the genus *Rousettus*, included here to avoid confusion); measurements from Koopman (1994).

- 1 Wing membrane (plagiopatagium) attached to second toe of foot 2
 - Wing membrane (plagiopatagium) attached to first toe of foot (subgenus *Rousettus*) 3
- 2 Braincase strongly deflected ventrally from a line drawn along the axis of the rostrum; premaxillaries not fused to each other; pm1 much larger in bulk than lower incisor; molars very narrow (width about one-half the length); antitragus of ear obsolete; forearm 84–92 mm (subgenus *Stenonycteris*) *R. lanosus*
 - Braincase slightly deflected; premaxillaries fused to each other; pm1 subequal in bulk to lower incisor; molars broad; antitragus of ear distinct; forearm 66–84 mm *Lissonycteris angolensis*
- 3 Median edge of plagiopatagium attached to body near the dorsal midline; forearm 79–89 mm (known from Sumatra and Borneo only) *R. spinalatus*
 - Median edge of plagiopatagium attached to the side of the body 4
- 4 Uropatagium well-furred for nearly entire anterior half;

- forearm 67–83 mm (known from Sulawesi and the Sanghir Islands only) *R. celebensis*
- If uropatagium has fur, it is well-furred only near root of tail; otherwise sparsely furred to nearly naked 5
- 5 Width of premolars and molars about equal to or very slightly greater than one-half their length (except m2 and m3 which are wider); forearm 65–76 mm (known from Madagascar only) *R. madagascariensis*
 - Width of premolars and molars broader 6
- 6 Pollex 30–38 mm; second phalanx of third digit 50–62 mm (forearm 81–102 mm) *R. egyptiacus*
 - Pollex 22–31 mm; second phalanx of third digit 36–51 mm 7
- 7 Skull deflection greater than in other species belonging to subgenus *Rousettus*, but not nearly as deflected as in *Rousettus* (*Stenonycteris*) *lanosus* (forearm 70–75 mm); endemic to Comoro Islands (between Africa and northern Madagascar) *R. oblioviosus*
 - Little to no skull deflection; distributed in southern Asia from Pakistan across India (and Sri Lanka) to southeastern China and Viet Nam and south through part of the Malay Peninsula, Sumatra, Java, and Bali (*leschenaulti*) or from Thailand through the Malay Peninsula and East Indies to the Philippines and Solomon Islands (*amplexicaudatus*) 8
- 8 Third lower molar elliptical in outline, about twice as long as broad; ears 14–16 mm in width; forearm 75–96 mm *R. leschenaulti*
 - Third lower molar subcircular in outline, only slightly longer than broad (breadth from $\frac{2}{3}$ to $\frac{5}{6}$ length); ears 10–13 mm in width; forearm 66–91 mm *R. amplexicaudatus*

Rousettus egyptiacus (É. Geoffroy, 1810)

Egyptian Rousette Bat

- Pteropus Egyptiacus* É. Geoffroy St.-Hilaire, 1810:96. Type locality: “la basse Egypte . . . le plafond d’une des chambres de la grande Pyramide” (Great pyramid, Giza, Egypt). Invalid emendation as *P. aegyptiacus* in É. Geoffroy St.-Hilaire, 1812:134, pl. 3, fig. 2.
Pteropus collaris Lichtenstein, 1823:5, not of Illiger, 1815:84. Type locality “Africa.”
Pteropus geoffroyi Temminck, 1825:197, pl. 15, figs. 14, 15. Type locality “Egypt, ‘Senegal’.”
Pteropus leachi Smith, 1829:433. Type locality “Gardens about Cape Town.”
Pteropus hottentottus Temminck, 1832:3. Type locality “circa urbem Capensem” (Cape area).
Eleutherura unicolor Gray, 1870:117. Type locality “Gaboan.”
Rousettus arabicus Anderson and de Winton, 1902:86, 88, 89–90. Type locality “Lahej, near Aden, southern Arabia.”
Rousettus sjöstedti Lönnberg, 1908:7. Type locality “Tanga,” Tanganyika Territory.

CONTEXT AND CONTENT. Context as given in the generic account above. Six subspecies are recognized:

- R. e. arabicus* (Anderson and de Winton, 1902:86, 88, 89–90), see above.
- R. e. egyptiacus* (É. Geoffroy, 1810:96), see above (*geoffroyi* Temminck is a synonym).
- R. e. leachi* (Smith, 1829:433), see above (*hottentottus* Temminck and *sjöstedti* Lönnberg are synonyms).
- R. e. princeps* (Juste and Ibañez, 1993:123). Type locality: “Roca



FIG. 1. Dorsal, ventral, and lateral views of cranium and dorsal and lateral views of mandible of male *Rousettus egyptiacus*, (USNM 463300). Greatest length of skull is 42.6 mm.

Bela Vista, 2 km S of Santo Antonio de Principe, Principe Island."

R. e. tomensis (Juste and Ibañez, 1993:124). Type locality: "Bindá (Santa Catarina), São Tomé Island."

R. e. unicolor (Gray, 1870:117), see above (*R. e. occidentalis* Eisentraut is a synonym).

DIAGNOSIS. *Rousettus egyptiacus* is the only species in the



FIG. 2. Adult female *Rousettus egyptiacus* and her young photographed in a captive colony, Buffalo, New York (courtesy of J. R. Cotter).

subgenus *Rousettus* on the African continent. In Africa, it may be differentiated from *R. (Stenonycteris) lanosus* and from *Lissonycteris angolensis* by the attachment of the wing membrane (plagiopatagium) to the foot (Koopman, 1994). In *R. egyptiacus* the plagiopatagium attaches to the first toe, whereas in *R. lanosus* (and *L. angolensis*) the plagiopatagium attaches to the second toe. *R. lanosus* (forearm, 84–91 mm) overlaps *R. egyptiacus* (forearm, 81–102 mm) in size, but differs from *R. egyptiacus* in having a sharply deflected braincase and very narrow molars (Koopman, 1994). *R. madagascariensis*, known only from Madagascar, differs from *R. egyptiacus* in being smaller (forearm, 65–76 mm) and having conspicuously narrow molars. *R. oblioviosus* from the Comoro Islands has relatively broad molars but is also a smaller bat (forearm, 70–75 mm). All other species in the subgenus *Rousettus* are known from the Far East and Southeastern Asia and are unlikely to be confused with *R. egyptiacus*, except that *R. leschenaulti* may overlap slightly in Pakistan. *R. leschenaulti* has a smaller thumb (23–31 mm) and a smaller second phalanx in its third finger (41–51 mm) than *R. egyptiacus* (thumb, 30–38 mm; second phalanx of third finger, 50–62 mm—Koopman, 1994).

