FAUNA *of* AUSTRALIA

37. PTEROPODIDAE

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DEFINITION AND GENERAL DESCRIPTION

The family Pteropodidae occurs throughout the Old World tropics and subtropics: Africa, southern Asia to Australia and the western Pacific islands. This family constitutes the Suborder Megachiroptera of the Order Chiroptera which, with 950 species, contains 25% of living mammals (Corbett & Hill 1980). Out of a world-wide total of 43 genera and 173 species of pteropodids, five genera and eight species occur in Australia.

In the Pteropodidae, the external ear is simple, has no tragus and the edge of the pinna forms an unbroken ring around the ear canal. The eyes are large with the choroid and outer layer of the retina uniquely folded into cones. No noseleaf is present. The second finger has three bony phalanges, the last of which is very small or rudimentary and usually bears a small claw. The tail is short, except for *Notopteris* species, or absent and the interfemoral membrane is absent or poorly developed. The shoulder joint is simple. The head has a fox-like or dog-like appearance, hence the common names flughunde and flying-fox. The dental formula is reduced to I 2/2 C 1/2 PM 3/3 M 2/3 = 34 or less. The canines are prominent and the molar teeth are highly modified for fruit eating. The palate has transverse ridges used in association with the tongue to crush soft foods. The stomach is simple. The penis is pendant.

The genus *Pteropus* was erected by Brisson (1762) from specimens collected from Bourbon Island, Réunion (see Andersen 1912, p. 219, for a discussion on this species, *P. niger*, whose type is destroyed). Gray (1821) first recognised the two suborders of bats (orders in his system), but his spelling Pteropidae has been replaced by Bonaparte's (1838) Pteropodidae. Dobson's (1878) major revision of the family (10 genera and 70 species) was expanded in 1912 by Andersen (35 genera and 186 species) to become the accepted taxonomy for the family.

HISTORY OF DISCOVERY

The Grey-headed Flying-fox (*Pteropus poliocephalus*) was first described from four specimens from 'la Nouvelle Hollande' (Temminck 1825) [Leyden Museum (2). Paris Museum (1) and British Museum (1)]. The Spectacled Flying-fox (*Pteropus conspicillatus*) was described by Gould (1850) from a specimen from Fitzroy Island, Queensland; this syntype (male) is in the British Museum. The Little Red Flying-fox (*Pteropus scapulatus*) was described by Peters (1862) from a specimen from Cape York and the holotype (female) is in the Berlin Museum. The Queensland Blossom Bat (*Syconycteris australis*) was described by Peters (1867) from a specimen from Rockhampton, Queensland (as *Macroglossus minimus* var *australis*) and the type (male subadult) is in the Berlin Museum [Matschie (1899) erected the genus *Syconycteris*]. The Queensland Tube-nosed Bat (*Nyctimene robinsoni*) was described by Thomas (1904) from a specimen from Cooktown, Queensland and the holotype (male) is in the British Museum. The *N. albiventer* reported from Australia are actually *N. robinsoni* (Winter & Allison 1980). The Black Flying-fox (*Pteropus alecto*) was described by Temminck (1837) from Menado and the Australian representative was first described by Peters (1867) as *Pteropus gouldii* from Rockhampton, Queensland. The syntypes are in the Berlin Museum.

The Bare-backed Fruit Bat (*Dobsonia moluccensis*) was described from a specimen collected in Amboina (Quoy & Gaimard 1830) and the first Australian specimen was reported from Coen (Allen 1935). The first Australian representative of *Macroglossus* was collected from Murray Islands, Torres Strait

and called *M. australis* (Ogilby 1892). The Australian forms have now been placed in the Northern Blossom Bat (*M. minimus*), originally collected from Java (see Corbett & Hill 1980; Honachki, Kinman & Koeppl 1982).

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

Australian species range in size from *Macroglossus* sp. (maximum weight 17g) and *Syconycteris* sp. (maximum weight 19g) to the *Pteropus* species (weighing up to 1000g) to. Males are larger and have larger canines in all species. All have dog-like faces except *Nyctimene* species which have tubular nostrils and short broad jaws (Fig. 37.1). In this genus the lower incisors are absent, but the lower canines meet so that there is no gap. The ears, wing and tail membranes bear yellow blotches. *Pteropus* species have a contrasting coloured mantle on the shoulders and upper back on which there are modified sebaceous glands. These glands are used to mark territories in the breeding season and are developed maximally at this time, more so in males (Nelson 1965a). In *Dobsonia*, the naked skin membranes extend to the midline of the back and there is a short tail. They have only one upper incisor between, not in front of, the canines and the first upper premolar has been lost (=28 teeth). The thumb has no claw and is used when climbing. Further illustrations of the Australian species are shown in Strahan (1983).

