FAUNA *of* AUSTRALIA

41. HIPPOSIDERIDAE

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DEFINITION AND GENERAL DESCRIPTION

Like their close relatives, the rhinolophids, members of the Hipposideridae possess an ornate noseleaf and have broad mobile ears. The noseleaf is basically a horseshoe shape, but it lacks a definite lancet and there is no structure that might be construed as the equivalent of the rhinolophid sella. Behind the anterior leaf, there is an intermediate swollen area which sometimes has a small central projection or ‘wart’. The intermediate leaf forms a base for a thinner, more elaborate, erect posterior element. This posterior leaf is not pointed, as in rhinolophids, but is usually rounded or flat across the top. In addition, the face of the posterior leaf may have several thin-walled compartments. The complexity of the noseleaf may be further enhanced by secondary foliations of skin from under the edges of the horseshoe.

In general, most hipposiderids are some shade of brown or reddish-brown, but fur colour can vary intraspecifically. The Orange Horseshoe-bat, *Rhinonycteris aurantius*, can be bright orange, brown, to almost white with brown tips. The Diadem Horseshoe-bat, *Hipposideros diadema*, often has pale shoulder patches.

The internal morphology of this group is similar to that of the Rhinolophidae, but the pectoral and pelvic girdles are more highly modified, the toes have two phalanges each and the lumbar vertebrae show a marked tendency to become fused into a solid rod. In the pectoral girdle, the fusion of the first and second ribs involves the entire bone, up to and including the corresponding thoracic vertebrae. This produces a solid ring of bone consisting of the seventh cervical and first and second thoracic vertebrae, first and second ribs and the entire presternum. The pelvic girdle is similar to that of the rhinolophids posteriorly, but anteriorly there is an additional bridge of bone connecting the acicular process with the front of the ilium, which produces a pre-acetabular foramen slightly exceeding the thyroid foramen in size.

While hipposiderids are closely related to the Rhinolophidae, the more highly modified character of the feet, the pectoral and pelvic girdles and separate distinctive features of the noseleaf are regarded as sufficient to allow the group to stand as a distinct family.

HISTORY OF DISCOVERY

The Hipposideridae was originally included in the Vespertilionidae along with the Rhinolophidae. Gray (1831) first described the genus *Hipposideros* and it was elevated to subfamilial level by Dobson (1875) as the Phyllorhininae (leaf-nosed bats). Miller (1907) recognised the Hipposideridae to be distinct from the Rhinolophidae at the family level. Hill (1963) gave a detailed account of the history of the Hipposideridae. Currently, there are nine extant genera in the Hipposideridae, two of which are represented in Australia: *Hipposideros*, with five species, and the monotypic *Rhinonycteris*.

The Dusky Horseshoe-bat, *Hipposideros ater*, was described by Templeton (1848) from a specimen from Colombo, Sri Lanka. Gray (1866) described a new bat, *H. albanensis*, collected from Port Albany, Cape York. This species was subsequently synonymised by Hill (1963) and McKean & Price (1967) with *H. ater aruensis* (Gray 1858), a New Guinea subspecies. Another subspecies from Oenpelli, Northern Territory, *H. ater gilberti*, was described by Johnson (1959) as *H. bicolor gilberti* and is now conspecific with *H. ater aruensis* (Hill 1963; McKean & Price 1967). Koopman (1984a) agreed that *H. albenensis* is a junior synonym of *H. ater\ aruensis*, but believed that the north-western

Australian specimens, once referred to as *gilberti*, are distinct from the Queensland form and that the Northern Territory specimens, also referred to as *gilberti*, are intergrades.

