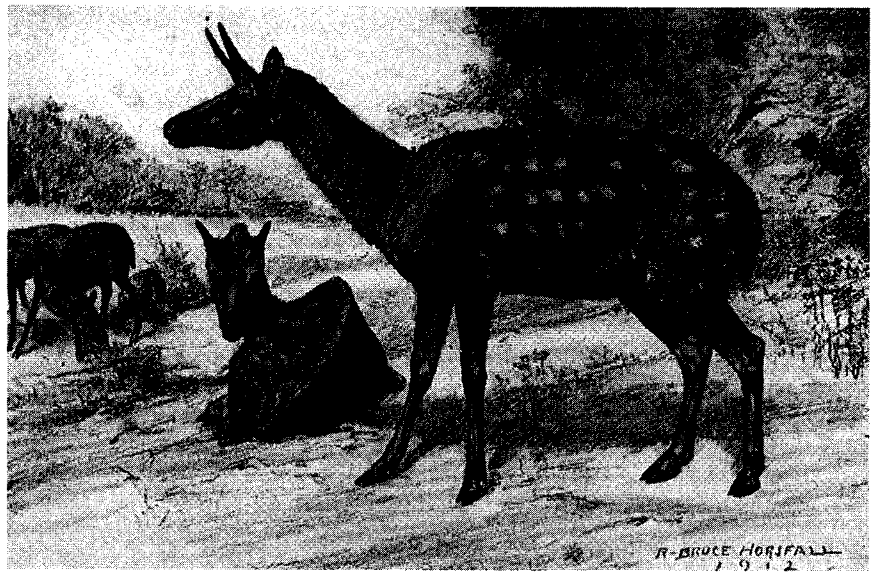

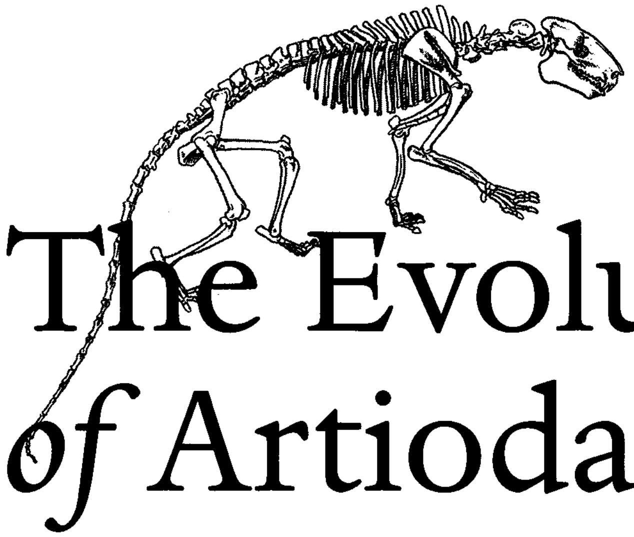

The Evolution of Artiodactyls

Edited by

DONALD R. PROTHERO *and* SCOTT E. FOSS

THE JOHNS HOPKINS UNIVERSITY PRESS, *Baltimore*

Printed in the United States of America on acid-free paper

9 8 7 6 5 4 3 2 1

The Johns Hopkins University Press
2715 North Charles Street
Baltimore, Maryland 21218-4363
www.press.jhu.edu

Frontispieces: Restoration of *Dromomeryx borealis* from Scott (1913) and *Agriochoerus antiquus* skeleton from Scott (1940).

Library of Congress Cataloging-in-Publication Data

The evolution of artiodactyls / edited by Donald R. Prothero and Scott E. Foss.
p. cm.
Includes bibliographical references and index.
ISBN-13: 978-0-8018-8735-2 (hardcover : alk. paper)
ISBN-10: 0-8018-8735-6 (hardcover : alk. paper)
1. Artiodactyla, Fossil—Evolution. 2. Phylogeny.
I. Prothero, Donald R. II. Foss, Scott E, 1968–
QE882.U3E96 2007
569′.63—dc22 2007009445

To our friends and colleagues
Dr. Jeremy Hooker and Dr. Alan Gentry
for their crucial contributions
to the study of fossil and living artiodactyls

CONTENTS

Acknowledgments *ix*
List of Contributors *xi*

1 Introduction 1
SCOTT E. FOSS AND DONALD R. PROTHERO

2 Molecular Phylogeny of Terrestrial Artiodactyls: Conflicts and Resolution 4
JONATHAN D. MARCOT

3 Phylogenetic Relationships of Cetaceans to Terrestrial Artiodactyls 19
JONATHAN H. GEISLER, JESSICA M. THEODOR, MARK D. UHEN, AND SCOTT E. FOSS

4 The Earliest Artiodactyls: Diacodexeidae, Dichobunidae, Homacodontidae, Leptochoeridae, and Raoellidae 32
JESSICA M. THEODOR, JÖRG ERFURT, AND GRÉGOIRE MÉTAIS

5 Endemic European Paleogene Artiodactyls: Cebochoeridae, Choeropotamidae, Mixtotheriidae, Cainotheriidae, Anoplotheriidae, Xiphodontidae, and Amphimerycidae 59
JÖRG ERFURT AND GRÉGOIRE MÉTAIS

6 Family Helohyidae 85
SCOTT E. FOSS

7 Family Anthracotheriidae 89
FABRICE LIHOREAU AND
STÉPHANE DUCROCQ

8 Family Hippopotamidae 106
JEAN-RENAUD BOISSERIE

9 Family Entelodontidae 120
SCOTT E. FOSS

10 Superfamily Suoidea 130
JOHN M. HARRIS AND LIU LI-PING

11 Family Agriochoeridae 151
JOSHUA A. LUDTKE

12 Family Merycoidodontidae 157
MARGARET SKEELS STEVENS AND
JAMES BOWIE STEVENS

13 Family Protoceratidae 169
DONALD R. PROTHERO AND
JOSHUA A. LUDTKE

14 Family Camelidae 177
JAMES G. HONEY

15 Basal Ruminants 189
GRÉGOIRE MÉTAIS AND
INESSA VISLOBOKOVA

16 Family Tragulidae 213
GERTRUD E. RÖSSNER

17 Family Moschidae 221
DONALD R. PROTHERO

18 Family Antilocapridae 227
EDWARD BYRD DAVIS

19 Family Palaeomerycidae 241
DONALD R. PROTHERO
AND MATTHEW R. LITER

20 Family Cervidae 249
COLIN P. GROVES

21 Family Giraffidae 257
NIKOS SOLOUNIAS

22 Family Bovidae 278
NIKOS SOLOUNIAS

23 Artiodactyl Paleoecology and Evolutionary Trends 292
CHRISTINE M. JANIS

24 Summary 303
DONALD R. PROTHERO
AND SCOTT E. FOSS

References 317

Index 363

ACKNOWLEDGMENTS

We thank each of the individual authors, who invested a huge amount of time, research, and passion into each of their respective chapters. Second only to the authors, we thank the many specialists who have donated time as peer reviewers. They are usually acknowledged in each chapter as appropriate. Jessica Theodor contributed enormously to this project by coordinating many of the European contributions, and this book would not be as complete as it is without her tireless input and assistance. We thank Carl Buell for his stunning cover painting, which captures the essence of this book so well. We also thank the Johns Hopkins University Press editorial staff, especially Vincent Burke, for their ongoing enthusiasm and support toward the publication of this book.

