

1 Introduction

Overview of Lorises and Pottos

K. A. I. Nekaris and Anne M. Burrows

This book started as a conversation in New Orleans back in 2016. A morphologist and a primatologist were sitting at the American Association of Physical Anthropologists annual meeting, bemoaning the scant presentations on lorises (slow lorises, slender lorises, angwantibos and pottos) relative to galagos, lemurs, monkeys and apes. Not only where were the talks on these primates, but where were the books on lorises? After a few minutes of this talk, we decided it was time to see to it ourselves. Using a cocktail napkin and later a more respectable legal pad, we started sketching out what we would each want to see in a collected, edited volume devoted to what we know about lorises, some of the least understood primates living today. What resulted from that afternoon in a New Orleans bar is this edited volume. The scope is intentionally broad and is primarily divided into sections on evolution and morphology, behaviour and conservation. We also purposefully focused on soliciting short contributions, set as boxes within the text, from young authors doing fieldwork in Asian range countries, places where scientific study and conservation efforts on *Loris* and *Nycticebus*, the Asian lorises, is producing previously unknown data on population density and specific challenges to conservation efforts.

Currently, there are too few data and field sites coming from the African range to include the same wealth of new information on *Arctocebus* and *Perodicticus*, the African lorises. These two genera remain incompletely understood due to a number of variables. While taxonomic revision has blossomed within the last 10 years on the Asian lorises (see, for example, Nekaris, 2014), the same has not happened for the African lorises, which remain as two recognised genera. We hope that the entries in this edited volume help stimulate renewed vigour in the establishment of new field sites and morphological, evolutionary and conservation studies on the African lorises.

The living Lorisidae family (Lorisiformes:Lorisoidea:Lorisidae) is widely dispersed in continental Africa and South and South-east Asia, and consists of the slender lorises (*Loris*), slow lorises (*Nycticebus*), pottos (*Perodicticus*) and angwantibos (*Arctocebus*). The Lorisoidea superfamily also includes the Galagidae family (bushbabies) and is interchangeable with the infraorder Lorisiformes for the purposes of this edited volume. A taxonomic note here: in this chapter we follow nomenclature from Grubb et al. (2003). Along with the bushbabies and lemurs, the lorises make up Strepsirrhini, the most 'primitive' of the living primates.

Lorisidae is further broken down into the subfamilies Perodicticinae (consisting of the African lorises *Perodicticus* and *Arctocebus*) and Lorisinae (consisting of the

2 K. A. I. Nekaris and Anne M. Burrows

Asian lorises *Loris* and *Nycticebus*). While phylogenetic debates persist, this arrangement of the extant (or living) lorises is widely accepted. The highly distinguished Professor Simon Bearder graciously provides our Foreword, taking us back to the very earliest days of field research into nocturnal strepsirrhines with a focus on African species. Professor Bearder's pioneering work in the field studies on nocturnal strepsirrhines set the stage for critical advances in tracking techniques, technology and equipment associated with learning about nocturnal strepsirrhines.

The first part of this edited volume concentrates on the evolution of lorises, including taxonomy (the actual scheme of classification) and phylogeny (how organisms are classified relative to one another), the fossil record of lorises and the unique morphological characteristics that help define lorises.

1.1 Part I: Evolution, Morphology and the Fossil Record

While lorises and bushbabies together make up the Lorisiformes and Lorisioidea, they are obviously different from one another. Lorises share a suite of traits that are not present in the galagids: cryptic (i.e. slow and quiet) locomotion, a derived hand/foot with the hallux (big toe) and pollex (first digit of the hand) highly extended, a reduced second digit on each hand and foot and a greatly reduced tail compared to most other primates (Nekaris, 2014).

Taxonomic categorisation of primates has been, and may always be, subject to challenges, disputes and advances in molecular genetics, the fossil record and historical writings. Taxonomy of lorises may arguably be the most contentious among all extant primate groups, due in part to their cryptic and nocturnal nature. Until recently, our understanding of lorisid taxonomy and their evolutionary history was poor. The sister family Galagidae has undergone remarkable taxonomic expansion in the last 20 years (see, for example, Grubb et al., 2003), but not so with Lorisidae. The Asian lorises, subfamily Lorisinae, currently include only two genera – *Loris* (slender lorises) and *Nycticebus* (slow lorises) – while the African lorises, subfamily Perodicticinae, similarly include only two genera – *Perodicticus* (pottos) and *Arctocebus* (angwantibos).

