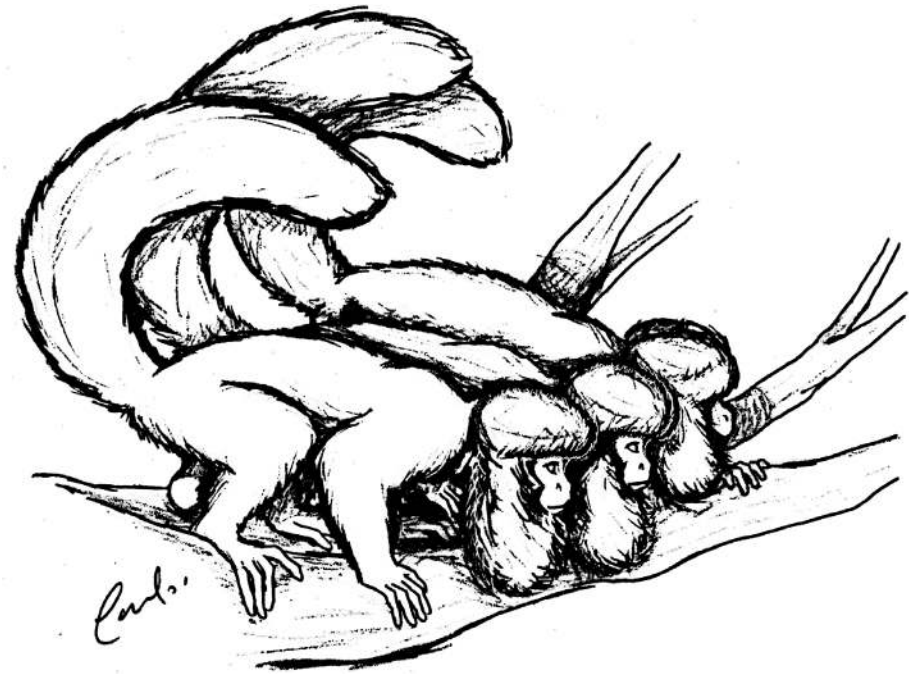
Part I

Fossil History, Zoogeography and Taxonomy of the Pitheciids

Walter C. Hartwig & Adrian Barnett



The five chapters in this section review current knowledge of the fossil record, evolutionary history, adaptive radiations, taxonomy and zoogeography of the closely related saki and uacari monkeys as well as the potentially closely related titi and owl monkeys. In the generation since *Living New World Monkeys* (*Platyrrhini*) (Philip Hershkovitz, University of Chicago Press, 1977), genetic investigations of primate evolutionary history have accelerated and now are the primary means of understanding interrelationships of the living species. In keeping with good scientific progress, the wealth of information we now have about pitheciines compared to 30 years ago opens new lines of inquiry and new needs for more detailed field and laboratory studies.

Titis, sakis and uacaris occupy a well-defined niche from a morphological perspective. They specialize in foraging on fruits with prohibitively hard pericarps. Using dental anatomy interpreted to be well-designed for puncturing and crushing the pericarp, the pitheciines are then able to access what most other species cannot – the soft inner pulp and seeds. The degree to which each living genus emphasizes sclerocarpy may underlie their evolutionary differentiation from one another within the pitheciine clade (see Kay *et al.* (Chapter 1) and Rosenberger and Tejedor (Chapter 2)).

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Given the nature of the fossil record to preserve hard tissues, it is no surprise that dental indicators of sclerocarpy have influenced paleontologists to identify some fossil taxa as ancestors of modern pitheciines. Some of the geologically earliest fossil New World monkeys display mandibular trends toward seed predation and indicate the existence of fossil pitheciids as of 15 million years ago. Kay *et al.* (Chapter 1) compare the competing opinions and conclude that other Patagonian early fossil platyrrhines resemble but are not related to the radiation of saki monkeys.

The fossil record of New World monkeys is sparsely distributed in areas where fortuitous geology makes ancient deposits available for survey. Paleontologists have long recognized that essentially tropical, Amazonian species have evolutionary histories largely invisible to the known South American fossil record. Pitheciines are no exception to this disconnect, because the living taxa are distributed tightly within equatorial and Neotropical riverine environments. And yet they are known in the fossil record. Indeed, apparent direct ancestors of sakis and uacaris have been found in 12-million-year-old deposits, and convergent if not distantly related taxa have been found in even older deposits. This strongly suggests that the adaptive radiation of pitheciines was a major vector of New World monkey evolutionary history.

The intrigue of New World monkey evolutionary history is such that the two living genera whose affinities are most debated – *Aotus* and *Callicebus* – are most often compared to the lineage whose relationships are most "secure" – the pitheciines. Rosenberger and Tejedor (Chapter 2) continue the story of *Aotus* and *Callicebus*, in apt tribute to the late Warren Kinzey, by detailing how the growing molecular evolution data bear on their standing interpretation of owl and titi monkeys as pitheciines. Because the molecular, morphological and ecological data are incongruent, they argue, we should anchor hypotheses of titi and owl monkey evolutionary history to what they do in the wild.

Figueiredo *et al.* (Chapter 3) demonstrate how far technology has come in their analysis of *Cacajao* molecular data. To obtain enough specimens for a competent genetic analysis they acquired data from living animals, cadaver, and museum skins and skulls. Their results further substantiate the monophyletic status of the genus, and probe more deeply into the relatedness of populations to their geographies. Pelage similarities compelled earlier morphologists to classify populations of uacaries into the same species. This practice may mask true phylogenetic differences driven by riverine isolation and panmictic population distributions as captured by genetic analysis.

Watersheds have influenced the zoogeography of *Callicebus* and *Chiropotes* species groups as well (see Silva Júnior *et al.*, Chapter 4). Primary field censuses of pitheciine habitats are logistically complicated, and this has led to a not unwelcome dilemma for taxonomists. Pitheciine diversity and population ranges are probably greater than estimated by the field surveys and museum analyses performed to date. Further detail would require greater intrusion into these poorly known habitats, which inevitably would reduce their "nativity" even as it would improve our sense of pitheciine ecological distribution.

Within the widely distributed *Callicebus personatus* species group are populations that exhibit the expected effects of reproductive isolation. Pelage traits have influenced the use of subspecies as population boundary names that often correspond to river systems or ecosystem transition zones at the edges of the Mata Atlantica (see Printes *et al.*, Chapter 5). Genetic sampling can now evaluate how well these taxonomies align with intrinsic biological markers, but is only now getting under way.