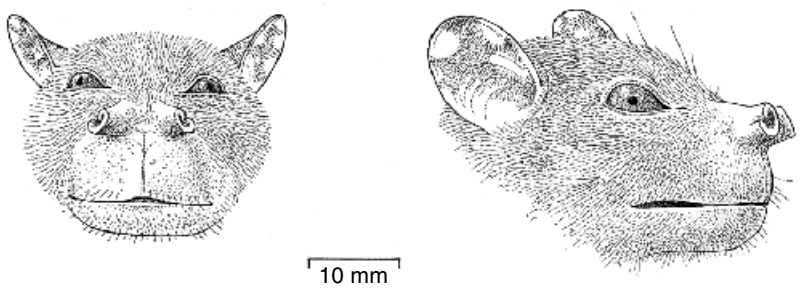

Figure 37.1 Front and lateral views of the head of *Nyctimene robinsoni*. (© ABRS) [F. Knight]

Feeding and Digestion

At night, pteropodids fly from their daytime roosts to feed on fruit or flowers. Several individuals often feed in the same tree and each may defend its portion of the tree. Soft fruits may be eaten completely, but fibrous foods usually are chewed, the juices swallowed and the remaining fibre spat out. An especially long tongue is found in those species that feed on blossom (Fig. 37.2). In all species, food passes completely through the gut in 30 minutes or less. In *Pteropus*, the stomach has marked cardiac and fundic regions, no caecum or appendix and no obvious demarcation between small and large intestine. Tedman & Hall (1985a, 1985b) examined the small intestine of the Black and Grey Flying-foxes histologically and suggested that the large absorptive area may compensate for the short food transit time. Steller (1986) determined the maintenance requirements for energy and nitrogen and compared the efficiency with which the nutrients in a native fig and an apple were utilised. The calculated minimal field energy budget (944 kJ $kg^{-0.75}$ day^{-1}) was high

compared to that of microchiropterans. *Pteropus* species fly over water, including salt water, and scoop up mouthfuls as they fly (Ratcliffe 1961; author personal communication). The author has seen Black and Grey Flying-foxes crawl down mangroves in their day roost to drink sea water in the estuary. The author, in an unpublished experiment over 15 days, found that both these species, when offered a choice between a salt solution (salt concentration half that of sea water) and tap water, drank two to eight times more solution than tap water. When the solution was equal to sea water, animals drank one and a half times more tap water than solution. The Black Flying-fox, offered a choice between tap water and a solution one and a half times sea water concentration, drank two to three times as much tap water. When the solution was changed to two times the concentration of sea water, animals drank nine times as much tap water. Even though fed the same food Black Flying-foxes drank three to four times more fluid than grey Flying-foxes. Richards (1986b) reported on the foraging behaviour and general ecology of the Queensland Tube-nosed Bat.

Skeletal System

The bacula of the Australian species are figured and described in Krutzsch (1959, 1962) and Lanza (1969). The skull of *Pteropus gouldi* is shown in Figure 37.3 and that of the Little Red Flying-fox by Andersen (1912).

Strickler (1977) commented on the shoulder osteology and myology of a specimen collected from Malaysia and wrongly identified as a Grey-headed Flying-fox which is endemic to Australia. His comments, however, are applicable to that species. He also examined the Northern Blossom Bat.

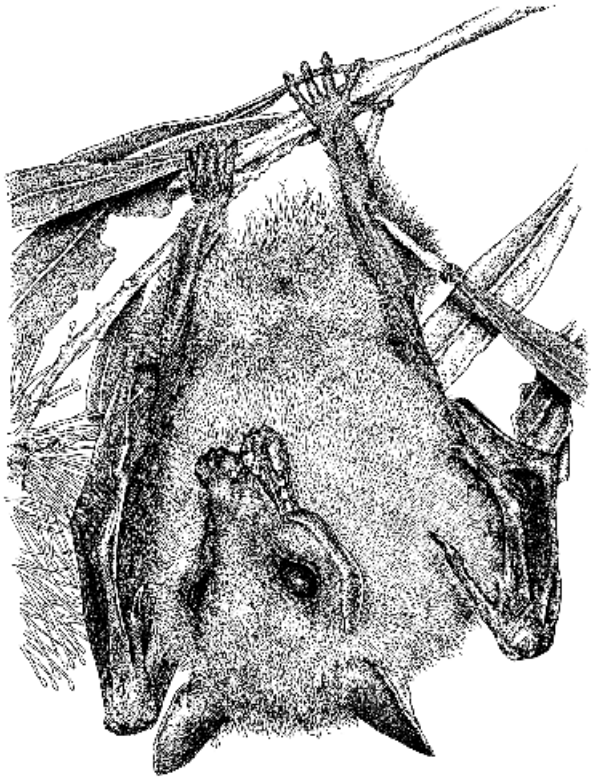

Figure 37.2 Blossom Bat, *Synconycteris australis*, hanging with toungue extended. (© ABRS) [K. Hollis]