The cyclic nature of 'lumping' and 'splitting' of taxa can leave the best of us lost, but Masters (Chapter 2) provides a deep taxonomic history of lorises and their shifting phylogenies over the last several centuries. With the shifting lumping and splitting of strepsirrhine taxa, this chapter helps set the stage for our current understanding of lorisid phylogeny and taxonomy.

With a more complete understanding of lorisid taxonomy available in this volume, where do we stand on evolution of lorises? We have a relatively good understanding of primate evolution, as well as evolution of the anthropoids and hominoids, but unfortunately our understanding of lorisid evolution is generally less complete and largely enigmatic. While it is widely accepted that lorises and bushbabies together make up the monophyletic Lorisiformes (or Lorisioidea), there is not as much certainty about monophyly (i.e. taxa descended from a single common ancestor) of the Lorisidae. Is Lorisidae a monophyletic group or instead diphyletic (i.e. taxa descended

from separate lines of ancestry)? Or perhaps paraphyletic? We conceptualise the first and early primates as most closely resembling extant strepsirrhines, and the living lorises (slender lorises, slow lorises, pottos and angwantibos) may be reasonable living models for what the earliest and first primates looked like and what they did, so a more complete understanding of loriseid evolution may not only benefit those of us keenly interested in lorises, but all of us with a stake in primate evolution.

Compared to anthropoids (monkeys and apes), our understanding of the strepsirrhine fossil record is relatively incomplete, especially so among the loriseoids (galagids and lorises). While the loriseid fossil record is relatively scarce, the geographic range of fossil lorises stretches from South-west Africa to South-east Asia, including a known record of lorises from the Middle East. This Middle East appearance is particularly intriguing because the geographic range of extant lorises does not include that historical bridge.

Until recently, fossil evidence dated loriseid origins to the Miocene of East Africa, around 20 Mya (million years ago). The three best known early Miocene forms are *Mioeuoticus*, *Progalago* and *Komba* (Rasmussen and Nekaris, 1998), and they are allied with either lorises or galagids based upon both cranial and postcranial features (Gebo, 1986; Le Gros Clark, 1956; McCrossin, 1992; Walker, 1969). Other authors have suggested that basal loriseoids may have demonstrated a combination of loriseid cranial characteristics and galagid postcranial adaptations (Rasmussen and Nekaris, 1998). *Karanisia* and *Saharagalago*, based on analysis of dental characteristics, are putative early lorises and galagids, respectively, from late Eocene sites at the Fayum Depression in Egypt (Seiffert et al., 2003). True, unrefuted lorises (*Nycticeboides simpsoni*) and galagids (*Galago howelli* and *G. sadimensis*) occur in the fossil record of the late Miocene of Pakistan and early Plio-Pleistocene of Ethiopia and Kenya, respectively.

López-Torres and Silcox (Chapter 3) synthesise our current, most up-to-date understanding of the loriseid fossil record. These authors note that extant loriseoids have few genera and species compared to other primate groups and that this pattern seems to have been true in the fossil record as well. López-Torres and Silcox compare the fossil record with the most recent molecular genetic evidence and come up with that rarity where they reinforce one another! The authors go on to review both *Karanisia* and *Mioeuoticus* and make suggestions on the biogeography of loriseid evolution.

While the fossil records of loriseoids may not be as robust as we would like, recent genetic evidence has resolved that bushbabies (galagids) diverged from lorises about 40 Mya, followed by a split within the lorises into lorises (the Asian lorises *Loris* and *Nycticebus*) and perodicticines (the African lorises *Arctocebus* and *Perodicticus*) only two million years later (38 Mya) (Pozzi et al., 2014). Clearly, at this time the environment selected for two different forms, with lorises specialised for non-leaping ‘slow’ climbing, and the bushbabies for rapid leaping.

Pozzi and colleagues (Chapter 5) pick things up from there and broadly cover our current understanding of loriseid phylogeny and taxonomy, but with an eye to recent molecular studies and the biogeographical questions surrounding loriseid evolution.

4 K. A. I. Nekaris and Anne M. Burrows

These authors make a particularly strong case for the utility of taxonomic data that emanate from molecular studies as tools to be employed in lorisid conservation efforts, as well as addressing the split into perodicticines and lorisesines.