A complex history surrounds the Fawn Horseshoe-bat, *Hipposideros cervinus*. Its close association with *H. galeritus* has frequently led to the application of the latter name to Australian specimens. Both species are possibly antedated by *Rhinolophus crumeniferus* (Hill 1963; Goodwin 1979). *Hipposideros cervinus* was described by Gould (1854) from specimens collected by MacGillivray from caves on Albany Island, Cape York as *Rhinolophus*? *cervinus*. Dobson (1878) recognised the similarities between *H. cervinus* and *H. galeritus* and although treating them as separate species, combined them with other forms which subsequently caused taxonomic confusion. Tate (1941c) variously considered *cervinus* as a valid species or a subspecies of *H. galeritus*. Jenkins & Hill (1981) recorded the sympatry of the two in Borneo thus establishing both as distinct species. The Australian form, as well as those found in the majority of islands and island groups from Sulawesi to the New Hebrides, is referred to as *H. c. cervinus*.

The Greater Wart-nosed Horseshoe-bat, *Hipposideros semoni*, was described by Matschie (1903) from a single female collected from Cooktown. Tate (1952b) listed this bat as a subspecies of the New Guinean *H. muscinus*, but Hill (1963) considered the two to be distinct species.

The Norwegian naturalist Dr. Knut Dahl first collected the Lesser Wart-nosed Horseshoe-bat, *Hipposideros stenotis*, from caves on the Mary River, Northern Territory, in 1894. The specimens were first identified by Collett (1897) as *H. muscinus*, a species described by Thomas & Doria (1886) from the Fly River in New Guinea. A specimen subsequently exchanged by Dahl (Christiana Museum) with the British Museum was identified by Thomas (1913) as *H. stenotis*, a species endemic in Australia.

Sixteen subspecies of the Diadem Horseshoe-bat have been designated since the Timorian type was described by Geoffroy St Hilaire (1813b). The type specimen is now in the Paris Museum (MNHP 918). Two distinct subspecies have been described in Australia, *H. d. reginae* from Cape York (Troughton 1937) and the smaller *H. d. inornatus* from the Northern Territory (McKean 1970).

The Orange Horseshoe-bat, *Rhinonycteris aurantius*, was first described by Gray (1845) as *Rhinolophus aurantius* in the Appendix to John Eyre's *Journals of Expeditions of Discovery into Central Australia in the Years 1840-41*. The specimen was found flying near the hospital at Port Essington on the Cobourg Peninsula by Dr. Sibbald. Gray (1847) proposed the genus *Rhinonicteris* for this species. The spelling of the generic name was emended by Hill (1982).

MORPHOLOGY AND PHYSIOLOGY

External characteristics

Although the noseleaf of hipposiderids is fundamentally similar to that of rhinolophids, there are distinct and characteristic differences between the two. The anterior leaflet lies above the upper lip and covers most of the top of the muzzle to the level of the eyes. The posterior leaflet never assumes the acute triangular form seen in rhinolophids, but has a rounded, arcuate outline and is, moreover, concave anteriorly and often divided into shallow cells by slight vertical folds. The intermediate noseleaf, or sella, is little more than a thickened transverse pad joined to the base of the posterior leaflet, lying between it and the nostrils. The nasal openings lie at the bottom of a central facial hollow and the exterior border of each is elevated into a shallow wing. Except in Dusky Horseshoe-bats, there are one or two supplementary leaflets under the main anterior noseleaf (see Fig. 41.1).

The ears are large, widely separated and often nearly as broad as they are long. The inner margin sweeps in an even convex curve from base to tip; the outer margin, while convexly rounded at the base, is straight or slightly concave for most of its length, with an indentation a short distance below the point. The antitragus is variable in size, but generally not as large as in *Rhinolophus*. The eye is of moderate size.

The wing of hipposiderids is similar to that of rhinolophids, the second digit comprising metacarpal only; the third, fourth and fifth have two phalanges. The wing is rather narrow and more or less parallel-sided from the back to the front owing to the close correspondence in length of the fourth and fifth digits. The interfemoral membrane is large and includes the whole of the tail except for the extreme tip. The hind margin of the membrane is strengthened by calcanea of a soft cartilaginous nature and varying length. The toes have only two joints.

The fur is fine, thick and in most species a brown-grey colour. Bright orange fur is common in many species and is the predominant colour morph in the Orange Horseshoe-bat. The fur of this species can also be white with brown tips. The brown-grey form of the Diadem Horseshoe-bat usually has pale, but conspicuous patches of fur on the shoulders.