CONTRIBUTORS

JEAN-RENAUD BOISSERIE, Département Histoire de la Terre, USM 0203, UMR 5143 CNRS, Unité Paléobiodiversité et Paléoenvironnement, Muséum National d'Histoire Naturelle, CP 38, 57 Rue Cuvier, Paris F-75005, France (jrboisserie@mnhn.fr)

EDWARD BYRD DAVIS, Department of Geological Sciences, University of Oregon, Eugene, OR 97403 (daviseb@berkeley.edu)

STÉPHANE DUCROCQ, Laboratoire de Géobiologie, Biochronologie et Paléontologie Humaine, UMR 6046 CNRS, Université de Poitiers, 40 Avenue du Recteur Pineau, F-86022 Poitiers cedex, France (stephane.ducrocq@univ-poitiers.fr)

JÖRG ERFURT, Institute for Geological Sciences and Geiseltalmuseum, Martin-Luther-Universität Halle-Wittenberg, Von-Seckendorff-Platz 3, D-06120 Halle (Saale), Germany (joerg.erfurt@geo.uni-halle.de)

SCOTT E. FOSS, Bureau of Land Management, Utah State Office, PO Box 45155, Salt Lake City, UT 84145 (scott_foss@blm.gov)

JONATHAN H. GEISLER, Department Geology/Geography and Georgia Southern Museum, Georgia Southern University, Statesboro, GA 30460-8149 (geislerj@georgiasouthern.edu)

COLIN P. GROVES, School of Archaeology and Anthropology, Building 14, Australian National University, Canberra, ACT 0200, Australia (colin.groves@anu.edu)

JOHN M. HARRIS, George C. Page Museum, 5801 Wilshire Boulevard, Los Angeles, CA 90036 (jharris @nhm.org)

JAMES G. HONEY, Department of Geological Sciences, University of Colorado, Boulder, CO 80309 (tiznat@hotmail.com)

CHRISTINE M. JANIS, Department of Ecology and Evolutionary Biology, Brown University, Providence, RI 02912 (christine_janis@brown.edu)

FABRICE LIHOREAU, Département de Paléontologie, FSEA, Université de N'Djaména, BP 1117, N'Djaména, Chad (flihoreau@intnet.td)

MATTHEW R. LITER, Department of Geology, Occidental College, Los Angeles, CA 90041 (liter@oxy.edu)

LIU LI-PING, Institute of Vertebrate Paleontology and Paleoanthropology, PO Box 643, Beijing 10044, China (liuliping@pa.ivpp.ac.cn)

JOSHUA A. LUDTKE, Department of Biology, San Diego State University, 5500 Campanile Drive, San Diego, CA 92182-4614 (joshualudtke@gmail.com)

JONATHAN D. MARCOT, Paleontology Section, University of Colorado Museum, UCB 265, Boulder, CO 80309 (jonathan.marcot@colorado.edu)

GRÉGOIRE MÉTAIS, Vertebrate Paleontology Section, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, PA 15213 (akssyria3@hotmail.com)

DONALD R. PROTHERO, Department of Geology, Occidental College, Los Angeles, CA 90041 (prothero@oxy.edu)

GERTRUD E. RÖSSNER, Department of Earth and Environmental Sciences, Palaeontology Section, and Geobio-Center of the Ludwig-Maximilians-Universität München, Richard-Wagner-Strasse 10, D-80333 Munich, Germany (g.roessner@lrz.uni-muenchen.de)

NIKOS SOLOUNIAS, Department of Paleontology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024; and Department of Anatomy, New York College of Osteopathic Medicine, Old Westbury, NY 11568-8000 (nsolouni@nyit.edu)

JAMES BOWIE STEVENS, PO Box 608, Terlingua, TX 79852 (stevensjb@hal.lamar.edu)

MARGARET SKEELS STEVENS, PO Box 608, Terlingua, TX 79852 (stevensjb@hal.lamar.edu)

JESSICA M. THEODOR, Department of Biological Sciences, University of Calgary, 2500 University Drive NW, Calgary, Alberta, Canada T2N 1N4 (jtheodor@ucalgary.ca)

MARK D. UHEN, PO Box 37012, Washington, DC 20013 (uhen@umich.edu)

INESSA VISLOBOKOVA, Paleontological Institute, Russian Academy of Sciences, ul. Profsoyuznaya 123, Moscow 117868, Russia (ivisl@paleo.ru)

The Evolution of Artiodactyls

was straight and pointed posteriorly. Frick (1937) transferred Cope's species *"Cosoryx" teres* to *Cranioceras* but added four additional species to the genus without adequate diagnoses or descriptions. Prothero and Liter (in press) recognized only two species in the genus *Cranioceras:* the larger species, *C. unicornis,* and the distinctly smaller species, *C. teres. Cranioceras* (Fig. 19.6) is distinct from *Procranioceras* in its long, upright supraorbital appendages that taper distally and curve slightly inward and long posteriorly directed occipital cranial appendage. *Cranioceras* actually occurs earlier (early Barstovian of California, New Mexico, and Nebraska) than the more primitive late Barstovian taxon *Procranioceras. Cranioceras* also occurs in the late Barstovian of Nebraska and New Mexico, the early Clarendonian of California, New Mexico, Texas, South Dakota, and Nebraska and persists until the late Clarendonian of California and Nebraska.

Yumaceras Frick, 1937, and *Pediomeryx* Stirton, 1936

Yumaceras figginsi was named by Frick (1937) based on very incomplete material from the middle Hemphillian Wray localities in Colorado. Just months earlier, Stirton (1936) had named *Pediomeryx hemphillensis* (Fig. 19.6) based on slightly better material from the late Hemphillian of Texas. Both genera were later shown by Webb (1983) to have long occipital cranial appendages, making them cranioceratins. Unlike *Cranioceras,* the occipital appendage is much longer and rises vertically, not posteriorly, and has an anteroposteriorly flattened tip. Stirton (1944) suggested that Frick's *Yumaceras* might be a junior synonym of his 1936 genus *Pediomeryx,* and Webb (1983) placed *Yumaceras* as a subgenus of *Pediomeryx.* This decision was also followed by Janis and Manning (1998b), although they also noted that the two genera were as distinct as any of the subgenera recognized in the Palaeomerycidae. Prothero and Liter (in press) argued that these genera deserve to be distinct because none of the subgenera in the family have proven justifiable. *Pediomeryx* can be distinguished from *Yumaceras* by its much more hypsodont cheek teeth and much smaller size. According to Webb (1983) and Janis and Manning (1998b), *Yumaceras* has three valid species, *Y. figginsi, Y. hamiltoni,* and *Y. ruminalis.* It occurs in the late Clarendonian of Florida and Texas, the early Hemphillian of Florida, Texas, Oklahoma, Oregon, and California, and the middle Hemphillian of California, Colorado, Nebraska, and Texas. *Pediomeryx* has only one valid species, *P. hemphillensis* (senior synonym of two Frick species). It is mostly known from the middle to late Hemphillian of Florida, California, Oklahoma, Texas, and Nebraska. As reported by Webb (1983: Fig. 7), the *Yumaceras-Pediomeryx* lineage shows increasing body size (*Yumaceras*) through the early and middle Hemphillian, then decreasing body size (*Pediomeryx*) until the lineage (and the family) vanished in the late Hemphillian.