1.1.1 The Perodicticines and Lorisesines

Due in part to the wide geographic separation between the Perodicticinae of Africa and the Lorisinae of Asia, we split Lorisidae into these subfamilies. However, they were once thought to comprise two monospecific genera, each containing a gracile (the perodicticine *Arctocebus* and the lorisine *Loris*) and a robust form (the perodicticine *Perodicticus* and the lorisine *Nycticebus*) (Yoder et al., 2001) (Table 1.1; Figure 1.1). Differences in behaviour, morphology, facial markings and genetic data have helped to build the picture of taxonomic diversity among these primates (Nekaris and Jaffe, 2007; Nekaris and Jayewardene, 2003; Nekaris and Munds, 2010; Roos, 2003; see also Chapter 2).

In the African lorises (the perodicticines), two gracile species are allopatric (species that occur in non-overlapping areas) and confined to the rainforests of Central

Table 1.1 Scientific names, common names, distribution, and body weight of lorisids

Latin name	Common name	Distribution	Body weight (g)
Perodicticinae			
<i>Perodicticus potto</i>	Western potto	Guinea, Guinea Bissau, Nigeria	600
<i>P. edwardsi</i>	Milne Edward's or Central potto	Nigeria, Zaire, Central African Republic	850-1600
<i>P. juju</i>	S. Nigerian potto	Guinea Coast of Nigeria	?
<i>P. ibeanus</i>	Bosman's or Eastern potto	Zaire, Burundi, Rwanda, Kenya	850-920
<i>Arctocebus aureus</i>	Golden angwantibo	Gabon	150-270
<i>A. calabarensis</i>	Calabar angwantibo	Cameroon, Gabon, Congo	270-325
Lorisinae			
<i>Loris lydekkerianus</i>	Mysore slender loris	South India, Sri Lanka	225-320
<i>L. tardigradus</i>	Red slender loris	Sri Lanka	105-170
<i>Nycticebus bengalensis</i>	Bengal slow loris	Burma, Bhutan, Cambodia, China, India, Laos, Thailand, Vietnam	1140-2100
<i>N. coucang</i>	Greater slow loris	Sumatra, peninsular Malaysia, Thailand, Singapore	635-850
<i>N. javanicus</i>	Javan slow loris	Indonesia (Java)	750-1150
<i>N. menagensis</i>	Philippine slow loris	Brunei, Indonesia, Malaysia,	265-800
<i>N. borneanus</i>	Bornean slow loris	Philippines	360-580
<i>N. kayan</i>	Kayan slow loris	Borneo	500-700
<i>N. bancanus</i>	Sody's slow loris	Borneo, Malaysia Banka, Belitung Indonesia	?
<i>N. hilleri</i>	Sumatran slow loris	Northern Sumatra	650-790
<i>N. pygmaeus</i>	Pygmy slow loris	Cambodia, China, Laos, Vietnam	360-580



Figure 1.1 The living genera of the perodicticine and lorisine primates – *Arctocebus calabarensis*, *Perodicticus ibeanus*, *Loris lydekkerianus nordicus*, *Nycticebus bengalensis* and *N. pymaeus*.

Africa: the golden angwantibo (*Arctocebus aureus*) and the Calabar angwantibo (*A. calabarensis*). The robust forms comprise three species: *Perodicticus edwardsi*, *P. ibeanus* and *P. potto*. *P. juju* from Nigeria most likely also represents a distinct species, with the Cross River forming the geographic barrier.

Within the Asian lorises (the lorisines), the gracile forms also seem to be allopatric (Kumara et al., 2006). The red slender loris (*Loris tardigradus*), the smallest of the lorisines, resides only in Sri Lanka's lowland and montane rainforests. The larger grey slender loris (*L. lydekkerianus*) is found in the northern part of Sri Lanka, but is also spread throughout southern India, south of the Tapti River. At the time of writing, nine species of robust slow lorises are recognised. Here we follow the taxonomy of Roos (2003) and Munds et al. (2013b): the Bengal, northern or ashy slow loris (*Nycticebus bengalensis*), greater slow loris (*N. coucang*), Javan slow loris (*N. javanicus*), Philippine slow loris (*N. menagensis*), Bornean slow loris (*N. borneanus*), Kayan slow loris (*N. kayan*), Sody's slow loris (*N. bancanus*), Sumatran or Hiller's slow loris (*N. hilleri*) and the pygmy or lesser slow loris (*N. pygmaeus*). By and large, these species are allopatric, apart from areas of Indochina where pygmy and Bengal slow lorises live in sympatry (species occupying the same geographic range); the range of the new Bornean species remains to be determined and may also contain some taxa in sympatry.

