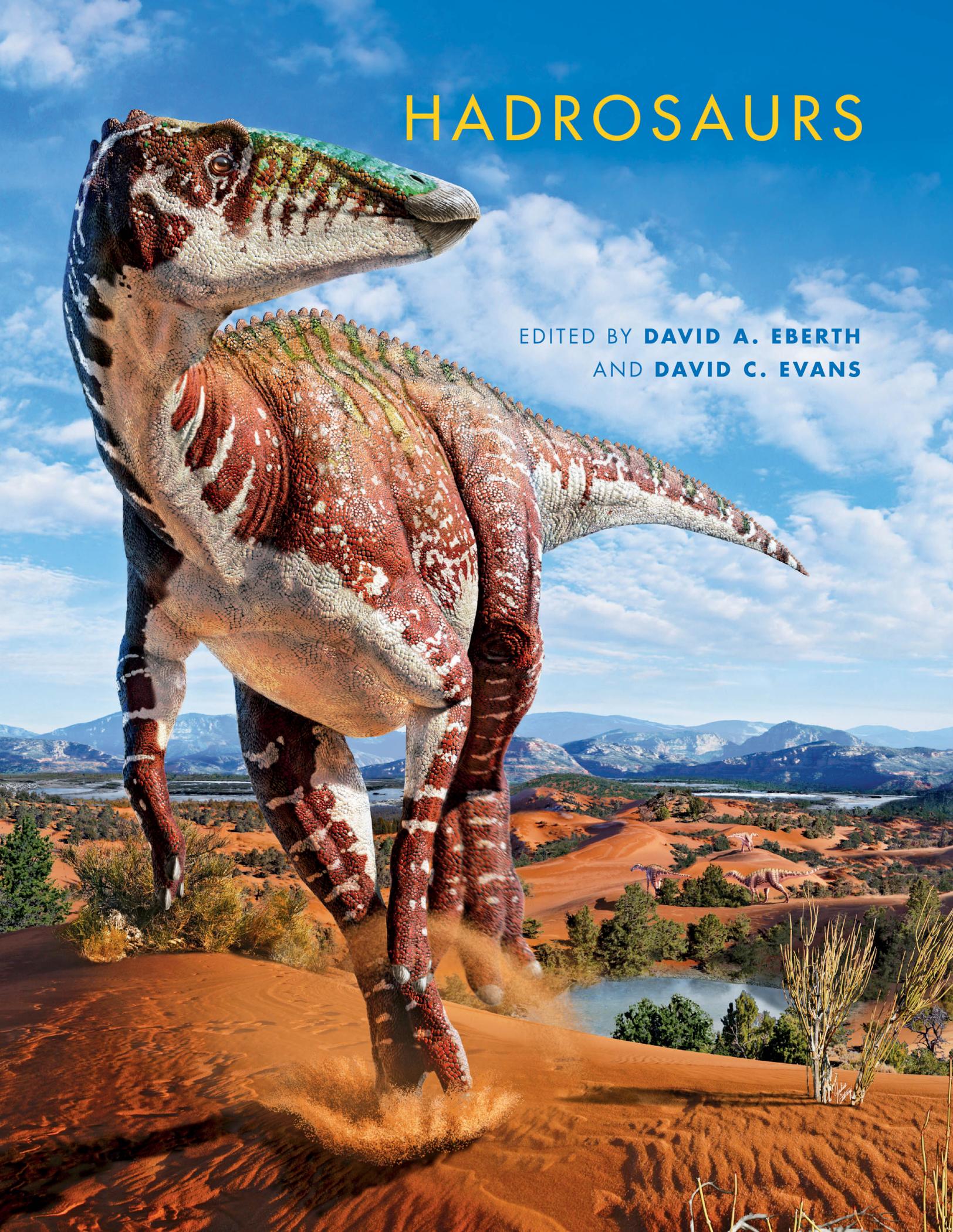


HADROSAURS

EDITED BY **DAVID A. EBERTH**
AND **DAVID C. EVANS**

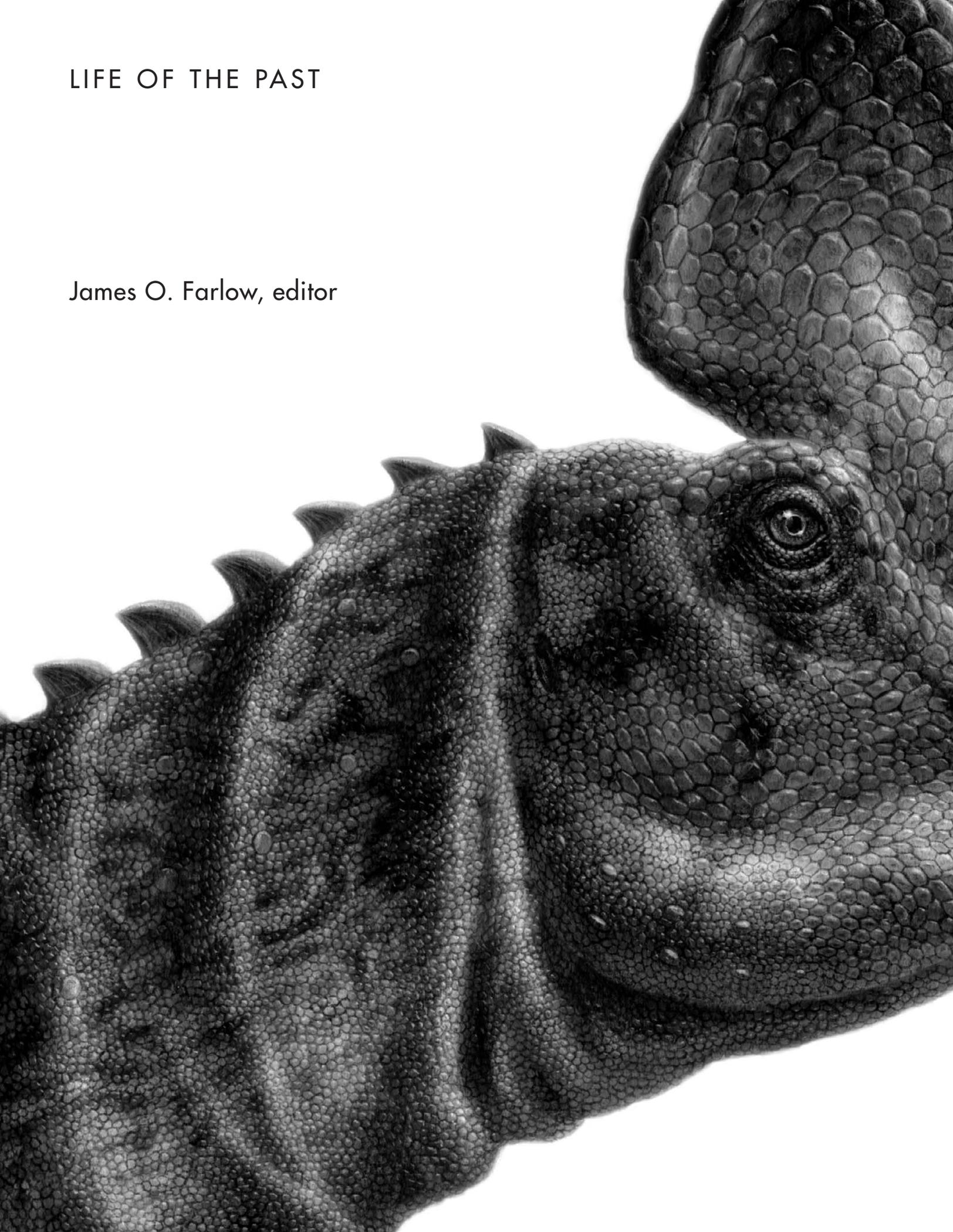


Hadrosaurs



LIFE OF THE PAST

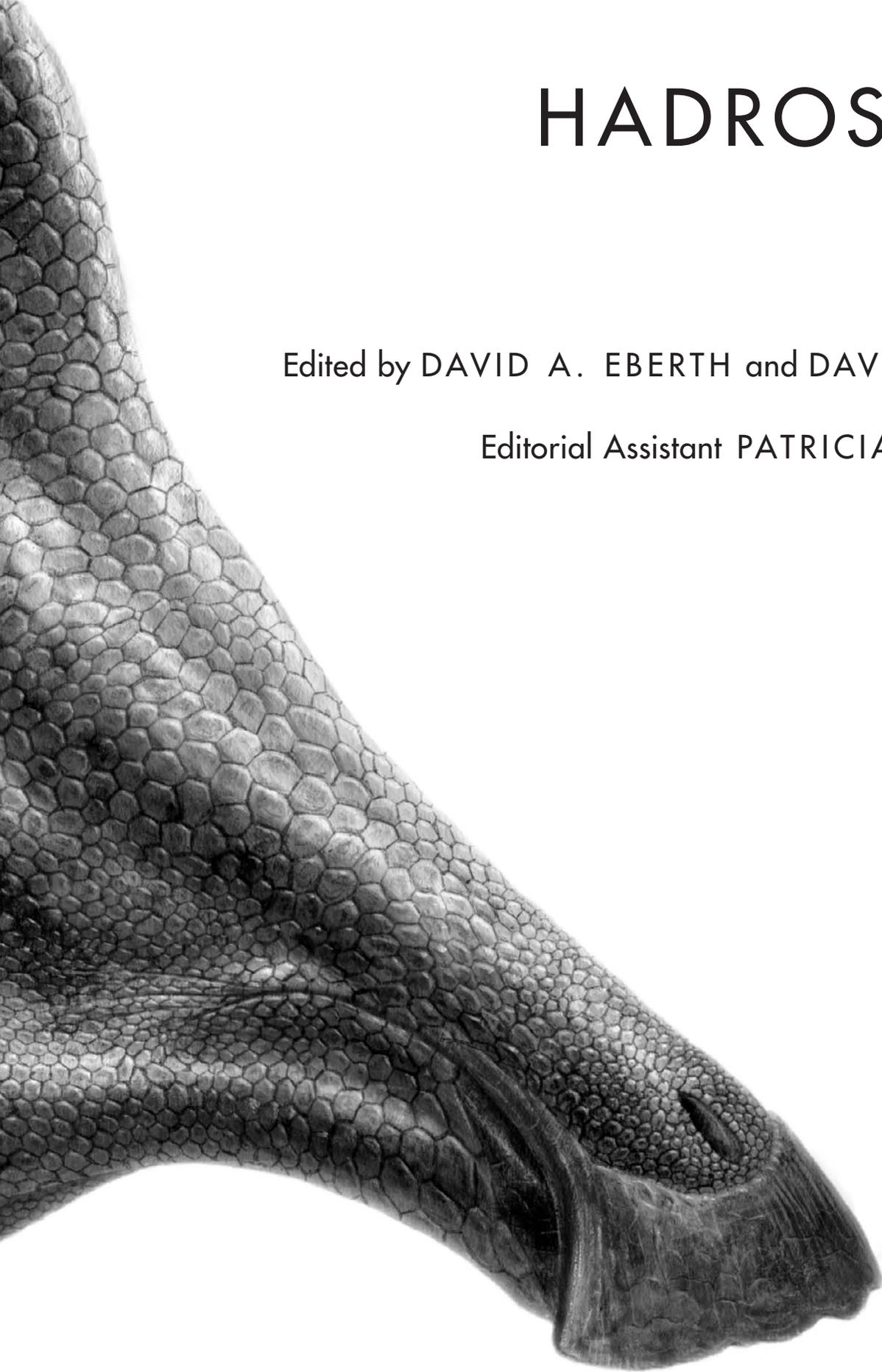
James O. Farlow, editor



HADROSAURS

Edited by DAVID A. EBERTH and DAVID C. EVANS

Editorial Assistant PATRICIA E. RALRICK



INDIANA UNIVERSITY PRESS

Bloomington & Indianapolis

This book is a publication of

Indiana University Press
Office of Scholarly Publishing
Herman B Wells Library 350
1320 East 10th Street
Bloomington, Indiana 47405 USA

iupress.indiana.edu

Telephone 800-842-6796
Fax 812-855-7931

© 2015 by Indiana University Press

All rights reserved

No part of this book may be reproduced or utilized in any form or by any means, electronic or mechanical, including photocopying and recording, or by any information storage and retrieval system, without permission in writing from the publisher. The Association of American University Presses' Resolution on Permissions constitutes the only exception to this prohibition.

© The paper used in this publication meets the minimum requirements of the American National Standard for Information Sciences—Permanence of Paper for Printed Library Materials, ANSI Z39.48–1992.

Manufactured in the United States of America

Library of Congress Cataloging-in-Publication Data

Hadrosaurs / edited by David A. Eberth and David C. Evans.

pages cm.—(Life of the past)

Includes bibliographical references and index.

ISBN 978-0-253-01385-9 (cloth : alk.

paper)—ISBN 978-0-253-01390-3 (ebook)

1. Hadrosauridae. 2. Hadrosauridae—Anatomy.

3. Hadrosauridae—Geographical distribution.

4. Dinosaurs. I. Eberth, David A. II. Evans, David C.

(David Christopher), [date]

QE862.O65H33 2014

567.914—dc23

2014011885

1 2 3 4 5 20 19 18 17 16 15

To David Weishampel and all those, from J. Leidy onward, who have contributed to our knowledge of hadrosaurs.