The pteropodid shoulder is of relatively simple construction, but some features are specialised. One is the lateral displacement of the primitive insertion of the omohyoides from the clavicle to the scapula (seen also in phyllostomatids and *Noctilio* species) and the other is an elaborate system of muscular slips which tie the tendon of occipitopollicalis muscle to the skin over the thoracic and lower cervical region. This latter muscle is important in maintaining tension in, and in manipulation of, the cranial edge of the propatagium. In the downstroke, the thumb is flexed strongly so that the lateral propatagium attached to it is drawn ventrally as is the proximal propatagium by the occipitopollicalis. The combined effects of these movements increases camber and lift. Several muscles that are important in the downstroke and flick phase of the upstroke are relatively large in highly manoeuvrable, slow to

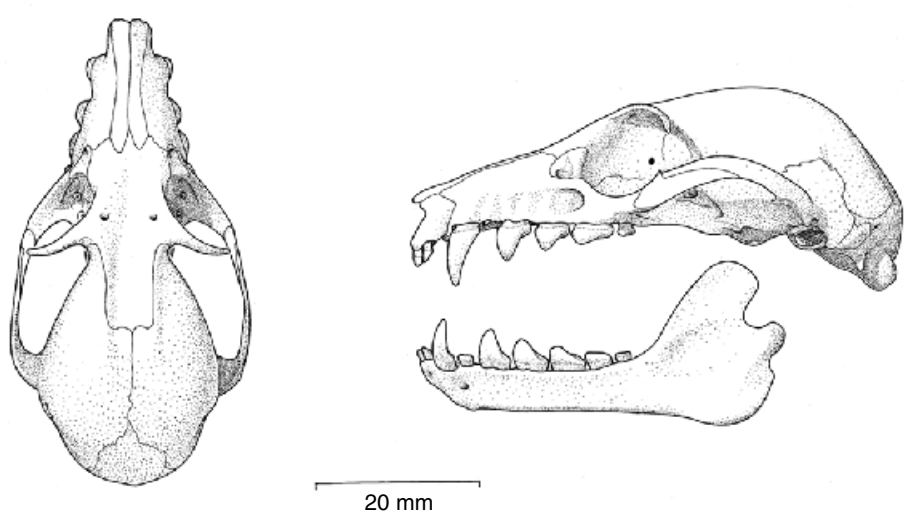

Figure 37.3 Dorsal and lateral views of the skull of Pteropus gouldi. (© ABRS) [K. Hollis]

moderately fast-flying and hovering bats, such as *Macroglossus* species. Wilson (1985) and Richards (1986a) commented on the flight mechanism of Bare-backed Fruit Bats.

Respiration

Bartholomew, Leitner & Nelson (1964) measured oxygen consumption, body temperature and heart rate of Grey-headed and Little Red Flying-foxes and Queensland Blossom Bats at rest in ambient temperatures from 0–40 °C. Bartholomew, Dawson & Lasiewski (1970) gave similar measurements for *Nyctimene albiventer* which could also apply to Queensland Tube-nosed Bats. At low temperatures all species wrap their wings around the body to enclose a layer of warm air against their ventral surface (Figure 37.7c). In Grey-headed Flying-foxes this reduced the lower critical temperature from 19°C to 15°C and at 5°C reduced the metabolism over that with wings not folded by half of the basal rate. At high temperatures, open-mouth panting, wing-fanning, salivation and licking of the muzzle, wrist, thumb, wing membranes and chest were used to increase heat loss. *Nyctimene* can be both homeothermic and heterothermic. At 25°C the ratio of metabolic rates in these states is 4 : 1. Bartholomew *et al.* (1970) suggested that many of the small megachiropterans (for example, *Syconycteris* and *Macroglossus*) can be both homeothermic and heterothermic. Thomas (1975, 1981) measured the metabolism of Black Flying-foxes while in flight. Although the metabolism of this species when in flight was 2.5–3.0 times greater than the highest metabolic rate of an exercising terrestrial mammal of similar size, only a quarter of the energy was required by the pteropodid, compared to the terrestrial mammal, to cover the same distance. There was a 17-fold increase in ventilation from rest to level flight by the Black Flying-fox.