6 K. A. I. Nekaris and Anne M. Burrows

1.1.2 Morphology

All taxonomic groups have unique morphologies relative to other taxonomic groups – it's one of the things that defines a grouping. Lorisids, though, arguably have some of the most unique morphologies among the primates. They are the only full-time arboreal primates to lack (or have substantially reduced) tails, they include the only venomous primates and some have scapular shields, just to name the most notable anatomical adaptations! Being strictly nocturnal and arboreal, very rarely descending to the earth, comes with a suite of ecological, locomotor, morphological and behavioural adaptations. One of the morphological adaptations that we typically associate with a highly nocturnal and arboreal primate lifestyle is 'face touch', the ability to use whiskers on the face to gather sensory information about the animal's position in space and what is around them. Muchlinski and colleagues (Chapter 4) describe the surprising diversity in loridid whisker morphology, with Asian loridids having barely perceptible whiskers and African loridids having robust, highly mobile whiskers. These authors describe the potential trade-offs between having robust 'face touch' versus sensory information gathered from olfaction, vision and ultrasonic vocalisations.

One of the most understudied areas of loridid social behaviour is that of olfactory communication. Aided by an acute sense of smell and the vomeronasal organ in the nasal chamber, which senses liquid chemicals transferred from the moist nose (Martin, 1990; Schilling, 1979), both bushbabies and lorises are in constant communication with each other via olfaction, using both a number of specialised scent glands and urine (Harcourt, 1981). The main advantage of olfactory communication via scent gland and urine marking in general is that it conveys information that is indirect and deferred in time, with a result that individuals do not have to come together in space or time in order to communicate. Information carried via scent includes kin and individual identity, gender and sexual receptivity.

Lundeen (Chapter 8) focuses her attention on the olfactory system of loridids. While strepsirrhines in general are thought to depend largely on olfaction as a means of communication, our understanding of loridid olfactory anatomy is surprisingly incomplete. Lundeen provides quantitative data on the olfactory anatomy in both perodicticines and lorisines, finding that perodicticines may rely on olfaction to a greater extent than lorisines.

Nett and Ravosa (Chapter 9) indirectly address vision in loridids by examining orbital convergence (eyes being close together) from skulls. Orbital convergence can be advantageous in creating accurate depth perception of one's surroundings, a desirable tool in a complex arboreal environment. These authors find that degree of orbital convergence may be strongly linked to dietary niches within loridids.

The highly derived hand of the African loridids (potto and angwantibo), with its hyper-extended pollex and almost vestigial second digit, has long been described as being an adaptation for increased grip strength. Boettcher and colleagues (Chapter 7) provide the first documented data on forearm and hand myology of the potto (*Perodicticus*) and compare it to one of the Asian loridids (*Nycticebus*), which lack

these hand specialisations. Despite the long-held belief that the hand of *Perodicticus* and its accompanying musculature are specialised to generate high grip strength, these authors find no evidence in their current investigation to support this notion, finding instead adaptations for increased dexterity.

1.1.3 Diet and Feeding Behaviour

Given an increased understanding of the diversity among lorises, it is no surprise that a variety of dietary specialists can be found among this group, including gummivores, frugivores and also the most faunivorous of all the primates (Das et al., 2014; Happold and Happold, 1992; Nekaris and Rasmussen, 2003; Starr and Nekaris, 2013).

The ability to consume and digest gum may be a fundamental adaptation of slow lorises (*Nycticebus*) and possibly pottos (*Perodicticus*) (Burrows et al., 2015, 2019a, 2019b; Nekaris, 2014; Oates, 1984). Gum is the preferred food of *N. bengalensis*, *N. javanicus*, *N. coucang* and *N. pygmaeus*, and these species gouge massive holes in trees in a matter of seconds in order to access gums (Nekaris, 2014; Starr et al., 2010). While field reports indicate that the slow loris is an obligate, full-time gummivore that possesses specific dental adaptations for this dietary niche, the evidence is not as clear for pottos, which are known to consume high percentages of fruit and some gums. Burrows and colleagues (Chapter 12) examine the dentition of pottos relative to slow lorises to try to answer questions about how pottos may feed on gums and whether gum as a food could have been influential in the evolution of lorises. These authors conclude that pottos have dental adaptations similar to those of slow lorises and that pottos may consume a high percentage of gums in their diets, and that gums may have played a role in the evolution of lorises.

Continuing with the question of the potential role of gums in the evolution of lorises, López-Torres and colleagues (Chapter 6) closely examine the toothcomb of *Karanisia* (a lorisid-like fossil strepsirrhine that represents the first appearance of a toothcombed primate fossil) in an attempt to answer whether it fed on gums. These authors conclude that *Karanisia* likely consumed gums but it is unknown how much of *Karanisia*'s overall diet gum comprised. This does, though, show a potential role for gums in the evolution of lorises.