PALEOECOLOGY

Janis (1982), Janis et al. (1994), and Janis and Manni (1998b) compared the diverse range of body sizes and crani appendages in palaeomerycids to the variation seen in mo ern antelopes of Africa. According to Janis and Mannin (1998b), the cranial appendages were skin covered (as ev denced by a healed broken horn in *Sinclairomeryx*) and proba bly used both for lateral display and for butting and nec wrestling. Most palaeomerycids were apparently dimorphi in their cranial appendages, and some had a deep lacrima vacuity, which may have housed a scent gland seen in most liv ing cervids. This combination of features suggested to Jani and Manning (1998b) that the more primitive palaeomerycid were territorial and lived in dense brush and woodlands, as d many modern antelopes. By contrast, the lack of dimorphis in *Aletomeryx,* combined with the proportionally longest limb of any palaeomerycid, suggests that these animals may hav preferred a more open habitat, as do modern gazelles.

Semprebon et al. (2004a) studied the mesowear, micr wear, and the skull proportions of the full range of Nor American palaeomerycids. They found that most had fe tures indicative of normal browsing habitat, consistent wit their relatively low-crowned teeth. Only the more derive late Clarendonian and Hemphillian cranioceratins (*Crani ceras, Yumaceras,* and *Pediomeryx*) show signs of mixed fee ing or some grazing, and some of these taxa are also mo hypsodont as well.

As already mentioned, Webb (1983) noticed a trend of in creasing size followed by size decrease in the *Yumaceras Pediomeryx* lineage, which is comparable to the size tren found in many other North American lineages during th Hemphillian. According to Webb (1983) and Janis and Ma ning (1998b), this may have represented an attempt by th last of the palaeomerycids to survive in the face of reduce woodland habitats and expanding grasslands. The last o the palaeomerycids occurs in the earliest Pliocene (lates Hemphillian) in Nebraska, where it coexists with the earli est true cervid in North America. This is proof that the tw groups briefly overlapped in time. The appearance o cervids may have driven the palaeomerycids to extinctio Alternatively, Janis and Manning (1998b) argue that th cervids may have been better adapted to the more open ar grassy habitats of the Pliocene, and dromomerycids coul not find a tropical forest refuge to ensure their survival.

ACKNOWLEDGMENTS

We thank G. Rössner and C. Janis for helpful reviews of this chapter. We thank J. J. Flynn, C. Norris, and J. Meng for ac cess to specimens in the AMNH. Funding for museum travel for this research was provided by the Donors of the Petroleum Research Fund, administered by the American Chemical Society, and by NSF grant EAR03-09538.

COLIN P. GROVES

20

Family Cervidae

THE DEER FAMILY CERVIDAE is the most diverse of the Artiodactyla/Cetartiodactyla after the Bovidae. The exact number of species is uncertain but has certainly been underestimated in the past, both because the important "catch-all" species *Cervus elaphus* has turned out to be nonmonophyletic (Pitra et al., 2004) and because an overzealous application of the biological species concept has led most authorities, up to the 1990s, to shoehorn allopatric taxa into as few species as possible. Proposals to rectify this as far as East Asian deer are concerned have been made by Groves (2006), and for Venezuelan *Odocoileus* by Molina and Molinari (1999).

In this chapter I attempt to combine disparate sources of evidence, including fossils and molecular genetics, into an overall picture of the Cervidae. Essentially, I attempt to fit confirmatory data from published sources into the jigsaw rather than bring forward new sources of evidence.

RELATIONSHIPS OF THE CERVIDAE

Among the living fauna there has long been an assumption that the sister group of Cervidae is the family Moschidae, the musk deer (see, for example, Gentry, 1994). Probably this is a legacy of old arrangements, lasting up to about the middle of the twentieth century (Ellerman and Morrison-Scott, 1951), whereby the musk deer were regarded as constituting a subfamily, Moschinae, of the Cervidae. A recent molecular study has cast doubt on this. Using three mitochondrial and four nuclear sequences, Hassanin and Douzery (2003) found that the Moschidae constitute a sister group not to the Cervidae but rather to the Bovidae, with 95% bootstrap support. Applying a molecular clock, these authors estimated that the Cervidae would have separated from the Bovidae/Moschidae clade about 27–28 million years ago; the combined group separated from a Giraffidae/Antilocapridae clade somewhat earlier.

The fossil relationships of the Cervidae were extensively reviewed by Janis and Scott (1987). These authors regarded *Lagomeryx* as the earliest member of the Cervidae; this early Miocene genus has frequently been assigned to its own family (to which two other Miocene genera, *Stephanocemas* and *Dicrocerus,* have often been assigned), but Janis and Scott (1987) drew attention to some apparently derived conditions that it shared with at least some of the Cervidae, including a lacrimal fossa (which is not, however, confined to the Cervidae) and a *Palaeomeryx* fold in the lower molars. It also had appendages that they identified as antlers—long pedicels crowned by an arrangement of palmated tines—although there is no sign that they were or could ever have been deciduous.

Certainly, there should be some objective criteria for combining taxa into a single family or separating them into different families (and, for that matter, similar criteria for designating genera as well). Goodman et al. (1997), working on primates, suggested a time criterion: in order to be considered distinct families, monophyletic clades should have separated at least by the Oligocene–Miocene boundary (and, for genera, by the Miocene–Pliocene boundary). Groves (2001: especially pp. 17–20) brought fossil data to bear on ungulates and carnivores and modified the proposals slightly. The time–depth criterion would work well for the living fauna; in combination with the plesion concept, it might not be too problematic for fossils either, given adequate evidence. The earliest *Lagomeryx* dates from MN 3, as does the earliest undoubted cervid, *Procervulus;* this makes its position a little equivocal, but an earliest Miocene separation is perfectly feasible, and including *Lagomeryx* in the Cervidae seems justifiable at least provisionally.

The fossil sister group to the Cervidae, according to both Janis and Scott (1987) and Gentry (1994), is the family Palaeomerycidae. Janis and Scott (1987) recognized a further family, Hoplitomerycidae for the genus *Hoplitomeryx,* but Gentry (1994) argued that this genus should be included in the Palaeomerycidae. The early Miocene genus *Dremotherium* would be plesion to the cervid/palaeomerycid clade (Ginsburg et al., 1994; Gentry, 1994).