GENERAL CHARACTERS. The South African *R. egyptiacus leachi* (Fig. 2) is a medium sized bat, with a wingspan ≤ 60 cm; total body length of adults ca. 15 cm (range, 14.0–16.2) and adult body mass ca. 130 g (Smithers, 1983). Eleven male specimens averaged 133.4 g (range, 88.1–166.0) and 18 females averaged 129.3 g (range, 117.1–166.0—Smithers, 1983). Forearm lengths of *R. e. leachi* from the Sudan ranged 90–98 mm for six adult males and 91–99 mm for 14 adult females (Koopman, 1975). The total length of eight males and five females of the nominate subspecies in Egypt were 150.7 mm (range, 140–167) and 139.8 mm (range, 119–160), respectively (Qumsiyeh, 1985). Forearms of 12 Egyptian males averaged 94.9 mm (90–97) and of six Egyptian females averaged 91.0 mm (84–94). Two male specimens of *R. egyptiacus unicolor*, captured in Rio Muni, Republic of Equatorial Guinea in west Africa, had measurements that averaged slightly larger than those of three females (Jones, 1971). Males had an average total length of 168.5 mm (145.0–192.0), an average forearm length of 93.5 mm (85.0–101.9) and an average mass of 131.5 g (92.4–170.6 g). Corresponding measurements of females were, total length, 144.3 mm (138.0–150.0), forearm length, 83.5 mm (81.1–85.9), and mass, 83.4 g (80.9–88.4 g). Forearm lengths of *R. e. unicolor* from west Africa ranged from 87 to 102 mm (Rosevear, 1965). Eight males and four females of *R. egyptiacus arabicus* from Iran were measured (DeBlase, 1980); total length of males averaged 135.1 mm (130.0–147.0); forearm length of seven males averaged 88.1 mm (85.0–92.4). Total length of females averaged 127.5 mm (121.0–132.0) and forearm length averaged 83.5 mm (82.0–87.0). Tail length is 6.6–25 mm (Andersen, 1912; Bergmans, 1979; Harrison, 1964; Qumsiyeh, 1985).

There is some variation in color within the species. In West Africa, the dorsal pelage is a very deep sepia-brown (Rosevear, 1965) with the belly fur several shades lighter. The dorsal fur is

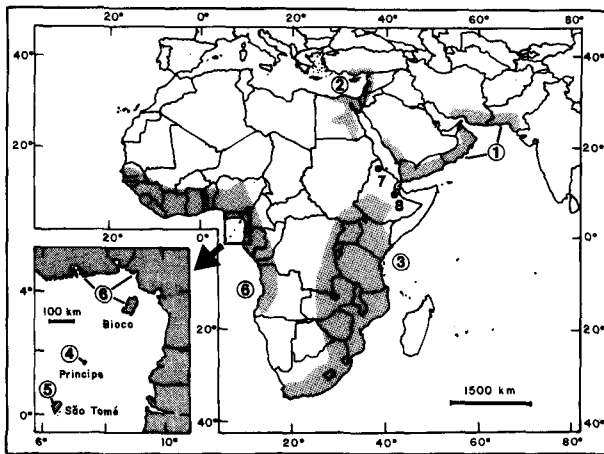


FIG. 3. Map of Africa and the Gulf of Guinea on the west African coast (inset) showing the geographic distribution of *Rousettus egyptiacus*, subspecies as follows: 1) *R. e. arabicus*, 2) *R. e. egyptiacus*, 3) *R. e. leachi*, 4) *R. e. princeps*, 5) *R. e. tomensis*, and 6) *R. e. unicolor*. Localities 7 and 8 represent specimens for which there is some question as to subspecific identity (see text).

dark brown in specimens taken in South Africa (Smithers, 1983) but is markedly lighter brown in specimens taken in Egypt. Specimens from Turkey and Cyprus are more accurately described as gray in color. Wings are dark brown in West and South Africa (sometimes nearly black), becoming lighter brown in specimens taken more to the north. Often there is a pale collar of lighter yellow or orange fur around the neck. Males have stiff hairs associated with glands on the throat which are more developed than on females, but there is no color dimorphism (Harrison, 1964). The fur extends onto the proximal half of the forearm both dorsally and ventrally, dorsally onto the legs to the ankles but ventrally only to the upper legs, and onto the dorsal surface of the narrow intermembral membrane. The facial fur is long on the forehead, shorter on the remainder of the head, but completely covers the face nearly to the tip of the muzzle. The eyes are large and conspicuous. The moderate-sized ears are dark and rounded at the apex.