Body wall

The fur of hipposiderids is thick and dense on the dorsal and ventral sides and around the head with the exception of the area of the noseleaf. A well-furred area is found on the inner medial border of the ear in Greater Wart-nosed Horseshoe-bats and this same area is lightly furred on the ears of all other hipposiderids. The dermis is thin on the wings and tail membrane and is thickest on the lips and soles of the feet. No arrectores pilorum have been found and the large numbers of skeletal muscle fibres found in the dermis are assumed to function as erectors (Quay 1970a). Median frontal glandular sacs behind the noseleaf of Dusky Horseshoe-bats can exude a clear liquid (McKean & Price 1967) and a median preanal gland was found in a hipposiderid by Allen, Lang & Chapin (1917).

Skeletal System

The skull has a distinct, though low and not specially developed, sagittal crest, small bullae and moderately large cochleae. The greatest depth of the braincase (bullae excluded) is at least equal to the depth of the rostrum, including molars. The zygomatic arch is abruptly expanded posteriorly, but the height of the expanded portion is much less than the distance from the last molar to the glenoid fossa.

The upper incisors are very small, but usually well formed, with a distinct, rounded crown with a slight cusp on the inner side. The lower incisors are trifid, the outer is the larger and the four incisors form a continuous row between the canines. The upper canines are heavy, but simple in form without a conspicuous cingula, though they frequently have a secondary cusp near the posterior base of the shaft. The lower canines are rather weak. The first upper premolar (PM^3) is small, functionless, closely crowded between cingula of canine and large premolar, or forced completely outward from the tooth row. The other teeth show no special peculiarities; M1 and M2 have normal main cusps and no hypocone, M3 usually has five cusps and three commissures, but the mesostyle and metacone are always closely approximated, the latter sometimes absent, leaving only two commissures. The lower molars have well-developed cusps and are normal in position. The dental formula is I 1/2 C 1/1 PM 1-2/2 M 3/3.