Threats to the biodiversity and conservation of pitheciines are recurring themes in this and other sections of this volume. From a taxonomic standpoint, recognizing more and more individual populations as distinct taxonomic entities – such as subspecies – helps to focus attention on what is most easily lost by anthropogenic habitat destruction. At the same time, micro-taxonomies may exaggerate the breadth of the *adaptive radiation* of the pitheciine lineage.

The chapters in this section exhibit the significant advances in understanding that have been made over the last 20 years. We are breaking away from divining taxonomy from skins and skulls. We understand more about pitheciine evolutionary history with every decade of fossil discoveries. And we are asking different questions about adaptive radiations and dispersal mechanisms because of more intensive fieldwork and preliminary comparative genetics. Students of the next decade are likely to be drawn to saki and uacari research less because they are exotic primates and more because of the myriad of specific and micro-evolutionary questions raised by the research reported here.

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Chapter 1

Pitheciidae and other platyrrhine seed predators

Richard F. Kay, D. Jeffrey Meldrum & Masanaru Takai

Phylogenetic and geochronologic background

Although a commonly agreed upon phylogeny for the platyrrhines generally, and the specific relationship of the pitheciid clade among other platyrrhines, has long been elusive, a growing consensus based on both molecules and morphology now appears to have emerged (Schneider *et al.* 1996, 2001; Ray *et al.* 2005; Horovitz 1999; Singer *et al.* 2002; Canavez *et al.* 1999; Barroso *et al.* 1997; Hodgson *et al.* 2009; Wildman *et al.* 2009). Figure 1.1A depicts a platyrrhine phylogeny based on nucleotide sequence data and *Alu* data.

Three family-rank clades supported by the molecular evidence are Cebidae (capuchins, squirrel monkeys, owl monkeys, tamarins, and marmosets), Atelidae (howlers, woolly, spider and woolly spider monkeys), and Pitheciidae (titis (*Callicebus*), sakis (*Pithecia* and *Chiropotes*) and uacaris (*Cacajao*)). The *Alu* data indicate that pitheciids are sister to a cebid–atelid clade. Some scientists consider the owl monkey *Aotus* to be a possible relative of *Callicebus*, and therefore a pitheciid *sensu lato* (Rosenberger & Tejedor, Chapter 2). However, all the recent molecular evidence confirms that *Aotus* is in fact a cebid with no close relationship to the pitheciids (Ray *et al.* 2005; Schneider *et al.* 2001; Hodgson *et al.* 2009; Wildman *et al.* 2009).

Recent work also has established a rough temporal framework for platyrrhine evolution (Schrago 2007). The estimated 20.1 Ma (Early Miocene) time of separation of Pitheciidae from other extant platyrrhine families and for the 15.6 Ma (Middle Miocene) separation of *Callicebus* from the stem lineage leading to Pitheciinae are consistent with the known, albeit sparse, fossil record. This evidence is not especially useful for palaeontologists, however. Assuming that the calibration of the branches is correct, the 95% probability intervals for these branch times are extremely broad. For the origin of the Pitheciidae, it is between 15.6 and 28.3 Ma and for the *Callicebus* branch from pitheciines, it is between 11.9 and 23.2 Ma. In most cases, fossil platyrrhines cannot be excluded from the pitheciid or pitheciine clade based on geologic age alone. Therefore, we must rely on the evidence of morphology and the fossil record itself to reconstruct more precisely the branch times related to pitheciid evolution.

Herein we make a few observations pertinent to the fossil evidence for the evolution of the Pitheciidae. We examine the anatomical attributes that correlate with the distinctive pattern of pitheciid behavior, especially with respect to the seed-predator niche. We survey the anatomical evidence of the fossils to get clues about the evolution of this behavior. We illustrate a remarkable instance of convergence of pitheciid-like anatomy and associated large-seed predation in a group of Early Miocene platyrrhines. Because emphasis is placed on the evolution of a sclerocarpic foraging niche (defined below), we have chosen to omit discussion of one proposed clade of extinct species (*Antillothrix*, *Xenothrix* and *Paralouatta*) that inhabited the Greater Antilles and that may be related to *Callicebus* (MacPhee & Horovitz 2004; Horovitz & MacPhee 1999; MacPhee *et al.* 1995; MacPhee & Fleagle 1991; MacPhee & Woods 1982; Rosenberger 1975). Of the three, only *Xenothrix* exhibits any morphology suggesting seed predation (Rosenberger 1975).

A word about systematic terminology

Systematists use the term “clade” to refer to a cluster of taxa (species, genera or families), the members of which trace back to a most recent (or last) common ancestor or LCA – Figure 1.1B (see Williams & Kay 1995 and Williams *et al.* 2010 for a discussion). The clade includes all the descendant species of the LCA, whether living or extinct. A “crown clade” is a clade that has living members. For example, the subfamily Pitheciinae is a crown clade consisting of species of the extant genera *Pithecia*, *Chiropotes* and *Cacajao*, their LCA, and all of the extinct species also descended from that LCA, and so on.

A stem taxon is one that is more closely related to one crown clade than another but is not a descendant of the LCA of any living clade. An example of a stem pitheciine is *Cebupithecia* from the Miocene of Colombia (see below). *Cebupithecia* is more closely related to living pitheciines than it is to Callicebinae, but it branched from the lineage leading to the LCA of extant pitheciines.