The origin of antlers has been discussed by Bubenik (1990, and elsewhere), Ginsburg and Azanza (1991), and Gentry (1994). Those of *Procervulus* apparently were never shed, in that they lacked a burr; they were present in males only (Ginsburg and Azanza, 1991), as in almost all modern cervids. Those of *Dicrocerus,* a genus known first from MN 5, were cast; specimens with small antlers were identified by Ginsburg and Azanza (1991) as females.

RELATIONSHIPS WITHIN THE CERVIDAE

Groves and Grubb (1987) divided the Cervidae into three subfamilies: Hydropotinae, for the antlerless Chinese water deer, genus *Hydropotes;* Odocoileinae for the New World deer ("neocervines") plus reindeer (*Rangifer*), moose (*Alces*), and roe deer (*Capreolus*); and Cervinae for the remaining Old World deer including the muntjacs. This was predicated on the fact that the reduction of lateral metacarpals has proceeded differently in the two antlered groups: the Odocoileinae have retained the distal ends, whereas the Cervinae have retained the proximal ends. These two types are known as telemetacarpal and plesiometacarpal, respectively, terms that are not available in a formal nomenclatural sense because they are not based on generic names but have nonetheless achieved wide currency. A cranial character separating the two antlered groups was described by Bouvrain et al. (1989). In all plesiometacarpal deer, the postglenoid foramen is entirely within the squamosal; in the telemetacarpal deer, on the contrary, the petrous forms its medial border. There appear, finally, to be behavioral features that also separate the two groups (Cap et al., 2002). These studies not only confirm that moose and roe deer truly are part of the neocervine clade but also render unnecessary the argument of Bubenik (1990) and Groves and Grubb (1990) that antlers evolved independently in muntjac and cervines.

Within Groves and Grubb's (1987) subfamily Odocoileinae, the neocervines and reindeer are characterized by a complete division of the choanae by the vomer, which forms a vertical partition. The common possession of this undoubted synapomorphy clearly unites them to the exclusion of moose and roe deer.

Does the only living antlerless genus, *Hydropotes,* fit into one of these two groups, or is it sister to them both? Implicit in the first view is that the lack of antlers of this genus is secondary; if *Hydropotes* occupies the second position, it might well have been antlerless from the start. *Hydropotes* is telemetacarpal, but a possibility exists that this condition may actually be primitive (it is also the condition in the Moschidae and Bovidae); its common occurrence in *Hydropotes* and the odocoileines would therefore be a symplesiomorph. Bouvrain et al. (1989) and Cap et al. (2002), however, both argued, using cranial and behavioral evidence, respectively, for the first view: that *Hydropotes* is related to the odocoileines.

Molecular studies have universally substantiated the telemetacarpal/plesiometacarpal split. Miyamoto et al. (1990) and Li and Sheng (1998), both using the mitochondrial cytochrome *b* gene, confirmed a close relationship between *Muntiacus* and *Cervus.* Randi et al. (1998a), using the same gene and the nuclear ê-casein gene, considered the monophyly of the telemetacarpal group probable but could not confirm it because of low support values and in the end opted for three equal clades: the telemetacarpalians with the choanal division, those without, and the plesiometacarpalians. Hassanin and Douzery (2003) and Pitra et al. (2004), however, found clear support for the two groups.

The hypothesis of Bouvrain et al. (1989) and Cap et al. (2002), that the affinities of *Hydropotes* lie with the other (antlered) telemetacarpalians, is abundantly confirmed by molecular studies. In addition, Randi et al. (1998a), Hassanin and Douzery (2003), and Pitra et al. (2004) have all positioned it as a clear sister group to *Capreolus.* Evidently, its ancestors had antlers, but these have been lost during evolution.

Finally, a reorganization of nomenclature has proved necessary (Grubb, 2000). The subfamilial name Odocoileinae, used by Groves and Grubb (1987) and many other authors, dates from 1923 and is antedated by more than a century by Capreolinae, Rangiferinae, and Alcinae. Accordingly, it is not the correct name for the telemetacarpalians.

In summary, the classification of genera of living deer accepted here is as follows (modified from Grubb, 2000):

Subfamily Lagomerycinae Pilgrim, 1941
Plesion *Procervulus*
Subfamily Pliocervinae Symeonidis, 1974
Subfamily Capreolinae Brookes, 1828
  Tribe Rangiferini Brookes, 1828
    Odocoileus
    Blastocerus
    Ozotoceros
    Hippocamelus
    Mazama
    Pudu
    Rangifer
  Tribe Capreolini Brookes, 1828
    Capreolus
    Hydropotes
  Tribe Alceini Brookes, 1828
    Alces
Subfamily Cervinae Goldfuss, 1820
  Tribe Muntiacini Knottnerus-Meyer, 1907
    Elaphodus
    Muntiacus
  Tribe Cervini Goldfuss, 1820
    Dama
    Axis
    Rucervus
    Panolia
    Elaphurus
    Cervus

MIOCENE CERVIDS

Pride of place among early cervids must go to *Procervulus dichotomus,* from the early Miocene (MN 3–5) of Europe (Gentry, 1994; Azanza and Menendez, 1990). The short antlers, confined to presumed males, sit on the end of long pedicels that are parallel to each other; most examples have two prongs, but a few have three. The surface sculpture of the antler suggests strong vascularization, implying the presence of velvet (Bubenik, 1990; Azanza, 1993a), but there is no burr, so it has been inferred that it was never shed. Ginsburg and Bulot (1987), however, found two antlers with sharp downwardly concave breaks, which they argued might after all represent the earliest form of natural shedding. Several species of *Procervulus* are known; they were revised by Rössner (1995), who cautioned that the relationships of the genus are still very difficult to resolve.

Procervulus was succeeded by *Heteroprox,* from MN 5–7, and the two are commonly combined in a subfamily Procervulinae; and by *Euprox,* from MN 6–10, which is considered by Gentry (1994) to be developing toward modern deer. In *Euprox,* the posterior of its two tines is longer and stronger than the anterior, as if it were antecedent to a beam. The immediate precursors to the crown-group cervids in Gentry's (1994) scheme were the late Miocene *Pliocervus, Cervavitus,* and *Cervocerus:* telemetacarpal deer (where this condition is known), retaining long maxillary canines and the *Palaeomeryx* fold, but with short pedicels and three or more tines.

In the phylogenetic scheme of Gentry (1994), the *Lagomeryx* clade includes *Stephanocemas* and *Dicrocerus,* but Azanza (1993b) identified a "protocoronet" in these two genera and assigned them a position intermediate between *Procervulus* and the crown group of modern deer. For Azanza (1993b), *Euprox* is within the crown group and belongs to the muntjac clade; like Bubenik (1990), she would place the muntjacs outside the clade to which all other modern deer, with their shortened pedicels, belong; this would require that the plesiometacarpal condition was acquired independently, and in addition such an interpretation now appears incompatible with the consistent molecular findings.