DISTRIBUTION. *Rousettus egyptiacus arabicus* is found along the Red Sea shore of Saudi Arabia from the vicinity of Mecca to Yemen, then northeast to Muscat, Oman and the eastern tip of the United Arab Emirates (Fig. 3). The subspecies *arabicus* continues in southcentral and southeastern Iran and then east to southern Pakistan and possibly to westernmost India (Anderson and de Winton, 1902; Bergmans, 1994; DeBlase, 1980). *R. e. egyptiacus* occurs along the coast of extreme southern Turkey, on the island of Cyprus, in western Syria, Lebanon, Israel, Jordan, in northern Egypt along the coast and then south along the Nile Valley to Abu Simbel Temple in far southern Egypt, and at the Dakhleh Oasis in the western Egyptian Desert (Andersen, 1912; Bergmans, 1994; Churcher, 1991; DeBlase, 1980; Eisenbraut, 1959; Hayman and Hill, 1971; Qumsiyeh, 1985). *R. e. leachi* has been reported from southwestern Ethiopia, southern Sudan, eastern and southeastern Congo (= Zaire), Uganda, Kenya, Tanzania, Zambia, Malawi, Zimbabwe (= Rhodesia), Mozambique, and extreme southern and eastern South Africa, Swaziland (= Natal) and Lesotho (Allen, 1957; Bergmans, 1979, 1994; Ellerman et al., 1953; Hayman et al., 1966; Kingdon, 1974; Koopman, 1975; Roberts, 1951; Smith, 1829). *R. e. princeps* is endemic to the island of Principe in the Gulf of Guinea (inset, Fig. 3) and *R. e. tomensis* is endemic to São Tomé (Juste and Ibañez, 1993; Juste et al., 1996). *R. e. unicolor* is known from Senegal and Gambia eastward through Liberia, Ivory Coast, Ghana, Togo, southern to northcentral Nigeria to western Cameroon, Bioko, and then south from Gabon and the Congo to western Zaire, and western Angola (Andersen, 1912; Bergmans, 1979, 1994; Eisenbraut, 1959; Ellerman et al., 1953; Hayman et al., 1966; Juste and Ibañez, 1993; Rosevear, 1965).

A specimen of *R. e. egyptiacus* was reported from northern Eritrea by Senna (1905). We have included it on our map (locality 7), but we note that *R. e. egyptiacus* has not otherwise been found further south than Abu Simbel Temple, Egypt. Bergmans (1994)

suggested that Senna's specimen instead might be *R. e. leachi*. Alternatively, it might be *R. e. arabicus*. A specimen from Harar in eastern Ethiopia (locality 8, Fig. 3) was identified as *R. e. arabicus*, but more recently has been suggested to be *R. e. leachi* (Bergmans, 1994). It is possible that specimens from east of the Ethiopian Central Rift may intergrade between eastern populations of *arabicus* and western *leachi*, and thus may be difficult to assign definitively to a subspecies (Bergmans, 1994).

There is no fossil record for this species.

FORM AND FUNCTION. The skin underlying the lighter-colored collar around the neck is composed of epidermis one to two cell layers thick. The dermis contains nests of alveolar sebaceous glands associated with hair follicles that are similar in morphology to those of other body regions, but larger. These glands are ca. 2 times larger in males than females (Mainoya and Howell, 1979).

A claw is present at the terminal phalanx of the first and second digits; all other fingers have a cartilaginous extremity. Toes have perforated claws. The os calcis is cartilaginous and articulates with the large, ventrolaterally curving calcaneus. Structures of bones in the hand and foot and ossification patterns are reviewed by Madkour (1975).

The external configuration of the femur is characteristic of Megachiroptera, with the condylar head close to the line of the diaphyseal axis and the greater and lesser trochanters almost diametrically opposed (Buckland-Wright, 1972). Average greatest length of the femur is 29.4 mm (28.5–30.8 mm). The compact cortical bone of the diaphysis has a maximum thickness of 24 μ m which diminishes abruptly to a thin cortex over most of the epiphysis (4–6 μ m). The spongiosa is sparse and most dense distally with no distinct interregional tracts of bone between diaphyses, trochanters, and condylar heads as described for other mammals. Histologically, the periosteal and endosteal surfaces are smooth, and no vascular channels exist, except those penetrating nutrient foramina. Cortical bone and trabecular bone consist of circumferential lamellae perforated with osteocytic lacunae but no osteons (Haversian systems). An osteocytic differential count revealed $55 \pm 3\%$ small osteocytes in the steady state, $37 \pm 3\%$ enlarged osteocytes with osteolytic or osteoplastic activity, and $8 \pm 1\%$ empty lacunae corresponding to dead osteocytes (Buckland-Wright, 1972). Such mammalian non-osteonic bone was hitherto undescribed.

Rousettus egyptiacus has one of the highest ratios of brain to body weight among chiropterans, nearly identical to the advanced insectivores, and exceeding the lowest encephalized primates (Pirilot and Stephan, 1970). This bat has an excellent visual system that is adapted for twilight vision and a keen sense of smell that facilitates food discrimination; these abilities are manifested by well-developed brain areas associated with these senses (Schneider, 1966). An atlas of brain structure is provided by Schneider (1966).

The eye of *R. egyptiacus*, like that of other Megachiroptera, contains minute choroidal papillae whose internal contours provide an undulating surface over which the photoreceptors are arranged (Kulzer, 1979). Various functions have been attributed to the papillae, the most popular being the provision of multiple focal planes circumventing the need for active accommodation, but even this explanation is doubted (Murphy et al., 1983). The visual system is well developed from the standpoint of bilaterality of optic projection, the differentiation of cytoarchitectural units in the visual centers of the brainstem, and the relative sizes of these centers (Cotter, 1981). There is substantial ipsilateral involvement of retinofugal projections to the ventrolateral geniculate nucleus, dorsolateral geniculate nucleus, pretectum and superior colliculus. The retinotopic organization of the superior colliculus resembles the pattern found in most mammals, being unlike other megachiropterans (Thiele et al., 1991).

Rousettus bats are an exception among Old World fruit bats in the use of echolocation within the roosting cave and while flying outside the cave (Pye and Pye, 1988; Thomas and Fenton, 1978). This is accomplished by emission of trains of clicks that are broadband, contain energy across a range of frequencies, and are audible to humans (Griffin et al., 1958). The start of each flight is accompanied by rhythmically repeated clicks that increase in frequency with the number of obstacles and flying bats. These clicks consist of a pair of sounds separated by 20–44 ms (Kulzer, 1958; Pye and Pye, 1988). The sounds are produced by the tongue, first on one

side of the mouth and then on the other, under the control of the hypoglossal nerve. The jaws are kept closed but the lips are parted on each side with sounds emerging between the teeth (Griffin et al., 1958; Kulzer, 1958). Pye (1967) suggested, and Roberts (1975) confirmed, that the buccal cavity contributes to sound production. The clicks have a broad bandwidth with appreciable energy in the range 7–60 kHz and a quick onset followed by a rapid decay (Pye and Pye, 1988). The lowest strong component is centered around 10–12 kHz with several higher partials yielding a complex spectrum. The cochlea shows none of the specialized characteristics found in the Microchiroptera (Hinchcliffe and Pye, 1968), and the hearing curve is sharply tuned at ca. 10 kHz. A hearing curve obtained for a single individual by behavioral conditioning (Suthers and Summers, 1980) showed a second small peak at 20 kHz, with greater sensitivity at the lower end of its emitted sound spectrum (Pye and Pye, 1988).