In particular, we recognize the efforts of Derek J. Main, a tireless promoter of Earth Science education and research. We value his contribution to this volume and mourn his all-too-soon passing.

Those animals of other days will give joy and pleasure to generations yet unborn.

Charles H. Stenberg

ix	Contributors		
xi	Reviewers		
xiii	Preface · David A. Eberth and David C. Evans		
xv	Acknowledgments		
	Part 1. Overview		
	A History of the Study of Ornithopods: Where Have We Been? Where Are We Now? and Where Are We Going?		
2	David B. Weishampel		
	Part 2. New Insights into Hadrosaur Origins		
	Iguanodonts from the Wealden of England: Do They Contribute to the Discussion Concerning Hadrosaur Origins?		
10	David B. Norman		
	Osteology of the Basal Hadrosauroid <i>Equijubus normani</i> (Dinosauria, Ornithopoda) from the Early Cretaceous of China		
44	Andrew T. McDonald, Susannah C. R. Maidment, Paul M. Barrett, Hai-lu You, and Peter Dodson		
	<i>Gongpoquansaurus mazongshanensis</i> (Lü, 1997) comb. nov. (Ornithischia: Hadrosauroidea) from the Early Cretaceous of Gansu Province, Northwestern China		
73	Hai-lu You, Da-Qing Li, and Peter Dodson		
	Postcranial Anatomy of a Basal Hadrosauroid (Dinosauria: Ornithopoda) from the Cretaceous (Cenomanian) Woodbine Formation of North Texas		
77	Derek J. Main, Christopher R. Noto, and David B. Weishampel		
	A Re-evaluation of Purported Hadrosaurid Dinosaur Specimens from the “Middle” Cretaceous of England		
96	Paul M. Barrett, David C. Evans, and Jason J. Head		
	A New Hadrosauroid (<i>Plesiohadros djadokhtaensis</i>) from the Late Cretaceous Djadokhtan Fauna of Southern Mongolia		
108	Khishigjav Tsogtbaatar, David B. Weishampel, David C. Evans, and Mahito Watabe		
	Hadrosauroid Material from the Santonian Milk River Formation of Southern Alberta, Canada		
136	Derek W. Larson, Nicolás E. Campione, Caleb M. Brown, David C. Evans, and Michael J. Ryan		
	Part 3. Hadrosaurid Anatomy and Variation		
	New Hadrosaurid (Dinosauria, Ornithopoda) Specimens from the Lower–Middle Campanian Wahweap Formation of Southern Utah		
156	Terry A. Gates, Zubair Jinnah, Carolyn Levitt, and Michael A. Getty		
	New Saurolophine Material from the Upper Campanian–Lower Maastrichtian Wapiti Formation, West-Central Alberta		
174	Phil R. Bell, Robin Sissons, Michael E. Burns, Federico Fanti, and Philip J. Currie		
	Variation in the Skull Roof of the Hadrosaur <i>Gryposaurus</i> Illustrated by a New Specimen from the Kaiparowits Formation (late Campanian) of Southern Utah		
191	Andrew A. Farke and Lucia Herrero		
	A Skull of <i>Prosaurolophus maximus</i> from Southeastern Alberta and the Spatiotemporal Distribution of Faunal Zones in the Dinosaur Park Formation		
200	David C. Evans, Christopher T. McGarrity, and Michael J. Ryan		
	Postcranial Anatomy of <i>Edmontosaurus regalis</i> (Hadrosauridae) from the Horseshoe Canyon Formation, Alberta, Canada		
208	Nicolás E. Campione		
	Cranial Morphology and Variation in <i>Hypacrosaurus stebingeri</i> (Ornithischia: Hadrosauridae)		
245	Kirstin S. Brink, Darla K. Zelenitsky, David C. Evans, John R. Horner, and François Therrien		
	Part 4. Biogeography and Biostratigraphy		
	An Overview of the Latest Cretaceous Hadrosauroid Record in Europe		
268	Fabio M. Dalla Vecchia		
	The Hadrosauroid Record in the Maastrichtian of the Eastern Tremp Syncline (Northern Spain)		
298	Fabio M. Dalla Vecchia, Rodrigo Gaete, Violeta Riera, Oriol Oms, Albert Prieto-Márquez, Bernat Vila, Albert Garcia Sellés, and Àngel Galobart		
	Hadrosaurs from the Far East: Historical Perspective and New <i>Amurosaurus</i> Material from Blagoveschensk (Amur Region, Russia)		
315	Yuri L. Bolotsky, Pascal Godefroit, Ivan Y. Bolotsky, and Andrey Atuchin		
	South American Hadrosaurs: Considerations on Their Diversity		
332	Rodolfo A. Coria		
	The Hadrosaurian Record from Mexico		
340	Angel A. Ramírez-Velasco, René Hernández-Rivera, and Ricardo Servin-Pichardo		
	Stratigraphic Distribution of Hadrosaurids in the Upper Cretaceous Fruitland, Kirtland, and Ojo Alamo Formations, San Juan Basin, New Mexico		
361	Robert M. Sullivan and Spencer G. Lucas		
	Relocating the Lost <i>Gryposaurus incurvimanus</i> Holotype Quarry, Dinosaur Provincial Park, Alberta, Canada		
385	Darren H. Tanke and David C. Evans		

Part 5. Function and Growth

- 22**
398 **Comparative Ontogenies (Appendicular Skeleton) for Three Hadrosaurids and a Basal Iguanodontian: Divergent Developmental Pathways in Hadrosaurinae and Lambeosaurinae**
Merrilee F. Guenther
- 23**
416 **The Size-Frequency Distribution of Hadrosaurs from the Dinosaur Park Formation of Alberta, Canada**
Donald B. Brinkman
- 24**
422 **Osteohistology and Occlusal Morphology of *Hypacrosaurus stebingeri* Teeth throughout Ontogeny with Comments on Wear-Induced Form and Function**
Gregory M. Erickson and Darla K. Zelenitsky
- 25**
433 **Three-Dimensional Computational Modeling of Pelvic Locomotor Muscle Moment Arms in *Edmontosaurus* (Dinosauria, Hadrosauridae) and Comparisons with Other Archosaurs**
Susannah C. R. Maidment, Karl T. Bates, and Paul M. Barrett
- 26**
449 **Duckbills on the Run: The Cursorial Abilities of Hadrosaurs and Implications for Tyrannosaur-Avoidance Strategies**
W. Scott Persons IV and Philip J. Currie
- 27**
459 **Duck Soup: The Floating Fates of Hadrosaurs and Ceratopsians at Dinosaur Provincial Park**
Donald M. Henderson
- 28**
467 **Hadrosauroid Jaw Mechanics and the Functional Significance of the Predentary Bone**
Ali Nabavizadeh