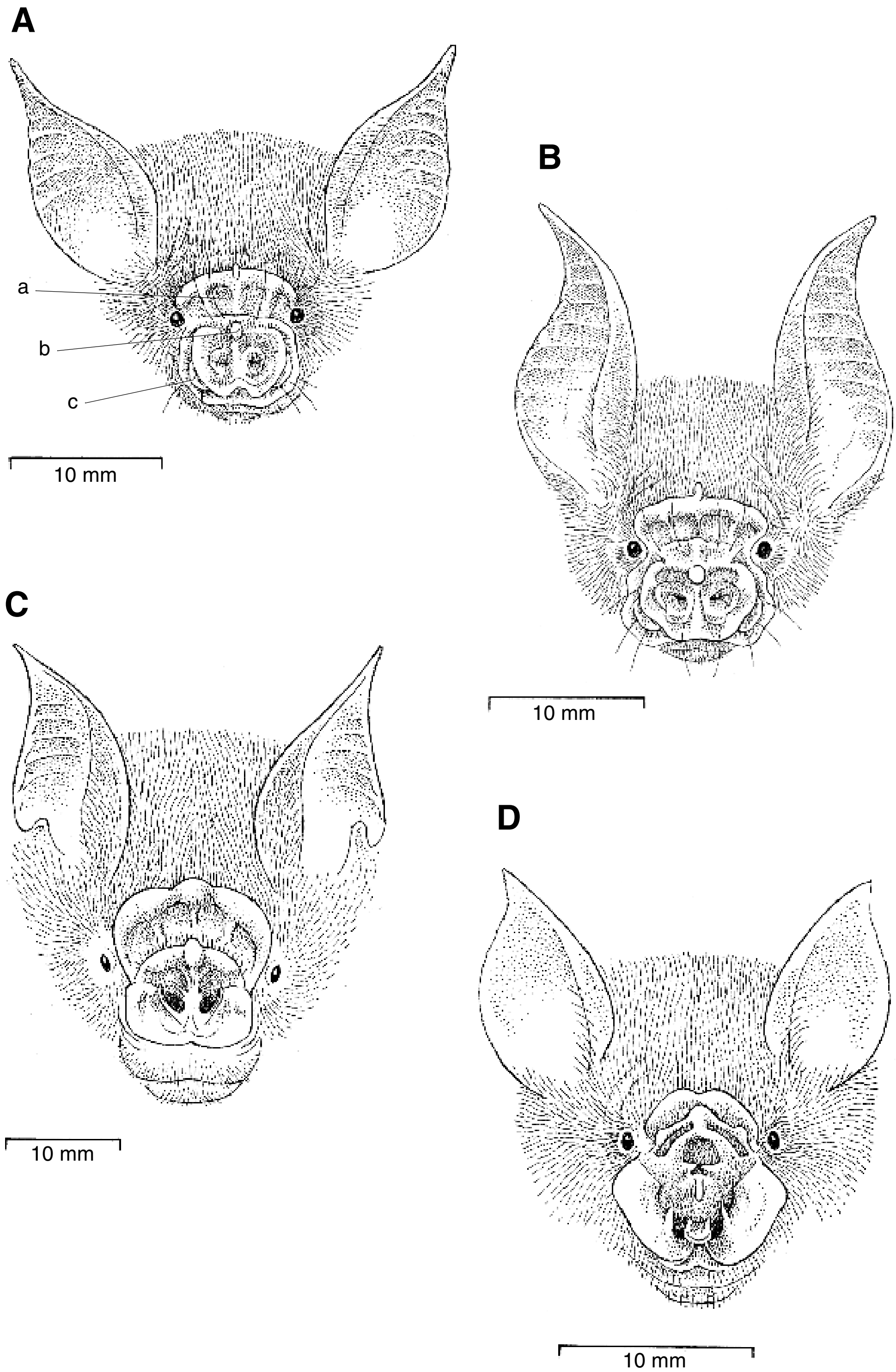

Figure 41.1 **A**, The head of the Lesser Wart-nosed Horseshoe-bat (*Hipposideros stenotis*) shows the characteristic square-shaped noseleaf complex of the family. The upper section (a) is sometimes called the coronet and in the Lesser Wart-nosed Horseshoe-bat it contains a centrally located 'wart'. There is another 'wart' on the main noseleaf (b) and supplementary noseleaves (c). **B**, the Greater Wart-nosed Horseshoe-bat (*Hipposideros semoni*) is another of the 'wart-nosed' bats. The upper 'wart' is larger than that of the Lesser Wart-nosed Horseshoe-bat, but the rest of the noseleaf is quite similar. This bat is endemic in tropical Australia. **C**, the Diadem Horseshoe-bat (*Hipposideros diadema*) has prominent eyes and large canines which it uses to secure prey such as large beetles. The fur colour of this bat can vary from grey-brown to bright reddish-orange. **D**, Orange Horseshoe-bat (*Rhinonycteris aurantius*). (© ABRS) [F. Knight]

The postcranial osteology of hipposiderids has changed little since the Miocene. The vertebral column is typically mammalian with seven cervical, 11 or 12 thoracic, six lumbar and three sacral vertebrae (Walton & Walton 1970). In hipposiderids the lumbar vertebrae are solidly fused (Walton & Walton 1970). Only a poorly developed vertical lobe is present on the presternum and the lateral lobes are pierced by two foramina which are formed as the result of incomplete fusion of the lateral processes with the second rib and costal cartilage. The manubrium of hipposiderids is more flattened and shield-like than in other bat families (Walton & Walton 1970). A secondary lateral process from the lateral lobes of the presternum is also present.

Like those of rhinolophids, the ribs are greatly flattened and the first and second ribs are coalesced. The space between the other ribs is well defined, but is almost obliterated (Allen 1893). There is a deep notch in the coracoid border of the scapula. The coracoid border also has a ventrally directed flange and another notch on its axillary border (Walton & Walton 1970). The clavicle is very large, quite long and curved. In the Rhinolophidae and Hipposideridae the clavicle forms a complex joint with the manubrium, first costal cartilage, first rib and, in the Hipposideridae, with the second costal cartilage and second rib (Walton & Walton 1968). The head of the humerus projects medially from the long axis of the shaft and has an elongated oval shape. The shaft of the radius is generally arched slightly in bats, but in hipposiderids it has a distinct bend.