Carpenter (1985, 1986) has made similar measurements on Grey-headed Flying-foxes flying in a wind tunnel. During flight there is an increase in oxygen consumption to a level about 24 times that of the basal rate and a corresponding increase in heat production. The 1 : 1 relationship between respiration rate and wing beat, however, limits the heat loss to a small fraction of heat production so that Grey-headed Flying-foxes quickly became hyperthermic at ambient temperatures above 25°C. For one bat the velocity of minimum power input was 7 ms^{-1}. The rate of oxygen consumption increased steeply at lower airspeeds where the wing beat was more frequent,

the plane of the beat was less vertical (because of the high angles of attack on the body) and the feet pulled the trailing edge of the proximal portions of the wings into a high camber. At higher airspeeds, the rate of oxygen consumption increased gradually and the wing beat became almost vertical as the body had a less inclined plane and the feet became more straight behind. The effect of velocity on the endurance of this species was such that the maximum range achieved was possible only at the velocity of minimum power input. The endurance of the Grey-headed Flying-fox while flying at 8.6 m s^{-1} was 32% and the range only 44% of that achieved at 7 m s^{-1}.

Sense Organs and Nervous System

The pteropodids have large olfactory bulbs. Olfaction is important in food location, and in recognition between mother and young and between mated individuals (Nelson 1965b). They also use a great variety of vocalisations in social interactions (Nelson 1964a), but do not utilise ultrasonic pulses for echolocation as do the Microchiroptera.

The eyes and visual system are well developed (Campbell, Graydon & Giorgi 1985; Graydon, Giorgi & Pettigrew 1987). Beasley, Graydon & Giorgi (1985) and Graydon, Pettigrew & Giorgi (1986) gave peak retinal ganglion cell counts in an area centralis of 7000/mm^2 for Grey-Headed Flying-foxes, 8000/mm^2 for Little Red Flying-foxes and 10 500/mm^2 for Black Flying-foxes. Driel, Graydon & Giorgi (1985) described the vasculature of the eye.

Calford *et al*. (1985a) mapped the somatosensory cortex of the Grey-headed Flying-fox and in the same species, recording from single neurones in the inferior colliculus, Calford *et al*. (1985b) found a frequency range from 2–50 KHz with maximal sensitivity at 15 KHz. Calford & McAnally (1987) reported a similar range in the Little Red Flying-fox of 2– >40 KHz, with a marked peak of sensitivity at 11 KHz. The peak in frequency sensitivity was found to be consistent with the biophysical characteristics of the external ear (pinna). Figure 37.4 shows a behavioural audiogram for the Grey-headed Flying-fox from an unpublished study by the author. The animals were observed in a triple walled soundproof box with viewing glass. One observer recorded ear movements by the animals on a time chart as an assistant turned on and off a pure tone of various frequencies and intensities. Maximal sensitivity was at 6 KHz. Sonographs of vocalisations indicated ranges mostly from 2–7 KHz (Nelson 1964a).

Stephan, Nelson & Frahm (1981) and Stephan & Nelson (1981) described the brains of the Black Flying-fox and the Queensland Tube-nosed Bat, and gave measurements for brain volumes and calculate encephalisation indices for six Australian megachiropterans. On their scale, the Australian species are close to the mean (193) of these species and 19 other megachiropterans (range 133 to 266). Values for the Australian species were Grey-headed Flying-fox (182), Queensland Tube-nosed Bat (196) , Black Flying-fox (197) , Spectacled Flying-fox (200) , Queensland Blossom Bat (201) and Little Red Flying-fox (206) .

Reproduction

General details of the breeding cycle of *Pteropus* species appear in Ratcliffe (1931) and Nelson (1965a, 1965b).

All *Pteropus* species regularly aggregate into camps occupying various types of vegetation such as mangroves, rainforest and wet sclerophyll forests. The Black Flying-fox has been reported by Stager & Hall (1983) to occupy a cave in Chillagoe (Queensland) and the author has seen them (June 1965) in a cave at Tunnel Creek (Western Australia) [mentioned in Marshall & Drysdale (1962), but species not identified].

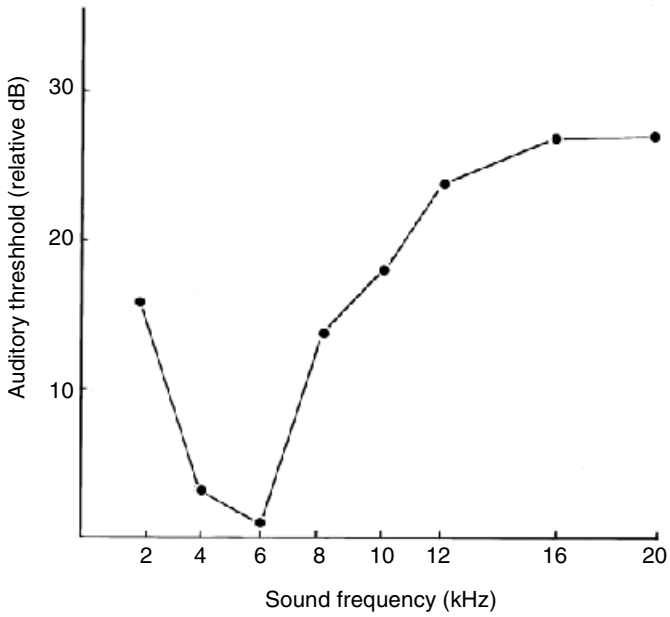

Figure 37.4 Audiogram for Pteropus poliocephalus, showing hearing sensitivity at different frequencies. (J.E. Nelson, unpublished data)