CERVINAE: MUNTIACINI

The muntjac group are not primitive antlered deer, *pace* Azanza (1993b) and Bubenik (1990), the latter of whom was impressed by the normally nondeciduous nature of the antlers of the Bornean endemic *Muntiacus atherodes;* rather, muntjacs have apparently reverted to a form with small antlers and long pedicels as part of a forest (mainly rainforest) adaptive strategy ("duiker syndrome"). Like another small deer, the telemetacarpal genus *Pudu,* the Muntiacini have fused their cubonavicular and external and median cuneiforms into a single bone.

The reputed diversity of species in *Muntiacus,* with several new species described over the past 10 years or so (beginning with the giant muntjac, originally placed in a separate genus and named *Megamuntiacus vuquangensis*), is getting out of hand. It is surely time to gather the available specimens of little black muntjac in one place and compare them morphologically and morphometrically and run several mtDNA and nDNA sequences. That said, we may all now agree that the revision by Groves and Grubb (1990) was somewhat overlumped. There is also a good deal of geographic variability in the sister genus *Elaphodus* (the only other living genus of the Muntiacini), but with so little available material, Groves and Grubb (1990) were unable to make much of it.

The earliest muntiacin is the late Miocene (7–9 Ma) *Muntiacus leilaoensis,* from Yuanmou, Yunnan (Dong et al., 2004). Like so many deer, this is known only from antlers and pedicels, and we do not know how close it is to living *Muntiacus* or *Elaphodus* in other aspects of its morphology. It does, however, seem to confirm that antlers are reduced in such small-antlered taxa as *Muntiacus atherodes* and *Elaphodus* spp. and makes the Cervini/Muntiacini split earlier than depicted by Pitra et al. (2004).

CERVINAE: CERVINI

The phylogeny of the Cervini has been most recently explored by Pitra et al. (2004). It is possible that four genera (*Axis, Rucervus, Dama,* and *Cervus*) should be recognized in the living fauna, but the recent discovery of a 7- to 9-million-year-old muntjac (Dong et al., 2004) indicates that the calibration chosen by Pitra et al. (2004) for their molecular clock has evidently been set too late, and I here propose to recognize two further genera, *Panolia* and *Elaphurus.*

The genus *Axis* is now shown to have but a single living species, the chital or spotted deer *A. axis* from India, Nepal, and Sri Lanka. The hog deer (*Cervus porcinus*) and its relatives are not closely related to it; their common possession of slender antlers, built on a plesiomorphic three-point plan (Geist, 1998), would seem to have misled most commentators. Actually, the presumed primitive antler type may be derived even in *Axis axis* itself because the early Pleistocene Mediterranean *A. nesti* and *A. eurygonos* had antlers built on a four-point plan (Di Stefano and Petronio, 2002). The skull of *Axis* is distinctive. The anterior ends of the nasal bones are bifid, the lateral prong of each nasal being equal to or longer than the median, so that together they form a concave anterior margin. The posterior ends form a shallow, blunt wedge into the frontals. There are no upper canines. The lower central incisors are very wide, their width exceeding the combined width of the two lateral incisors plus the canine.

Rucervus contains the swamp deer (traditionally a single species, *R. duvauceli*) of Nepal and India and the presumed-extinct Schomburgk's deer (*R. schomburgki*) of Thailand. Pitra et al. (2004) extracted DNA from a Schombrugk's deer specimen and showed that it is indeed the sister species of the swamp deer and not a representative of a separate genus or subgenus *Thaocervus* as had sometimes been thought. Cranially, *Rucervus* resembles *Dama* and is readily distinguished from other Cervini by the form of the nasofrontal suture: the nasal bones together make a deep, acute-angled wedge back into the frontals. At their free ends, each has two prongs, a very long lateral one and a rudimentary median one, as in *Axis.* There are no upper canines.

The genus *Dama* (fallow deer) is closer to *Cervus* than are the previous two genera, according to Pitra et al. (2004). It contains two living species, the European (*D. dama*) and Persian (*D. mesopotamica*); these are quite distinct, despite the urge of many authors to make them subspecies of a single species. The fossil record of the genus does not begin until the middle Pleistocene, with *D. clactoniana,* of which the modern *D. mesopotamica* is essentially a size-reduced version, although Pfeiffer (1999) plausibly ascribed some late Pliocene fossils to the *Dama* stem. The nasal bones resemble those of *Rucervus.* There are no upper canines (except as an anomaly). The lower central incisors are widened, as in *Axis.*

The giant deer, *Megaloceros,* has long been postulated to be closely related to *Dama* (Lister, 1994), a hypothesis that has recently been spectacularly confirmed by the sequencing of its DNA (Lister et al., 2005). The genus is first known from the middle Pleistocene of Europe and western Siberia; Lister (1994) documented the changes over time from the early *M. verticornis* and *M. savini* to the terminal Pleistocene/early Holocene *M. giganteus* and showed changes in body shape between open and woodland habitats. Lister et al. (2005) placed the split between *Megaloceros* and *Dama* at 4–5 Ma, which would be on the cusp of generic recognition in the scheme of Goodman et al. (1997), but they accepted the 7-Ma muntiacin–cervin split postulated by Pitra et al. (2004) as their calibration point, and, as suggested above, this might be too late. Azzaroli (1994) and Azzaroli and Mazza (1992b) noted resemblances between *Eucladoceros boulei* from Nihewan (China) and *Megaloceros* and suggested that they might represent an ancestor–descendant series.

The Eld's deer complex, here tentatively regarded as forming a separate genus *Panolia,* is cranially distinct from other Cervini, especially in that the posterior ends of the nasal bones form only a blunt, shallow wedge into the frontals, whereas anteriorly each nasal is single pointed, the points diverging from one another leaving a midline V-shaped gap—the form usually seen in *Cervus.* The antlers of this genus are highly distinctive, the brow tine and the beam forming a continuous, almost unbroken arc. Traditionally only a single species, *P.* (formerly *Cervus*) *eldi,* has been recognized. Balakrishnan et al. (2003) showed, however, that there is a deep split between a western clade, from Burma and Manipur, and an eastern clade, from the Indochinese region and Hainan. There are also considerable morphological differences between the two as well as between the dryland-living thamin of Burma and the critically endangered sangai, confined to the floating reed beds (phumdi) of Logtak Lake in Manipur. Groves (2006) suggests that Eld's deer be reexamined with a view to ascertaining whether they ought to be reclassified into two or even three distinct species.