The pollex has two phalanges and a claw is borne on the distal phalanx. Only the metacarpal is present on the second digit; the metacarpal that represents this digit lies close to the metacarpal of the third digit and serves to strengthen the wing's leading edge (Miller 1907). The usual number of phalanges present in digits III, IV and V is three, but only two are present in the hipposiderids.

Fossil pelves of Tertiary hipposiderids do not differ significantly from those of modern forms (Dechaseaux 1958). Friant (1963) records that the pre-acetabular foramen is formed and distinct in Tertiary hipposiderids. This feature is unique among mammals (Dobson 1878). It is formed by a supplemental bridge of bone which connects the anterior tip of the pubic spine with antero-lateral end of the ilium. Sutures are not evident in this junction and this was also reported in fossil hipposiderids (Friant 1963). A small sesamoid bone is embedded in the anterior cartilaginous rim of the acetabulum. This small bone may be present in other families, but is often lost in skeletal preparations (Walton & Walton 1970).

The neck of the femur is either very short or absent. Two trochanters are present, both subequal in size, and drawn backward. The shaft of the femur is straight, but some fossil hipposiderids have femora which arch slightly (Revilliod 1917).

The tibia is broadest at its upper end; the lateral condyle projects abruptly from the main axis and is covered by cartilage. The fibula is complete and the tarsus is short and composed of seven bones. The calcar is associated with the first row of tarsal bones and help to spread the interfemoral membrane.

The phalangeal formula for the foot of bats is 2–3–3–3–3 except in hipposiderids, where it is 2–2–2–2–2 (Miller 1907). The hindlimb is poorly developed and rotated caudally 180°. Its primary purpose is to spread the flight membranes, although it is also used for hanging in the roost.

Locomotion

Because of the low aspect ratio of their wings, the smaller hipposiderids have a slow, weaving flight. This allows them to hunt in and around vegetation, usually about 1–2 metres above the ground. The larger Diadem Horseshoe-bat has a higher aspect ratio than the small species and is consequently a faster and more direct flier. All hipposiderids are reluctant to crawl and generally move their roost position by taking off and landing again.

The forearm musculature is larger and heavier than in molossids or vespertilionids, but the major muscles powering the downstroke (the pectoralis, the posterior division of the serratus anterior and the subscapularis) are fairly uniform, even between distantly related bats (Vaughan 1970a).

Feeding and Digestive System

All the hipposiderids are aerial insectivores and there are no records of them landing on the ground or gleaning insects from vegetation. Prey is captured in their wing or tail membrane and passed to the mouth while flying. Hipposiderids have been seen feeding in small groups and typically forage close to the ground. Food is crushed in the mouth by tribosphenic molars and passed to a saccular stomach. Faecal material contains finely mashed remnants of insects; the scales of Lepidoptera are prominent.

Circulatory System

The circulatory system for the hipposiderids is typical of the Microchiroptera. Hipposiderids exhibit wide-range homeothermy with partial torpidity at intermediate temperatures. Kulzer *et al*. (1970) showed that the body temperature of Dusky and Orange Horseshoe-bats was close to ambient when the bats were at rest. Orange Horseshoe-bats are slower to rewarm and extended exposure to cold leads to uncontrolled hypothermia and exhaustion.

Respiration

The upper respiratory tract of the hipposiderids consists of a complex set of nasal chambers. The latter are believed to cause resonance of the call produced by the larynx and play an important part in the emitted ultrasonic call (Novic 1977). The lung is comparatively large for the small body size. Single ultrasonic calls or multiples are given with each respiratory cycle.

Excretion

Paired, equi-sized kidneys are located dorsally in the peritoneal cavity. The renal bodies tend to be located lower in the peritoneal cavity in relation to overall body length than is the case with most laboratory animals (Rosenbaum 1970) and appear to be unmodified for a volant lifestyle. There are slight variations in kidney shape amongst species, but most tend to be bean-shaped, the external border is more convex and the internal border concave at the hilus. The renal pelvis has a variable shape and the hilus protrudes beyond the renal body. (Rosenbaum 1970).