During December and January males begin to associate with one or more females to form territories in late January. Males mark these by rubbing their scapular glands along the branches of trees within the territory. Both sexes may defend the territory although the male is usually more active. Females initially have young at the breast, but as the breeding season progresses the young leave the female to associate with other young (Figure 37.7d).

Mating in Grey-headed and Black Flying-foxes occurs in March-April. Males have sperm in the epididymis all the year and will attempt to mate with females at any time. Testes activity, as judged by the weight of the testes and the size of tubules and accessory glands, is greatest in the month preceding copulation and least from June to September (Nelson 1965b). Towers & Martin (1985) and Martin *et al*. (1987) measured progesterone and oestradiol levels in Grey-headed Flying-foxes and discussed the local endometrial reaction and possible factors regulating female receptivity.

The male usually initiates precopulatory behaviour by grooming the wings and body of the female and by licking the vaginal opening. Initially, the female may rebuff the male, but these rebuffs become less intense and less frequent so that more time is spent licking the vaginal opening. Such activity may last for 3/4 hour before the male moves behind the female, holds her wings between his upper arm and forearm, grasps her neck in his teeth and copulates with her. The penis, which has a species-specific arrangement of spines on it, is very flexible and can be moved independently of pelvic movements. Throughout the breeding season such bouts of precopulatory and copulatory behaviour may be repeated several times each day and are accompanied by much movement and vocalisation (Nelson 1965b).

The sexes segregate in late April and early May and at this time the males show little aggressive behaviour, even mutually grooming each other. During winter (June to September) the population is usually dispersed, but some animals may aggregate in winter camps. In September, the population begins to reappear again in the summer camps where the single young is born in late September to late October.

There are no published data on the embryology of the Australian species. Some of the author's unpublished data on the Little Red Flying-fox are shown in Table 37.1.

Table 37.1 The relationship between date and size of embryos of *Pteropus scapulatus* in 1959-60.

DATE	EMBRYO WEIGHT (g)		
	Average	Range	Number
January 18	1.8	0.1–6.9	109
February 22	14.1	3.0–26.0	30
March 12	21.3	8.0–32.5	57
March 25	28.1	11.5–36.0	7
April 14	42.0	23.0–62.0	11
April 25	51.0	40.0–74.5	7
April 27	First birth seen		

In Grey-headed Flying-foxes the uterus is bicornuate and successive pregnancies occur in alternate horns. The placenta is discoidal and at full term has a yolk sac gland covering about a third of the placenta (Figure 37.5). The placenta is sometimes ejected while attached to the neonate and may be eaten.

A young animal weighs about 70 g at birth though there is wide variation in this weight (45–118 g). It is naked on its ventral surface and is dependent on its mother for the regulation of body temperature. It is carried everywhere by the mother to whom it clings by gripping her fur with the claws of the thumbs and feet and by grasping her axillary teat in its mouth. By about 4 weeks they weigh about 150 g, the fur on the ventral surface has grown and the young can regulate its body temperature (Figure 37.7d). Now, it is left in the trees at night with other young when mothers go to feed. The mothers and young call to each other on the mother's return. The mother recognises her own young's call, but the final recognition is by smell. The young are able to fly at 3 months when they weigh about 250 g. They eventually leave the females and associate with other young. They are mature at 18 months with a body weight of 595 ± 55 g for males and 575 ± 25 g for females. All females above 600 g become pregnant in the breeding season.

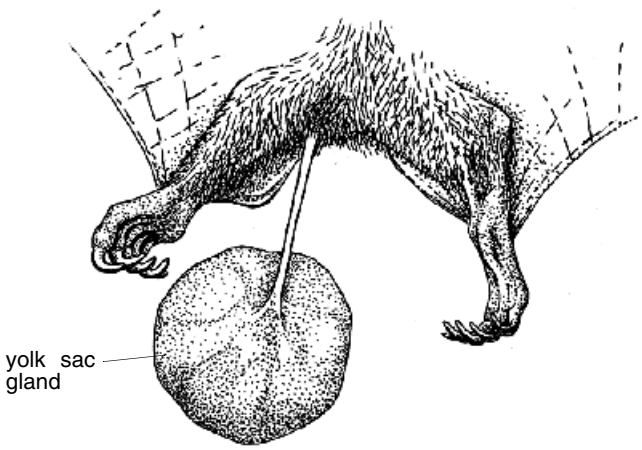

Figure 37.5 A newborn bat showing the large placenta found in this group.(© ABRS) [G. Scott]

As is apparent in Table 37.1, the breeding season of the Little Red Flying-fox is reversed compared to other *Pteropus* species in that mating occurs in late December–early January and births occur in late April–early May. Length of gestation is about 4 months rather than the 5–6 months observed in the other species (see also Prociv 1983a).