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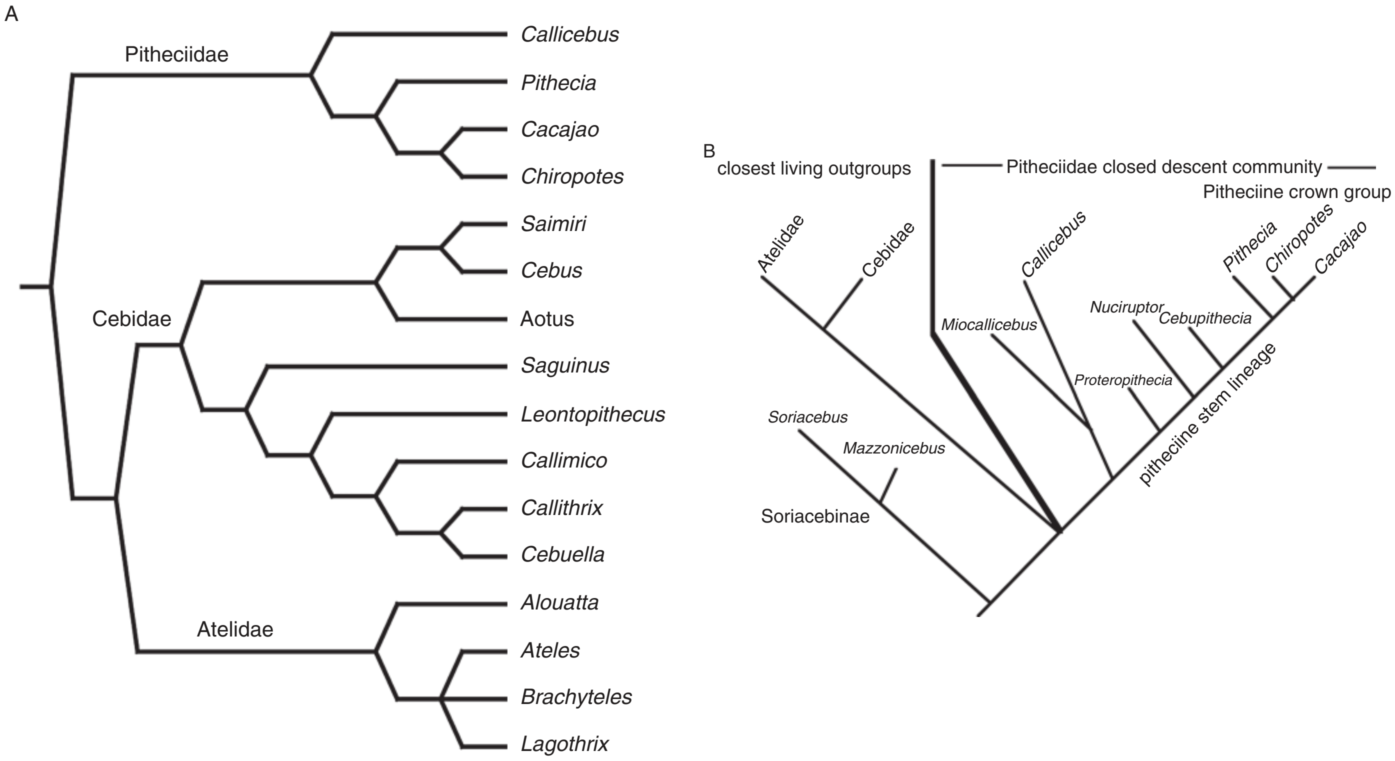

Figure 1.1 A. Cladogram of extant platyrrhine genera based on molecular sequences and *Alu* data. *Alu* elements (short interspersed nuclear elements or SINEs) complement molecular sequences because their mode of evolution is predominantly unidirectional and virtually homoplasy-free (Hillis 1999; Bashir *et al*. 2005). Molecular data strongly support the monophyly of the Platyrrhini and recognition of three clades: Atelidae, Cebidae and Pitheciidae (Harada *et al*. 1995; Barroso *et al*. 1997; Schneider *et al*. 1996, 2001; Singer *et al*. 2002). Platyrrhine monophyly is supported by 87 *Alu* elements (Singer *et al*. 2002; Ray *et al*. 2005). The tree is resolved at nodes with bootstrap values ≥ 90%, or when one or more *Alu* supports it. The *Alu* data indicate that Atelidae and Cebidae are sister taxa to the exclusion of Pitheciidae (Ray *et al*. 2005). Linkage of callitrichines with *Aotus* and a *Saimiri/Cebus* group is strongly supported by molecular data and three *Alu*s, and one *Alu* links cebines with *Aotus*. *Callicebus* is supported strongly as a basal pitheciid by sequences and three *Alus*. *Aotus* is excluded consistently from the *Callicebus*–pitheciine clade (*contra* Rosenberger 1981; Rosenberger & Tejedor, Chapter 2). Atelidae has strong molecular support (including six *Alu*s), with *Alouatta* as the sister to a clade consisting of *Ateles*, *Brachyteles*, and *Lagothrix* (Meireles *et al*. 1999a, 1999b). B. Simplified cladogram of platyrrhine phylogeny illustrating the systematic terms used in the text and the proposed phylogenetic position of key fossil taxa.

Pitheciid adaptations for sclerocarpy

Fruit is a major element in the diet of platyrrhines. Typically, the soft, outer layers of the fruit (the pericarp) are the parts preferred. The soft parts are obtained by swallowing the fruit whole, or by removing the edible portions with teeth and/or hands and then dropping the seed. Whole seeds ingested together with the soft outer layers can germinate if passed intact through the gastrointestinal tract. Pitheciines follow a different pattern: they extract the seed from the fruit and chew it before swallowing, and are thus known as “seed predators”. A number of primate species in South America are occasional seed predators, but pitheciines are specialized to varying degrees in seed predation (van Roosmalen *et al*. 1988).

Kinzey & Norconk (1990, 1993) examined the hardness of the foods ingested by *Pithecia pithecia* and *Chiropotes satanas*. Compared to the frugivore *Ateles paniscus*, these specialist seed predators select soft seeds from fruits with very hard pericarps. Data on the hardness of the pericarp of these fruits is provided by Kinzey & Norconk (1990). The maximum hardness of the pericarp ingested by *Pithecia* is nearly five times that of fruits ingested by *Ateles*. *Chiropotes* breaks open even harder fruit pericarps to access and eat seeds – the maximum recorded fruit hardness was 27 times that of the hardest fruit opened by *Ateles* (Kinzey & Norconk 1990). Once the fruit is opened, the seed itself is soft and easily chewed (Kinzey & Norconk 1990). Kinzey and Norconk refer to this foraging adaptation as sclerocarpic foraging or sclerocarpic harvesting, which is comparable to that of avian seed predators such as parrots and macaws (Boubli 1999).

Van Roosmalen *et al*. (1988) offer the best description of how pitheciines eat these fruits. For example, with *Eschweilera* fruits from the Brazil nut family (Lecythidaceae), *Chiropotes* bites a hole into the fruit at the edge of the operculum, then uses its procumbent incisors rather like a can opener to pop it off and gain access to the seeds inside. When feeding on very hard seed pods of larger Lecythidaceae such as *Lecythis davisii* and other physically similar seed pods, the saki uses its powerful wedge-shaped canines rather than its incisors (van Roosmalen *et al*. 1988, pp. 14–15).