There are five individual pinna muscles (Friauf and Herbert, 1985). Their motor neurons lie within the facial motor nucleus (mean = 4,126 multipolar neurons, $n = 11$ animals) in the anterior medulla. The facial motor nucleus is ca. 1.0 mm long and 0.9 mm wide and is bordered rostrally by the superior olivary complex and caudally by the inferior olivary complex and the nucleus ambiguus. No overlap of motor neurons was found, and the high number of motor neurons allows sophisticated pinnae movements (Friauf and Herbert, 1985).

In proportion to body weight, adrenal glands from *R. egyptiacus* are smaller than in many other mammals (Baranga, 1980). Adrenal weights increase with age, and maximal weight is attained before sexual maturity. There was a 27% incidence of macroscopic accessory adrenocortical bodies and numerous microscopic accessory bodies (Baranga, 1984), which, histologically, consist of cortical tissue like the main gland. Baseline plasma corticosterone levels (36 ± 4 ng/ml) were comparable to those of other mammals (Widmaier and Kunz, 1993). Spleens become smaller in response to stress, contradicting findings for rodent spleens which become larger in response to stress (Baranga, 1978).

In *R. egyptiacus*, unlike many mammal species, the small intestine is freely permeable to calcium with no active transport mechanism (Keegan et al., 1980). Serum levels of the hormonally active vitamin D metabolite, 1,25-(OH)₂-vitamin D₃, were very low (14 ± 6.7 pg/ml), and the immediate precursor, 25-(OH)-vitamin D₃, was not detectable (Opperman and Ross, 1990). Kidneys and a fibroblast cell line derived from skin and lung showed immunohistochemically detectable 9 kDa vitamin D-dependent calcium binding protein (calbindin-D9K), but the 28 kDa vitamin D-dependent calcium binding protein (calbindin-D28K) was not demonstrable (Opperman and Ross, 1990; Venter and Manchester, 1993). The absence of calbindin-D28K from the kidneys is unusual for mammals (Opperman and Ross, 1990).

Heart rate, determined by telemetry (5 adult males, 5 days), paralleled basal diurnal values and peak nocturnal values of oxygen consumption and body temperature (Noll, 1979a). Average resting heart rate was 248 ± 3 beats/min during the daytime resting period and 444 ± 5 beats/min during the night activity period. The thermoneutral zone of the normally hydrated bat was 31–36°C (Korine and Arad, 1993; Kulzer, 1979; Noll, 1979b), and oxygen consumption (basal metabolic rate, BMR) in this range averaged 0.95 ± 0.15 ml g⁻¹ h⁻¹ (Korine and Arad, 1993) and 0.84 ± 0.02 ml g⁻¹ h⁻¹ (Noll, 1979b). The BMR during the day was followed by a period of sustained, elevated O₂ consumption (1.7 – $2.6 \times$ BMR—Noll, 1979a) beginning at darkness. During the second half of the night, O₂ consumption gradually returned to resting level. The circadian cycle of body temperature also was determined telemetrically in 3 adult males for 10 days (Noll, 1979b). With the beginning of darkness, a resting level of $34.8 \pm 0.03^\circ\text{C}$ changed abruptly and remained 2.2°C higher before returning to resting level during the second half of the night. The average temperature of a male during a 24 hour period was $35.6 \pm 0.2^\circ\text{C}$.

Roussettus egyptiacus is adapted to a warm climate with a suite of thermoregulatory adaptations. Evaporative water loss and respiratory frequency during normal hydration increase as power functions of ambient temperature (Korine and Arad, 1993). The normally hydrated, heat-exposed bat effectively regulates body temperature and dissipates heat by dry thermal conductance and evaporative cooling, including dilating blood vessels of wing and interfemoral membranes, extending the tongue, panting, salivating copiously, licking most of its body, and descension of the testes

(Kulzer, 1963a, 1963b; Laburn and Mitchell, 1975). In water restricted bats, oxygen consumption and dry thermal conductance increased, whereas evaporative water loss decreased (Korine and Arad, 1993). Cold-acclimated bats cluster, elevate heat production, use nonshivering thermogenesis, and develop brown fat tissue (Noll, 1979b).

For wild-caught bats (males and females, respectively), plasma white cell counts were $8.8 \pm 2.5 \times 10^9/\text{l}$ and $8.8 \pm 5.8 \times 10^9/\text{l}$; red cell counts were $11.95 \pm 0.94 \times 10^{12}/\text{l}$ and $13.88 \pm 1.52 \times 10^{12}/\text{l}$; hematocrit levels were $43.9 \pm 2.4\%$ and $57.0 \pm 6.2\%$; hemoglobin levels were 17.1 ± 1.1 g/dl and 17.4 ± 2.0 g/dl; mean corpuscular volumes were 36.8 ± 1.4 fl and 41.1 ± 1.7 fl; and mean cell hemoglobin concentrations were 39.0 ± 1.6 and 30.6 ± 0.8 pg. There were no differences in hematological indices from lactating and non-lactating bats (van der Westhuyzen, 1988). Hematological indices also are provided by Arad and Korine (1993), Kulzer (1979), Noll (1979a), and Widmaier and Kunz (1993).

Blood hemolysates consist of one hemoglobin component with an isoelectric point of 7.3–7.4 (Condo et al., 1989). Bat hemoglobin, with no bound oxygen, has a much lower affinity for oxygen and a significantly broader temperature sensitivity than human hemoglobin, and the affinity increases if concentration of chloride ions is ≥ 50 mmol/l (Condo et al., 1989). Although oxygen affinities of bat hemoglobin are higher than those of comparable, small, nonflying mammals, Bohr curves of purified hemoglobin, and purified hemoglobin in the presence of CO₂ and 2,3-DPG, indicate allosteric regulation of oxygen binding affinities similar to that of other mammals. The higher specific oxygen uptake, when compared with similar-sized, non-volant mammals, is achieved by a larger heart, higher carrying capacity for blood oxygen, and higher hemoglobin concentration (Jurgens et al., 1981; Noll, 1979a).