Little is known about the other Australian species. Nelson's (1964b) suggestion that the Queensland Blossom Bat may have two or more gestations in a year and that aggregations are formed in October when the young are born, needs to be verified with further studies. These smaller megachiropterans are assumed to roost singly or in small groups, either in tree hollows or under large hanging leaves. The Bare-backed Flying-fox roosts in caves.

NATURAL HISTORY

Life History

Flower (1931) recorded that a Grey-headed Flying-fox was kept in the London Zoo for 6 years 11 months and 9 days.

Ecology and Behaviour

Although they eat fruit, the Australian species are predominantly flower eaters and the seasonal patterns of movements of the *Pteropus* species are correlated with the availability of blossom, predominantly that of *Eucalyptus* species (Nelson 1965a).

Flying foxes gather in large numbers to roost and in the evening leave camps in large numbers (Figure 37.6). Grey-headed Flying-foxes occupy summer camps in spring (September), the number of resident animals peaking in December and January and then decreasing until the camps are deserted in April and May. Many of these camps have been occupied regularly for over 100 years. The number of animals in these camps vary from year to year and from month to month each year and can be correlated with the relative abundance of blossom. Winter camps are occupied usually from April to September. These camps are not common, may arise suddenly in a particular year and are occupied predominantly by young born in the previous October. In later years these new winter camps may be occupied continuously with an increase in numbers about April and a decrease about September (presumably corresponding with movements by animals from and to summer camps, respectively). They may cease to be occupied after a number of years. Such winter camps first appear when blossom is unseasonally abundant.

This general pattern can be modified greatly by the relative abundance of blossom. Summer camps may not be deserted until June if blossom is more abundant than normal. During the winter, when blossom is not normally abundant, the population is dispersed.

The Little Red Flying-fox also forms large camps in November and December, but Nelson (1965a) did not find camps of the species during winter and so assumed that birth occurred when the species was dispersed. Prociv (1983a) found a winter camp in which young were born and juvenile packs and territories formed. Such behaviour was seen in the summer camps of Grey-headed Flying-foxes.

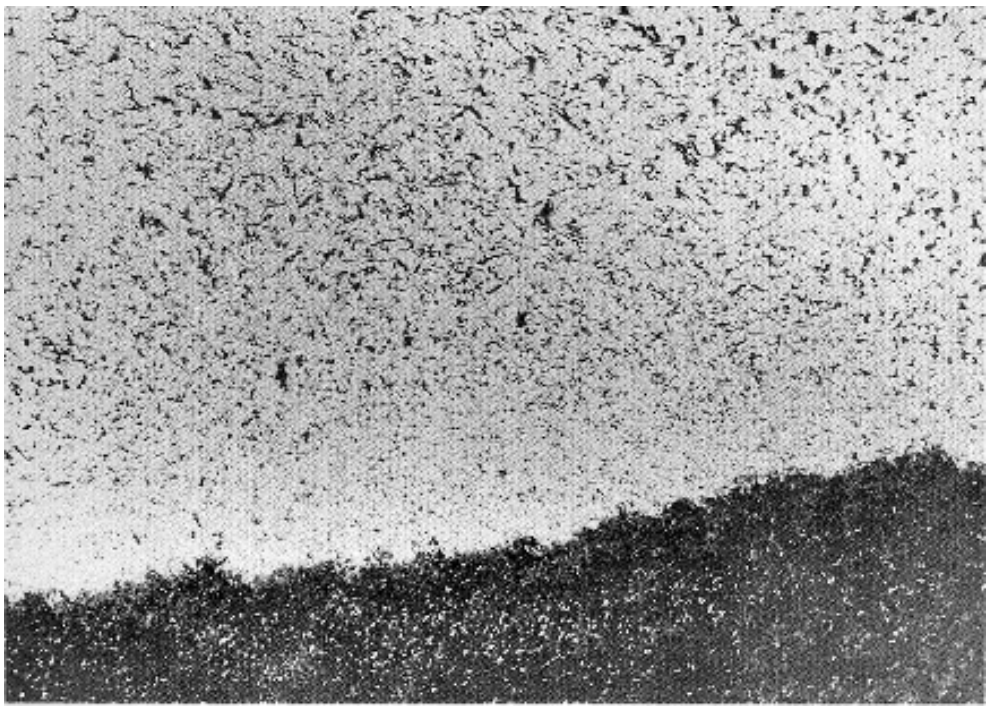

Figure 37.6 A large flight of pteropodids taking off at dusk.