Part 6. Preservation, Tracks, and Traces

- 29**
486 **Debris Flow Origin of an Unusual Late Cretaceous Hadrosaur Bonebed in the Two Medicine Formation of Western Montana**
James G. Schmitt, Frankie D. Jackson, and Rebecca R. Hanna

- 30**
502 **Occurrence and Taphonomy of the First Documented Hadrosaurid Bonebed from the Dinosaur Park Formation (Belly River Group, Campanian) at Dinosaur Provincial Park, Alberta, Canada**
David A. Eberth, David C. Evans, and David W. H. Lloyd

- 31**
524 **Body Size Distribution in a Death Assemblage of a Colossal Hadrosaurid from the Upper Cretaceous of Zhucheng, Shandong Province, China**
David W. E. Hone, Corwin Sullivan, Qi Zhao, Kebai Wang, and Xing Xu

- 32**
532 **First Hadrosaur Trackway from the Upper Cretaceous (Late Campanian) Oldman Formation, Southeastern Alberta**
François Therrien, Darla K. Zelenitsky, Kohei Tanaka, and Wendy J. Sloboda

- 33**
540 **Paleopathology in Late Cretaceous Hadrosauridae from Alberta, Canada**
Darren H. Tanke and Bruce M. Rothschild

- 34**
572 **A Review of Hadrosaurid Skin Impressions**
Phil R. Bell

- 35**
591 **Soft-Tissue Structures of the Nasal Vestibular Region of Saurolophine Hadrosaurids (Dinosauria, Ornithopoda) Revealed in a "Mummified" Specimen of *Edmontosaurus annectens***
Albert Prieto-Márquez and Jonathan R. Wagner

- 36**
600 **The Role and Biochemistry of Melanin Pigment in the Exceptional Preservation of Hadrosaur Skin**
Phillip L. Manning, Roy A. Wogelius, Bart Van Dongen, Tyler R. Lyson, Uwe Bergmann, Sam Webb, Michael Buckley, Victoria M. Egerton, and William I. Sellers

611 Afterword · John R. Horner

613 Subject Index

615 Locality Index (by country)

616 Stratigraphy Index (by country)

617 Taxonomic Index

Andrey Atuchin, Palaeontological Laboratory of the Institute of Geology and Nature Management, Far East Branch, Russian Academy of Sciences, per. Relochny 1, 675000 Blagoveschensk, Russia

Karl T. Bates, Department of Musculoskeletal Biology II, Institute of Aging and Chronic Disease, University of Liverpool, Sherrington Buildings, Ashton Street, Liverpool, U.K. L69 3GE

Paul M. Barrett, Department of Earth Sciences, Natural History Museum, Cromwell Road, London, U.K. SW7 5BD

Phil R. Bell, School of Environmental and Rural Science, University of New England, Armidale 2351, NSW, Australia

Uwe Bergmann, Stanford Synchrotron Radiation Lightsource, Stanford University, Menlo Park, California 94305

Ivan Y. Bolotsky, Research Center for Paleontology and Stratigraphy, Jilin University, Changchun 130061, China

Yuri L. Bolotsky, Palaeontological Laboratory of the Institute of Geology and Nature Management, Far East Branch, Russian Academy of Sciences, per. Relochny 1, 675000 Blagoveschensk, Russia

Kirstin S. Brink, Department of Ecology and Evolutionary Biology, University of Toronto Mississauga, 3359 Mississauga Road N., Mississauga, Ontario L5L 1C6

Donald B. Brinkman, Royal Tyrrell Museum of Palaeontology, Box 7500, Drumheller, Alberta T0J 0Y0

Caleb M. Brown, Royal Tyrrell Museum of Palaeontology, Box 7500, Drumheller, Alberta T0J 0Y0

Michael Buckley, Faculty of Life Sciences, University of Manchester, Manchester, U.K. M13 9PL

Michael E. Burns, Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9

Nicolás E. Campione, Departments of Earth Science and Organismal Biology, Uppsala University, Box 256, 751 05 Uppsala, Sweden

Rodolfo A. Coria, CONICET–University of Rio Negro–Museo Carmen Funes, Av. Córdoba 55 (8318) Plaza Huinca, Neuquén, Argentina

Philip J. Currie, Department of Biological Sciences, Zoo. 413, Biological Sciences Building, University of Alberta, Edmonton, Alberta T6G 2E9

Fabio M. Dalla Vecchia, Grup de Recerca del Mesozoic, Institut Català de Paleontologia Miquel Crusafont (ICP), Escola Industrial 23, E-08201 Sabadell, Spain

Peter Dodson, School of Veterinary Medicine, University of Pennsylvania, 3800 Spruce Street, Philadelphia, Pennsylvania 19104-6045

David A. Eberth, Royal Tyrrell Museum of Palaeontology, Box 7500, Drumheller, Alberta T0J 0Y0

Victoria M. Egerton, School of Earth, Atmospheric and Environmental Sciences, University of Manchester, Manchester, U.K. M13 9PL

Gregory M. Erickson, Department of Biological Science, Florida State University, Tallahassee, Florida, 32306-4295

David C. Evans, Department of Natural History, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario M5S 2C6

Federico Fanti, Dipartimento di Scienze della Terra e Geologico-Ambientali, Università di Bologna, Italy

Andrew A. Farke, Raymond M. Alf Museum of Paleontology, 1175 West Baseline Road, Claremont, California 91711

Rodrigo Gaete, Museu de la Conca Dellà, Carrer del Museu 4, Isona, E-25650, Spain

Àngel Galobart, Grup de Recerca del Mesozoic, Institut Català de Paleontologia Miquel Crusafont (ICP), Escola Industrial 23, E-08201 Sabadell, Spain

Albert Garcia Sellés, Grup de Recerca del Mesozoic, Institut Català de Paleontologia Miquel Crusafont (ICP), Escola Industrial 23, E-08201 Sabadell, Spain

Terry A. Gates, Department of Biological Sciences, North Carolina State University, Raleigh, NC 27695; North Carolina Museum of Natural Sciences, Raleigh, NC 27601

Michael A. Getty, Denver Museum of Nature and Science, 2001 Colorado Boulevard, Denver, Colorado 80205-5732

