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# The Primate Fossil Record

Edited by

**WALTER CARL HARTWIG**

TOURO UNIVERSITY



PUBLISHED BY THE PRESS SYNDICATE OF THE UNIVERSITY OF CAMBRIDGE  
The Pitt Building, Trumpington Street, Cambridge, United Kingdom

CAMBRIDGE UNIVERSITY PRESS

The Edinburgh Building, Cambridge CB2 2RU, UK  
40 West 20th Street, New York NY 10011-4211, USA  
477 Williamstown Road, Port Melbourne, VIC 3207, Australia  
Ruiz de Alarcón 13, 28014 Madrid, Spain  
Dock House, The Waterfront, Cape Town 8001, South Africa

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First published 2002

Printed in the United Kingdom at the University Press, Cambridge

Typeset Joanna 10.25/12.5pt System Poltype® [vN]

A catalogue record for this book is available from the British Library

Library of Congress Cataloguing in Publication data

The primate fossil record / edited by Walter Carl Hartwig.

p. cm.

Includes bibliographical references and index.

ISBN 0 521 66315 6

1. Primates, Fossil. I. Hartwig, Walter Carl, 1964–

QE882.P7 P75 2002

569'.8 – dc21 2001037847

ISBN 0 521 66315 6 hardback

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# 15 | The Pliopithecoidea

DAVID R. BEGUN

## Introduction

A primitive catarrhine group with no known descendants, pliopithecoids were a diverse and fascinating group of primates ranging from southwestern France to China, from about 17 to 7 million years ago. Equally impressive is the range of morphological diversity within the Pliopithecoidea. Pliopithecoids were highly diverse and successful, varying in size from approximately 3 to 20 kg, and spanning dietary adaptations from generalized frugivory to highly specialized folivory. Smaller taxa were probably more monkey-like in their positional behavior, moving along the tops of branches, while the larger forms appear to have been more suspensory. The fossil record of the Pliopithecoidea displays widespread homoplasy, or parallel evolution, and adaptive radiation. Pliopithecoids resemble South American monkeys in diversity and adaptation and, indeed, are an example of the “Splendid Isolation” phenomenon typified by the faunas of Australia and South America (Simpson, 1980). In contrast, the evolutionary relations remain unclear, both within the Pliopithecoidea and between it and other anthropoids.

## History of discovery and debate

Pliopithecoids were among the first fossil primates to be discovered and described. The famous femur from Eppelsheim and the famous lower jaw from Sansan set the stage for both the catarrhine fossil record and the sciences of paleo-primatology and paleoanthropology. However, discovery of fossil catarrhines more closely resembling great apes and humans shifted attention away from the Pliopithecoidea. After discovery and recognition of *Pliopithecus antiquus* only a few specimens from several localities, and a large collection of mostly isolated teeth from one (Göriach, Austria), were discovered in the next 100 years. Overall they attracted relatively little attention from the scientific community.

Paul Gervais (1849a) nominated *Pliopithecus* from discoveries first announced by Édouard Amand Isidore Hippolyte Lartet in 1837 and referred by Henri-Marie Ducrotay de Blainville (1839, 1840) to *Pithecus antiquus*. Several years later, a new and slightly larger species of *Pliopithecus*, *P. platyodon*, was described from collections in Switzerland by Biedermann (1863). A much larger collection of jaws and isolated teeth, first described by Hofmann (1863) from Göriach, was attributed to *Pliopithecus antiquus*, but eventually moved into *P. platyodon* (Hürzeler, 1954a; Harrison et al., 1991). More speci-

mens were recovered from Sansan and another locality in France, La Grive St. Alban (Depéret, 1887). Isolated teeth were found in various localities in the Loire valley of central France (Gervais, 1867; Lecomte, 1912), in Germany near Augsburg and in Bavaria (Roger, 1898; Schlosser, 1900) and in Poland (Wegner, 1913). These highly fragmentary partial dentitions or isolated teeth expanded the known geographic range of *Pliopithecus*, but offered little insight into the nature of *Pliopithecus*. Researchers assumed with little doubt, based on the simple and primitive morphology of the teeth and their small size, that this taxon was directly ancestral to hylobatids.

During the middle of the twentieth century the pace of discovery of, and scientific interest in, pliopithecoid fossils, continued to lag behind that of the hominoids. New isolated teeth from Switzerland (Stehlin, 1914) and an older specimen from Dĕvínská Nová Ves, known since the end of the previous century but only described in Glässner (1931), preceded the exceptional review monograph by Johannes Hürzeler (1954a). He referred to recent discoveries to be described elsewhere, including the remains of several skeletons of a pliopithecoid from the Dĕvínská Nová Ves fissures (Zapfe, 1952; Zapfe & Hürzeler, 1957). Eventual publication of these specimens would jump-start research and interest in this group.

The spectacular discoveries made by Helmuth Zapfe in the fissures of Dĕvínská Nová Ves culminated in what many consider the best monograph ever written on a fossil primate – Zapfe’s monumental treatise on *Pliopithecus (Epipliopithecus) vindobonensis* (Zapfe, 1960). These specimens include the first postcranial fossils described for a pliopithecoid, although Lartet (1837b) noted some in his announcement. Major portions of three individuals are preserved at Dĕvínská Nová Ves, including a well-preserved skull, associated limb bones, vertebrae, scapulae and an ilium, which indicated extreme primitiveness. While he stressed resemblances to gibbons, Zapfe (1960) noted numerous similarities to platyrrhines, and even suggested that had they not been found in association, the humerus and the ear region of the temporal bone would scarcely have been recognized as anthropoid (Zapfe, 1958).

Along with more isolated specimens found at this time, a new type of pliopithecoid was discovered in 1959 and named *Plesiopliopithecus* (Zapfe, 1961; Bergounioux & Crouzel, 1965), which several authors have recognized as belonging to a distinct subfamily, the Crouzeliinae (Ginsburg & Mein, 1980; Andrews et al., 1996). In fact, most of the more

recently discovered pliopithecoids have been placed in the Crouzeliinae by these authors, though the justification for this is by no means clear (see below). This includes large samples of jaws, teeth and postcrania from Rudabánya, Hungary and Lufeng, Yunnan Province, China (Kretzoi, 1975; Pan, 1988). These latter specimens are also among the latest surviving members of the Pliopithecoidea, and dentally the most peculiar. Interestingly, these most recently discovered specimens may clear up one of the oldest controversies of paleoanthropology, the affinities of the famous femur from Eppelsheim (see below). Also discovered and described in this most recent phase of research are the oldest and most primitive pliopithecoids, *Dionysopithecus* and *Platodontopithecus*, from the early Miocene of China (Li, 1978; Gu & Lin, 1983), as well as a more advanced form, *Pliopithecus zhanxiangqi* (Harrison et al., 1991).

Beginning with Cuvier and his apparent dismissal of the Eppelsheim femur, through the great breakthrough by Lartet, and up to the present, pliopithecoids have been in and out of the limelight. Hürzeler and Zapfe did much to revive interest in this group, as did the discovery of “gibbon-like” fossils from east Africa (Le Gros Clark & Thomas, 1951; Ferembach, 1958; Fleagle, 1975; Andrews & Simons, 1977). However, in the final analysis, pliopithecoids tell us more about the dynamics of macroevolution than about the evolutionary history of gibbons, which remains shrouded in mystery.

## Taxonomy

### Systematic framework

#### The Pliopithecoidea

Because they are extinct, distant relatives of living catarrhines, a brief description of their defining features, assuming there are some, is appropriate before embarking on their systematics. Beyond the fact that they have only two premolars per quadrant in their adult dentitions, few characters define them as catarrhines and none offers convincing evidence that they are more closely related to modern catarrhines than are the earliest members of this group, the propliopithecoids of the Eocene and Oligocene of Egypt. In their recent review of the pliopithecoids, Harrison & Gu (1999) cite only three characters linking pliopithecoids to Old World monkeys and apes, and these are relatively unimpressive. They suggest that upper molars are narrower than those of *Propliopithecus* or *Aegyptopithecus*, lower molars are broader than *Propliopithecus* or *Aegyptopithecus*, and that the tubular ectotympanic is partially ossified. However, neither of the molar features is consistent in all pliopithecoids, and is also variable in propliopithecoids and platyrrhines. Worse still, the ectotympanic character is a presumed intermediate morphology and not an actual synapomorphy.

Most authors have assumed a unilinear direction in the evolutionary transformation (morphocline) of the catarrhine

ectotympanic (e.g., Szalay, 1975a; Szalay & Delson, 1979; Andrews et al., 1996). The scenario is as follows: the ectotympanic resembles a short bony tube fused to the outer surface of the auditory bulla in New World monkeys; it becomes an elongated tube, forming the canal of the outer ear (external auditory meatus). This occurs, it is assumed, through the intermediate step of a partially ossified tube, as seen in *Epipliopithecus vindobonensis* and superficially resembling some very young modern catarrhines. Direct evidence for this is lacking, however, and it is just as probable that the ectotympanic morphology of *Epipliopithecus vindobonensis* is either unique to that species or to the Pliopithecoidea, and independent of the evolution of an ectotympanic tube in Old World monkeys and apes, or primitive for Anthropoidea. In fact, among anthropoids the external auditory meatus in *Epipliopithecus* resembles those of *Tremacebus harringtoni*, a primitive platyrrhine from the late Oligocene of Argentina (Hershkovitz, 1974), and *Aegyptopithecus*, from the Oligocene of Egypt (Szalay & Delson, 1979; Fleagle & Kay, 1983). These forms also resemble much more primitive primates or primate relatives such as *Ignacius* and *Shoshonius* (Kay et al., 1992; Beard & MacPhee, 1994). While the inferior or ventral portions of the ectotympanic tube may be slightly more ossified in *Epipliopithecus*, convergence in the evolution of ectotympanics in fossil and living prosimians, plesiadapiforms and tarsiers is well noted (e.g., Szalay, 1975a; MacPhee, 1977, 1981; MacPhee & Cartmill, 1986; Kay et al., 1992; Beard & MacPhee, 1994) and there is no reason to think that anthropoids were immune to such phenomena.

In many ways pliopithecoid dental morphology is more similar to platyrrhines than to propliopithecoids. Pliopithecoids tend to have narrow lower incisors, occasionally waisted, or constricted at the junction of the crown and the root (the cervix), and this morphology is also found in a number of platyrrhines. In addition, one of the few defining traits that seems to be consistently present in pliopithecoids is a  $P_3$  with a tall crown, roughly triangular in outline, with a comparatively short, vertically oriented mesiobuccal face. The mesiobuccal face of the anterior premolar is not expanded to accommodate the upper canine, which in catarrhines is honed or sharpened by this structure (the sectorial premolar) (Andrews, 1978a; Harrison & Gu, 1999).

In most pliopithecoids the protoconid and metaconid are not transversely aligned, but slightly offset such that the protoconid is mesial to the metaconid. In some cases the fovea mesial to these cusps is also expanded and bears a small mesial cusp that may be homologous to the paraconid. These features are never found in even the most primitive hominoid or Old World monkey, but they are common in platyrrhines and many adapids and living prosimians (Begun, 1989b). Some pliopithecoids appear to have had shorter faces and larger brains than propliopithecoids, and these features are shared with catarrhines (Fleagle & Kay, 1983), but also with many platyrrhines. Ford (1994) found no unambiguous derived postcranial character shared between

*Epipliopithecus* and catarrhines. Unlike any catarrhine, *Epipliopithecus vindobonensis* retains such primitive features as an entepicondylar foramen at the distal end of the humerus, a hinge-like carpometacarpal joint of the thumb, a rectangular as opposed to squared posterior articular facet of the calcaneus, a posterior position of the anterior articular facet of the calcaneus, and possibly a prehallux bone in the foot (Zapfe, 1960; Fleagle, 1983; Ford, 1994; Andrews et al., 1996).

The point of this brief review of the Pliopithecoidea is to dispel the impression that they are little apes (Szalay & Delson, 1979; Fleagle, 1988) and focus attention on their primitiveness, as Zapfe (1958) noted long ago. All researchers who have analyzed pliopithecoids in some detail agree that they are not hominoids, and that they pre-date the division of Old World monkeys and apes. Pliopithecoids may be related to living catarrhines, may be an independent descendant lineage of the propliopithecoids, or may even be the sister clade to living anthropoids. More interesting, perhaps, is their diversity and success as the first modern-looking anthropoid to evolve and radiate in Eurasia. In many ways they mirror the evolutionary history of the New World monkeys, having found their way onto a land mass devoid of anthropoids.