Sense Organs and Nervous System

The eyes of most hipposiderids are small, a feature common to cave-dwelling, sedentary, insectivorous bats that possess a well-developed echolocation system. The eye is probably used in conjunction with echolocation to monitor the environment.

The auditory centres are particularly well developed. The superior and inferior colliculi of the brain are exposed and the cochlear nuclei are extramedullary. The basilar membrane in the cochlear of the ear has large specialised thickenings (Henson 1970a). The tympanic membrane and auditory ossicles are small in Fawn and Dusky Horseshoe-bats, reflecting the very high frequencies used by these bats. The middle ear muscles of hipposiderids are large, richly innervated and capable of contracting and relaxing at rapid rates. The external ear moves in synchrony with pulse emission in *Hipposideros* and also assumes a variety of shapes, so that ears appear to examine a sound field environment. The control of these movements and that of the laryngeal musculature is probably under the influence of the corticobulbar tracts in the cerebral cortex (Henson 1970a). A vomeronasal organ has been found in *Hipposideros lankadiva* by Cooper & Bhatnagar (1977).

Endocrine and Exocrine Systems

The endocrine system of hipposiderids is typically mammalian. The ovaries are bilaterally flattened, ovoid structures with the left slightly larger than the right (Bernard & Meester 1982). The ovary consists of a thick outer cortex containing large numbers of primordial follicles and a thin medulla. The corpus luteum is extruded from the left ovary and persists only for a brief period during gestation (Bernard & Meester 1982). No detailed observations have been made on the endocrine or exocrine organs in Australian hipposiderids.

Reproduction and Development

The reproductive biology of hipposiderids in Australia is poorly known and consists mainly of anecdotal observations. Some inferences can be made from observations on overseas hipposiderids. Hipposiderids are monotocous and monoestrous. Both ovaries and cornua are functional (Carter 1970). As pregnancy advances, the foetus comes to occupy the entire uterus, the cornua no longer being visible. Females have inguinal teats which function only as holdfast organs. In July in the north-western Kimberley, McKenzie *et al*. (1978) collected a female Lesser Wart-nosed Horseshoe-bat with enlarged uteri and developed mammae, together with a sub-adult specimen. The young of the Dusky Horseshoe-bat in Queensland are born during December (McKean & Price 1967), but Johnson (1964) recorded a hairless young, with a head-and-body length of 28 mm, clinging to a female in late October at Douglas River in the Northern Territory. These records indicate that the date of parturition in hipposiderids could vary inter- and intraspecifically or geographically.

Gestation requires about 90 days in *Hipposideros cyclops* (Carter 1970). The young of hipposiderids are born head first and are carried by their mother for some time after birth. When not sucking the pectoral (lactating) teats, the young attach to inguinal teats and cling to their mother’s fur using their well-developed thumb and toe claws. At birth, hipposiderids are blind, naked and of a pinkish colour. Growth and development are rapid and young attain adult proportions by 2 months.

Ultrasonics

Like rhinolophids, the hipposiderid call is of a constant frequency with a short terminal downsweep. The call is emitted via the nostrils. There is an inverse relationship between the size of the hipposiderid and the frequency of its call. Larger hipposiderids catching larger prey are able to use a lower frequency, but smaller species need a high frequency (shorter wavelength) to detect smaller prey. The frequency of the call also correlates with ear size and the distance separating the nostrils. Hipposiderids appear to be specialised for short range hunting (Novic 1977). The duration of the call is 10–15 ms, shorter than that for rhinolophids.

The call of Diadem Horseshoe-bats has its maximum energy at 54.9 kHz with its terminal downsweep going to 50.9 kHz (Fenton 1982b). Slightly different recordings were made for this species in New Guinea by Grinnell & Hagiwara (1972). Their studies showed that its call consisted of a dominant second harmonic of 58 kHz, dropping to 47 kHz. They also noted that the fundamental and third harmonic were faint and that there was a strong fourth harmonic. The pulse duration is about 10 ms (Novic 1977).