Pascal Godefroit, Department of Palaeontology, Royal Belgian Institute of Natural Sciences, rue Vautier 29, 1000 Brussels, Belgium

Merrilee F. Guenther, Department of Biology, Elmhurst College, Elmhurst, Illinois 60126

Rebecca R. Hanna, Museum of the Rockies, Montana State University, Bozeman, Montana 59717

Jason J. Head, Department of Earth and Atmospheric Sciences, University of Nebraska–Lincoln, 228 Bessey Hall, Lincoln, Nebraska 68588

Donald M. Henderson, Royal Tyrrell Museum of Palaeontology, Box 7500, Drumheller, Alberta T0J 0Y0

René Hernández-Rivera, Instituto de Geología, Universidad Nacional Autónoma de México, Circuito de Investigación Científica, Cuidad Universitaria, Delegación Coyoacán, 04510 México

Lucía Herrero, The Webb Schools, 1175 West Baseline Road, Claremont, California 91711; Stanford University, 450 Serra Mall, Stanford, California 94305

David W. E. Hone, School of Biological and Chemical Sciences, Queen Mary University of London, Mile End Road, London, U.K. E1 4NS

John R. Horner, Museum of the Rockies, Montana State University, Bozeman, Montana 59717-0040

Frankie D. Jackson, Department of Earth Sciences, Montana State University, Bozeman, Montana 59717

Zubair Jinnah, School of Geosciences, University of the Witwatersrand, Johannesburg, Wits 2050, South Africa

Derek W. Larson, Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, Ontario M5S 2C6

Carolyn Levitt, University of Utah, Department of Geology and Geophysics, Salt Lake City, Utah 84112

Da-Qing Li, Gansu Geological Museum, 6 Tuanjie Road, Chengguan District, Lanzhou, Gansu Province, 730010, China

David W. H. Lloyd, Royal Tyrrell Museum of Palaeontology, Box 7500, Drumheller, Alberta T0J 0Y0

Spencer G. Lucas, New Mexico Museum of Natural History and Science, 1801 Mountain Road NW, Albuquerque, New Mexico 87104

Tyler R. Lyson, Smithsonian Institution, National Museum of Natural History, Washington, D.C. 20560

Susannah C. R. Maidment, Department of Palaeontology, The Natural History Museum, Cromwell Road, London, U.K. SW7 5BD

Derek J. Main (deceased), Department of Earth and Environmental Sciences, University of Texas at Arlington, Arlington, Texas 76019

Phillip L. Manning, School of Earth, Atmospheric and Environmental Sciences, University of Manchester, Manchester, U.K. M13 9PL

Andrew T. McDonald, Department of Earth and Environmental Science, University of Pennsylvania, 254-b Hayden Hall, 240 South 33rd Street, Philadelphia, Pennsylvania 19104

Christopher T. McGarrity, Department of Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks Street, Toronto, Ontario M5S 3B2

Ali Nabavizadeh, Center for Functional Anatomy and Evolution, Johns Hopkins University School of Medicine, Baltimore, Maryland 21287

David B. Norman, Sedgwick Museum and Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge, U.K. CB2 3EQ

Christopher R. Noto, Department of Biological Sciences, University of Wisconsin–Parkside, Kenosha, Wisconsin 53144

Oriol Oms, Universitat Autònoma de Barcelona, Departament de Geologia, Cerdanyola del Vallès, Barcelona, E-08193, Spain

W. Scott Persons IV, Department of Biological Sciences, Zoo. 418, Biological Sciences Building, University of Alberta, Edmonton, Alberta T6G 2E9

Albert Prieto-Márquez, School of Earth Sciences, University of Bristol, Wills Memorial Building, Queens Road, Bristol, U.K. BS8 1RJ

Angel A. Ramírez-Velasco, Posgrado Facultad de Medicina Veterinaria y Zootecnia, Universidad Nacional Autónoma de México, Circuito de Investigación Científica, Ciudad Universitaria, Delegación Coyoacán, 04510 México

Violeta Riera, Universitat Autònoma de Barcelona, Departament de Geologia, Cerdanyola del Vallès, Barcelona, E-08193, Spain

Bruce M. Rothschild, Department of Vertebrate Paleontology, Carnegie Museum of Natural History, 4400 Forbes Ave. Pittsburgh, Pennsylvania 15213

Michael J. Ryan, Department of Vertebrate Paleontology, Cleveland Museum of Natural History, 1 Wade Oval Drive, University Circle, Cleveland, Ohio 44106

James G. Schmitt, Department of Earth Sciences, Montana State University, Bozeman, Montana 59717

William I. Sellers, Faculty of Life Sciences, University of Manchester, Manchester, U.K. M13 9PL

Ricardo Servin-Pichardo, Facultad de Ciencias, Universidad Nacional Autónoma de México, Circuito de Investigación Científica, Ciudad Universitaria, Delegación Coyoacán, 04510 México

Robin Sissons, Philip J. Currie Dinosaur Museum, Pipestone Creek Dinosaur Initiative, County of Grande Prairie No. 1, 10001 84 Ave., Clairmont, Alberta T0H 0W0

Wendy J. Sloboda, Warner, Alberta T0K 2L0

Corwin Sullivan, Key Laboratory of Vertebrate Evolution and Human Origin, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, PO Box 643, Beijing 100044, China

Robert M. Sullivan, New Mexico Museum of Natural History and Science, 1801 Mountain Road NW, Albuquerque, New Mexico 87104

Kohei Tanaka, Department of Geoscience, University of Calgary, 2500 University Dr NW, Calgary, Alberta T2N 1N4

Darren H. Tanke, Royal Tyrrell Museum of Palaeontology, Box 7500, Drumheller, Alberta T0J 0Y0

François Therrien, Royal Tyrrell Museum of Palaeontology, Box 7500, Drumheller, Alberta T0J 0Y0

Khishigjav Tsogtbaatar, Mongolian Paleontological Center, Ulaanbaatar 210351, Mongolia

Bart Van Dongen, Williamson Research Centre for Molecular Environmental Science, University of Manchester, Manchester, U.K. M13 9PL

Bernat Vila, Grupo Aragosaurus-Instituto Universitario de Ciencias Ambientales, Paleontología, Facultad de Ciencias, Universidad de Zaragoza, Pedro Cerbuna 12, E-50009 Zaragoza, Spain

Jonathan R. Wagner, Texas State University–San Marcos, Department of Geography ELA 139, 601 University Drive, San Marcos, Texas 78666-4684

Kebai Wang, Key Laboratory of Vertebrate Evolution and Human Origin, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, PO Box 643, Beijing 100044, China