The apparent affinities of the East Asian genus *Elaphurus,* Père David's deer, vary according to what system is being studied. As listed by Meijaard and Groves (2004b; Table 7), its morphological features (except for its unique antler conformation) generally recall those of *Cervus;* protein electrophoresis and a nDNA sequence (κ-casein) similarly align it *Cervus;* yet mtDNA puts it in a clade with *Panolia.* The best explanation of this at present is that it originates from an ancient hybridization between stem representatives of *Cervus* (male) and *Panolia* (female) (Meijaard and Groves, 2004b; Pitra et al., 2004). *Elaphurus* is known as far back as the late Pliocene (*E. bifurcatus*), and according to the modification of the molecular clock of Pitra et al. (2004) that I propose here, its separation from *Panolia* would date from about the Miocene–Pliocene boundary. Deer hybridize readily, at least within the same genus, and it may be that other species will also be shown to be of hybrid origin, but no case at present seems as plausible as that of Père David's deer. Y-chromosome DNA analysis in the Cervidae would be of enormous interest.

The genus *Cervus* is cranially most similar to *Panolia,* except that the posterior nasal bones form a distinct, but relatively short, point. The males possess small canines. Even shorn of some of its erstwhile components, the genus is large and unwieldy. As argued by Pitra et al. (2004), specializations of the display organs (antlers, mane, rump patch, voice) are indicators of habitat and reproductive seasonality rather than of phylogenetic affinity. The three well-separated clades are as follows:

1. Tropical clade, including *C. porcinus* (hog deer) and its relatives, *C. timorensis* (rusa) and *C. unicolor* (sambar) and its relatives. The so-called *Axis lydekkeri,* from 1.5-million-year-old deposits at Sangiran, Java, is related to *C. porcinus* and may reflect the plesiomorphic morphology of this clade, according to Meijaard and Groves (2004b). Di Stefano and Petronio (2002) suggest that the so-called *Rusa elegans* and *R. hilzheimeri* of the late Pliocene already possess derived conditions in common with *Cervus unicolor;* if so, then the diversification of the lineage must have begun at least by then. Nothing is known of the fossil antecedents of *C. timorensis.*
2. Western temperate clade, *C. elaphus* and its relatives. Pitra et al. (2004) suggested that the geographically isolated Central Asian *C. yarkandensis* (including *bactrianus?*) constitutes a distinct species; the spotted form *C. maral* of Turkey and Iran and the small, secondarily simplified North African deer (introduced to Corsica and Sardinia) are further candidates for species status. The earliest representative of what is presumably this clade is the early Pleistocene *C. magnus,* which has a relatively simple four-point antler plan resembling that of a sika. The European/West Siberian *Cervus acoronatus,* which resembles modern *C. yarkandensis* in lacking the multitine antler "crown" of *C. elaphus sensu stricto,* appears at the time of the Matuyama/Brunhes boundary, 0.8 Ma; it is not until about 0.5 Ma that the earliest "crowned" deer, *C. eostephanoceros,* appears.
3. Eastern temperate clade, recently treated by Groves (2006). This includes *C. albirostris* (white-lipped deer), and a subclade containing the *C. nippon* group (sika) and the large Sino-Rosso-American deer (wapiti and shou), which form a progressive cline running southwest-northeast from *C. wallichi* (Tibet) via *C. macneilli* (Sichuan) and *C. xanthopygus* (Primoriye, Manchuria, East Mongolia) to *C. canadensis* of the Central Asian mountains and North America. One of the most unexpected but most consistently corroborated findings of molecular studies on deer has been that the wapiti and shou are not eastern subspecies of *C. elaphus,* as had always been assumed, but are from an entirely separate clade, to which sika also belong. The early Pleistocene Chinese *Cervus grayi* is very close to sika (Di Stefano and Petronio, 2002); the fossil history of wapiti and shou is unknown.

The origin of the tribe Cervini itself is uncertain, but a number of European Pliocene and Pleistocene genera are assigned to it: *Croizetoceros, Arvernoceros, Eucladoceros, Pseudodama* (probably a synonym of *Dama*), and the enigmatic *Candiacervus* from the Pleistocene of Crete (Heintz and Aguirre, 1976; Heintz and Dubar, 1981; Lister, 1994; Azzaroli, 1992; Azzaroli and Mazza, 1992a, 1992b). Perhaps the best known of these is *Eucladoceros,* characterized by its complex multibranched antlers; it is best known from the late Pliocene to early Pleistocene of Europe but extended well outside Europe to the late Pliocene site of Nihewan in China. As noted above, Azzaroli (1994) and Azzaroli and Mazza (1992b) hypothesized that the Chinese species, *E. boulei* would constitute a plausible ancestor for *Megaloceros.*

CAPREOLINAE: CAPREOLINI

It has been clear for some time that living roe deer (*Capreolus*) belong to two species, although the relative distributions of the two have yet to be completely delimited (they may have changed historically: the western *C. capreolus* seems to have extended its range at the expense of the eastern *C. pygargus*). Mitochondrial control region sequences separate them completely and indicate that the split between them goes back 2 to 3 million years; there are two clusters within each of the species, opening the possibility that the taxonomic diversity is still underestimated (Randi et al., 1998a).

The earliest known fossil of the tribe, *Procapreolus ucrainicus,* is late middle Miocene in age (about 10 Ma according to Lister et al. [1998], but 12 Ma according to Azanza and Menendez [1990]). Other species assigned to the same genus are known as late as the early Pliocene (Di Stefano and Petronio, 2002). Compared to *Capreolus,* the antlers are very similar but with weaker development of the "pearling" so characteristic of modern roe deer, and the two top tines are sometimes each bifurcated; there are primitive features in the teeth, and large canines are present in a specimen of *P. wenzensis* (Lister et al., 1998). The earliest species assigned to *Capreolus, C. constantini* from the middle Pliocene of Central Asia, more resembles modern *C. pygargus* according to Lister et al. (1998), who were uncertain whether this represents the beginning of geographic separation or indicates that *C. pygargus* is the more plesiomorphic of the two living species.

Because it now seems evident that *Hydropotes,* the Chinese water deer, is a second genus of this tribe, some of the evolutionary trends seen in the *Capreolus* lineage may make sense. The possession of more complex antlers in *Procapreolus ucrainicus* is evidently the primitive state, which became somewhat reduced in *Capreolus* and lost altogether in *Hy-*

dropotes, and the large canines of *P. wenzensis* may well be not primitive but derived in the direction of *Hydropotes.* These hypotheses will be tested by later discoveries.

CAPREOLINAE: ALCEINI

Most authors place all living *Alces* (elk [Europe] or moose [North America]) in a single species, but Boyeskorov (1999) has convincingly argued that there are in fact two species: *A. alces* from Europe and western Siberia, and *A. americanus* from eastern Siberia and North America. The boundary seems to be the Enisei River. They differ in chromosome number, color and color pattern, body proportions, skull characters, and antler form. The small moose from the Manchuria/Primoriye region, which Boyeskorov refers to as *A. americanus cameloides,* has single-palm antlers like those of *A. alces* rather than the double-palm antlers of the larger *A. americanus* and may rank as a third species. The status of the recently extinct Caucasus moose has yet to be settled.