Due to close morphological resemblance (in particular body size and morphometrics) the calls of *Hipposideros galeritus* are likely to be very similar to those of the Fawn Horseshoe-bat. Grinnell & Hagiwara (1972) recorded *H. galeritus* calls in New Guinea which had a frequency of 144–145 kHz, dropping to 120 kHz.

The calls of Dusky, Greater and Lesser Wart-nosed, and Orange Horseshoe-bats have not yet been analysed.

NATURAL HISTORY

Life History

Very few studies have been conducted on the life history of these bats in Australia. There have been no long-term investigations and most of the information is either anecdotal or has been derived from overseas reports on the same species.

Females probably do not breed until their second year. All records indicate that only one young is born per year. Young have been recorded for Dusky Horseshoe-bats in October, but most births occur in November and December. Life expectancy of the large Diadem Horseshoe-bat could be in excess of 10 years, but for the smaller hipposiderids it is probably less than this. The overall sex ratio of each species tends to be even, but at various times of the year colonies have been observed with a bias towards one sex, such as congregations of females at maternity sites.

Ecology

All hipposiderid bats are cave dwelling insectivores. The diet includes a variety of moths and beetles. Most hipposiderids fly 1–2 m above the ground, frequently avoiding bushes and using their short broad wings for slow and manoeuvrable flight. Diadem Horseshoe-bats are known to hang on a favourite perch and scan the surrounds for suitable insect prey. Such perches can be from 1–3 m above the ground. Caves or mines selected for roosting are generally warm and humid. Exceptionally, the Lesser Wart-nosed Horseshoe-bat roosts in dry, open caves and mines. Because of their similar choice of roosting sites, several species can be found in the same cave. Different species usually roost in separate locations, but occasionally mixed roosts occur. Hipposiderids hang free by their toes and usually space themselves on a cave ceiling. Clustering is not usually observed, but does occur in young bats.

Most hipposiderids appear to be reasonably sedentary with only small cave to cave migrations occurring. In *Rhinonycteris*, however, there are large-scale dispersal patterns related to season and possibly to cave microclimate.

Predators include snakes and large dasyurids which enter the roost. Bats disturbed from their roost during the daytime are pursued by a number of birds, including black kites and butcherbirds.

Vestjens & Hall (1977) recorded moths, cockroaches, beetles, ants and an unidentified orthopteran in the stomachs of Australian hipposiderids. All Orange Horseshoe-bat stomachs contained moths and in several there were traces of ground beetles, click-beetles, chafers, weevils, shieldbugs, parasitic wasps, unidentified Coleoptera and ants (Vestjens & Hall 1977), indicating that this species could occasionally feed on the ground. In captivity, Diadem Horseshoe-bats will eat a wide variety of food types including large insects, small vertebrates and fresh meat.

Behaviour

Hipposiderids are nocturnal, emerging from their roosts just after dusk. They spend the first couple of hours feeding and then return to a roost (often their daytime roost), where they groom themselves. Several feeding sorties can occur during the night and are dependent on insect availability. Social behaviour, such as closely following one another and dive-bombing, is interspersed with feeding activities. The foraging behaviour of Diadem Horseshoe-bats has been observed by Fenton (1982b) using cyalume and radio-tracking. It is the only species so far recorded to use a perch and engage in sallies for insect prey. Often this species patrols an area between two such perches. Because of their short, broad wings, hipposiderids have a slow fluttery flight. They remain active throughout the year and always appear alert when approached in their roost. Hanging free from the ceiling, they invariably face an approaching intruder while slightly flicking their ears forwards to sideways, movement that helps to accurately locate it.

Grooming is done with the hind feet, thumb and, occasionally, teeth. Young that are still clinging to their mother are groomed by their mother licking their fur.

Economic Significance

It is unknown whether any of the food items recorded by Vestjens & Hall (1977) are pest species, but as hipposiderids occur in remote areas, their food items probably are not of agricultural importance. No pathogens or parasites harmful to humans or domestic stock have been reported from hipposiderids in Australia.