This bat assimilates 15–20 g of monosaccharides/night (Keegan, 1977). The intestinal transit time is 18–100 minutes, but <10% of sugars reappear in the feces. There is a very rapid uptake of fructose; its maximum assimilation is reached in 5 min, whereas maximum uptake of glucose occurs in 30 min (Keegan, 1975). The microvilli of intestinal mucosal cells (Keegan and Modinger, 1979) are long and slender, average length is 3.6 μm (3 times that of the laboratory rat, *R. norvegicus*), average diameter is 0.1 μm , there are 57/mm², and they increase surface area 57 times (3.2 times that of *R. norvegicus*). Plasma levels of glucose are 108 ± 13 mg/dl (Widmaier and Kunz, 1993). Bats (average mass = 144 g) require a mean intake of dry matter of 6 g/day for nitrogen balance and a mean intake of 11 g/day for energy requirements, suggesting that energy, rather than nitrogen, is the daily limiting component of their diet (Korine et al., 1996). The daily energy requirement is 167.7 kJ/day, and the maintenance nitrogen requirement (0.247 g N kg^{-0.75}/day) is 55% lower than expected from allometric relations.

Mean daily total water intake averages 71.7 ml (Kulzer, 1979). Urine flow is 17.2% of body mass, fecal water output is 4.8% of body mass, and evaporative water loss is 28% of body mass (Kulzer, 1979). Kidney structure consists of an extremely short papilla and a thin medulla, indicating an ability to produce a dilute urine (Kulzer, 1979). The average density of glomeruli is 7/mm² and the cortex consists primarily of convoluted tubules. Urine concentration varies from 113 ± 25 mosmol/kg H₂O to 1800 mosmol/kg H₂O under various dietary regimes (Arad and Korine, 1993; Kulzer, 1979).

ONTOGENY AND REPRODUCTION. *Roussettus egyptiacus* has cyclic and acyclic breeding patterns, possibly as adaptations to local geo-climatic conditions. Mating of this bat in Egypt occurs year round (Madkour et al., 1983) and in South Africa, from June through September (Lombard, 1961). Pregnant bats were found in Liberia in March (Verschuren, 1976), August (Wolton et al., 1982), and October to November (Coe, 1975); in Rhodesia and South Africa in October (Ansell, 1960; Jacobsen and du Plessis, 1976); in Uganda from December to March and July to September (Mutere, 1968a, 1968b); in Saudi Arabia in January and June (Nader, 1975); and in Yemen in March and July (Nader, 1975). Births were observed in Egypt in February and March (Anderson and de Winton, 1902); in Lebanon from June to August (Atallah, 1977); in Liberia in December (Coe, 1975); in Uganda and East Africa in March and September (Mutere, 1968a, 1968b); in South Africa from October to June (Herzig-Straschil and Robinson, 1978) and November to December (Jacobsen and du Plessis, 1976); and in Zaire and Rwanda year round (Anciaux de Faveaux, 1978). Lac-

tation was reported in Egypt from March to May (Qumsiyeh, 1985); in West Africa in February (Jones, 1971); in Saudi Arabia in July (Nader, 1975); and in Yemen in March and October (Nader, 1975). In captivity, these bats breed all year (Anderson and de Winton, 1902; Kulzer, 1958, 1969a; Zuckerman, 1953) and young are born in every month (Baker and Baker, 1936; Kulzer, 1958, 1969a; Noll, 1979b).

The testes of subadults are abdominal whereas those of adults are scrotal. Testes are ovoid or round and during mating are ca. 13 mm in length (Penzhorn and Rautenbach, 1988), and seminal vesicles increase in size (1.5 times testis length) during mating (Penzhorn and Rautenbach, 1988). Paired Cowper's glands, a tripartite prostate gland that does not completely surround the urethra, and ampullary glands have been described (Madkour et al., 1983). A microscopic description of the cauda epididymis and testis and descriptions of the reproductive tract and relationship to kidney, ureter, and urethra is provided by Madkour et al. (1983). The glans penis has prominent corpora cavernosa and the os penis is ca. 6.1 mm long and 2.8 mm wide (Qumsiyeh, 1985). Spermatogenic activity was found throughout the year in Egypt, with diameter of seminiferous tubules maximal in May and minimal in December (Madkour et al., 1983). In South Africa, spermatogenic activity was found throughout the year, peaking in May (Penzhorn and Rautenbach, 1988). Globular seminal vesicle secretions were prominent during copulations in July and August, and spermiphagy by macrophages in the cauda epididymis occurred November to January. Some adult males were aspermatogenic and spermiphagic (September to January), indicating some males were seasonally reproductive (Penzhorn and Rautenbach, 1988). In Uganda, the testicular cycle had two peaks (Mutere, 1968b). Maximal testis weight (3.5 ± 0.5 g) was in April and September and minimal weight (0.9 ± 0.1 g) in January. Maximal testis weight coincided with distended epididymis and copulations.

The female uterus is duplex, symmetric, and the two uterine horns are externally united (caudally) but their lumina open at the vagina by separate cervical canals (Bernard, 1988). Reproductive asymmetry is common in the Pteropodidae, and in female *R. egyptiacus* the restriction of follicular development and preovulatory Graafian follicles to one ovary, and an involuted corpus luteum in the opposite ovary, indicate alternating ovarian function (Bernard, 1988). The unilateral endometrial reaction during late follicular development is restricted to the uterine horn on the same side as the ovary in which follicles develop. An ovarian rete system between the ovarian artery and vein provides a local transport system and plays a role in local control of the unilateral reaction (Bernard, 1988). During pregnancy, there is a single corpus luteum and developing embryo in the same side of the reproductive tract, whereas the contralateral ovary contains primary and secondary follicles (Bernard, 1988). The corpus luteum of pregnancy persists until the next ovulation (Bernard, 1988).