The following taxonomy cautiously recognizes the Pliopithecoidea as primitive catarrhines, based only on their dental formula. The superfamily is subdivided into two families, which differs from the classification of Harrison & Gu (1999), who only recognize subfamilial distinctions. Within the two families few synapomorphies unite the included taxa, and there remains the distinct possibility that they, particularly the Pliopithecidae, will be found to be paraphyletic.

Order Primates Linnaeus, 1758

Infraorder Catarrhini É. Geoffroy Saint-Hilaire, 1812

Superfamily Pliopithecoidea Zapfe, 1960

Family Pliopithecidae Zapfe, 1960

Subfamily Dionysopithecinae

Genus *Dionysopithecus* Li, 1978

*Dionysopithecus shuangouensis* Li, 1978

*Dionysopithecus orientalis* Suteethorn et al., 1990

Genus *Platodontopithecus* Li, 1978

*Platodontopithecus jianghuaiensis* Li, 1978

Subfamily Pliopithecinae Zapfe, 1960

Genus *Pliopithecus* Gervais, 1849

*Pliopithecus piveteaui* Hürzeler, 1954

*Pliopithecus antiquus* Gervais, 1849

*Pliopithecus platyodon* Biedermann, 1863

*Pliopithecus zhanxiangi* Harrison et al., 1991

*Pliopithecus* sp.

Genus *Epipliopithecus* Zapfe & Hürzeler, 1957

*Epipliopithecus vindobonensis* Zapfe & Hürzeler, 1957

Genus *Egarapithecus* Moyà-Solà et al., 2001

*Egarapithecus narcisoi* Moyà-Solà et al., 2001

Family Crouzeliidae

Subfamily Crouzeliinae

Genus *Plesiopliopithecus* Zapfe, 1961

*Plesiopliopithecus lockeri* Zapfe, 1961

*Plesiopliopithecus ausitanensis* Bergounioux & Crouzel, 1965

*Plesiopliopithecus rhodanica* Ginsburg & Mein, 1980

*Plesiopliopithecus priensis* Welcomme et al., 1991

Genus *Anapithecus* Kretzoi, 1975

*Anapithecus hemyaki* Kretzoi, 1975

Genus *Laccopithecus* Wu & Pan, 1984

*Laccopithecus robustus* Wu & Pan, 1984

Family incertae sedis

Genus *Paidopithecus* Pohlig, 1895

*Paidopithecus rhenanus* Pohlig, 1895

## Superfamily Pliopithecoidea

### Family Pliopithecidae

#### Subfamily Dionysopithecinae

**GENUS** *Dionysopithecus* Li, 1978

A genus of small primitive catarrhine approximating the size of gibbons. Of the two species recognized here one is known only from a single lower molar. Thus, the genus is defined essentially by the morphology of the better-known species, *Dionysopithecus shuangouensis*. Four isolated teeth from Pakistan are also referred to *Dionysopithecus* but no species is defined, so these teeth are not described here (Bernor et al., 1988).

**INCLUDED SPECIES** *D. orientalis*, *D. shuangouensis*

**SPECIES** *Dionysopithecus shuangouensis* Li, 1978

**TYPE SPECIMEN** IVPP V5597 (from Songlinzhuang, Sihong County, Jiangsu Province, People's Republic of China), a left maxillary fragment with  $M^{1-3}$ .

**AGE AND GEOGRAPHIC RANGE** The earliest species of the genus, known from the Xiaocowan Formation at the type locality of Songlinzhuang, dated by faunal associations to between 17 and 18 Ma; also recognized from the Zhenji locality, thought to be of similar age (Harrison & Gu, 1999; Qiu et al., 1999).

#### **ANATOMICAL DEFINITION**

*Dionysopithecus shuangouensis* is known only from isolated teeth. It has a broad  $I^1$  with a pronounced lingual cingulum and female upper canines that are triangular in horizontal cross-section. Upper premolars are narrow while upper molars are comparatively broad with well-developed lingual cingula and moderately developed buccal cingula.  $M^3$  has strongly reduced distal cusps. Incisors are tall-crowned, narrow and waisted.  $P_3$  is vertical and lacks the crown flare of a structurally sectorial  $P_3$  (see above).  $P_4$  has a lingual cusp (metaconid) that is lower in cusp height



than the buccal cusp (protoconid), a feature not found in other currently recognized pliopithecoids, but possibly present in one specimen from Kenya (see below). The lower molars are long and narrow, often preserving the paraconid, a mesial cusp otherwise only found in prosimians and the most primitive anthropoids. The other mesial cusps are not aligned transversely, as in most other catarrhines, but, common to pliopithecoids, the buccal cusp (protoconid) is more anterior or mesial than the lingual cusp (metaconid). The cristid obliquid is obliquely oriented, again as in most pliopithecoids and more primitive anthropoids, and unlike most other catarrhines. Finally, a pliopithecine triangle, one of the few defining characters of the Pliopithecoidae, is present. This feature consists of a subtle set of ridges on the buccal side of the crown defining a small triangular shaped pit between the protocone and hypocone (Hürzeler, 1954a). *Dionysopithecus shuangouensis* (and *Platodontopithecus jianghuaiensis*) are distinguished from other pliopithecoids in having relatively rounded molar cusps and moderately developed upper molar buccal cingula, narrow  $M^1$  with a distinctively convex lingual edge, and small  $M^3$  with reduced lingual cusps (Ginsburg & Mein, 1980; Harrison & Gu, 1999).

**SPECIES** *Dionysopithecus orientalis* Suteethorn et al., 1990

**TYPE SPECIMEN** TF 2451, an  $M_1$

**AGE AND GEOGRAPHIC RANGE** Known only from a single tooth dated by faunal association to between 16 and 17 Ma (Ducrocq et al., 1994; Qiu et al., 1999), from Ban San Klang, northern Thailand

**ANATOMICAL DEFINITION**

Though originally referred to the east African genus *Dendropithecus*, *Dionysopithecus orientalis* is referred to *Dionysopithecus* in Harrison & Gu (1999) based on strong similarities to the type species, *D. shuangouensis*. These include size and basic morphological attributes of the occlusal surface typical of pliopithecoids. For example, *D. orientalis* has mesial cusps that are offset, such that the buccal cusp is more mesial than the lingual cusp, as in most pliopithecoids, but unlike *Dendropithecus* and hominoids. It should be noted however, that while the morphology of the Ban San Klang molar is clearly pliopithecoid, its distinctiveness from the type species of *Dionysopithecus* remains to be proven. Harrison & Gu (1999) are cautious in recognizing a separate species, and this is wise given the known range of variation in molar morphology among pliopithecoids.

**GENUS** *Platodontopithecus* Li, 1978

**INCLUDED SPECIES** *P. jianghuaiensis*

**SPECIES** *Platodontopithecus jianghuaiensis* Li, 1978

**TYPE SPECIMEN** PA 870, currently in the collections of the IVPP, Beijing, PRC. a left  $M^3$

**AGE AND GEOGRAPHIC RANGE** Known from the Xiaocowan Formation at the type locality of Songlinzhuang, Sihong County, Jiangsu Province, PRC, dated by faunal associations to between 17 and 18 Ma; also recognized from the Zhenji locality, thought to be of similar age (Harrison & Gu, 1999; Qiu et al., 1999)

**ANATOMICAL DEFINITION**

*Platodontopithecus jianghuaiensis* is known only from isolated teeth, which are considerably larger than those of *D. shuangouensis*, being somewhat larger than siamang teeth. Harrison & Gu (1999) estimate the body mass at about 15 kg. Presumed male upper canines are tall and bilaterally compressed. The upper premolars are broader than in *Dionysopithecus*, and the lower  $P_4$  has subequal mesial cusps unlike *Dionysopithecus*. The molars are like *Dionysopithecus* but slightly narrower, with higher cusps and crests, including a better developed pliopithecine triangle.

**Subfamily Pliopithecinae**

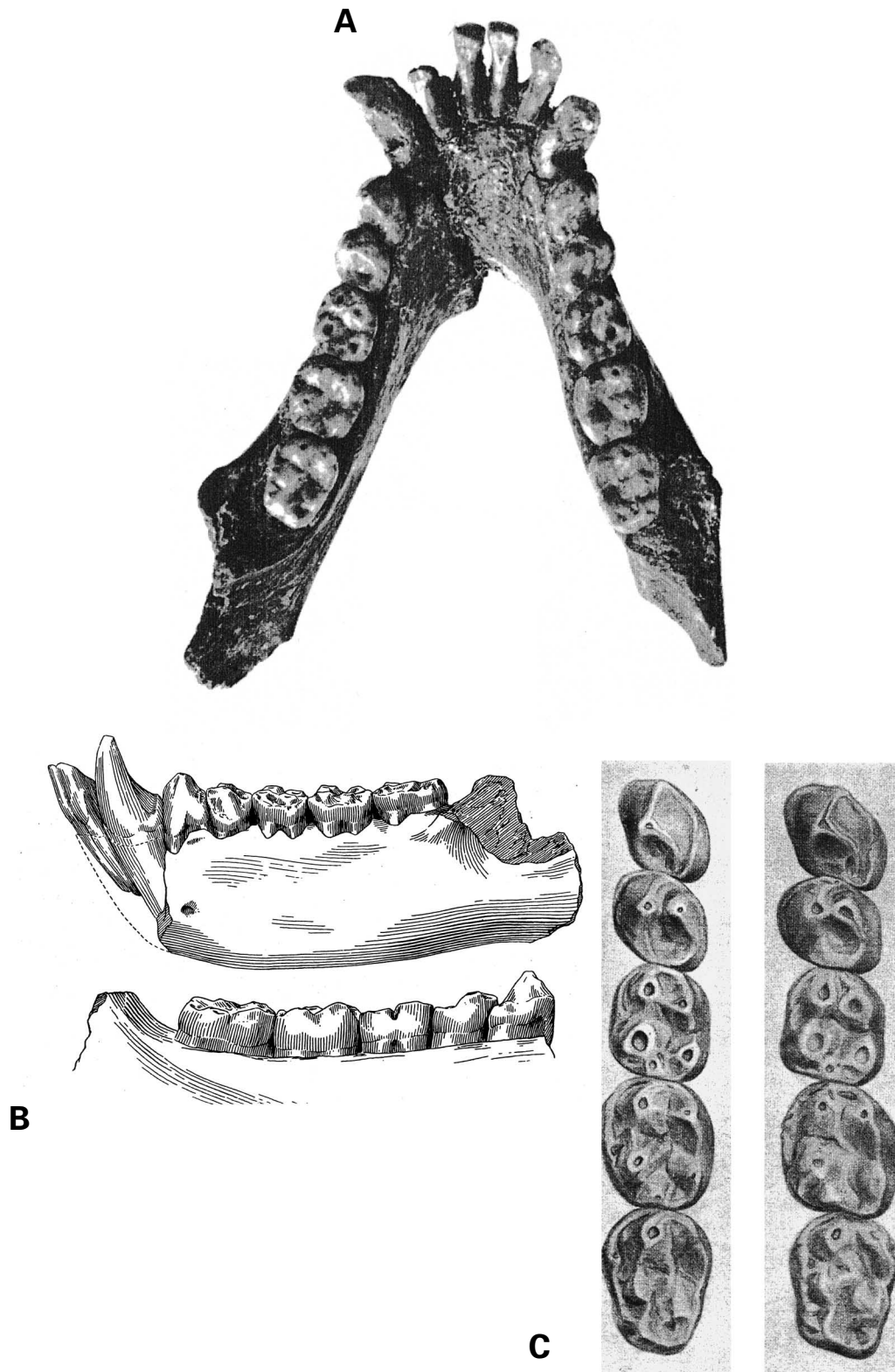
**GENUS** *Pliopithecus* Gervais, 1849

A genus of small primitive catarrhine approximating the size range of hylobatids. Pliopithecines share with dionysopithecines a suite of dental characters that are almost all primitive for anthropoids. These include incisors that are tall-crowned, narrow and waisted, spatulate but labiolingually flat upper central incisors, narrow, pointed and asymmetrical upper lateral incisors, tall, broad  $P_3$  crown lacking a truly sectorial morphology, long and narrow lower molars, often preserving a paraconid, mesial cusps that are aligned obliquely, an obliquely oriented cristid obliquid, and a pliopithecine triangle. In most species of *Pliopithecus* the  $P_4$  and lower molars tend to be long and narrow with large anterior or mesial pits (fovea) and well-developed buccal cingula. Though most species have teeth close in size to *Hylobates*, the mandibles tend to be more massive. Upper premolars and molars tend to be broad and short. The premolars have heteromorphic cusps, the buccal ones always the more prominent. The upper molars usually have well-developed, shelf-like lingual cingula, and commonly buccal cingula or stylar shelves. Upper molars commonly lack a distal transverse ridge between the hypocone and metacone, but have a ridge connecting the hypocone to the protocone or the crista obliqua (this is true of crouzelines as well, in contrast to the opinion of Andrews et al. (1996)).