All hipposiderids are protected by law in Australia and several species occur in specific reserves. Tunnel Creek and Geike Gorge in Western Australia, Cutta Cutta, Katherine Gorge and Kakadu in the Northern Territory and Camooweal and Chillagoe Caves in Queensland have colonies or numbers of Dusky, Lesser Wart-nosed, Diadem and Orange Horseshoe-bats. In northern Queensland, the Fawn Horseshoe-bat has a limited distribution and several of its known locations are in abandoned mines that are subject to cave-ins.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

Hipposiderids are found throughout the tropical areas of the Old World from Africa, Madagascar through India to south-eastern Asia, the Philippines, New Guinea, Australia, New Caledonia and the New Hebrides (Vanuatu). They are known as fossils from as early as the Middle or Late Eocene of Europe. Their distribution within Australia is tropical. The most widespread species, the Dusky Horeshoe Bat, is found on the eastern coast north of Townsville, in western and central northern Queensland, the top end of the Northern Territory and the Kimberley region of Western Australia. They are widespread in south-eastern Asia from India to the Philippines. The Fawn, and Greater Wart-nosed Horseshoe-bats are both found in New Guinea and Diadem Horseshoe-bats are widespread throughout south-eastern Asia. Lesser Wart-nosed Horseshoe-bats are endemic in northern Australia.

Affinities with other Groups

The Hipposideridae is included in the superfamily Rhinolophoidea along with the Nycteridae, Megadermatidae and Rhinolophidae. The close relationship of the Hipposideridae to the latter family is discussed above.

Affinities within the Hipposideridae

There are nine extant genera and one extinct genus in the family Hipposideridae. Of the 60 species in the family, 48 are placed in *Hipposideridos*; other genera are represented by one or two species.

Since the caves favoured by hipposiderids are available south of their distribution, the temperature regulating ability of this group probably is a factor in their tropical distribution.

Fossil Record

The family appeared rather suddenly in the Early Miocene faunas of Europe without any evident autochthonous ancestors. They may have immigrated into Europe in the Late Oligocene from an Asiatic or African palaeotropical area of the Old World from a more generalised, but as yet unrecognised ancestral hipposiderid (Sigé, Hand & Archer 1982). From the Early Miocene to the mid-Late Miocene, a period of about 12 million years, different localities show the persistence and radiation of this group in western Europe. Sigé *et al*. (1982) described *Brachipposideros nooraleebus* from the bat-rich Middle Miocene deposits from Riversleigh, Queensland. This species is closely related to other *Brachipposideros* species from Europe and the Australian endemic, the Orange Horseshoe-bat, is regarded as a descendent of an ancestral species of *Brachipposideros*.

The palaeoecological setting of the fossil bats from the Riversleigh deposit appears to have been a relatively quiet, sunny, lime-enriched tropical pool that contained tortoises, crocodiles and fish. The bats may have been washed into the pool from an adjacent cave (Sigé *et al*. 1982).

COLLECTION AND PRESERVATION

Collection

Outside of their cave environment, hipposiderids are generally difficult to catch. Both mist-nets and bat traps have been used successfully. Because the smaller species are slow fliers, mist-nets need to be set in dense vegetation or in a maze pattern to be successful. Catching at their roost site with either a hand net or a small mist-net set across a narrow passageway is generally the most successful technique.

Preservation

Total immersion in 70% ethyl alcohol containing 2% glycerine is the best method of preservation. A small cut in the abdominal wall is needed to allow penetration of preservative into the body cavities. Skins are best prepared from fresh specimens but study skins can be prepared from frozen material. Since the small leaflets of the noseleaf wrinkle and lose their shape when skins are dried, specimens are best stored in alcohol.

Laboratory Maintenance

Hipposiderids are generally difficult to keep in captivity, particularly Orange Horseshoe-bats. An exception is the Diadem Horseshoe-bat, which readily accepts captivity and can be fed on a wide range of food such as fresh meat, grasshoppers, meal-worms, beetles and cicadas.

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