Gestation has been estimated to be four months based on field data (Kulzer, 1958; Mutere, 1968a, 1968b) and 105–107 days based on captive observations (Kulzer, 1966). In South Africa, pregnancy rates were 95% (Penzhorn and Rautenbach, 1988) and 90% and 96% in two consecutive breeding seasons (Jacobsen and du Plessis, 1976), compared with 80% per cycle in Uganda (Mutere, 1968b). Usually one young is born at a time (Ansell, 1960; Coe, 1975; Herzig-Straschil and Robinson, 1978; Jacobsen and du Plessis, 1976; Kulzer, 1966; Mutere, 1968b; Nader, 1975; Oika, 1987; Verschuren, 1966, 1976), but twins have been reported (Herzig-Straschil and Robinson, 1978; Kulzer, 1966; Oika, 1987).

During parturition, the female is quiescent except for licking the young as it squirms out of the vagina aided by uterine contractions (Kulzer, 1966). Forelimbs are freed before hindlimbs. With umbilicus still attached, the newborn climbs on the mother's abdomen and within minutes attaches with deciduous teeth to one of its mother's teats. The mother licks the newborn extensively before chewing the placenta, leaving only a small piece, which dries with the umbilical cord. Weights of neonates were 17.9 g, $n = 1$ (Baranga, 1980); 18.7 g as the lowest weight (Mutere, 1968b); 22.5 g, $n = 1$ (Kulzer, 1958); 23–24 g (Jacobsen and du Plessis, 1976); and 22.7 ± 2.5 g, $n = 11$ (Noll, 1979b). Neonatal crown-rump length was 56 mm (Kulzer, 1958) and forearm length was 38.2 ± 0.2 mm ($n = 11$ —Noll, 1979b).

Neonates are born with folded ears and closed eyes. They are also born naked except for a thin, downy covering on head and dorsum (Kulzer, 1958, 1969a). After 10 days, the ears become erect

and mobile and the eyes open (Kulzer, 1958). Body temperature after birth is 33–34°C, the first signs of thermoregulatory control appear at 7 days, and full control of body temperature at an ambient temperature of 20°C is achieved at ca. 21–27 days (Noll, 1979b). By 36 days, forearm length is 60 mm, wing span is 75% of the adult span, and body mass has doubled since birth (Noll, 1979b). Growth curves of forearm length and body mass of males and females indicate the same rate of growth for both sexes (Mutere, 1968b). At ca. 9 months both sexes attain adult body weights of ca. 90 g and forearm length of 88–99 mm (Anderson and de Winton, 1902; Mutere, 1968b).

Lactation in *R. egyptiacus* lasted 70 days in Egypt (Kulzer, 1958) and ca. 60 days in South Africa (Penzhorn and Rautenbach, 1988). Captive animals lactated for 6 weeks (Mutere, 1968b). Weaning mass was 63.1 g (Baranga, 1980) and 67–98 g (mean of 84.5 g—Jacobsen and du Plessis, 1976).

ECOLOGY. *Rousettus egyptiacus* occurs from sea level to altitudes of 4,000 m and from arid to moist tropical biomes (Kulzer, 1979). The variety of ecological conditions indicates no single factor as a barrier, beyond the requirement for abundant plant food and dark roosts. These bats usually roost during the day in moist (high humidity) caves, and they also use damp, artificial structures (e.g., tombs, mines, military bunkers) but not trees (Atallah, 1977; Kulzer, 1979; Lewis and Harrison, 1962; Qumsiyeh, 1985).

Food includes a variety of fruit, flowers, and leaves. Egyptian rousette bats eat apple, apricot, banana, carob, date, fig, grape, jamba, litchis, loquat, mango, mulberry, orange, pawpaw, and peach, while in drier regions, date and fig may be their staple food for a large part of the year. The amount of food consumed per bat is higher for single bats than for clustered bats (Coe, 1975; van der Westhuyzen, 1976). Fruit consumption by these bats has been considered an economic nuisance (Harrison, 1964; Jacobsen and Du Plessis, 1976).

The lanner falcon (*Falco biarmicus*) and the genet (*Genetta*) prey upon *R. egyptiacus* (Jacobsen and Du Plessis, 1976). In Cairo, they were attacked by hawks (species not identified) when leaving their roost (Kulzer, 1969b), and falcons and owls (*Bubo bubo*) also take them (Qumsiyeh, 1985).

Ectoparasites of *Rousettus egyptiacus* include mites *Spinturnix lateralis*, *Ancystropus leleupi*, and *Ancystropus zelebori* in Republic of the Congo (Anciaux de Faveaux, 1965), *Ancystropus lateralis* in Egypt, Palestine, and Cyprus (Stiles and Nolan, 1930), and *A. zeleborii*, *Liponyssus glutinosus*, and *L. longimanus* in Egypt (Stiles and Nolan, 1930); flies *Eucampisipoda africanum*, *Nycteribosca africana* and *N. alluaudi* in Republic of the Congo (Anciaux de Faveaux, 1965), *Eucampisipoda hyrtlui* and *Nycteribosca diversa* in Egypt (Stiles and Nolan, 1930), *Thaumapsylla breviceps* in South Africa (Stiles and Nolan, 1930), *Nycteribia pedicularia*, *N. schmidlii*, and *E. hyrtlui* in Palestine (Theodor and Moscona, 1957), *E. hyrtlui* in Lebanon (Lewis and Harrison, 1962), and *E. africana* in Liberia (Wolton et al., 1982); the bedbug *Afronemex leleupi* in Republic of the Congo (Anciaux de Faveaux, 1965); fleas *Thaumapsylla breviceps* in Republic of the Congo (Anciaux de Faveaux, 1965) and *Archaeopsylla metallescens* in Egypt (Stiles and Nolan, 1930); and the tick *Alectorobius (Reticulinasus) camicasi* in Senegal (Sylla et al., 1997).