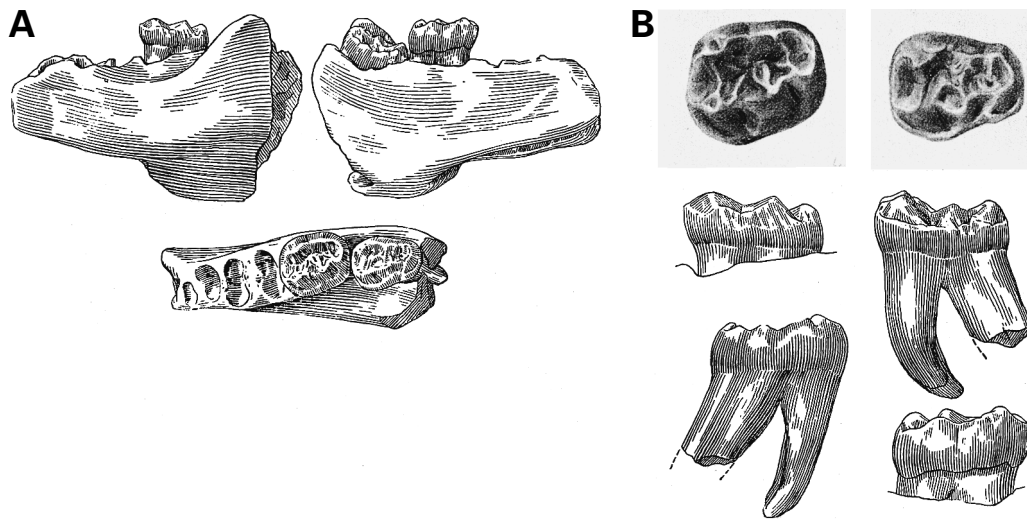
**INCLUDED SPECIES** *P. antiquus*, *P. piveteaui*, *P. platyodon*, *P. zhanxiangi*

**SPECIES** *Pliopithecus antiquus* Gervais, 1849 (Fig. 15.1)

**TYPE SPECIMEN** From the E. Lartet collection from Sansan at the Muséum National d'Histoire Naturelle, Paris, a mandible lacking only the rami and portions of the right canine and left  $I_2$  crowns



**Fig. 15.1** *Pliopithecus antiquus*. (A) The type mandible in occlusal view; (B) buccal and lingual view of the type; (C) occlusal drawings of the type (both appear to be from the left side, but in fact the row on the left is a photographically reversed image of the right side dentition, for ease of comparison with the left side and with other dentitions). Adapted from Simons (1972) and Hürzeler (1954a).



**Fig. 15.2** *Pliopithecus piveteaui*. (A) Three views of the type and only specimen, a right mandible photographically reversed here; (B) studies of the  $M_2$  (left) and  $M_3$  (right). Adapted from Hürzeler (1954a).

**AGE AND GEOGRAPHIC RANGE** *Pliopithecus antiquus* is definitively identified only at Sansan and La Grive, both in France and dated to MN 6 (about 15 Ma). Hürzeler (1954a) was of the view that the species is only known from Sansan, but most subsequent authors also include the La Grive specimen, which comes from older sediments than the *Dryopithecus* teeth from the same site (Ginsburg, 1975, 1986). *Pliopithecus antiquus* may also be known from other MN 6 localities in Germany (Diessen am Ammersee, Stätzing, Ziemetshausen, Gallenboch) and Switzerland (Kreuzlingen and Rümikon), though these are isolated teeth and their species attribution is uncertain. Similarly, *P. antiquus* has been tentatively identified at later localities in Poland (MN 7 of Opole, Poland; MN 8 of Castel de Barbera, Spain and Przeworno II, Poland; MN 9 of Doué-la-fontaine and Meigné-le-vicomte, France), though again only on the basis of isolated teeth. In a number of cases however, authors note similarities to the sample from Göriach referred previously to *P. antiquus* but here, following Andrews et al. (1996), referred to *P. platyodon*. In addition, one of these samples, from Castel de Barbera, is recognized here as a distinct species (see below). Conservatively, we can conclude that *P. antiquus* is an MN 6 taxon from France that may have persisted into later periods (MN 6–9) in more central areas of Europe.

#### **ANATOMICAL DEFINITION**

*Pliopithecus antiquus* is dentally among the smallest species of *Pliopithecus*, though there is extensive overlap among the European species (Fig. 15.1). In addition to size, *P. antiquus* can be distinguished from some other species only by a number of subtle dental characters. To avoid repetition, these are listed in the anatomical definitions of the other species.

**SPECIES** *Pliopithecus piveteaui* Hürzeler, 1954 (Fig. 15.2)

**TYPE SPECIMEN** In the Lecoindre collections at la Chapelle-Blanche, Mantelhan (Indre et Loire), a right mandibular fragment with  $M_{2-3}$  and alveoli for the roots of the  $P_4$  and  $M_1$

**AGE AND GEOGRAPHIC RANGE** Dated to MN 5 (16–17 Ma), only from the Loire valley of France (Faluns de Touraine, Anjou, Pontevoy-Thenay, Mantelhan) (Ginsburg & Mein, 1980; Ginsburg, 1986).

#### **ANATOMICAL DEFINITION**

The combination of subtle morphological differences, more primitive morphology, geography and greater age suggest that *P. piveteaui* is a distinct species, as originally recognized by Hürzeler (1954a) and more recently by Ginsburg (1975, 1986) and Ginsburg & Mein (1980). The type specimen is unusual for pliopithecines in having a very small  $M_3$  in relation to  $M_2$ . The teeth are small but within the range of *P. antiquus*. They are considerably smaller than in other most species, but close to those of the small species from Castel de Barbera (see below). Both teeth narrow distally, a feature common in  $M_3$  but unusual in  $M_2$ . The  $M_3$  of the type has an even more tapered morphology than is typical for the genus. The  $M_3$  has a very reduced entoconid (the distal lingual cusp) and the  $M_2$  has a smooth and flared, or bulging buccal surface lacking the buccal cingulum typical of *P. antiquus*. Finally, the cusps on both molars are more bilaterally compressed, the crests that connect them more strongly defined, and the fovea and basins that separate them are larger, all compared to *P. antiquus*. These latter features are found in a number of other pliopithecoids, including *P. platyodon*, *P. sp.* from Spain and in most crouzeliines, and thus may be primitive for the superfamily. The right  $P_4$  is broad and also has a more bulging buccal surface than in *P. antiquus*, with a larger talonid basin, a lower protoconid and a more strongly developed hypoconid (Ginsburg, 1975). Ginsburg (1975)

also described additional lower molars that resemble the type. Finally, two upper teeth are known, a  $P^4$  and  $M^3$ , which cannot be compared directly to *P. antiquus* from Sansan. Compared to an isolated  $P^4$  from Poland that may belong to *P. antiquus* or *P. platyodon* (Kowalski & Zapfe, 1974) the *P. piveteaui*  $P^4$  is smaller, and relatively broader or shorter, with a relatively larger protocone, a pronounced lingual cingulum, and a much shorter talon. Both upper teeth more closely resemble *P. platyodon*  $P^4$  specimens from Göriach, though again they are much smaller (Fig. 15.4).

A number of researchers have recently suggested that *P. piveteaui* is indistinguishable from *P. antiquus* (Harrison et al., 1991; Andrews et al., 1996). Andrews et al. (1996) consider the relative size of the  $M_3$  and its unusual morphology, which distinguishes *P. piveteaui* from *P. antiquus*, to be unreliable given known ranges of variability in this tooth. They do not comment on other aspects of the dental morphology of *P. piveteaui*. In light of the number of differences from *P. antiquus* and the consistency of those differences in the larger samples described by Ginsburg (1975), *P. piveteaui* is recognized here as a separate species. Its apparently primitive morphology may be an important hint to understanding some aspects of the evolutionary history of the Pliopithecoidea (Ginsburg & Mein, 1980, and see below).

**SPECIES** *Pliopithecus platyodon* Biedermann, 1863 (Fig. 15.3)

**TYPE SPECIMEN** In the collections of the Museum of Winterthur, Zurich, a damaged female maxilla with heavily worn dentition

**AGE AND GEOGRAPHIC RANGE** *Pliopithecus platyodon* from Elgg (near Zurich) is considered to be MN 5 in age, based on biostratigraphic correlations (Ginsburg, 1986); however, the bulk of the sample currently attributed to this taxon is from the MN 6 locality of Göriach, Austria

**ANATOMICAL DEFINITION**

*Pliopithecus platyodon*, based on the sample from Göriach, is dentally larger on average than *P. antiquus*. According to Andrews et al. (1996), *P. platyodon* has a relatively broader  $P_3$  and slightly longer, more rectangular lower molars that increase in size from  $M_1$  to  $M_3$  more than in *P. antiquus*. However, these characters are very variable in the Göriach sample. It is safe to say that *P. antiquus* and *P. platyodon* are very similar and essentially differ only in size (Fig. 15.3).

Hürzeler (1954) and Zapfe (1960) both suggested that the Elgg and Göriach samples may represent the same species, but were reluctant to attribute the Göriach material to *P. platyodon* due to the poorly preserved occlusal morphology of the type. Harrison et al. (1991) formally combined the two samples. Andrews et al. (1996) cite a number of differences between the Göriach and Sansan samples as evidence of their taxonomic distinction (see below). Of course, it remains unclear if Elgg and Göriach are really the same taxon or if another species of *Pliopithecus*, *P. goeriachensis* (Sera, 1917) should be recognized. Here I

follow Harrison et al. (1991). As noted above, a number of other specimens usually attributed to *P. antiquus* may in fact belong to *P. platyodon* (Hürzeler, 1954).

**SPECIES** *Pliopithecus zhanxiangi* Harrison et al., 1991

**TYPE SPECIMEN** BPV-1021 (found at Maerzuizigou (BN 87021), Tongxin County, People's Republic of China, and in the collections of the IVPP, Beijing), a damaged female cranium

**AGE AND GEOGRAPHIC RANGE** Considered to be contemporary with Sansan (MN 6), based on faunal similarities (Harrison et al., 1991; Qiu et al., 1999), China

**ANATOMICAL DEFINITION**

*Pliopithecus zhanxiangi* is the largest species of the genus. Lower molars, which bear pliopithecine triangles, increase markedly in size from  $M_1$  to  $M_3$ . They commonly show secondary wrinkling of the occlusal surface. The mandible is robust with a large extramolar sulcus. The upper canine is thick and relatively low-crowned, and the upper premolars and molars are very broad with strong buccal cingula (Harrison et al., 1991). On the buccal sides of the  $M_{2-3}$  there is a depression or notch that gives the tooth a waisted appearance.

Unlike other species of the genus, *P. zhanxiangi* is also known from a partial cranium, distinguished from *E. vindobonensis* primarily by size. The anterior palate is somewhat more complete in *P. zhanxiangi*, revealing large, broad incisive foramina, similar to those of hylobatids and other non-hominid primates. The inferior orbital fissure is large, a feature also more typical of non-catarrhine primates (e.g., Hershkovitz, 1974). *Pliopithecus zhanxiangi* shares with *E. vindobonensis* a short face with narrow premaxilla, broad incisive foramina, narrow, oval-shaped nasal apertures, broad orbits with mildly projecting rims, low cheek bones (zygoma), and restricted maxillary sinuses.