Mahito Watabe, Hayashibara Museum of Natural Science, 2-3. Shimoiishi-1, Okayama 700-0907, Japan

Sam Webb, Stanford Synchrotron Radiation Lightsource, Stanford University, Menlo Park, California 94305

David B. Weishampel, Center for Functional Anatomy and Evolution, Johns Hopkins University School of Medicine, Baltimore, Maryland 21287

Roy A. Wogelius, Williamson Research Centre for Molecular Environmental Science, University of Manchester, Manchester, U.K. M13 9PL

Xing Xu, Key Laboratory of Vertebrate Evolution and Human Origin, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, PO Box 643, Beijing 100044, China

Hai-lu You, Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, 142 Xizhimenwai Street, Beijing 100044, China

Darla K. Zelenitsky, Department of Geoscience, University of Calgary, 2500 University Dr NW, Calgary, Alberta T2N 1N4

Qi Zhao, Key Laboratory of Vertebrate Evolution and Human Origins, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, PO Box 643, Beijing 100044, China

Paul M. Barrett, Department of Earth Sciences, Natural History Museum, Cromwell Road, London, U.K. SW7 5BD

Kirstin S. Brink, Department of Ecology and Evolutionary Biology, University of Toronto Mississauga, 3359 Mississauga Road N., Mississauga, Ontario L5L 1C6

Brooks B. Britt, Department of Geology, Brigham Young University, S-387 ESC, PO Box 24606, Provo, Utah 84602

Caleb M. Brown, Royal Tyrrell Museum of Palaeontology, Box 7500, Drumheller, Alberta T0J 0Y0

Nicolás E. Campione, Departments of Earth Sciences and Organismal Biology, Uppsala University, Box 256, 751 05 Uppsala, Sweden

Katherine Clayton, Paleontology Collections, Natural History Museum of Utah, 301 Wakara Way, Salt Lake City, Utah 84108

Penelope Cruzado-Caballero, Universidad de Zaragoza, Departamento de Ciencias de la Tierra, c/ Pedro Cerbuna, 12 c.p. 50009 Zaragoza, Spain

David Dilkes, Department of Biology and Microbiology, University of Wisconsin Oshkosh, 800 Algona Boulevard, Oshkosh, Wisconsin 54901

Peter Dodson, School of Veterinary Medicine, University of Pennsylvania, 3800 Spruce Street, Philadelphia, Pennsylvania 19104-6045

David A. Eberth, Royal Tyrrell Museum of Palaeontology, Box 7500, Drumheller, Alberta T0J 0Y0

David C. Evans, Department of Natural History, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario M5S 2C6

Andrew A. Farke, Raymond M. Alf Museum of Paleontology, 1175 West Baseline Road, Claremont, California 91711

Denver Fowler, Museum of the Rockies, Paleontology Department, 600 West Kagy Boulevard, Bozeman, Montana 59717

Roland Gangloff, University of California Museum of Paleontology, 1101 Valley Life Sciences Building, Berkeley, California 94720-4780

James Gardner, Royal Tyrrell Museum of Palaeontology, Box 7500, Drumheller, Alberta T0J 0Y0

Terry A. Gates, Department of Biological Sciences, North Carolina State University, Raleigh, NC 27695; North Carolina Museum of Natural Sciences, Raleigh, NC 27601

Pascal Godefroit, Department of Palaeontology, Royal Belgian Institute of Natural Sciences, rue Vautier 29, 1000 Brussels, Belgium

Merrilee F. Guenther, Department of Biology, Elmhurst College, Elmhurst, Illinois 60126

Jason J. Head, Department of Earth and Atmospheric Sciences, University of Nebraska–Lincoln, 228 Bessey Hall, Lincoln, Nebraska 68588

Donald M. Henderson, Royal Tyrrell Museum of Palaeontology, Box 7500, Drumheller, Alberta T0J 0Y0

Casey Holliday, Department of Pathology and Anatomical Sciences, University of Missouri, M318 Medical Sciences Building, Columbia, Missouri 65212

James Kirkland, Utah Geological Survey, PO Box 146100, Salt Lake City, Utah 84114

Derek W. Larson, Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, Ontario M5S 2C6

Jordan Mallon, Canadian Museum of Nature, Palaeobiology Department, PO Box 3443 Stn. "D," Ottawa, Ontario K1P 6P4

Richard McCrea, Peace Region Palaeontology Research Centre, 255 Murray Drive, Box 1540, Tumbler Ridge, British Columbia V0C 2W0

Andrew T. McDonald, Department of Earth and Environmental Science, University of Pennsylvania, 254-b Hayden Hall, 240 South 33rd Street, Philadelphia, Pennsylvania 19104

David B. Norman, Sedgwick Museum and Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge, U.K. CB2 3EQ

Albert Prieto-Márquez, School of Earth Sciences, University of Bristol, Wills Memorial Building, Queens Road, Bristol, U.K. BS8 1RJ

Patricia E. Ralrick, Royal Tyrrell Museum of Palaeontology, Box 7500, Drumheller, Alberta, T0J 0Y0

Raymond R. Rogers, Geology Department, Macalester College, 1600 Grand Avenue, Saint Paul, Minnesota 55105

Eric Snively, Department of Biology, University of Wisconsin-La Crosse, 1725 State Street, La Crosse, Wisconsin 54601

David Spalding, 1105 Ogden Road, Pender Island, British Columbia V0N 2M1

Daisuke Suzuki, Sapporo Medical University, South 1 West 17, Chuo-ku, Sapporo 060-8556 Japan

François Therrien, Royal Tyrrell Museum of Palaeontology, Box 7500, Drumheller, Alberta T0J 0Y0

Khishigjav Tsogtbaatar, Mongolian Paleontological Center, Ulaanbaatar 210351, Mongolia

David B. Weishampel, Center for Functional Anatomy and Evolution, Johns Hopkins University School of Medicine, Baltimore, Maryland 21287

Lawrence Witmer, Department of Biomedical Sciences, College of Osteopathic Medicine, Ohio University, Life Sciences Building, Room 123, Athens, Ohio 45701

Holly Woodward, Oklahoma State University Center for Health Sciences, 1111 West 17th Street, Tulsa, Oklahoma 74107

Hai-lu You, Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, 142 Xizhimenwai Street, Beijing 100044, China



HADROSAURS—ALSO KNOWN AS DUCK-BILLED DINOSAURS—are one of the best-known groups within Dinosauria due to their abundance in the fossil record, notable diversity, and near global distribution in the Late Cretaceous. Their success was likely driven by a combination of factors that included, most importantly, anatomically-unique and functionally-complex jaws and dentitions that processed plants more efficiently than those of any “reptile” before or since. Ultimately, the ubiquity of hadrosaurs in the Cretaceous fossil record has allowed us to learn more about dinosaurian paleobiology and paleoecology than we have from any other group.