Locomotion is one feature used to characterise lorises and is possibly the best-studied aspect of their behaviour, forming the basis for field studies (Crompton, 1980, 1983, 1984) and captive studies (e.g. Demes et al., 1998; Dykyj, 1980; Glassman and Wells, 1984; Ishida et al., 1992; Oxnard et al., 1990). Locomotion among lorises is so characteristic that some of the morphological traits linked to locomotion differentiate bushbabies from the lorises (Charles-Dominique and Bearder, 1979). All bushbabies have long tails, elongated tarsal bones in the hindlimbs and longer hindlimbs than forelimbs (indicative of leaping), whereas lorises, to varying degrees, have reduced or lost their tails and have hindlimbs and forelimbs of relatively even lengths (Martin, 1990). As a result, bushbabies can cross gaps by hopping and leaping, while lorises do this by cantilevering, bridging or extending the body.

8 **K. A. I. Nekaris and Anne M. Burrows**

The ‘slowness’ of loris movement is reviewed in Chapter 11 by Hanna, along with the unique biomechanical aspects associated with their locomotion. Hanna provides quantitative data for the relatively slow, purposeful locomotory style of lorises and reviews specific joint mechanics during movement. The characteristic ‘cantilever’ method that lorises use to bridge a gap is described in biomechanical detail here and Hanna compares the loriseid cantilever to the methods that arboreal snakes use to bridge gaps.

1.1.4 The Social Behaviour of Lorises

Primatologists have long considered the nocturnal strepsirrhines to generally be non-social, especially when we consider them relative to the anthropoids. However, this couldn’t be more wrong! Nocturnal primates have rich social lives but they may not be the social lives that we diurnal species think about first. While many diurnal primates live in large groups, most nocturnal primates do not. This does not make them necessarily *asocial*. Lorises engage in considerable amounts of social behaviour. Many slender lorises (*Loris*) spend time together outside the breeding season grooming, foraging and feeding together (Bearder and Martin, 1980b; Clark, 1985; Rhadakrishna and Singh, 2002).

Additionally, physical contact alone does not define sociality – home range overlap is also very important, and animals that are physically dispersed will still maintain regular vocal and olfactory contact with conspecifics. Determination of home range overlap via radio tracking or simply by all-night follows of known individuals further elucidates the varied social relationships of lorises, and defines the *spacing system*. Adult sex composition mirrors that seen among diurnal primate social organisations, with single male and female units, single male and multiple female groups, single female with multiple male groups and multiple male and female groups. In the case of rainforest primates, where observation by any other means might prove impossible, radio tracking has become invaluable to infer social organisation based on spatial patterns.

Exactly *how* the social behaviour and organisation of lorises evolved, though, is uncertain. Poindexter and Nekaris (Chapter 10) use quantitative data to reconstruct the likely ancestral social behaviour of Loriformes (both bushbabies and lorises). They conclude that the most likely social organisation was a dispersed family group/social monogamy, and describe the potential advantages that this social organisation may have provided.

1.2 Part II: Ecology and Captive Management

1.2.1 The Ecology of Lorises

Ecology is such an enormous, over-arching topic that it is difficult to confine it to one small discussion. For the purposes of this introductory section, we here talk about ecology as preferences related to habitat, home range, nutrition and nutritional

requirements, predation pressures, activity budgets, mother–infant behaviours, feeding behaviours and the interplay among all of these. This broad basket of factors related to ecology has important implications for captive management and husbandry of lorises as well, thus our decision to combine ecology and captive management into the second section of this edited volume.

1.2.2 Habitat Use

Lorises show a wide preference for use of both substrates and strata in the forest (e.g. Nekaris, 2001; Nekaris et al., 2005; Pimley et al., 2005a). Substrate size selection is almost always related to the body weight of the animal, with smaller animals moving on smaller gauged twigs, branches and lianas, and larger animals negotiating sturdier supports with greater girth. Small species, such as *Arctocebus aureus* and *Loris lydekkerianus*, thrive in the undergrowth and in tree fall zones, whereas larger species, such as *Nycticebus coucang*, prefer the canopy (Butynski et al., 1998). This ecological division is what allows the African lorises in particular to occur in sympatry in many places throughout their range (cf. Charles-Dominique, 1977a), and may also influence the distribution of sympatric Asian lorises (Duckworth, 1994).