**GENUS** *Epipliopithecus* Zapfe & Hürzeler, 1957

**INCLUDED SPECIES** *E. vindobonensis*

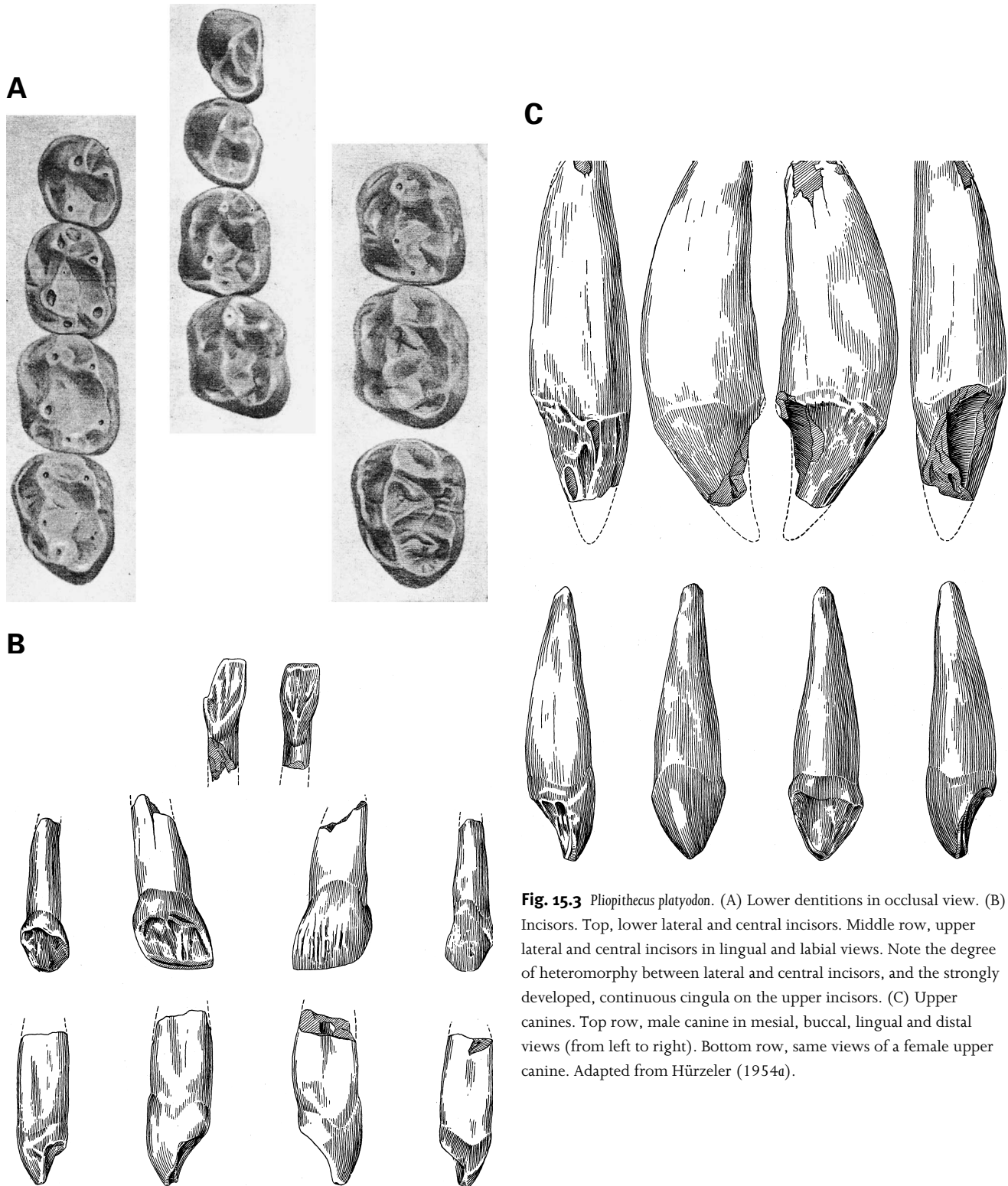
**SPECIES** *Epipliopithecus vindobonensis* Zapfe & Hürzeler, 1957 (Figs. 15.4–15.6; see also Fig. 20.1)

**TYPE SPECIMEN** In the collections of the Naturhistorische Museum, Vienna, Individual III from the Děvinská Nová Ves fissures (Harrison et al. (1991) describe a palate as part of the holotype, but this is from Individual II (Zapfe, 1960); their Figure 9 with a view of the type (Individual III) is correct), portions of a mandible, maxilla, cranial fragments, vertebrae, a left clavicle, left humerus, distal left ulna, carpals, metacarpals and phalanges

**AGE AND GEOGRAPHIC RANGE** Based on faunal comparisons, generally considered to be lower MN 6 or upper MN 5 in age, about 15 to 15.5 Ma (Zapfe, 1958; Ginsburg, 1986; Rögl, 1999), eastern Europe

**ANATOMICAL DEFINITION**

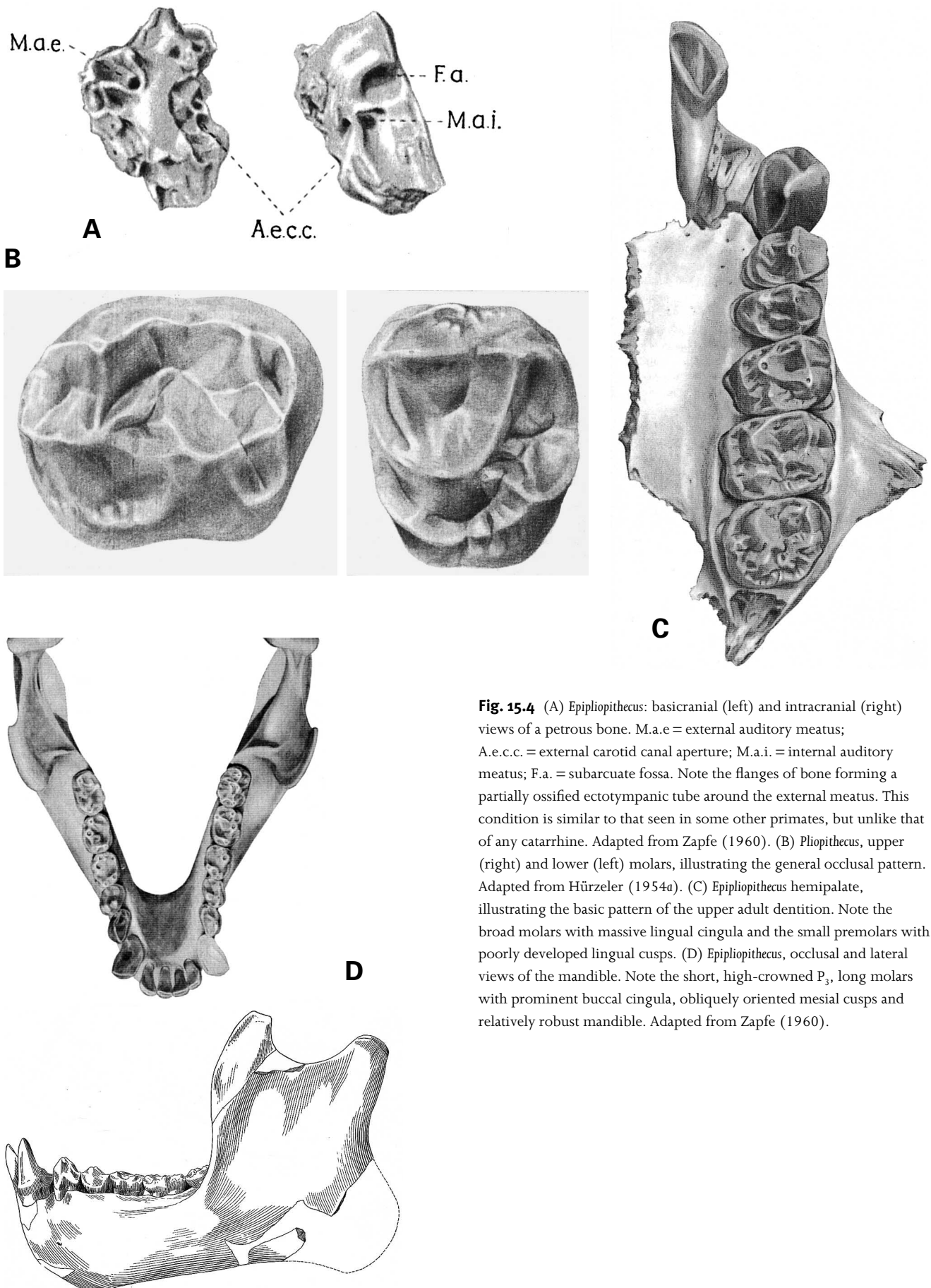
*Epipliopithecus vindobonensis* was originally named as a subgenus of *Pliopithecus*, *P. (Epipliopithecus) vindobonensis* (Zapfe &



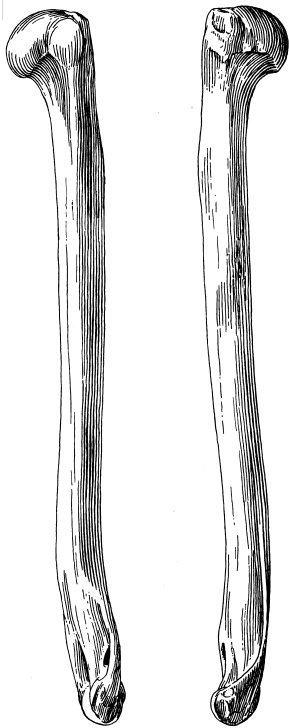
**Fig. 15.3** *Pliopithecus platyodon*. (A) Lower dentitions in occlusal view. (B) Incisors. Top, lower lateral and central incisors. Middle row, upper lateral and central incisors in lingual and labial views. Note the degree of heteromorphy between lateral and central incisors, and the strongly developed, continuous cingula on the upper incisors. (C) Upper canines. Top row, male canine in mesial, buccal, lingual and distal views (from left to right). Bottom row, same views of a female upper canine. Adapted from Hürzeler (1954a).

Hürzeler, 1957). In addition to the impressive type specimen, *E. vindobonensis* is known from two more partial skeletons and a number of isolated remains, all from the same fissure deposit. Dentally *E. vindobonensis* can be distinguished from *Pliopithecus* by a number of features. These include differences from *P. antiquus* in overall larger dental size, higher-crowned lower incisors, upper central

incisor broad with a notched lingual cingulum,  $P_4$  and lower molars slightly narrower, indistinct or missing pliopithecine triangle, slightly broader upper molars, small trigone basin on molars, less well-developed buccal cingulum on upper molars, and greater size differences between molars. It is due to this more impressive suite of dental differences, particularly the absence of a



**Fig. 15.4** (A) *Epipithecus*: basicranial (left) and intracranial (right) views of a petrous bone. M.a.e = external auditory meatus; A.e.c.c. = external carotid canal aperture; M.a.i. = internal auditory meatus; F.a. = subarcuate fossa. Note the flanges of bone forming a partially ossified ectotympanic tube around the external meatus. This condition is similar to that seen in some other primates, but unlike that of any catarrhine. Adapted from Zapfe (1960). (B) *Pliopithecus*, upper (right) and lower (left) molars, illustrating the general occlusal pattern. Adapted from Hürzeler (1954a). (C) *Epipithecus* hemipalate, illustrating the basic pattern of the upper adult dentition. Note the broad molars with massive lingual cingula and the small premolars with poorly developed lingual cusps. (D) *Epipithecus*, occlusal and lateral views of the mandible. Note the short, high-crowned  $P_3$ , long molars with prominent buccal cingula, obliquely oriented mesial cusps and relatively robust mandible. Adapted from Zapfe (1960).



**Fig. 15.5** *Epipliopithecus vindobonensis*. Medial (left) and lateral (right) views of the humerus illustrating the primitive nature of this taxon. Note the entepicondylar foramen. Adapted from Zapfe (1960).

pliopithecine triangle and the distinctive morphology of the incisors that *E. vindobonensis* is recognized here as a separate genus from *Pliopithecus*.

*Epipliopithecus vindobonensis* has a fairly large and globular braincase with well-developed temporal lines (in one specimen meeting in the midline to form a low sagittal crest), a relatively projecting snout (though less than in *Aegyptopithecus*), orbits slightly laterally deviated with a prominent, projecting glabellar region, supraorbital costae that do not meet in the midline to form a torus, depressed frontal trigon, relatively short but vertical frontal squama, broad interorbital space, prominent lacrimal crest obscuring the lacrimal fossa from anterior view, petrous bones with a large subarcuate fossa, and an incompletely ossified ectotympanic tube. The mandibles are long and have robust corpora and broad rami with prominent, flared gonial angles. Postcranially *E. vindobonensis* most closely resembles long-limbed New World monkeys but also relatively leggy Old World monkeys. In brachial index it is more like suspensory New World monkeys and prosimians, but hindlimb overall length and the crural index are closer to Old World monkeys (Zapfe, 1960). However, the crural index of *E. vindobonensis* is also very close to gibbons and chimpanzees, and within the human range (Zapfe, 1960). Unlike apes, however, the forelimb was slightly shorter than the hindlimb, being most comparable to howling monkeys but also baboons (Zapfe, 1960). The trunk was long and slender, and probably had seven lumbar vertebrae,

a long sacrum and possibly a tail (Zapfe, 1960; Ankel, 1965). *Epipliopithecus vindobonensis* had comparatively long hands and feet, and long, curved fingers, and was mostly likely an agile climber. This is also suggested by the morphology of the joint surfaces of the limb bones (Fig. 15.6).