The fossil history of *Alces* is fairly well known. Azzaroli (1981, 1985) recognized a separate genus *Cervalces* for all the fossil species, reserving *Alces* for just the living forms. Lister (1993), on the other hand, incorporated them all in the same genus and traced the changes from early Pleistocene *Alces gallarum* via middle Pleistocene *A. latifrons* to the modern European *A. alces,* which appeared in the late Pleistocene. (An intermediate species, *A. carnutorum,* has sometimes been recognized at the early/middle Pleistocene boundary, between *A. gallarum* and *A. latifrons* [Heintz and Poplin, 1981].) The changes involved fluctuation in body size and directional modification of skull form and shortening of the antler beam, indicating the adoption of a more forested, less steppic environment (see also Breda and Marchetti, 2005, who retain the genus *Cervalces*).

In North America, modern moose appeared only at the end of the Pleistocene, where they replaced a late surviving population of *A. latifrons* (classed by Azzaroli as a distinct, endemic North American species, *A. scotti*).

CAPREOLINAE: RANGIFERINI

The living genera of Rangiferini (as understood here) are *Rangifer* (Holarctic reindeer and caribou), *Odocoileus* (whitetail, blacktail, and mule deer, from North America and the northwestern part of South America), *Mazama* (brockets, mainly South American but extending into southern Mexico), and the entirely South American *Hippocamelus* (huemul), *Blastocerus* (marsh deer), *Ozotoceros* (pampas deer), and *Pudu* (pudu). These genera form a well-defined clade, and, despite such unusual features as the possession of antlers in the female, *Rangifer* is an integral member, although it may well be sister taxon to the other genera (Pitra et al., 2004). The tribe is distinguished from Capreolini and Alceini by the derived condition of the vomer (mentioned above), by the presence of a stylohyoid–paroccipital contact, and by the antler pedicels being well separated (Webb, 2000).

A cladogram has been proposed by Webb (2000), as follows:

((*Pudu* (*Rangifer* (*Hippocamelus*)))(*Mazama* (*Ozotoceros* (*Blastocerus, Odocoileus*))))

This was based on craniodental characters, but the molecular data of Pitra et al. (2004) indicate instead the following:

(*Rangifer* (*Blastocerus, Pudu*)(*Odocoileus, Mazama*))

The remaining two genera were not available.

Much work remains to be done on the distinctiveness and α-taxonomy of all these genera. At present, both *Hippocamelus* and *Pudu* are assigned two species, and there is no indication that this is not correct. *Blastocerus* and *Ozotoceros* are each considered monotypic, although the status of the supposed subspecies, especially of the latter, needs to be reexamined.

Odocoileus is a very difficult genus taxonomically. In North America there are two species groups, each currently being classed as a single species, but this is almost certainly overlumped. One problem is that white-tailed deer (*O. virginianus:* if this really is a single species, rather than a species complex) and mule deer (*O.* cf. *hemionus*) are known to interbreed in West Texas. It was discovered 20 years ago that in this region the two share a mtDNA restriction type characteristic of white tail, suggesting that interbreeding had occurred between male mule deer and female whitetails, and the whitetail phenotypic characteristics have been lost by generations of backcrossing with mule deer (Carr et al., 1986). A subsequent study (Cathey et al., 1998) confirmed that F_1 hybrids are rare and found that Y chromosome DNA, by contrast with mtDNA, assorted more clearly along species lines.

There is a decline in size down the east coast of North America, culminating in the diminutive deer of the Florida Keys (currently known as *Odocoileus virginianus clavium*). Study of mtDNA of deer in Florida, including Key deer, found three different haplotypes, but these corresponded only poorly with the described subspecies, including *clavium* (Ellsworth et al., 1994). This raises the question, frequently posed in recent years, of whether putative subspecies would better be defined as possessors of unique mitochondrial haplotypes rather than, as traditionally, on morphological characters. It has been argued that the function of the subspecies category is to delimit geographically restricted lineages; against this, I would maintain first that of course mtDNA is inherited only matrilineally, and the depicted lineages might be entirely different if Y chromosome DNA were studied (as in the West Texas hybridization study cited above). In any case, morphological characters are themselves (broadly speaking) heritable, and there is some value

in continuing to recognize gene pools that are strongly divergent as a whole.

An analogous situation recurs in Venezuela, at the southern end of the distribution of whitetails. Molina and Molinari (1999) recognized three distinct species in Venezuela and suggested that there was evidence for a fourth. These are *O. margaritae* (Margarita I.), *O. lasiotis* (Mérida Andean Highlands), and *O. cariacou* (from the rest of the range). In contrast, a study of mtDNA by Moscarella et al. (2003) identified four clades, but these corresponded rather poorly with the proposed species. It is clearly time for a new look, utilizing both methods and using the same samples for both.

Mazama is also a taxonomically complex genus, with more species than the four that had been previously assigned to it (see, for example, Medellín et al., 1998, who identified a distinct species for Yucatan).

Rangifer (called reindeer in Europe, caribou in North America) are currently regarded as a single species, *R. tarandus,* which is broadly divided into woodland, tundra, and high-Arctic subspecies. The woodland forms (*R. t. fennicus* in the Old World, *R. t. caribou* in the New World) are very different in appearance—antler form, color, and build—from the tundra forms (*R. t. tarandus* in the Old World, *R. t. granti* and *groenlandicus* in the New), and there is said to be some seasonal overlap in range when tundra reindeer/caribou enter the northern fringes of the coniferous forest. Precisely how much interbreeding there may be, however, is not known. This situation suggests that speciation is well under way or complete, but before we can contemplate a new taxonomic arrangement, we need to know whether Old and New World woodland forms constitute a clade separate from the tundra forms or are separately derived from them (or even vice versa). The monophyly of the three high-Arctic forms, however, has already been investigated: the two New World forms, *R. t. pearyi* and *eogroendlandicus,* do indeed form a clade, related to the nearest tundra subspecies, *R. t. groenlandicus* (known as barren-ground caribou in Canada), whereas the Svalbard reindeer, *R. t. platyrhynchus,* although morphologically not dissimilar, is a clear derivative of Old World tundra reindeer (Gravlund et al., 1998). Tundra and high-Arctic reindeer are said to be seasonally sympatric on some of the Canadian high-Arctic islands and are strikingly different in appearance, but in this case one wonders how much the differences might be the result of phenotypic plasticity.

The earliest example of a living genus in the Americas is a species of *Odocoileus* from the early Pliocene; the earliest known of all American deer is *Eocoileus gentryorum* Webb, 2000, of the late Miocene (5 Ma) of Florida, which according to its describer is "most comparable to *Ozotoceros* and *Mazama.*" His placement of it on one of two major New World clades (see above), rather than at the base, implies that still earlier deer fossils may be expected in North America—as indeed would be predicted on molecular clock grounds (Pitra et al., 2004). Other genera described from the Americas are as follows:

Bretzia. Best known from the Rancholabrean (latest Pleistocene), the earliest possible occurrence of this genus, consisting of a small palmated antler, is also late Pliocene in age (Webb, 2000). Morejohn et al. (2005) recently added further material to the known sample of the genus, describing some unusual features of the carpals and tracing the evolution of its antler form from earliest through intermediate to latest occurrences.