Nelson (1964a) described mother-young, agonistic, reproductive, warning and alarm vocalisations for Grey-headed Flying-foxes with some brief references to Black and Little Red Flying-foxes. In most calls the fundamental frequency is about 2 KHz. Aspects of the behaviour of the Grey-headed Flying-fox are shown in Figure 37.7.

Parasites

Prociv (1983a, 1983b, 1985) found the ascaridoid nematode *Toxocara pteropodis* in all of the Australian *Pteropus* species. Adult *T. pteropodis* are found only in the intestines of suckling young. Eggs are passed in the faeces of young more than 5 weeks of age and adult flying foxes acquire the parasite by ingesting faeces, which need to be older than 10 days to be infective, from foliage in the camps. Eggs hatch in the intestine and larvae move to the liver and remain there for the life of the male flying fox. In the female, the larvae pass through the mammary glands to the neonate.

Mackerras (1958) found the protozoan *Hepatocystis pteropi* in the blood of all four *Pteropus* species and *Trypanosoma pteropi* in the Black Flying-fox. Doherty, Carley & Gorman (1964) found no antibodies to group B arboviruses in 23 sera samples of Spectacled Flying-foxes from Innisfail, and Doherty *et al*. (1966) found none to group A arboviruses in seven sera samples from *Pteropus* species collected from Innisfail (most likely Spectacled Flying-foxes). O'Connor & Rowan (1955) found no antibodies to the virus of dengue fever in six Black Flying-foxes and 18 Little Red Flying-foxes. Gard & Marshall (1973) found 25% of Grey-headed Flying-foxes obtained from Nelson Bay (New South Wales) had antibodies to Ross River Virus, but could detect no viraemia in laboratory trials. Johnston, Wharton & Calaby (1968) found no cattle ticks (*Boophilus microplus*) on three Black Flying-foxes and one Little Red Flying-fox on Magnetic Island. Mackerras (1958) listed a cestode, *Hymenolepis* species and a nematode, *Filaria* species, in the Grey-headed Flying-fox. Prociv (1987) provided a review of parasites associated with Australian pteropodids.