**GENUS** *Egarapithecus* Moyà-Solà et al., 2001

**INCLUDED SPECIES** *E. narcisoi*

**SPECIES** *Egarapithecus narcisoi* Moyà-Solà et al., 2001

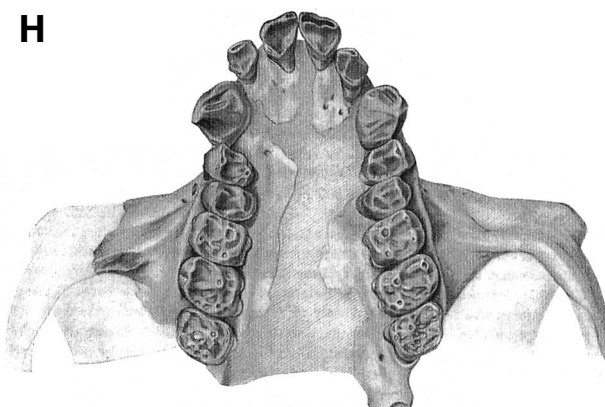
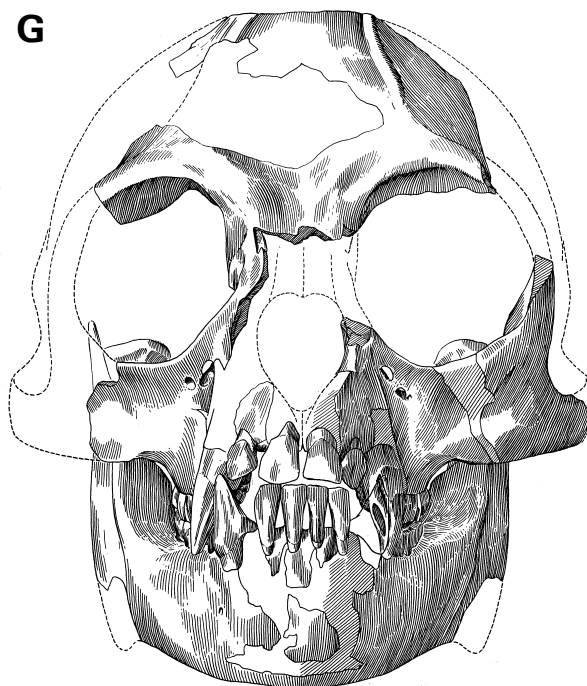
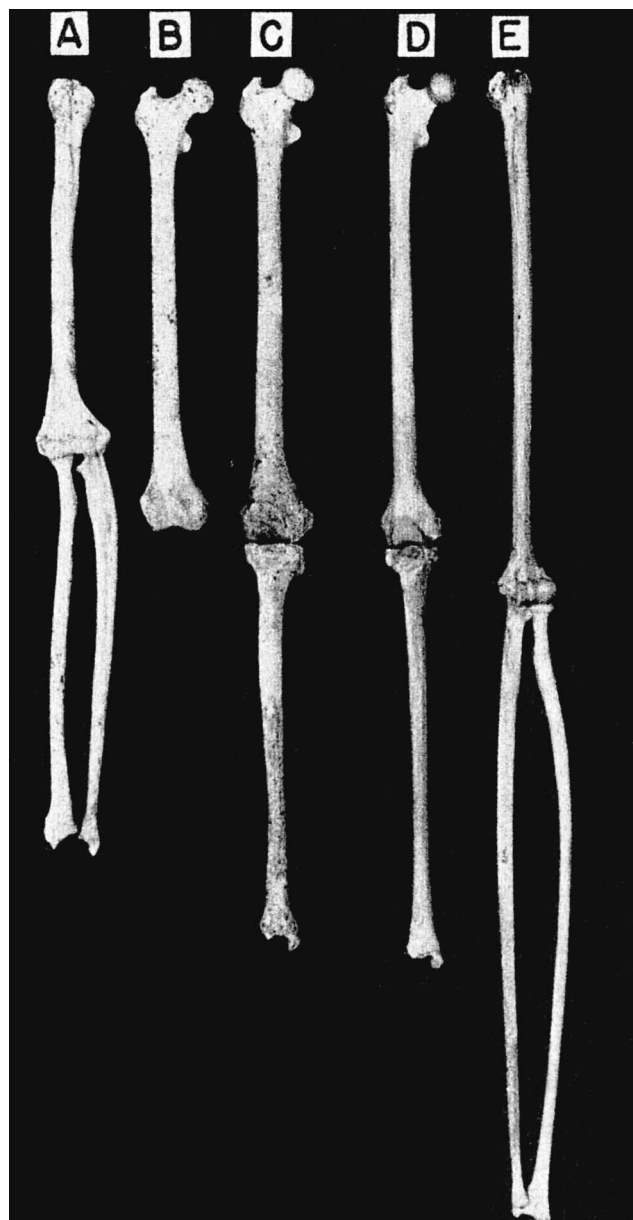
**TYPE SPECIMEN** IPS 2943, a fragmentary mandible

**AGE AND GEOGRAPHIC RANGE** Torrent de Febulines, in the Vallés Penedés basin of Catalonia near Barcelona, is biostratigraphically dated to MN 10 and is placed in Chron C4An of the Geomagnetic Polarity Time Scale, indicating an age of about 9 Ma (Moyà-Solà et al., 2001).

**ANATOMICAL DEFINITION**

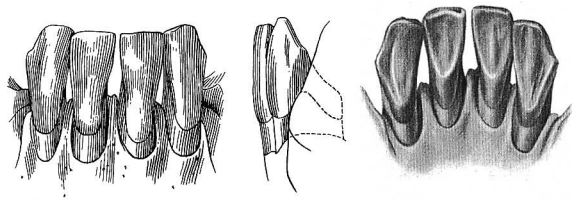
The type specimen and an associated palatal fragment with a right P<sup>3</sup> have been mentioned in the literature by Golpe-Posse (1982) and Andrews et al. (1996), and recently named to a new genus by Moyà-Solà et al. (2001). *Egarapithecus* has a very distinctive occlusal morphology that surely merits a genus-level distinction. The lower teeth are narrow and elongated with sharply defined occlusal crests and large talonid basins. The P<sub>3</sub> has a strong metaconid and the P<sub>4</sub> an exceptionally elongated talonid with well-formed distal cusps. The molars have small mesial fovea and larger distal fovea, opposite the condition in *Anapithecus*. The M<sub>3</sub> is exceptionally long and narrow. The mandible is extremely deep relative to transverse breadth compared to *Epipliopithecus*, *Anapithecus* and *Pliopithecus*. Moyà-Solà et al. (2001) suggest that the small canines in the symphyseal fragment are unerupted, despite the wear on the M<sub>3</sub> (canines almost always erupt before the M<sub>3</sub> in catarrhines). However, unerupted canines lack root apical closure, while the canines in the *Egarapithecus* type have completed roots. The fact that the canines in *Egarapithecus* remain embedded in the mandible probably results from a pathology, another possibility suggested by Moyà-Solà et al. (2001). The incisors (based on the exposed roots) and canines are very small, even for a female, but it is not clear to what extent this is normal for the genus. The palatal fragment preserves the distal surface of the canine alveolus indicating the presence of a large upper canine, probably of a male. Thus it is unlikely to have come from the same individual as the type. The P<sup>3</sup> is also unusual in being rectangular with roughly equal mesial and distal moieties, unlike most other pliopithecoids.

As noted by Andrews et al. (1996) and Moyà-Solà et al. (2001), *Egarapithecus* has some crouzeliine similarities, and indeed these authors assign this taxon to the Crouzeliinae. These similarities mainly involve lower dental elongation and sharply developed occlusal crests, which, while more strongly developed in crouzeliines, are nevertheless present

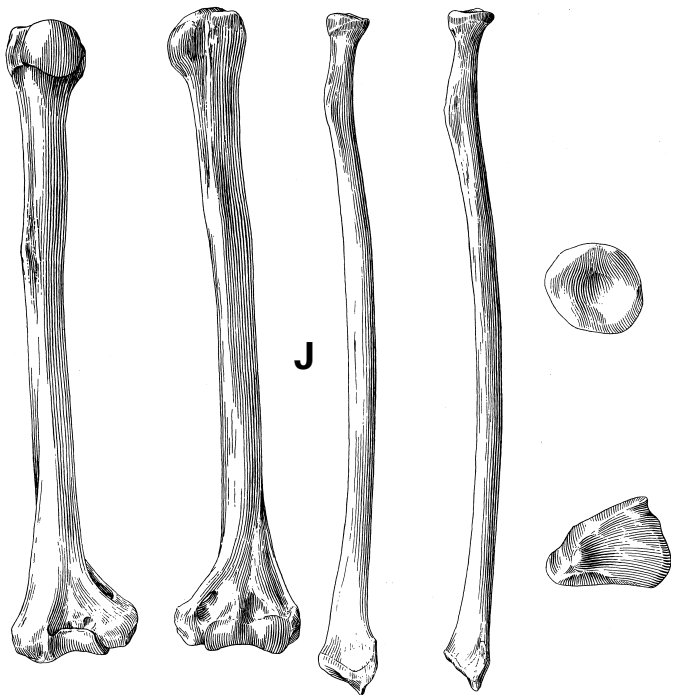
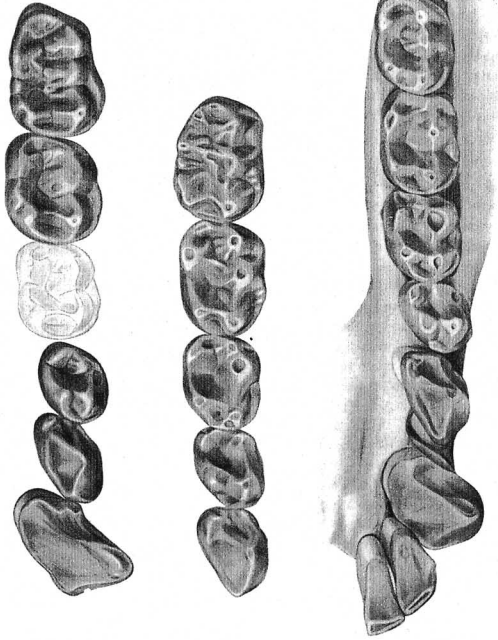


**Fig. 15.6** *Epipliothecus vindobonensis*. (A–H) The best preserved cranium and limbs. The limb bones of *Epipliothecus* (A–C) are compared to those of a gibbon (D,E); (F) lateral view of the skull; (G) frontal and (H) palatal views. (I) (overleaf) Lower dentitions. Note the tall, narrow, heteromorphic lower incisors (top) and the absent or poorly defined pliothecine triangle on the lower molars. (J) Upper limb bones (humerus left, radius right). (K) Study of the ulna. Note the prominent olecranon process, unkeeled trochlear notch, small, anteriorly placed and facing radial facet and the deep shaft (top row). Note also the very prominent and robust ulnar styloid (bottom row). (L) Hands and feet. Top row, articulated left hand skeleton and dorsal, left lateral, right lateral and palmar views of a 2nd hand proximal phalanx. Bottom row, same views of a hallux proximal phalanx and a 3rd proximal phalanx of the foot, and an articulated left foot. (M) Cranial (top) and caudal (bottom) views of the sacrum. Note the large sacral canal, suggesting the presence of a long tail (Ankel, 1965). Adapted from Zapfe (1960).