Titi monkeys share the seed-eating habits of pitheciines but to a lesser degree, although almost half the diet of *Callicebus lugens* may be immature seeds (Palacios *et al*. 1997). Similarly,

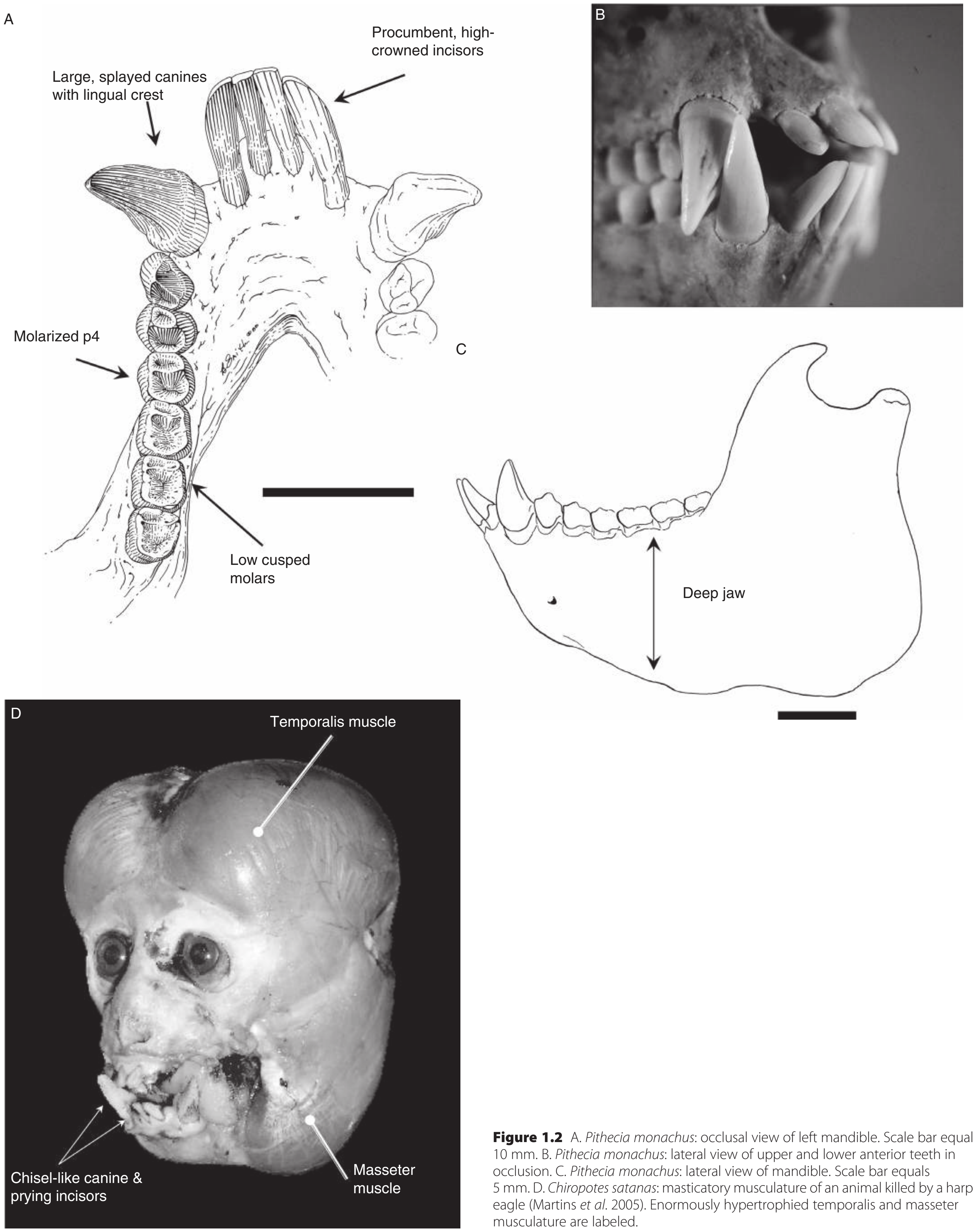

Figure 1.2 A. *Pithecia monachus*: occlusal view of left mandible. Scale bar equals 10 mm. B. *Pithecia monachus*: lateral view of upper and lower anterior teeth in occlusion. C. *Pithecia monachus*: lateral view of mandible. Scale bar equals 5 mm. D. *Chiropotes satanas*: masticatory musculature of an animal killed by a harpy eagle (Martins *et al*. 2005). Enormously hypertrophied temporalis and masseter musculature are labeled.

seeds may make up at least a quarter of the diet of *Callicebus melanochir*, but the hardness of these items is not recorded (Müller 1996).

A pattern of derived features related to sclerocarpic harvesting using the anterior dentition distinguish the living pitheciids from other extant platyrrhines (Kay 1990; Rosenberger 1992). In the pitheciines, the incisor–canine complex forms a specialized puncturing and prying mechanism (Figure 1.2A,B). The lower incisors are procumbent, narrow and styliform, forming a gouge. The canines are enlarged, laterally splayed, and have a sharp lingual crest (entocristid), producing a triangular cross-section. The specialized large-seed scraping and splitting is powered by enormously hypertrophied adductor musculature with attendant jaw deepening posteriorly (Figure 1.2C,D). The first lower molars are enlarged as well. Further specializations of the post-canine dentition include a molarized last premolar and low-cusped molars with low relief and blunt, weakly developed cutting edges (Figure 1.3A). There is virtually no disparity of height between the trigonid and talonid, with the intervening protocristid represented by a low, often indistinct ridge. Molar enamel is relatively thin and often crenulated.