Navahoceros. A somewhat stockily built mountain deer with small antlers. Best known from Rancholabrean deposits, it may go back to some 3 Ma (Webb, 2000).

Sangamona. Described by Kurtén (1979) as a stilt-legged deer from the late Pleistocene, is a phantom. Churcher (1984) performed a notable hatchet job on it, showing that the type specimen is indeterminable and that every other specimen that has been referred to it from time to time is also either indeterminable or else demonstrably something else (usually *Odocoileus*). No such deer ever existed.

Torontoceros. Described by Churcher and Peterson (1982), this genus is known only from a partial skull with heavy, horizontal but otherwise reindeer-like antlers, dated by ^{14}C at 11,315 ± 325 B.P.

Morenelaphus, Epieuryceros, Agalmoceros, Chaitocerus. These are poorly known deer from the middle (?) Pleistocene of South America. Their relationships are unclear.

CONCLUSION

The broad outlines of cervid phylogeny and taxonomy are now clear, but the details remain to be filled in. Further DNA work—nuclear, including Y-chromosome, as well as mitochondrial—is needed, and renewed morphological and behavioral studies are necessary to find where the species (*sensu* phylogenetic species concept) begin and end, and hence, what are the units of biodiversity in the genus.

EPILOGUE

During a visit in 1994 to the Institute of Ecology and Biological Resources, Hanoi, the late Shantini Dawson drew my attention to a very unusual frontlet and antlers labeled "Black Muntjac," collected on September 9, 1974, at Gia Lai, Kontum. It bears an uncanny resemblance to *Procervulus* in the symmetrical lack of a brow tine as well as in the remarkably straight, parallel antler beams. I sent the photos (see Fig. 20.1) to the late Tony Bubenik, who was extremely intrigued and excited by the resemblance.

Careful examination suggests, however, that this may be an unusual example of hog deer, *Cervus porcinus.* It does have a clear burr, unlike *Procervulus,* and the antlers are bent back just above the burr, as if to accommodate a brow tine whose development has been suppressed.

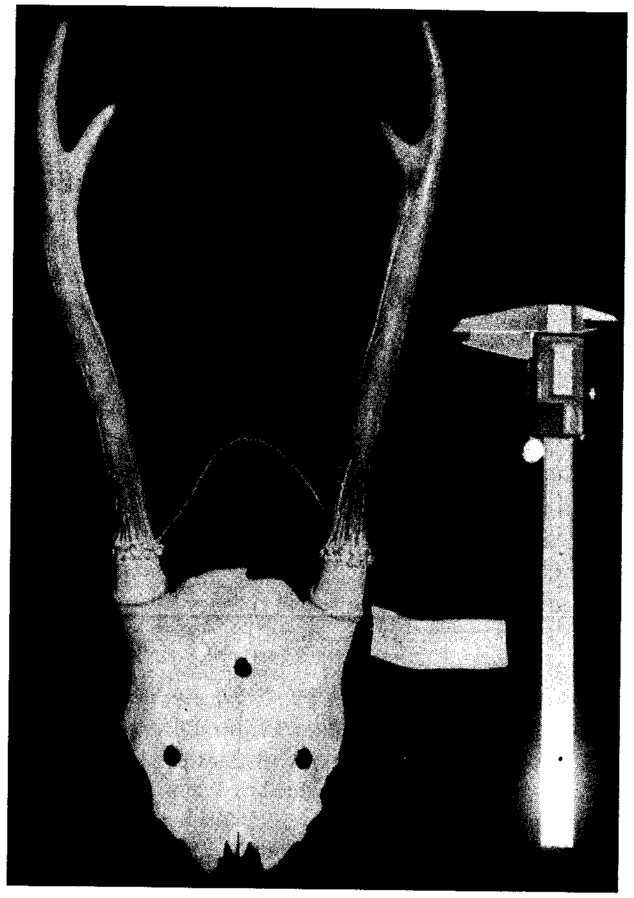

Fig. 20.1. "Black Muntjac" from Gia Lai, Kontum. Probably an unusual example of hog deer, *Cervus porcinus*.

The significance of the specimen is that it shows the degree to which occasional anomalies can mislead one's assessment of affinities but that the sort of crown cervid features elucidated by Janis and Scott (1987), Bubenik (1990), and Azanza (1993a) are sure guides to the true nature of a deer, however bizarre.

ACKNOWLEDGMENTS

I thank Nikos Solounias, Alan Gentry, and another referee for their useful comments. Erik Meijaard and the late Peter Grubb have been valued collaborators over the years, and without them, a chapter such as this could never have been written. My association with molecular workers, especially Christian Pitra and Joerns Fickel, has been fruitful, and I have learned from it. I learned more than I can say from my all too brief association with the late Tony Bubenik. Finally, I thank Don Prothero for inviting me to contribute to this volume.

NIKOS SOLOUNIAS

21

Family Giraffidae

THE GIRAFFE AND THE OKAPI are the only living species of the Giraffidae. A celebrated species on its own merit, the giraffe also represents Africa. Every person knows of the giraffe, and Sherr (1997) has shown many of its popular expressions. Its trivial name, *Giraffa camelopardalis*, means spotted (pardali) camel (camela) in Greek. There are many extinct species of giraffids from Eurasia and Africa, and they were common in Eurasian and African faunas during the late Miocene (Bohlin, 1926; Hamilton, 1978a). The okapi (*Okapia johnstoni*) is not well known to the public but is fascinating to zoologists and to paleontologists because it resembles the many now extinct species in having a simple ruminant form with a short neck. Little is known about the okapi because it inhabits forbidding dense forests in Zaire, so it has not been well studied, and its relationship with the giraffe and the extinct giraffids is problematic. The okapi was discovered in 1901, and it was immediately envisioned as a modern representative of already known fossil forms such as *Palaeotragus*, *Helladotherium*, and *Samotherium*, taxa from the localities of Pikermi and or Samos in Greece. Its discovery was reminiscent to that of the coelacanth (*Latimeria*), which was found living long after similar fossils had been unearthed and studied. Even the Hollywood film industry's notion of unexplored deep rain forests containing still living taxa formerly presumed extinct, including dinosaurs, is in part inspired by the discovery of the okapi. Was the okapi, then, a survivor like a Miocene taxon of *Helladotherium* or *Palaeotragus*? Scientists have compared the okapi to other giraffids (Colbert, 1938c; Hamilton, 1978a; Lankester, 1907a, 1907b). A more recent interesting approach was that of Geraads (1986), who suggested a close affinity of the okapi to the giraffe on the basis of the presence of ossicones and strong pneumatization of the frontals. Fossil taxa did not have ossicones, but instead the horns were