Endoparasites include the hemosporidian *Plasmodium rousetti* (causes malaria) in Zaire (Garnham, 1973) and Republic of the Congo (Anciaux de Faveaux, 1965), and the roundworm *Nycteridocoptes rousetti* in Republic of the Congo (Anciaux de Faveaux, 1965). Rabies affects *R. egyptiacus* in Republic of the Congo (Anciaux de Faveaux, 1965).

Colonies in caves range from ca. 100 to several thousand individuals (Herzig-Straschil and Robinson, 1978; Kingdon, 1974). Within roosts the bats hang in densely packed clusters which form wherever there are suitable footholds. The availability of dark places may regulate population size in caves, because they change roosting sites often, continually seeking and fighting for the darkest corner or crevice they can attain (Herzig-Straschil and Robinson, 1978; Kingdon, 1974; Kulzer, 1979). Most flight activity and roost changes occur during daytime when the sun is reflected into the cave (Herzig-Straschil and Robinson, 1978). Colony size can be stable (Mutere, 1968b) or it can fluctuate (Jacobsen and Du Plessis, 1976; Lombard, 1961). Reduction in colony size in the eastern Mediterranean region during winter presumably indicated migration to warmer climates and more abundant food (Atallah, 1977). Colony

size may vary when the sexes segregate during reproductive efforts (Kingdon, 1974; Korine et al., 1994; Lombard, 1961; Oika, 1987). Seasonal changes in the abundance of fruit induces migration, but reliance on suitable roosts may limit foraging distances (Kingdon, 1974). In South Africa, marked individuals of *R. e. leachi* moved between roosts 32 km apart and one adult female relocated 500 km away (Jacobsen and du Plessis, 1976).

Rousettus egyptiacus often roosts with other bats, including emballonurids, hipposiderids, rhinolophids, and vespertilionids (Herzig-Straschil and Robinson, 1978; Kingdon, 1974). In French Guinea, *Lissonycteris angolensis* was found in the same cave (Eisentraut and Knorr, 1957). In northern Rhodesia (Zimbabwe), *R. e. leachi* occurred with *Hipposideros commersoni*, *Miniopterus*, and *Rhinolophus* (Ansell, 1960). In Israel, *Myotis capaccinii*, shrews *Crocidura leucodon*, *C. russula*, and the rodent *Acomys cahirinus* were found with *R. egyptiacus* (Harrison, 1964). The spiny mouse (*Acomys dimidiatus*) appeared to be commensal with *R. egyptiacus* in a tomb in Aswan, Egypt (Maser, 1966).

Disease in wild populations has not been reported, but a calcium-phosphorous imbalance and vitamin D deficiency (Buckland-Wright and Pye, 1973), osteoproliferation due to fluorosis (Duncan et al., 1996), and neurological impairment associated with cobalamin (vitamin B₁₂) deficiency (Green et al., 1983) were found in captive animals. Continuous exposure to cold (2.5–7.0°C for 24 h) causes loss of body temperature and eventual death (Kulzer, 1969b), indicating *R. egyptiacus*, which shows no signs of torpor or hibernation, cannot survive in a continuous cold or temperate climate. Maximum longevity is 25 years for individuals kept in captivity (Kulzer, 1979).

BEHAVIOR. *Rousettus egyptiacus* clusters within day roosts, maintaining close body contact among individuals, reducing the influence of environmental conditions, surface-to-volume ratio, and energetic costs of homeothermy (Kulzer, 1979; Noll, 1979a). Captive bats space themselves only when ambient temperatures are $\geq 30^{\circ}\text{C}$ (Kulzer, 1979). If a colony of *Rousettus* is disturbed, individuals try to escape to darker places and form compact clusters (Kulzer, 1979). This fright reaction can be induced in bats kept in captivity (Kulzer, 1979).

Within their roost, these bats chatter noisily for much of the day. They have a wide range of squawks and cries that play roles in individual and social communication. Recognition does not depend only on vocalizations or hearing, but to a great extent on scent (Kulzer, 1969b). Grooming activities during roosting include combing their fur with foot claws and licking of the abdomen, chest, head, and wing membranes. The wings and face are very thoroughly licked by the long tongue and receive the most attention (Kingdon, 1974; Kulzer, 1969a). These bats become more active during the afternoon as the closely packed clusters spread out, and grooming and social activities intensify (Kulzer, 1969b). After feeding, there is another thorough grooming session. The hair on the chest, sometimes matted with fruit, is thoroughly combed with the hindfeet, toes are cleaned with the mouth, and the teeth are vigorously scratched with toenails (Lombard, 1961). It has been estimated that half the night is spent grooming (Kulzer, 1969a). When urinating or defecating, or when climbing a wall or tree trunk, these bats go into an upright position, turn around, and hang by their thumbs (Lombard, 1961).

Jacobsen and du Plessis (1976) observed a colony of *R. e. leachi* crowded together in a cave. Frequent squabbling occurred, especially if a bat was shuffled out of position and then attempted to regain its former place. These bats (sex or age class not identified) fought by striking with the forearm and hooking with the clawed thumb (Jacobsen and du Plessis, 1976). They sparred with an open mouth, frequently biting when managing to hook another bat. These fights were usually accompanied by loud screams. This activity persisted throughout daylight hours.

The sexes segregate, females forming nursery colonies and males establishing bachelor groups, in geographical areas where breeding is seasonal (Kingdon, 1974; Korine et al., 1994; Lombard, 1961; Oika, 1987). Elsewhere, there are large stable colonies (Mutere, 1968b). In Uganda, births occur just before seasonal peaks in rainfall (Mutere, 1968b). In South Africa, bat numbers increased during the hot rainy season (October–February) when food was most abundant (Jacobsen and du Plessis, 1976), and numbers peaked March–April, when young of the year accompanied foraging adults.

In captivity, the male initiates sexual activity, whereas the fe-

male appears unwilling, resisting and protesting as he encircles her (Kulzer, 1958). The male climbs on the female's back, embraces her while beating her with his wings, and grips her by biting her nape. This struggle continues until her resistance subsides and she becomes excited, clinging to his belly with her claws while he copulates. He licks her muzzle continuously, enhancing receptivity (Kingdon, 1974; Kulzer, 1969b). After an initial copulation is effected, subsequent copulations may occur (Kulzer, 1958).