One method of quantifying dietary adaptations is to measure the relative development of the shearing crests on the molar crowns. A “shearing quotient” (or SQ) can be calculated by regressing the log total crest length (y) on log tooth length (x). Deviations away from the isometric line derived from mean log x and mean log y are expressed as a percent difference: SQ $= 100$ (observed $-$ expected)/expected. The molar shearing crests are poorly developed in pitheciines. In Figure 1.3B, the SQs for living platyrrhines are clustered by dietary preference. Species that eat considerable amounts of fibrous foods such as cellulose-rich leaves (*Alouatta*), or insects (chitinous exoskeletons) and fungi, which are rich in structural carbohydrate (*Callimico*), have large shearing quotients. In contrast, species that feed on less-fibrous, soft fruits (*Ateles*) or tree gum (*Callithrix*) have relatively flatter teeth, with shorter, more rounded crests. The teeth of species that specialize in eating hard seeds or splitting open tough, hard fruits (*Cebus* and the pitheciines) tend to have even less shearing crest development (Kay *et al.* 2002; Anthony & Kay 1993; Fleagle *et al.* 1997),

Pitheciidae as a morphocline

Callicebus–Pithecia–Chiropotes–Cacajao represent a morphocline of increasingly specialized dental features for sclerocarpic foraging (Kinzey 1992; Meldrum & Kay 1997a; Kay 1990; Rosenberger 1992). *Callicebus* is least specialized for seed predation among the pitheciids, but does possess some dental and mandibular morphologies associated with sclerocarpy, including posterior deepening of the mandible, and narrow, elongate incisors (Figure 1.4). However, the canines are not enlarged and the premolars are not molarized, nor is the molar structure specialized in the manner described above (cresting is more evident and the trigonid is slightly elevated above the talonid).

Pithecia, *Chiropotes* and *Cacajao* demonstrate adaptations for sclerocarpy in increasing degrees. All these species have procumbent, laterally compressed lower incisors arranged like a shovel. In a stout mandibular symphysis, the canines are progressively larger and more flared, and the chisel-like cross-sectional profile more pronounced. The last premolar looks more like a molar and the molars themselves are flatter with more poorly developed cutting crests and a tendency for the surfaces to become crenulated.

The extant pitheciines occupy an intermediate position in the morphospace defined by the shape of the platyrrhine ankle bone, the talus (Meldrum 1990). They fall between the cebids, characterized generally as small-bodied quadrupedal runners and leapers, and the atelids, which are generalized as prehensile-tailed suspensors. These distinctions are further reflected in other postcranial features such as limb

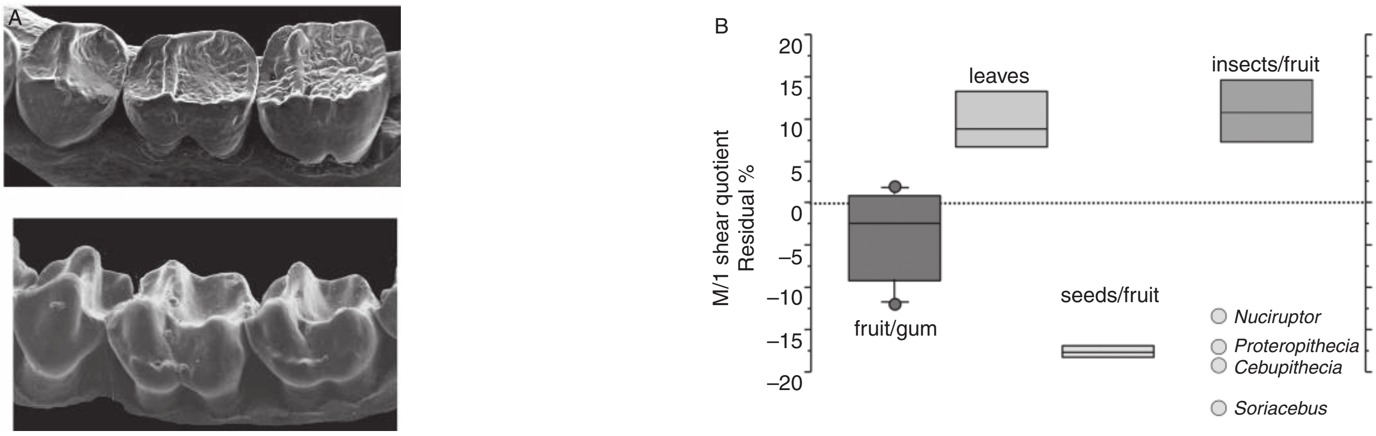

Figure 1.3 A. Occlusolateral scanning electron micrographs of the mandibular cheek teeth P_4–M_2 of *Cacajao calvus*, a seed eater (above), and *Saimiri sciureus*, a mixed insect and soft fruit eater (below), illustrating the range of shearing crest development among extant platyrrhines. The two images are bnot to the same scale. B. Shearing quotients (SQs) for living platyrrhines clustered by dietary preference. *Nuciruptor*, *Cebupithecia* and *Soriacebus* have very poorly developed shearing surfaces on their molars suggesting a diet of fruit, seeds, or gum.

proportions and the morphology of the joints of the extremities. Among the pitheciines there exists some differentiation of the details of locomotor adaptation. Fleagle & Meldrum (1988) have shown that *Pithecia* displays postcranial adaptations for vertical clinging and leaping correlated with its habit of occupying the understory. *Chiropotes* and *Cacajao*, on the other hand, show adaptations for quadrupedalism and hindlimb suspension. Hindlimb suspension may be a correlate of below-branch foraging, which provides access to suspended fruits (Meldrum 1998).

The fossil record of platyrrhine sclerocarpy

The fossil record of platyrrhines begins in the latest Oligocene (26 Ma) (Kay *et al.* 1998). For the most part, the specimens documenting platyrrhine history come from outside the current distribution of living platyrrhines. This is especially evident in the great southward extension of the range in early Miocene times, related to the "Mid-Miocene climatic optimum" between ~17 and 15 million years ago (Figure 1.5). Two distinct clades of platyrrhines demonstrate remarkable convergence in the masticatory apparatus. One group, the extant Pitheciidae and their fossil relatives, extend back to the early Middle Miocene, about 15.5 million years ago, and seem to have occupied all or most of the tropical zone. A second, older and more geographically restricted group, the *Soriacebus* clade, despite their resemblance to living pitheciines, are more probably stem platyrrhines.

Figure 1.4 *Callicebus moloch*: right lateral view of skull. *Callicebus* is least-specialized for seed predation among the pitheciids, but does possess incipient dental and mandibular morphologies associated with sclerocarpy, including posterior deepening of the mandible and narrow incisors. Skull length equals ~6 cm.