In recent years, a number of dinosaur groups have been the subject of renewed scientific interest. In 2005, sauropod studies experienced a scientific renaissance with the benchmark publications *The Sauropods: Evolution and Paleobiology* and Indiana University Press’s *Thunder Lizards: The Sauropodomorph Dinosaurs*. In 2010, after a decade-long surge of interest in horned dinosaurs, that group received similar treatment in Indiana University Press’s *New Perspectives on Horned Dinosaurs*. During the last five years it has been the hadrosaurs’ time in the spotlight. Due to the rapidly growing fossil record as well as widespread international collaborations, researchers from around the world are now studying new specimens and taxa of hadrosaurs to clarify their origins, patterns of evolution, function, paleobiology, paleobiogeography, and preservation.

It was with this perspective that we (Davids 1 and 2) convened the International Hadrosaur Symposium (September 22–23, 2011). A collaboration between the Royal Tyrrell Museum and the Royal Ontario Museum, the goal of the IHS was to bring together an international slate of scientists and enthusiasts to share their research on and passion for duck-billed dinosaurs. Hosting the event at the Royal Tyrrell Museum made perfect sense to us; after all, few places in the world can boast the abundance and quality of hadrosaur fossils as are found in the classic Upper Cretaceous nonmarine strata of southern Alberta, and the Tyrrell’s collections.

Fifty-plus presentations by an international roster of dinosaur specialists and up-and-coming students rounded out two days of hardcore hadrophilia (apologies to Peter Dodson for

blatantly ripping off his terminology). The IHS was also an opportunity for all of us to honor the contributions of David Weishampel (David 3).

Setting the international tone were our five keynote presenters: Rodolfo Coria (Argentina), Pascal Godefroit (Belgium), Jack Horner (U.S.A.), Khishigjav Tsogtbaatar (Mongolia), and our honored guest, David Weishampel (U.S.A.). The watershed nature of the meeting was recognized by all attendees and, collectively, we managed to overcome unanticipated obstacles such as an impending strike by Air Canada employees, which resulted in last minute rerouting of flights and late appearances by some attendees. Be it known that we truly appreciate the efforts everyone made to attend the symposium.

This volume comprises most of the content from the symposium, and more. Because we believe this volume and its contents to be a uniquely comprehensive treatment of hadrosaurs, we chose simply to call it *Hadrosaurs*. The scope of the volume encompasses not only the well-known hadrosaurids proper, but also Hadrosoidea, which allows the former group to be evaluated in a broader perspective.

The volume’s 36 chapters are organized into the following six parts, followed by an afterword by Jack Horner:

Overview includes only one chapter, written by David Weishampel. David has spent a large part of his career studying dinosaurian paleobiology and, arguably, his most significant contributions are hadrosaurian. He has conducted pioneering work on hadrosaurian parental care, feeding mechanisms, functional morphology of bizarre structures, and phylogeny. In this chapter he uses data from the second edition of *The Dinosauria* to document patterns of research on ornithomorphs over the past two centuries, and uses his wisdom to surmise where researchers may be focusing in the future.

New Insights Into Hadrosaur Origins includes six chapters that document new and historical materials that shed light on the evolution and diversity of hadrosauroids before the origins of true hadrosaurids. David Norman (David 4) reviews taxa that have been implicated in the origin of Hadrosoidea, and presents some provocative ideas about the evolution of ornithomorphs leading up to hadrosaurids. A

standout chapter by Tsogtbataar et al. describes an exciting new taxon from the Djadokhta Formation of Mongolia, important for understanding the origin of hadrosaurids (it is rendered beautifully on the cover of the book by Julius Csotonyi). McDonald et al., You et al., and Barrett et al. provide new information about known specimens, and help sort out some long-standing questions about these specimens. Similarly, Main et al. and Larson et al. remind us of the importance of the North American hadrosauroid record for understanding the origins of Hadrosauridae.

Hadrosaurid Anatomy and Variation includes contributions by Gates, Bell, Farke and Herrero, Evans, Campione, Brink, and colleagues, and focuses on the anatomy of a variety of hadrosaurid taxa from western North America. Gates, Bell, Farke and Herrero, and colleagues describe new specimens from stratigraphic units that are rapidly proving to be important sources of new information about hadrosaur diversity and distributions, whereas the contributions by Evans, Campione, Brink, and colleagues provide in-depth descriptions and interpretations of known taxa and specimens. The morphological details provided here will lead undoubtedly to improved comparative studies.

Biogeography and Biostratigraphy documents the distribution of hadrosaurids in time and space. Here, chapters by Ramírez-Velasco et al. and Dalla Vecchia and colleagues stand out as exceptionally detailed overviews of hadrosaur occurrences in Mexico and Europe, respectively. Similarly, contributions by Bolotsky et al., Coria, and Sullivan and Lucas go a long way to help improve our understanding of hadrosaurian diversity in eastern Asia, South America, and the Southwestern U.S.A. The contribution by Tanke and Evans underscores the importance of properly documenting locality data for specimens.

Function and Growth includes seven contributions that address function, growth, and life habits. Studies of hadrosaur morphology, locomotion, and function by Maidment et al., Persons and Currie, and Henderson employ evolving techniques in computer modeling and engineering that we hope will spark discussion and renewed interest in this topic. Nabavizadeh revisits the all-important question of jaw kinetics via predeontary morphology, and Guenther's com-

parison of postcrania is a step toward identifying different developmental pathways in hadrosaurs. Erickson and Zelenitsky describe ontogenetic changes in tooth morphology/histology in *Hypacrosaurus stebingeri* that reflect dietary changes during development. Lastly, Brinkman's size-distribution data are the basis of conclusions that challenge conventional wisdom related to growth rates in hadrosaurs.

Preservation, Tracks, and Traces is the last part of the volume and includes eight chapters, including contributions by Manning et al., Prieto-Márquez and Wagner, and Bell on skin and skin traces. Of particular note is the chapter on the origins of the classic *Maiasaura* bonebed by Schmitt et al., which many of us have awaited for years (no pressure anymore, Jim!). Contributions by Eberth et al. and Hone et al. present more evidence that some hadrosaurs lived in large, segregated herds, perhaps rivaling in size those of centrosaurian ceratopsians. Back in Alberta, Therrien et al. provide the first evidence of hadrosaur tracks from the Oldman Formation of Alberta, and Tanke and Rothschild provide an exhaustive survey of paleo-osteopathologies in hadrosaurs from Dinosaur Provincial Park.