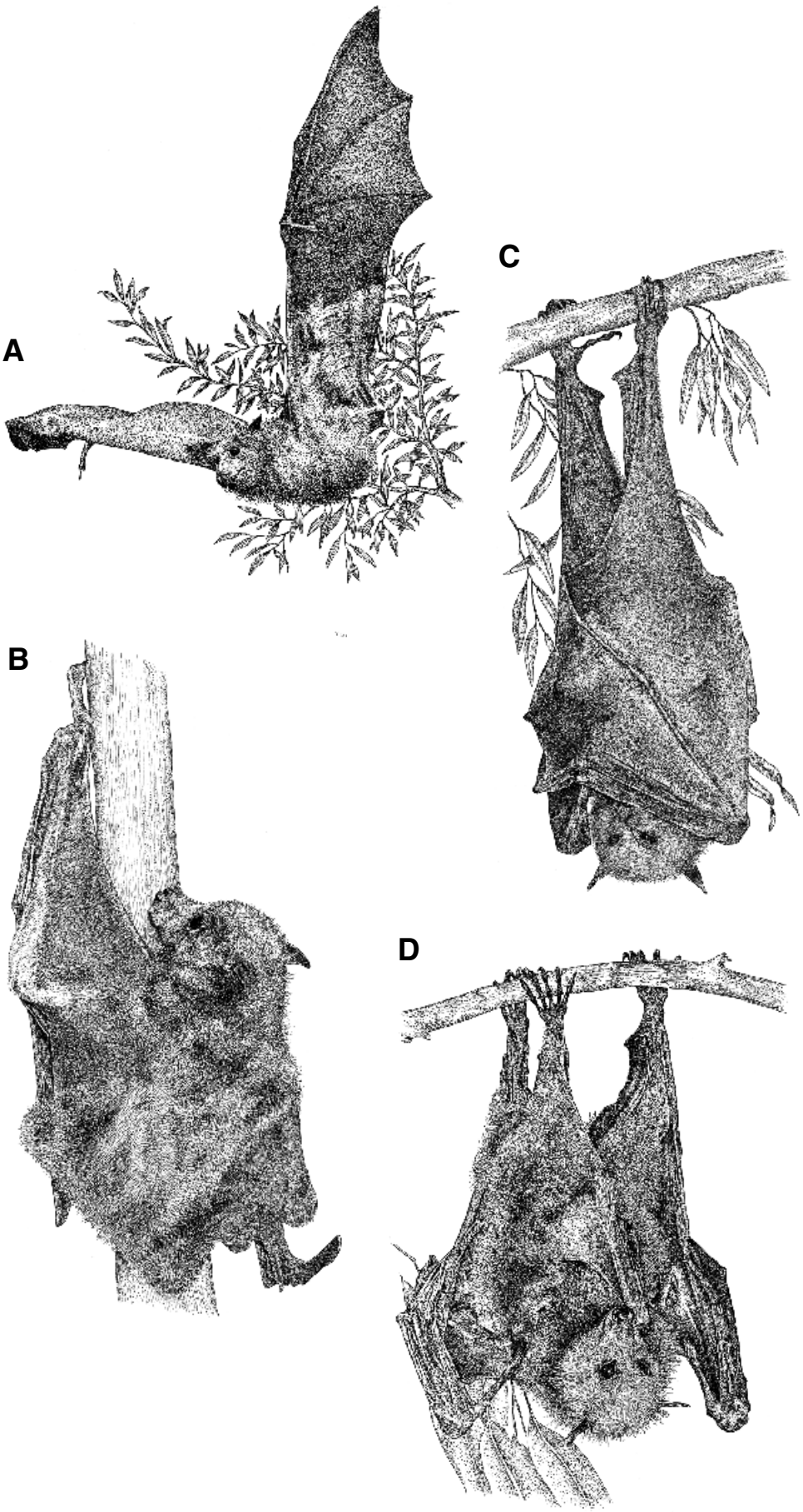

Figure 37.7 Behaviour in *Pteropus poliocephalus*; **A**, in flight; **B**, climbing; **C**, roosting, **D**, mother and baby. (© ABRS) [K. Hollis]

Maa (1971) and Allison (1987) listed Nycteribiidae ectoparasites on Australian Megachiroptera. Domrow (1961, 1963) recorded laelaptid mites on the first two tergites of the batflies. Two species of batflies, *Cyclopodia albertisii* and *C. australis*, were found on the same host. The former species of batfly is widespread and occurs on three or four *Pteropus* species outside of Australia whereas the latter species of batfly is endemic to Australia. They have identical distribution and host ranges in Australia, but *C. albertisii* shows strong preference for Black and Grey-headed Flying-foxes (which also occur outside of Australia) while *C. australis* favours the Little Red Flying-fox. Two nycteribiids are recorded from the Bare-backed Fruit Bat in Australia, *Leptocyclopodia macrura* and *Archinycteribia actena*. *Cyclopodia sycophanta* is recorded from the Queensland Blossom Bat and *C. tenuis* from the Northern Blossom Bat. Durden & Wilson (1985) listed ectoparasites of the Grey-headed and Little Red Flying-foxes including the first record of a species of *Amblyomma*.

Economic Significance

Ratcliffe (1931) examined the economic effects of flying foxes on the agricultural industry. Most of his observations are relevant today. When conditions are unfavourable for *Eucalyptus* blossom generally, they also are unfavourable for commercial blossom (fruit trees *etc.*). The economic losses of an already poor blossom and a poor harvest are increased many times when flying foxes eat some of the small amount of fruit that is available in poor years. In good blossom years flying foxes cause minor economic loss. Management and control of flying foxes was one of the subjects of a symposium, the relevant papers of which were published in 1987 (*Australian Mammalogy* 10: 125-157).

Flying foxes have been considered by health authorities to be possible vectors for human disease, but as the references above indicate, there has been no evidence to support this.

BIOGEOGRAPHY AND PHYLOGENY

Hall (1984, 1987) discusses the biogeography of the Pteropodidae and distribution maps for Australian members of this family are shown in Strahan (1983). Robson (1986) extended the range of the Bare-backed Fruit Bat to Chillagoe, Queensland. The Grey-headed and Little Red Flying-foxes, and the Queensland Tube-nosed Bat are endemic, but the other species also occur in New Guinea and Indonesia. *Pteropus melanotus* is present on the Australian territory of Christmas Island (Tidemann 1987). The greater proportion of megachiropteran species occurs in south-eastern Asia which is probably the centre of evolution for the group. There have been no reported fossils in Australia, although fossils are known from the Oligocene and Miocene of Europe, Miocene of Africa and Pleistocene of Madagascar and Indonesia.

Pettigrew (1986) and Pettigrew & Jamieson (1987) have resurrected the debate on the mono- di- or polyphyletic origin of Chiroptera. Although they have not yet examined fruit eating Microchiroptera, they consider that their own studies on brain characters and the studies of various authors on other characters indicate that the Megachiroptera are more closely related to Primates than to Microchiroptera.

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