Pitheciidae

Patagonian Argentina has a rich assemblage of fossil primates of Early Miocene age. From Patagonian Argentina south of 40° S comes a single, and oldest, fossil pitheciine species. It also represents the youngest occurrence of a fossil primate in Argentina, after which climatic conditions became more arid and cooler, less suitable for occupation by forest-dwelling monkeys. *Proteropithecia* consists of teeth, jaw fragments, and a talus (Kay *et al.* 1998, 1999). This meagre material establishes only that the front-tooth specializations of the pitheciines (sakis and uacaris), associated with seed predation, were present (Figure 1.6A). The lower incisor has a stout root and the crown is projecting. Incisor crowns and roots are compressed sideways, conforming to the gouging mechanism of extant Pitheciinae. The molars of *Proteropithecia* are also flattened, although a low, rather distinct cross crest (a protocristid)

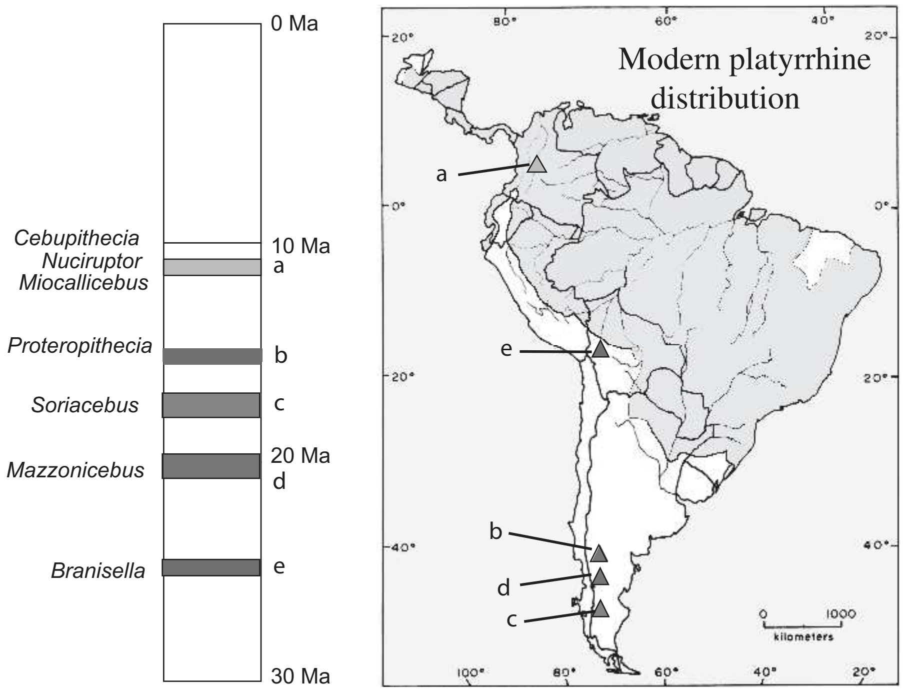

Figure 1.5 A map and timescale of the fossil platyrrhines discussed in the text. The temporal positions of the taxa are marked on the timescale at left. The modern range of platyrrhines in South America is indicated by the shaded area on the map. The positions of the localities of the fossil platyrrhines discussed in the text are indicated by triangles on the map. Symbols: a, La Venta, Neiva, Colombia; b, Cañadon del Tordillo, Neuquen, Argentina; c, Río Pinturas, Santa Cruz, Argentina; d, Gran Barranca, Chubut, Argentina; e, Salla, Bolivia.