Within day roosts, young cling to the mother for about six weeks (Kulzer, 1966; Rosevear, 1965). When at rest, the mother's wings are folded to cover the neonate completely. After the 16th day, the young bat leaves the teat for several minutes at a time, cleans itself, begins to swing actively backwards and forwards, turns about in all directions, and unfolds its wings. Wing beating begins after day 25 (Kulzer, 1966). The first flight excursions of young are 63–70 days after birth (Kulzer, 1966; Rosevear, 1965). These first flights are near the mother and during the daytime rest period only. After 100 days, the young leaves the day roost but flies close to its mother. At this stage, while in the roost, the young bat's behavior resembles that of the adults. Young continuously observe adults (Kulzer, 1966), and each individual that approaches is intensely sniffed and smelled by the young. As young approach weaning, they lick excess fruit from the mother's lips and several days later take mouthfuls of fruit (Lombard, 1961).

Nightly pre-emergence activity of *R. egyptiacus* includes movement towards the entrance of the cave and flying to the cave mouth. The time of emergence, under natural light conditions, begins after sunset (Jacobsen and du Plessis, 1976; van der Westhuyzen, 1976). Bats begin to return to the day roost before sunrise. Feeding patterns in captives indicate a circadian rhythm which is adjusted or synchronized to the light-dark cycle (van der Westhuyzen, 1976). Maximum activity depends on there being light intensity of 10^{-5} – 10^{-2} lx (Kulzer, 1979), which agrees with field observations (Jacobsen and du Plessis, 1976). Under conditions of constant light, a circadian rhythm of activity persists (Erkert, 1970).

Times of emergence and return to the cave for *R. e. leachi* indicate a different winter and summer pattern of activity (Herzig-Straschil and Robinson, 1978). During summer, the period of activity is longer than during the winter, despite a shortened dark phase. Bright moonlight delays the onset of emergence (Herzig-Straschil and Robinson, 1978). In Israel, reproductively active adult females emerged before juveniles and adult males, and first emergence was correlated with light intensity rather than with time of sunset (Korine et al., 1994). Lags in emergence indicate the need for males to defend territories and the need for females to have longer feeding bouts because of the increased energy and nutritional demands of pregnancy and lactation.

In the branches of trees, *R. egyptiacus* can move quickly and surely, using their thumb claws as hooks (Kulzer, 1969b). Grounded bats move slowly with clumsy movements, but they can take flight from smooth surfaces (Bergmans, 1978). They can fly at 4.4 m/s (Kulzer, 1958) and glide at 5.3–11.0 m/s (Pennycuik, 1971). They can hover (Kulzer, 1958) and are more maneuverable than most birds (Pennycuik, 1971). Caged bats could fly through openings of 25 by 20 cm without touching the sides, despite a wingspan ≤ 60 cm (Kulzer, 1958).

Smell is a important sense for these bats when selecting food, as demonstrated by their ability to distinguish between a minute quantity of hidden banana and a synthetic banana scent (Kulzer, 1969b). Jacobsen and du Plessis (1976) describe *R. e. leachi* hovering by fruit-laden branches, before alighting on one and selecting a ripe fruit. After plucking a fruit, the bat flies to a roost, grasps the fruit against its chest, bites out pieces, and masticates. Juice and liquefied pulp are swallowed, and a small ball of fibers, seeds, and rind are spat out. Hard skinned food items (e.g., litchis) are first peeled by rotating the fruit with wings, hind foot, and mouth (Jacobsen and du Plessis, 1976). The bats discard up to 25% of the fruit gathered, much of it resulting from attempted pilfering by other bats, which may terminate in agonistic behavior (Jacobsen and du Plessis, 1976). Adult bats consume 50–150% of their body mass/day (Izhaki et al., 1995). Feeding roosts were located up to 459 m from feeding trees (Izhaki et al., 1995). Seed dispersal by bats has no effect on seed germination per se, other than temporal asynchrony in germination and preventing consumption by other seed predators (Izhaki et al., 1995). *Epomophorus gambianus* and *R. egyptiacus* were observed feeding at the same *Diospyros senensis* bush in Zimbabwe where as many as five *R. egyptiacus* simul-

taneously arrived at and departed from the same bush (Thomas and Fenton, 1978). Approximately a hundred bats were observed feeding from baobab flowers (*Adansonia digitata*), where they flew to a bloom from below, alighted upside down using their feet and forelimb claws, and fed 10–15 s (Start, 1972). When feeding, the bats are aggressive and their audible cries may attract other bats (Brosset, 1966; Thomas and Fenton, 1978).

GENETICS. Examination of 200 mitotic divisions from three males and one female *R. e. leachi* from the forests of Magamoto, Uganda Occidental, indicated $2n = 36$ and $FN = 66$ (Dulic and Mutere, 1973). Autosomes consist of twelve pairs of metacentrics, two pairs of submetacentrics, two pairs of subtelocentrics, and one pair that is very small and punctiform. Of the metacentrics, one pair has an unusually long central constriction; these morphologically identical marker chromosomes have been described for all megachiropteran species (Peterson and Nagorsen, 1975). The X chromosome is submetacentric and the Y chromosome is small and punctiform.

REMARKS. The generic name *Rousettus* comes from the French *rousse*, meaning reddish or reddish brown, the fur color of the earliest specimens taken in Egypt. The specific name *egyptiacus* refers to the type locality for the species. Skull photographs courtesy of D. E. Wilson.

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Editors of this account were SYDNEY ANDERSON, LESLIE CARRAWAY, and KARL F. KOOPMAN. Managing Editor was BARBARA H. BLAKE.

GARY G. KWIECINSKI, DEPARTMENT OF BIOLOGY, UNIVERSITY OF SCRANTON, SCRANTON, PENNSYLVANIA 18510-4625; THOMAS A. GRIFFITHS, DEPARTMENT OF BIOLOGY, ILLINOIS WESLEYAN UNIVERSITY, BLOOMINGTON, ILLINOIS 61702-2900.