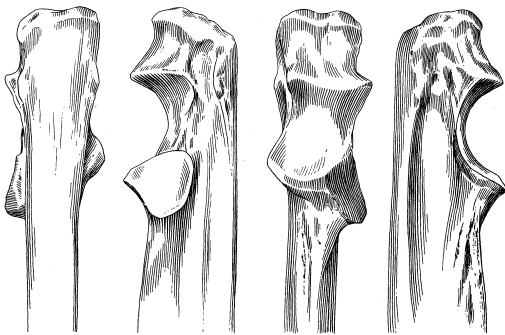




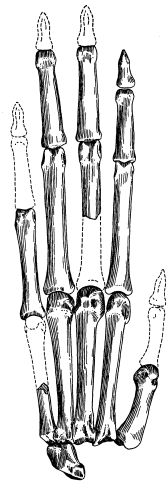
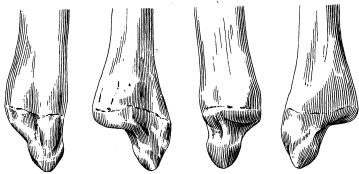
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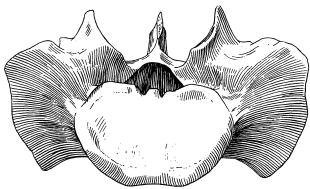
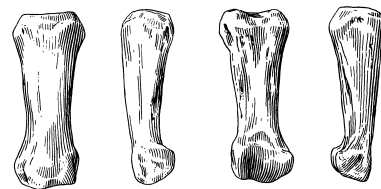
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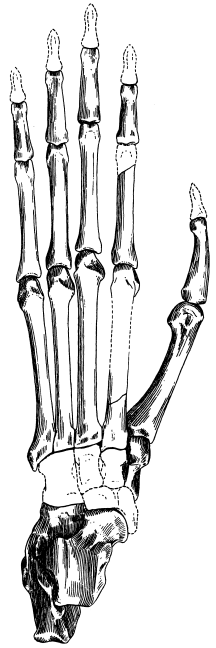
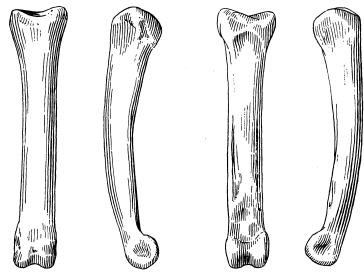
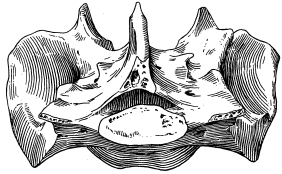


Fig. 15.6 (cont.)

in some pliopithecids, including those from the nearby and somewhat older locality of Castel de Barbera (see below). However, *Egarapithecus* lacks key features, such as large mesial basins, and has unique characters, such as very long molars and premolars,  $P_4$  with large distal cusps, very obliquely oriented oblique crests and very small lower anterior teeth, suggesting that this taxon evolved independently from the crouzeliines, the view adopted here. It may be a descendant of the Castel de Barbera taxon, which has some similar characteristics but in a less well-developed state.

## New pliopithecine

At least one new taxon belonging to this subfamily is probably present in Spain, but given the scope of this work it is not formally named here. A new species of *Pliopithecus* is represented by specimens from two other localities in the Vallés Penedés basin. The most informative specimen is an associated upper and lower dentition of a small catarrhine from the MN 8 locality of Castel de Barbera. Recognition of a new but unnamed species here contrasts with the view of Andrews et al. (1996), who consider these teeth to belong to *P. antiquus*. However, the Castel de Barbera specimens are smaller on average than *P. antiquus*, and are morphologically distinctive. They have bilaterally compressed cusps with well-developed crests and large occlusal basins. In some respects these are similarities with *P. piveteaui*, but they are more strongly developed in the Spanish taxon. In addition, a right  $dP_4$  is known from Can Feliu, also considered to be of MN 8 age (Ginsburg, 1986). Andrews et al. (1996) consider this specimen to be a crouzeliine based on the fact that in size it is more consistent with *Egarapithecus*, which they consider to be a crouzeliine. As noted above, *Egarapithecus* lacks diagnostic crouzeliine characters. In addition, the Can Feliu specimen is morphologically closer to homologous *Pliopithecus* teeth from Göriach than to crouzeliine specimens from Rudabánya. It is long compared to breadth and has a narrower talonid, a more mesial protoconid and a distinctive trigonid with a long basin divided by a transverse ridge ending mesiolingually at a small paraconid. It is probably from a larger individual of the same taxon as the Castel de Barbera dentitions. An isolated male canine from Castel de Barbera (IPS 1823), considerably larger than that from the associated dentitions, may also represent this taxon.

## Family Crouzeliidae

### Subfamily Crouzeliinae

Ginsburg & Mein (1980) defined Crouzeliinae based on the type genus *Crouzelia*. Subsequent authors (e.g., Andrews et al., 1996) have recognized that *Crouzelia* cannot be distinguished from *Plesiopliopithecus*, but the suprageneric taxon remains valid. Here it is elevated to a family based on the numerous differences from the Pliopithecidae.

Crouzeliids in general differ from pliopithecids in having sharper, more bilaterally compressed cusps more displaced toward the margins of the crowns, resulting in larger, relatively deep occlusal basins (except the distal basin, which is restricted and lingually offset) (Ginsburg & Mein, 1980; Begun, 1989b; Andrews et al., 1996). These traits are similar to those in pliopithecines from Spain, but more strongly expressed. Crouzeliines also differ in having elongated molars and premolars with sharp, well-developed crests, particularly between the trigonids and talonids and along the crown margins.

### GENUS *Plesiopliopithecus* Zapfe, 1961

*Plesiopliopithecus* is a small primitive catarrhine, most of the species of which are, on average, smaller in dental size than *Pliopithecus*. Like *Epipliopithecus*, *Plesiopliopithecus* was originally recognized as a subgenus of *Pliopithecus* by Zapfe (1961). I follow Ginsburg & Mein (1980) in elevating *Plesiopliopithecus* to genus status here. *Plesiopliopithecus* species are only known from lower teeth. They are distinguished from other crouzeliines in being much smaller and in having very reduced hypoconulids. In addition to their crouzeliine characters, they retain typical features of the pliopithecoids including a variably expressed pliopithecine triangle, obliquely oriented oblique crest and a protoconid that is mesial to the metaconid.

**INCLUDED SPECIES** *P. auscitanensis*, *P. lockeri*, *P. priensis*, *P. rhodanica*

**SPECIES** *Plesiopliopithecus lockeri* Zapfe, 1961 (Fig. 15.7)

**TYPE SPECIMEN** In the collections of the Naturhistorische Museum, Vienna, a left mandibular fragment from Trimmelkam, Austria

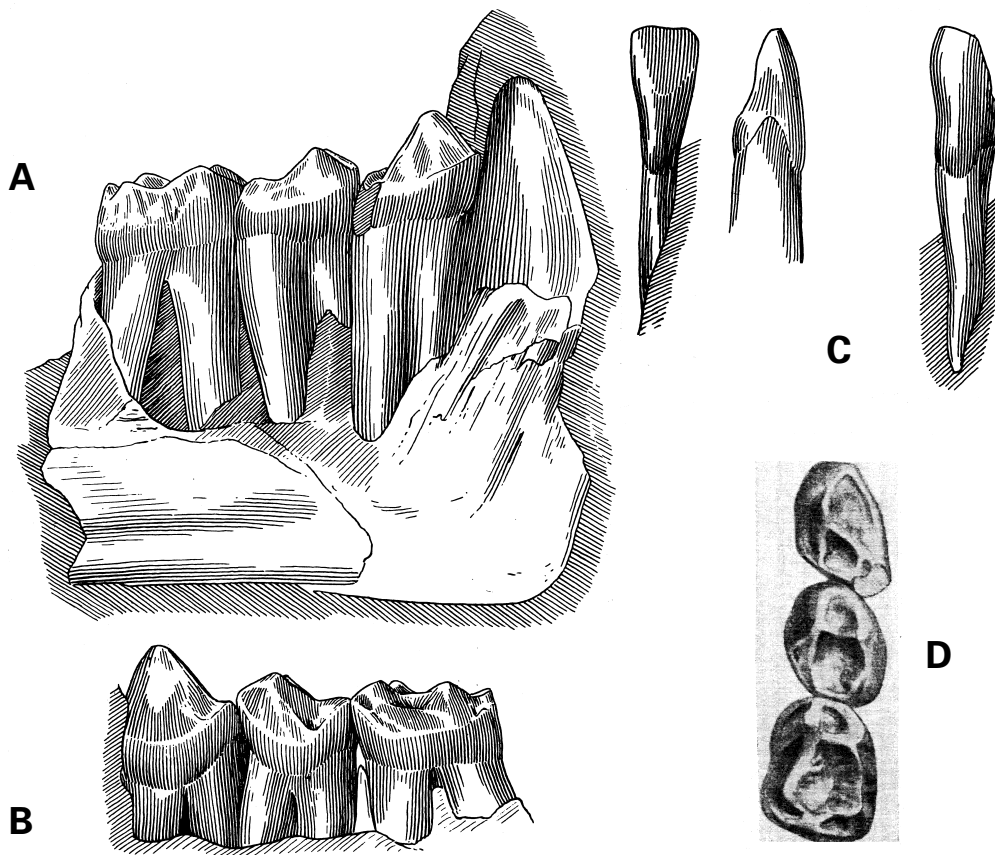
**AGE AND GEOGRAPHIC RANGE** Trimmelkam is considered to date to MN 6, but the fauna from the site is poor (Ginsburg, 1986); the only other taxon definitively identified at the site, *Palaeomeryx eminens*, is generally considered to be an MN 7/8 taxon (Gentry et al., 1999)

### ANATOMICAL DEFINITION

Like all the species of *Plesiopliopithecus*, *P. lockeri* is known from one individual. The  $P_3$  is long and oval with a small distal fovea, compared to the other crouzeliines *Anapithecus* and *Laccopithecus*. The  $P_4$  is like other crouzeliines in being elongated with a particularly large talonid surrounded by tall, sharp crests (Zapfe, 1961; Ginsburg & Mein, 1980). Like *P. auscitanensis* the  $P_4$  has a distinct entoconid. Like *P. auscitanensis* and *Laccopithecus*, but unlike *Anapithecus*, the  $M_1$  is broader distally due to the presence of a large, buccally displaced hypoconid. The lower incisors are tall-crowned and narrow. The  $I_1$  is flared or wider at the occlusal edge than at the cervix and the  $I_2$  is asymmetrical (Fig. 15.7).

**SPECIES** *Plesiopliopithecus auscitanensis* Bergounioux & Crouzel, 1965 (Fig. 15.8C, D)

**TYPE SPECIMEN** Sa 999 (MNHN), a left mandibular fragment with  $P_4$ – $M_1$



**Fig. 15.7** *Plesiopliopithecus lockeri*. (A) Lingual and (B) buccal views of  $P_3$  to  $M_1$  and the impression in the matrix of the canine. (C) Lower incisors and (D) an occlusal view of the postcanine dentition. Note the oblique cristid obliquid between the protoconid and hypoconid and the broad, distally flared talonid basin, and reduced hypoconulid. Adapted from Zapfe (1961).

**AGE AND GEOGRAPHIC RANGE** Sansan, France is in MN 6 (by definition, since it is the reference locality for this zone); it is considered to date to about the middle of this zone, roughly 14.5 Ma

**ANATOMICAL DEFINITION**

*Plesiopliopithecus auscitanensis* is very difficult to distinguish from *P. lockeri*. According to Ginsburg & Mein (1980) it has a somewhat smaller  $P_4$  talonid and an  $M_1$  with compressed mesial cusps and a reduced hypoconulid. According to Andrews et al. (1996) it has a less well-developed  $M_1$  buccal cingulum and a less well-defined distal fovea, lacking the ridge that separates this basin from the talonid in *P. lockeri*. Unfortunately, these apparently distinct morphologies are found together in larger single species samples of pliopithecoids, such as *Anapithecus hemyaki* and *Pliopithecus platyodon*. *Plesiopliopithecus auscitanensis* is dentally smaller than *P. lockeri*, but the only specimen of *P. lockeri* is a male, which can be expected to have been in the upper end of the range of variation in dental size. Reluctantly, two separate species are recognized here (Fig. 15.8).