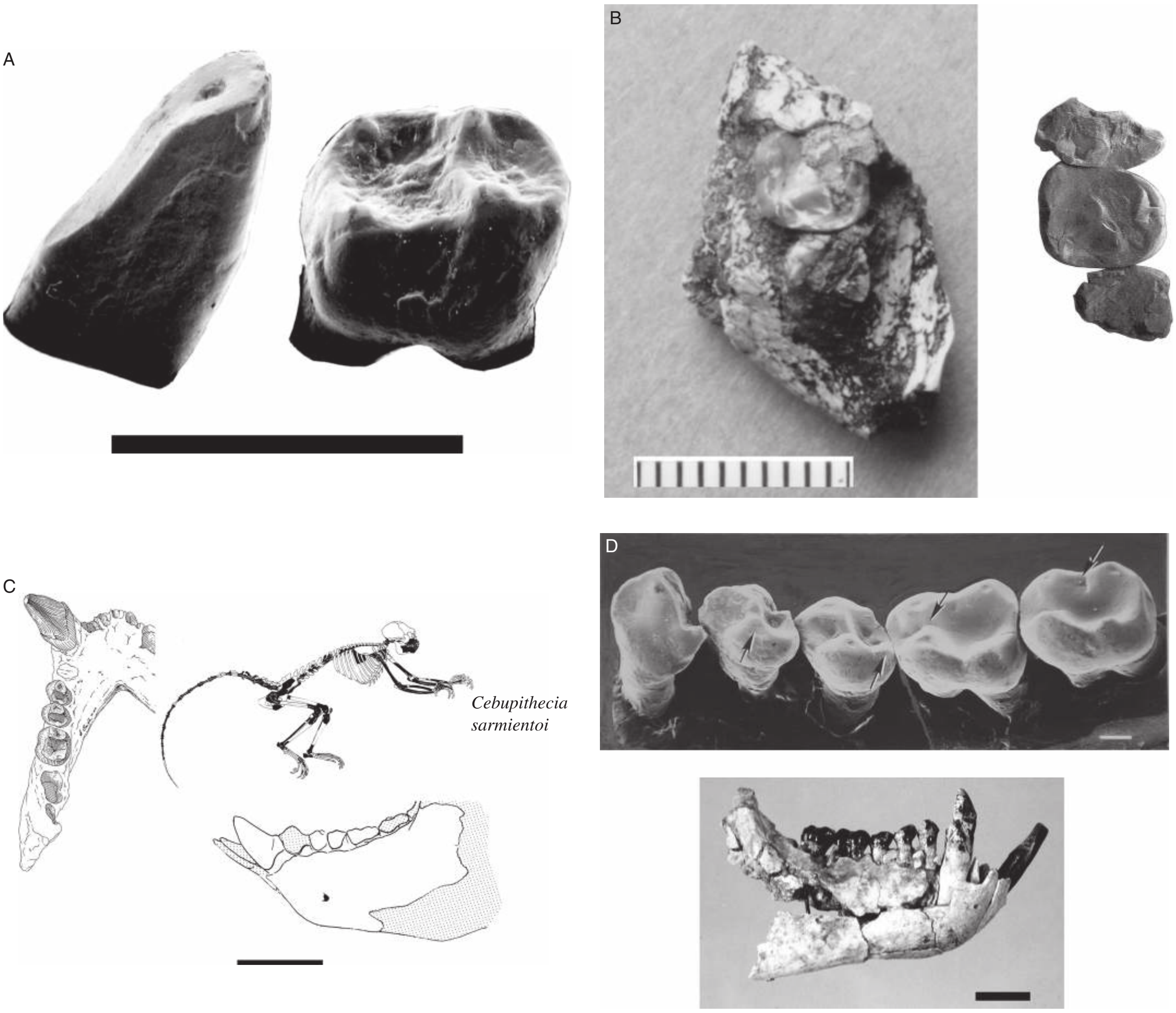

Figure 1.6 A. *Proteropithecia*, Middle Miocene, northern Patagonia, an isolated lower molar and lower incisor. Scale bar equals 5 mm. B. *Miocallicebus villaviejai*, middle Miocene, Colombia. Maxilla with right upper cheek teeth. Scale bar equals 10 mm. C. *Cebupithecia sarmientoi*, Middle Miocene, Colombia. Jaws, teeth and partial skeleton. Scale bar for lateral view of jaw equals 10 mm. D. *Nuciruptor*, Middle Miocene, Colombia. Lower jaw in lateral view and view of the cheek teeth. Scale bar for mandible equals 5 mm.

remains. The associated ankle bone resembles that of *Callicebus*, suggesting that *Proteropithecia* was a generalized arboreal quadruped.

Because *Proteropithecia* is surely a pitheciine, by inference, this species establishes that the titi-monkey (*Callicebus*) clade must already have separated from pitheciines by 15.5 Ma. Another slightly older Patagonian species, *Homunculus* (about 16.5 million years old), has been related to *Callicebus* (Rosenberger 2000, 2002; Fleagle & Tejedor 2002). However, it appears more likely that the similarities between *Homunculus* and *Callicebus* are merely shared primitive characters and evince no special affinity between the two. Several new, exceptionally well-preserved crania of *Homunculus* retain many primitive platyrrhine features and have a relatively small brain (Kay *et al*. 2006a, 2006b, 2012).

The next record of fossil pitheciids comes from 11–12-million-year-old Miocene rocks in the Tatacoa Desert, Colombia. The sites are situated at 5°N in the modern-day valley of the Magdalena River, which drains northward into the Caribbean and is separated from the Amazon and Orinoco basins by the eastern Andean Cordillera. In Miocene times, the cordillera had not yet arisen and the faunas of the Magdalena valley were in continuity with present day Orinoco and Amazon basins (Hoorn *et al*. 1995; Lundberg *et al*. 1986). Thus, the fossil monkeys from Colombia give us a Middle Miocene snapshot of the northwestern Amazon/Orinoco Basin. The Colombian

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fossil record documents the first definite record of titi monkeys – *Miocallicebus villaviejai* (Takai *et al.* 2001) and two stem pitheciines, *Nuciruptor* and *Cebupithecia*. We have no fossil record of any crown pitheciine species. Another Middle Miocene primate from Colombia, *Mohanamico hershkovitzi*, has been related to pitheciids (Luchterhand *et al.* 1986). Others have since suggested its affinities lie with callitriichines (Rosenberger *et al.* 1990) or express uncertainty about its phylogenetic position (Horovitz 1999; Meldrum & Kay 1997a).

Not much is known about *Miocallicebus*. The type specimen (Figure 1.6B) consists of a maxillary fragment preserving a partial root of the first upper molar, the complete second molar and a damaged third molar (Takai *et al.* 2001). Except for its much larger size, the upper second molar of *Miocallicebus* is very similar to that of extant *Callicebus*, with a nearly rectangular occlusal outline, a distinct hypocone, and a distinctive well-developed mesiolingual cingulum. The dental evidence of *Miocallicebus* confirms what we knew from the existence of *Proteropithecia*: callicebines and pitheciines had diverged from each other by the Middle Miocene.

Cebupithecia (Figure 1.6C) shares many diagnostic similarities of the jaws and teeth with living pitheciines (Orlosky 1973; Rosenberger 1979; Kay 1990). The alveolar process of the mandible deepens posteriorly as in living pitheciines, and the two sides of the lower jaw are joined at a robust symphysis. Like extant pitheciines, the incisors (as observed from the preserved roots) are modified into a gouging mechanism, being mesiodistally compressed and procumbent. A wide space separates the incisors from the robust, splayed canines, which have a chisel-like crest at the apex, lending the tooth a triangular cross-section. The first lower premolar is quite large but the others are small and do not resemble molars (i.e. they are not molariform). The molars have low relief like living pitheciines, but with smooth rather than crenulated enamel (Meldrum & Kay 1997a).

Nuciruptor is another Colombian Miocene pitheciine (Meldrum & Kay 1997a) (Figure 1.6D). A virtual contemporary of *Cebupithecia*, *Nuciruptor* has the same distinctive incisor specialization, but does not display the same degree of specialization of the canine evident in the former. The anterior premolar is not enlarged and the posterior premolar is not molariform. The molars of both *Nuciruptor* and *Cebupithecia* have very poorly developed shearing crests, with even lower SQs than any of the living pitheciines (Figure 1.3B). This strongly suggests that they were masticating hard seeds, although the molar enamel is not crenulated. In short, the mosaic of features displayed by *Nuciruptor* would seem to bear out Kinzey's (1992) prediction that specializations of the anterior dentition preceded those of the post-canine dentition in the evolution of sclerocarpy.

Given the rarity of postcranial remains for fossil pitheciines, limited conclusions can be drawn about correlations between locomotor adaptations and dietary adaptations. There is simply too little representation of the diversity of postcranial derivations, or lack thereof, to confidently correlate adaptations of limbs to those of the dentition, even if such a correlation were expected to exist. The most extensive fossil skeleton represents a single specimen of *Cebupithecia* (Figure 1.6C) (Stirton & Savage 1951; Stirton 1951). The skeleton is structurally similar to *Pithecia*, but lacks many of the derived traits of the extant pitheciine postcranium (Fleagle & Meldrum 1988; Meldrum 1993; Meldrum & Kay 1997b). For example, the distal femur (knee) has deep condyles, and the patellar groove, across which the kneecap slides, is narrow with a raised lateral margin. This suggests locomotion dominated by above-branch quadrupedal running with considerable leaping ability, whereas living pitheciines engage more frequently in climbing and suspensory behaviors as well as leaping. Similarly, extant pitheciines exhibit relatively longer limbs compared to the length of the trunk and configurations of other joints that bear some resemblances to the ateline condition. These correlates of climbing and suspensory behaviors are lacking in *Cebupithecia*. Furthermore, *Cebupithecia* has an elongate tail, unlike living, short-tailed sakis and uacaris (Meldrum & Lemelin 1991).