Al-Razi and colleagues (Chapter 16) describe how Bengal slow lorises (*Nycticebus bengalensis*) use their habitat and home ranges. These authors found that Bengal slow lorises persisted in disturbed habitats and this may be partially due to opportunities to feed on exudates in those disturbed habitats. Starr and Nekaris (Chapter 20) describe ranging patterns for pygmy slow lorises (*N. pygmaeus*) and demonstrate that these small primates are quite territorial and require large areas, having important implications for reintroduction efforts as well as captive management. Svensson and Luhrs (Chapter 17) describe habitat use and ranging patterns of the African lorises: pottos (*Perodicticus*) and angwantibos (*Arctocebus*). These authors provide data on feeding behaviour, vocalisations, mating behaviour and maternal care that are much needed in planning for conservation efforts, especially in the rapidly changing habitats that these primates inhabit.

1.2.3 Activity Cycles and Sleeping Sites

All lorises are nocturnal in their activity patterns, with no diurnal or cathemeral species. Animals may occasionally become active in daylight to change position for thermoregulatory purposes, to eat during periods of intense food scarcity and to avoid predators (Bearder et al., 2006), but across species it is the amount of light that dictates amount of activity. *Loris lydekkerianus*, for example, maintains activity regardless of moon phase (Bearder et al., 2002), whereas *N. pygmaeus* decreases its activity during the light moon phases (Starr et al., 2012b).

Veilleux (Chapter 14) ties visual function in lorises and pottos to anti-predation and foraging strategies. Amount of moonlight on any given night influences the activity in lorises and Veilleux considers this in her review of lorisid vision, ending with predictions on visual acuity in these primates.

10 K. A. I. Nekaris and Anne M. Burrows

Feeding and foraging behaviours span a variety of topics, but in this section we examine these behaviours in light of sexual differences. Anirudh and colleagues (Chapter 19) describe sex-based differences in feeding and foraging behaviours, with a focus on rehabilitating rescued slow lorises (*Nycticebus menagensis*) in Borneo. This is the first publication focusing on these behaviours in rehabilitated and released slow lorises in Borneo, an important consideration for ensuring the best possible outcomes for released animals.

Another incredibly unusual behaviour among lorises is their ability to moderate their body temperature. Streicher and Reinhardt (Chapter 15) review our understanding of how lorises use hibernation, torpor and fat storage in thermoregulation as well as managing food scarcity periods. To date, we only know about hibernation and torpor in the Asian lorises but this doesn't necessarily mean that the African lorises do not engage in torpor or hibernation.

1.2.4 Predation

Lorises and pottos have developed a suite of morphological characteristics that allow them to remain still for prolonged periods, and to provide camouflage and protection if attacked (Bearder, 1987; Charles-Dominique, 1977a; Nekaris, 2001). Lorises, which lack speed, have had to go to other morphological extremes against predators (Nekaris et al., 2007). An important defence is their cryptic locomotion; usually these silent primates can move away undetected. They can also remain still for long periods. This adaptive positional and locomotor behaviour is covered in Chapter 18 by Das and Nekaris. They present data from a field study on *Nycticebus bengalensis* with special regard to substrate size, sitting and quadrupedal walking. Overall, this study provides evidence that both positional and locomotor behaviours may be conserved among the Asian lorises.

When there is no possibility of escape, *Perodicticus* turns and faces the danger, adopting a defensive posture and making violent thrusts and growls at the predator. Physical adaptations make this posture a formidable weapon, including (1) a scapular shield, produced by a combination of raised cervical spines, some of which protrude above the skin in the form of tubercles, which are covered by thick skin and bristles of sensory hair, offering protection, defence and acute sensitivity; and (2) muscular hands which allow the potto to grip firmly without falling off (a potto can support up to 10 times its weight!). In extreme danger, pottos, and indeed other lorises, simply drop to the ground, move rapidly through the undergrowth and seemingly disappear to safety (Jewell and Oates, 1969a; Nekaris et al., 2007; Oates, 1984). The angwantibo does not face its predator but turns away, revealing a conspicuous target-like tail. As with the potto, an angwantibo keeps its head beneath its forelimbs. If the predator gets too close, it lifts its leg and bites the attacker on the nose! Genets and some snakes are known predators of pottos.

Known predators of slender and slow lorises include pythons, monitor lizards, orang-utans, hawk eagles and domestic dogs (Nekaris et al., 2007). Although stealth is their main defence, slow lorises (*Nycticebus*) have developed an even more