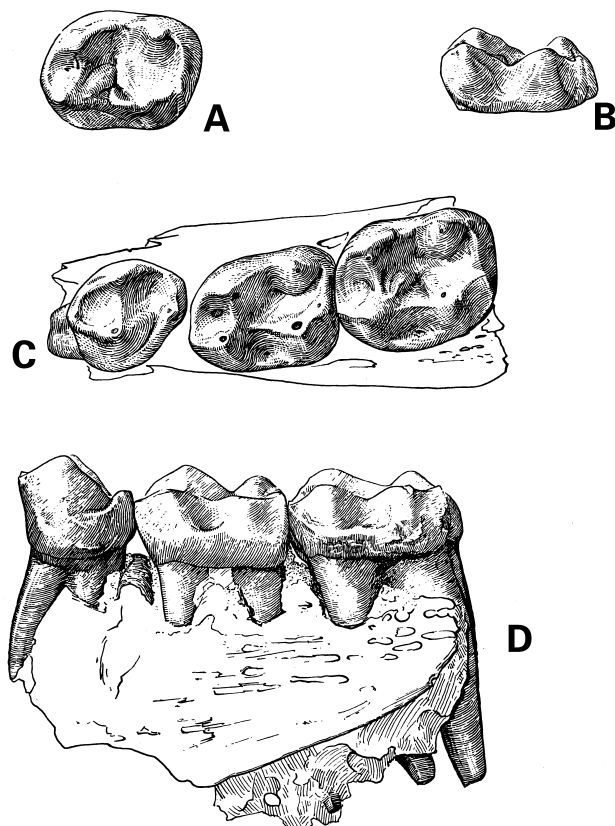
**SPECIES** *Plesiopliopithecus rhodanica* Ginsburg & Mein, 1980 (Fig. 15.8A, B)

**TYPE SPECIMEN** FSL 65626, collections of the Faculté des Science, Université Claude-Bernard, Lyon, an  $M_2$

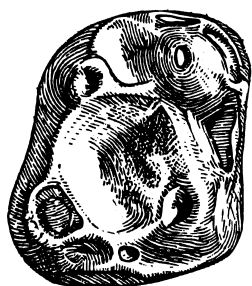
**AGE AND GEOGRAPHIC RANGE** La Grive Saint Alban, Isère, France, has primate-bearing sediments of differing ages; Fissure L7 is dated to MN 7 (Ginsburg, 1986). Many authors currently combine MN 7 and MN 8, so that the ages of the crouzeliine and hominid from La Grive may in fact be quite close. This would be an interesting combination of primates, already known from a number of localities (Salmendingen, Austria, Rudabánya, Hungary and Lufeng, China)

**ANATOMICAL DEFINITION**

*Plesiopliopithecus rhodanica* is even more difficult to distinguish because it is only known from one tooth. Differences include smaller size, slightly narrower crown, elongated crests, reduced buccal cingulum, smaller mesial fovea and very small hypoconulid (Andrews et al., 1996), but again, a similar range of variation is easy to match in larger samples of other pliopithecoids. Ginsburg & Mein (1980) consider these characters, which tend to distinguish pliopithecids from crouzeliines, better developed in *P. rhodanica* (apart from size). Given this evidence of an evolutionary change, and given the temporal separation of the samples, this



**Fig. 15.8** *Plesiopithecus*. (A,B) *P. rhodanica* in occlusal (A) and buccal (B) views. (C,D) *P. auscitanensis* in occlusal (C) and buccal (D) views. Adapted from Ginsburg and Mein (1980).



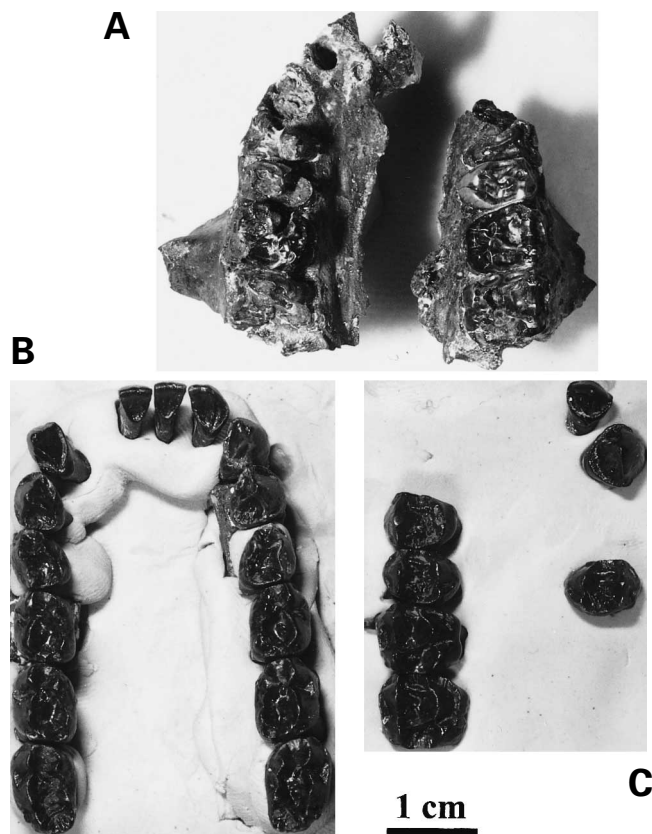
**Fig. 15.9** *Plesiopithecus priensis*. Occlusal view.

species is recognized here as distinct as well (Fig. 15.8).

**SPECIES** *Plesiopithecus priensis* Welcomme et al., 1991 (Fig. 15.9)

**TYPE SPECIMEN** Specimen in the collections of the Muséum Nationale d'Histoire Naturelle, Paris, a right mandibular fragment

**AGE AND GEOGRAPHIC RANGE** Priay (Ain, France) contains a good micromammal assemblage that unambiguously dates the locality to the upper part of MN 9, or about 9.5 Ma, considerably younger than other species of the genus (Welcomme et al., 1991)



**Fig. 15.10** *Anapithecus hemyaki*. (A) Palatal view from a partial cranium of a female with a heavily worn and damaged dentition, and, bottom, well-preserved lower (B) and upper (C) dentitions of a subadult female.

#### ANATOMICAL DEFINITION

*Plesiopithecus priensis* can be distinguished by its much larger size, but it retains the typical morphology of the genus with its broad talonid and reduced hypoconulid. The buccal cingulum is also more strongly developed than is typical for *Anapithecus*. This specimen has been attributed to *Pliopithecus* in Welcomme et al. (1991) and Andrews et al. (1996), but it is clearly distinct as described in general for crouzeliines and more specifically for *Plesiopithecus* (see above).

**GENUS** *Anapithecus* Kretzoi, 1975

**INCLUDED SPECIES** *A. hemyaki*

**SPECIES** *Anapithecus hemyaki* Kretzoi, 1975 (Fig. 15.10)

**TYPE SPECIMEN** RUD 9, in the collections of the Geological Museum of Hungary but currently stored in the National Museum of Hungary, a mandibular fragment

**AGE AND GEOGRAPHIC RANGE** *Anapithecus hemyaki* is known from several localities at Rudabánya, Hungary, the ages of which are essentially contemporaneous at MN 9. Unlike other pliopithecoids, *Anapithecus* appears to have had a broad distribution. It is identified at Salmendingen and Götzendorf, in the Vienna basin of Austria. Götzendorf is considered to be slightly younger than Rudabánya although

still in MN 9, while Salmendingen is considered to be MN 10 (Rögl *et al.*, 1993; and see Chapter 20, this volume).

#### **ANATOMICAL DEFINITION**

*Anapithecus hemyaki* is medium-sized primitive catarrhine that is larger than all other pliopithecoids on average. It was originally recognized as a subgenus of *Pliopithecus*. Ginsburg & Mein (1980) elevated it to a distinct genus assigned to the crouzeliines. A distinctive system of crests between the mesial cusps and the  $M_1$  hypoconid unambiguously identifies *Anapithecus*. These crests form a Y, with the vertical component represented by the cristid obliquid and the arms represented by crests going to the protoconid and metaconid (Begun, 1989b). While this looks superficially like catarrhine deciduous molar morphology there are fundamental differences in crest development, orientation and in overall crown morphology (Begun, 1991). In contrast to the opinion of Andrews *et al.* (1996), a careful examination of the original specimens from all three localities clearly reveals their morphological similarities.

*Anapithecus hemyaki* is dentally somewhat larger than a siamang and probably weighed about 15 kg. The specimens suggest little body-mass sexual dimorphism but substantial canine dimorphism. Lower incisors are tall-crowned but also relatively robust transversely (long), and lack the “waisting” of other pliopithecoids. Upper central incisors are broad and low-crowned with marked lingual cingula. Upper lateral incisors are very distinctive, being much smaller than the centrals, pointed, symmetrical and relatively flat labiolingually, resembling miniature upper female canines. Lower premolars and molars are long with very large mesial fovea and talonids and small, lingually displaced distal fovea. The  $M_3$  is especially long and tapered distally. These characters are more strongly developed in *A. hemyaki* than in other crouzeliines. In addition, lower molars have typical crouzeliine and pliopithecoid characters including mesially placed protoconids, obliquely oriented oblique crests, bilaterally compressed, marginalized cusps and prominent occlusal crests. Many specimens preserve either remnants or well-developed pliopithecine triangles. Upper molars and premolars are broad with large basins as well. Premolars have substantial cusp heteromorphy, the buccal cusps being taller than the lingual ones, and a distinctive, hexagonal shape (L. Kordos, pers. comm.). The upper molars have strong lingual and buccal cingula, relatively large talons, and well-developed ridges connecting the hypocone to the protocone. Though poorly preserved it is clear that the mandible was transversely robust, as in many pliopithecoids.

One cranial specimen is broadly similar to *Pliopithecus zhanxiangi* and *Epiplioptithecus vindobonensis* but much larger. Shared characters include short faces with short premaxilla, fenestrated palates, narrow, oval shaped nasal apertures, broad orbits with projecting rims, low cheek bones (zygoma), and restricted maxillary sinuses (Kordos & Begun, 2000). Like *E. vindobonensis*, *Anapithecus hemyaki* has a

fairly large and globular neurocranium. The orbits also face slightly laterally and are surrounded laterally by prominent, projecting supraorbital costae and infraorbital rims, and the frontal bone has a depressed frontal trigon and a relatively short but vertical frontal squama, and broad interorbital space. Reconstruction suggests that the interorbital region was relatively somewhat narrower than in *E. vindobonensis*, and that the medial ends of the supraorbital costae dipped down toward glabella, as in *E. vindobonensis* and hylobatids. Compared to *E. vindobonensis* the temporal lines are less well-developed and the snout relatively less projecting. The orbits are more elongated, the root of the zygomatic on the maxilla is higher and positioned more anteriorly, the postorbital breadth is relatively greater, and the frontal is shorter and more vertical (Kordos & Begun, 2000). Compared to *Pliopithecus zhanxiangi* and *Epiplioptithecus vindobonensis* the anterior palate is broad. The few postcranial fragments include phalanges and some foot bones that are also broadly similar to *Epiplioptithecus vindobonensis*, but with features that suggest more suspensory postures (e.g., more strongly curved phalanges) (Begun, 1988a, 1993a).

**GENUS** *Laccopithecus* Wu & Pan, 1984

**INCLUDED SPECIES** *L. robustus*

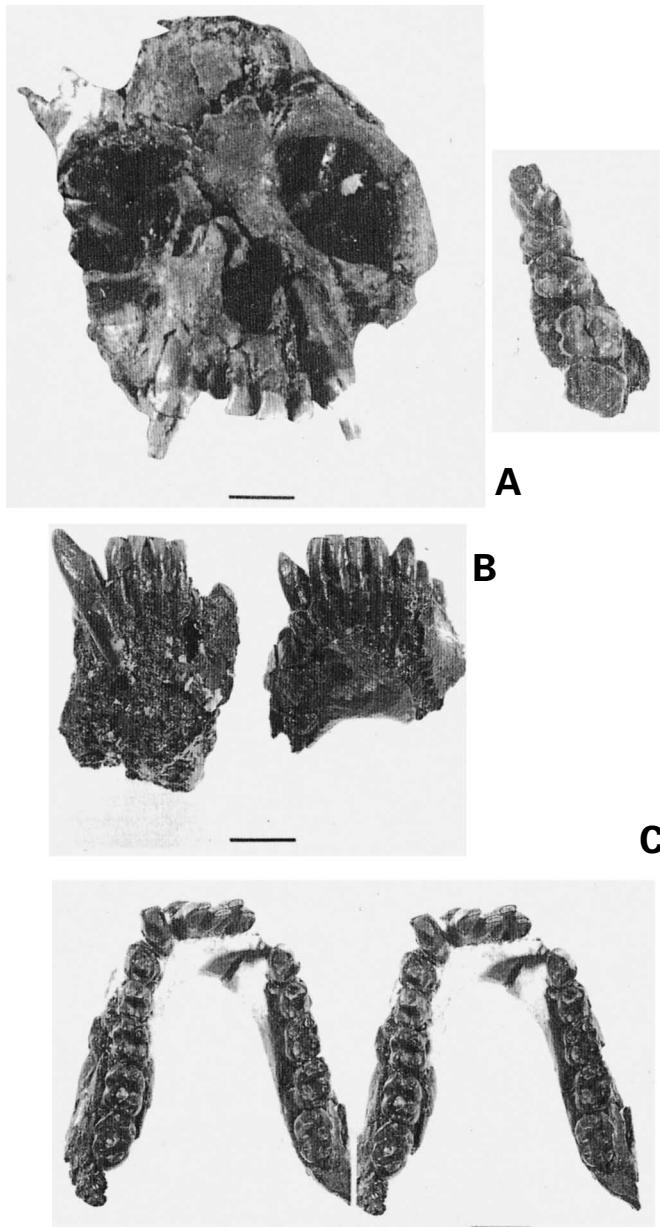
**SPECIES** *Laccopithecus robustus* Wu & Pan, 1984 (Fig. 15.11)

**TYPE SPECIMEN** PA 880, a nearly complete female lower dentition and fragmentary mandible, and PA 876, two halves of a badly damaged maxilla. Wu & Pan (1984) interpreted these specimens to be parts of a single individual, but PA 876 is clearly a male, based on canine size and morphology (Pan *et al.*, 1989). Technically these specimens are thus syntypes rather than a holotype, because they are different specimens and different individuals. In view of the fact that PA 880 has a better preserved dentition, was figured first in the original publication, has been figured elsewhere in a higher-quality image (Pan *et al.*, 1989), and is more directly comparable to most other type specimens of pliopithecoids, it should be designated as the lectotype. All specimens are from Lufeng County, Yunnan Province, and are in the collections of the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, PRC.