The *Soriacebus* clade

A second clade of platyrrhine sclerocarpic foragers consists of two genera, *Soriacebus* (Figure 1.7) and *Mazzonicebus* (Kay, 2010). The two are found in the Early Miocene of Patagonian Argentina (at > 45°S). *Soriacebus* occurs in the early part of the Santacrucian South American Land Mammal Age (SALMA) at about 17 Ma. *Mazzonicebus* appears to be its ancestor or sister taxon, and appears at 20.0 and 20.2 Ma in the Colhuehuapian SALMA (Kay 2010). Most of what we have to say about this clade is based on the published specimens of *Soriacebus* but applies equally to *Mazzonicebus*.

Soriacebus is considered by some scientists to be an extinct tribe of pitheciines (Fleagle & Tejedor, 2002; Tejedor 2005a,b), but others argue that it represents a distinct clade of early platyrrhines, unrelated to pitheciines (Meldrum & Kay 1997a; Kay *et al.* 1998). We return to these conflicting hypotheses below. *Soriacebus* resembles pitheciids in a constellation of dental and jaw anatomy associated with sclerocarpic harvesting. It possesses

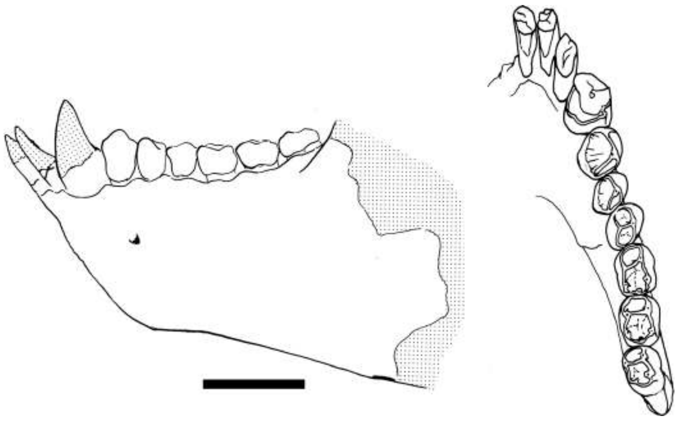

Figure 1.7 Left mandible of *Soriacebus sarmiento*, an early Miocene platyrrhine from Patagonia with convergent specializations for seed predation. Occlusal (left) and lateral (right) views. Scale bar equals 10 mm.

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procumbent styliform incisors that must have served as a gouging mechanism. The lower canine is extremely robust. A large and projecting anterior premolar served as a puncturing device. A swelling on the outside of the tooth seems to have provided a sharpening edge for the large splayed pitheciine-like upper canine (Fleagle *et al.* 1997; Fleagle 1990; Tejedor 2005a,b). The lower jaw has a robust symphysis allowing recruitment of muscle forces from both sides of the jaw during powerful incisal and canine biting. The mandibular ramus deepens posteriorly, increasing its strength against powerful bending forces engendered by the action of the front teeth, and serving as an expanded surface for large chewing adductor muscles. The front teeth are extremely large in proportion to the cheek teeth behind the anterior premolar. The cutting edges of the cheek teeth are weakly developed, as in pitheciines.

Colhuehuapian-age *Mazzonicebus* from the Patagonian locality of Gran Barranca (~45°S) resembles *Soriacebus* in having robust jaws that deepen posteriorly, gouging incisors, enlarged canines and anterior premolars, and poorly developed cutting edges on its molars. However, the size disparity between the front teeth and cheek teeth is not as pronounced as in *Soriacebus* and the molar structure is markedly different in several details of the cusps.

The structural details of the premolars and molars of *Soriacebus* appear to be those of a stem platyrrhine (Kay 2010). The lower premolars have weakly developed medial cusps (metaconids), the anterior upper premolars have small hypocones and the last premolar is not molariform. Advanced soriacebine molars have elongate trigonids, versus short ones in pitheciines. This combination of clear specializations for sclerocarpic harvesting on the one hand, but differences in the details of how this adaptation is achieved, on the other, leave little doubt that the *Soriacebus* clade acquired their sclerocarpous feeding adaptations independently from pitheciines.

Concluding observations

The evolutionary history of pitheciids is characterized by an increased reliance upon large-seed predation. Pitheciids engage in "sclerocarpic harvesting", involving the removal with the incisors and canines of a hard or tough outer pericarp to obtain and chew up relatively soft nutrient-rich seeds. Although precise data about *Callicebus* are not available from the literature, *Callicebus* shows a more limited version of this adaptation with some but not all of its morphological features.

No pitheciine fossils are known from continental South America between the Recent and the middle Miocene. Stem pitheciines are represented between 15.5 and 11.5 Ma by three genera ranging from Patagonia to Colombia. Only one specimen, from the middle Miocene of Colombia, documents the *Callicebus* lineage.

In spite of this impoverished record, a few constraints can be identified with regard to the otherwise broad branch times for the separation of pitheciids from other platyrrhines and the cladogenesis between the *Callicebus* lineage and that of the saki–uacaris is provided by the fossil record. The earliest definite appearance of the *Callicebus* clade (*Miocallicebus*) is dated to the Laventan SALMA, about 12 Ma. Pitheciines present a more pronounced version of the sclerocarpic foraging jaw adaptations. They first appear as fragmentary fossil remains described as *Proteropithecia* in the later parts of the Santacrucian SALMA at about 15.5 Ma. These two species establish that the branching times for the origin of Pitheciidae and *Callicebus*–pitheciine cladogenesis must have occurred before 15.5 Ma.

The Early Miocene *Soriacebus* clade is a remarkable parallel to pitheciines in terms of anterior dental and jaw structure. *Soriacebus* offers another example from the primate fossil record of distinct clades arriving at similar solutions to common adaptive challenges, in this case, the exploitation of seeds encased within hard or tough pericarps.

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