**AGE AND GEOGRAPHIC RANGE** Lufeng appears to be one of the latest occurrences of non-cercopithecoid primates in Eurasia, and has been correlated to NMU 10, the Chinese mammal unit equivalent to MN 11–12 of Europe (Qiu, 1990; Qiu & Storch, 1990; Qiu *et al.*, 1999), about 8 Ma; only *Oreopithecus* persists beyond this time in Eurasia

#### **ANATOMICAL DEFINITION**

*Laccopithecus robustus* is known from a rich sample of about 90 specimens, including a partial cranium with a well-preserved face and palate, as well as a number of more fragmentary jaws, associated dentitions, isolated teeth and a proximal phalanx (Pan, 1998). *Laccopithecus robustus* is a



**Fig. 15.11** *Laccopithecus robustus*. (A) The best-preserved cranium and an occlusal view of an upper tooth row; (B) anterior views of a male (left) and female (right) mandible illustrating the degree of sexual dimorphism; (C) stereophotograph of the lower dentition (type specimen). Adapted from Pan et al. (1989).

medium-sized primitive catarrhine, in most dimensions dentally smaller than *Anapithecus*. Females are close in molar size to siamangs, whereas males are somewhat larger. It has a number of typical crouzeliine characters such as large occlusal basins, compressed, marginalized cusps, and obliquely oriented oblique crests. Like *Anapithecus*, *L. robustus* has a fairly broad  $P_3$  but like *Plesiopithecus* the molars and premolars are less elongated than in *Anapithecus*, the occlusal basins are less expanded, especially the mesial fovea, and the hypoconulid is rather small, though not with the degree

of reduction seen in *Plesiopithecus*. There are no pliopithecine triangles on any of the lower molars and the buccal cingula are minimally developed. The lower canines are more massive than in *Anapithecus* while the lower incisors more closely resemble *P. lockeri* in that they are mesiodistally shorter. Two damaged mandibular symphyses suggest that the anterior part of the mandible was robust with well-developed transverse tori while the posterior portion appears to have been relatively gracile in transverse dimensions. Upper incisors lack the strong size differential of *Anapithecus*, the  $I^1$  being a very short tooth barely longer than the  $I^2$ . Both upper incisors are labiolingually robust. The male upper canine is very large and strongly bilaterally compressed. All three upper anterior teeth in fact closely resemble their homologues in hylobatids, though this is not the case for the lower incisors, which are lower-crowned and broader in hylobatids. Another important distinction from hylobatids is the presence of sexual dimorphism in canine morphology, as in nearly all other anthropoids. The upper premolars are longer or less broad than in *Anapithecus*, and lack the degree of cusp heteromorphy of this taxon. The upper molars are also less broad than in *Anapithecus* with minimally developed lingual cingula and no stelar shelves. The talons tend to be smaller and the cusps more rounded.

The cranium of *L. robustus* is badly damaged, as is the case for most specimens from Lufeng. The palate is narrow anteriorly, as in *Epipliopithecus* and it appears to have been fenestrated. As in *Epipliopithecus*, *Anapithecus* and *Hylobates*, the nasal aperture is tall but small and narrow overall, with a narrow base and an apex that reaches above the lower level of the orbits. As in *Epipliopithecus* the orbits appear to have been more squared, or less elongated than in *Anapithecus*, though they are distorted. Relative to orbital dimensions the interorbital space is similar to that of *Epipliopithecus*. The root of the zygomatic is placed fairly high on the maxilla, and the zygomatic bone itself is robust and separated from the body of the maxilla by a prominent malar notch, all more like *Anapithecus* than *Epipliopithecus*, while the orbital rims are less prominent than in *Anapithecus*, more like the condition in *Epipliopithecus* (Fig. 15.11). Finally, the single proximal phalanx of *Laccopithecus* is long and curved, with strong muscle markings suggestive of suspensory positional behavior (Meldrum & Pan, 1988).

### Family *incertae sedis*

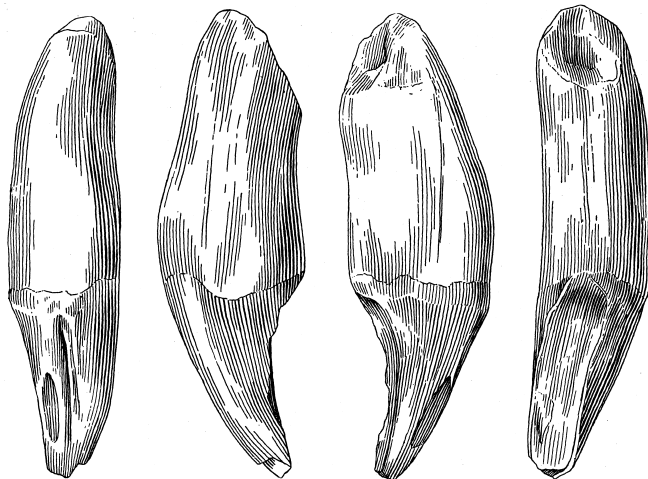
**GENUS** *Paidopithecus* Pohlig, 1895

**INCLUDED SPECIES** *P. rhenanus*

**SPECIES** *Paidopithecus rhenanus* Pohlig, 1895 (Fig. 15.12; see also Fig. 20.1)

**TYPE SPECIMEN** The Eppelsheim femur, a nearly complete specimen first described in Kaup (1861), in the collections of the Hessisches Landesmuseum, Darmstadt, Germany

**AGE AND GEOGRAPHIC RANGE** Known only from



**Fig. 15.12** *Paidopithecus rhenanus*. Upper male canine in mesial, buccal, lingual and distal views. Adapted from Hürzeler (1954).

Eppelsheim, dated securely to MN 9 based on its rich associated fauna (Mein, 1986)

#### ANATOMICAL DEFINITION

*Paidopithecus rhenanus* is a large primitive catarrhine known from the type femur and an upper male canine (Fig. 15.12). Both specimens resemble *Epipliopithecus* but are much larger. The femur routinely is attributed to *Dryopithecus*, but is different from any fossil or living hominoid (Begun, 1992a) as confirmed by the recent discovery of femoral fragments of *Dryopithecus* from Spain (Moyà-Solà & Köhler, 1996). Recently recovered femora from Rudabánya possibly attributable to *Anapithecus* based mostly on size, are very different in morphology from *Paidopithecus rhenanus* (Kordos & Begun, 1999). *Paidopithecus rhenanus* can be distinguished morphologically from hominoids but in terms of size it is consistent with a number of pliopithecoids. Here it is considered to be pliopithecoid but left unassigned beyond the superfamily level.

The femur of *Paidopithecus rhenanus* is long and gracile with a comparatively short neck with a lower neck–shaft angle than in hominoids generally, including *Dryopithecus*, and in comparison to the Rudabánya femora (Kordos & Begun, 1999). The shaft is straight and the condyles are shallow and separated by a broad patella groove. The canine is long and dagger-like, closely resembling the canines of *Epipliopithecus* and *Laccopithecus*. The root and cervix are similar in dimensions to the single upper male canine specimen of *Anapithecus*, which unfortunately does not preserve much of the crown. It is smaller and less robust than *Dryopithecus* upper male canines (Fig. 15.12).

### Evolution of European Miocene catarrhines

#### What if anything is a pliopithecoid?

Distinguishing among many of the species of pliopithecoids

is difficult due to their exceptionally primitive and conservative dental morphology. It is possible that the dionysopithecines are broadly ancestral to all other pliopithecoids, though more fossils are required to establish the affinities of these primitive Asian catarrhines. Within the Pliopithecinae it appears that *Pliopithecus platyodon* and *P. antiquus* are most closely related, differing essentially only in size. *Pliopithecus piveteaui* is smaller and more primitive than the other European species, and may be their ancestor. Technically this should require a new genus name for the older sample to distinguish it from the more closely related descendants. *Pliopithecus zhanxiangi* and *Epipliopithecus vindobonensis* are more distinctive, and it may be justified to recognize separate genera for both of these taxa. Because *E. vindobonensis* lacks one of the few diagnostic characters of the pliopithecines, a pliopithecine triangle on the lower molars, it is recognized here as a distinct genus. In fact, *E. vindobonensis* is no more morphologically like *Pliopithecus* than are some specimens attributed tentatively to *Limnopithecus*, such as KNM-FT 20 from Fort Ternan, Kenya (Andrews, 1978a).

Within the Crouzeliinae a morphological gradient is apparent from the more conservative *Plesiopliopithecus lockeri* to the more derived *Anapithecus henyaki*. *Laccopithecus* does not fit clearly with this trend and may have diverged early in the evolutionary history of the crouzeliines. The dionysopithecines are most similar to early Miocene African taxa (Bernor et al., 1988; Harrison & Gu, 1999).

The early Miocene of Africa seems the most likely origin for the pliopithecoids (Thomas, 1985; Made, 1999). *Limnopithecus* shares the distinctive  $P_3$  morphology with the Pliopithecoidae. In addition, the lower  $P_4$  of the specimen tentatively identified as *Limnopithecus* from Fort Ternan, Kenya has a metaconid that is much lower than the buccal cusp, as in *Dionysopithecus* (see above). This however is not true of other *Limnopithecus*, and it may well be that the specimen from Fort Ternan is not *Limnopithecus* but a pliopithecoid. If this is the case, the Fort Ternan specimen may represent the dispersal of a pliopithecoid into Africa, since Fort Ternan is considerably younger than much of the record of pliopithecoids in Europe and China (Pickford, 1986a). A number of Fort Ternan taxa, including rodents, ruminants and carnivores, are also thought to be Eurasian in origin (Tong & Jaeger, 1993; Gentry & Heizmann, 1996; Werdelin & Solounias, 1996; Made, 1999). At Wadi Moghara in Egypt, a humerus is known with a relatively modern elbow joint, as in proconsulids and more modern hominoids, and an entepicondylar foramen, reminiscent of prosimians, many New World monkeys, Oligocene catarrhines and, of course, *Epipliopithecus* (Simons, 1994a). This early Miocene specimen may also be associated with the ancestry of the Pliopithecoidae. At any rate, these fossil samples suggest a complex connection between the Miocene primate faunas of Asia and Africa. It may be, as suggested by Harrison et al. (1991) that the earliest pliopithecoids lived in East Asia. They seem to diversify however in Europe. If the taxonomy proposed here is

correct, then it appears that on two separate occasions the pliopithecoids sent representatives to Asia, once in the form of the pliopithecine *P. zhanxiangi* and another time the crouzeliine *Laccopithecus*. The evolutionary relations within the Pliopithecoidea are so poorly defined that it is possible that the Asian taxa evolved independently from the European taxa. However, given the evidence of migration of other mammalian genera between Asia and Europe during the middle and late Miocene (Flynn et al., 1986; Bernor et al., 1988; Qiu, 1990; Pickford, 1993b; Qiu & Qiu, 1995; Qiu et al., 1999; Made, 1999), a similarly complex pattern of biogeography in the Pliopithecoidea is certainly possible.

In conclusion, the systematics and evolutionary history of the Pliopithecoidea are about as simple as those of the Platyrrhini. This is no coincidence. The histories of both groups are remarkably similar. Both emerge from a primitive ancestor on a new land mass devoid of anthropoids, and both diverge into their respective major groups very shortly after their first appearance. Both undergo evolutionary changes that seem to be emergent or structurally inevitable in anthropoids: molarization, encephalization, reduction of the snout, limb gracilization and the development of suspensory positional behavior. Pliopithecoids were unable to maintain their splendid isolation, having been joined first by hominoids and then by cercopithecoids during the Miocene. Like the hominoids, they were unable to adapt to changing climates. It may be this more than anything else that led to the extinction of both groups at practically the same moment at the end of the Miocene.

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