Nomenclature note—Unlike most forms of science, taxonomy can be quite democratic. Over the last two decades, numerous clade names and definitions have been proposed for the hadrosaurian part of the ornithomimid family tree. Rather than imposing a particular taxonomic scheme on the book's contributors, we chose to allow contributors to employ their preferred taxonomy. Not surprisingly, the book reveals little consensus. In particular, readers may find differential use of the terms Hadrosauridae, Hadrosaurinae, and Saurolophinae across the book's chapters a bit confusing. In order to address this, and other similar confusions, we asked authors to cite their taxonomic sources where necessary.

In summary, we have tried our best to present a group of well-balanced and consistently edited manuscripts, while allowing the authors to express their individual styles. We hope that you all enjoy the volume and find it useful for years to come.

David A. Eberth

David C. Evans

WE THANK ALL OF THE PARTICIPANTS WHO ATTENDED THE International Hadrosaur Symposium in 2011 and helped us realize that this volume would be a successful venture. We thank the authors for helping provide a cohesive and coherent product, and especially for being so patient as the clock kept ticking. Special thanks to the reviewers who did their jobs in a timely manner and were often willing to look at manuscripts more than once, thus ensuring that contributions were of high quality both scientifically and editorially.

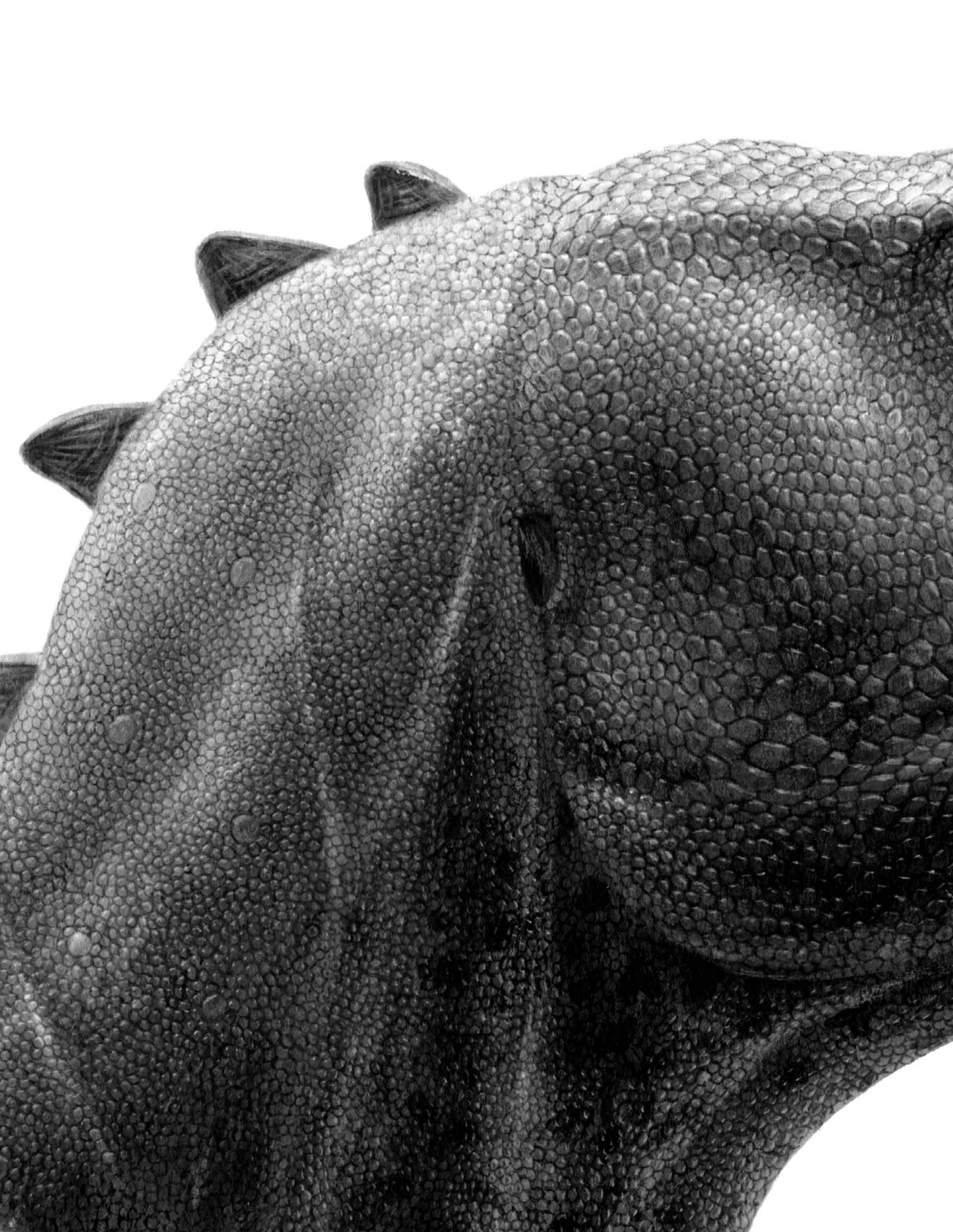
Our sincere gratitude goes to Bob Sloan and Jim Farlow, and the rest of the great team at Indiana University Press for all their help with this project.

We thank our respective home organizations who gave freely of their time, physical resources, and manpower. Special thanks to the Royal Tyrrell Museum for providing the FTP site, printing services, physical layout space, and so much else that was critical to the compilation of this volume. DAE thanks J. Gardner, D. Brinkman, F. Therrien, and D. Henderson for advice on numerous scientific and editorial items, and W. Taylor and D. Braman for editorial assistance. DCE thanks N. Campione and D. Larson for editorial and scientific assistance.

We are particularly grateful to A. Keibel and the Royal Tyrrell Museum Cooperating Society for financial and administrative support during the symposium and throughout this project.

We thank J. Csotonyi for the exceptional cover artwork of *Plesiohadros djadokhtaensis* and the wonderful (and first) artistic rendering of Djadokhtan paleoenvironments during a wet climatic phase. We also thank D. Dufault and L. Panzarin for their original artistic contributions to the volume.

Last, but certainly not least, we recognize P. Ralrick for her colossal contributions to this project. Patty served as our technical editor and editorial assistant, helped review manuscripts, listened to the occasional rant, and also indexed the volume. Without her attention to detail, this project would have taken twice as long and would not have been done half as well. Thanks, Patty, we hope that now you are very satisfied.





A History of the Study of Ornithopods: Where Have We Been? Where Are We Now? and Where Are We Going?

1

David B. Weishampel

ABSTRACT

Where ornithopod studies have been and where they are going is fascinating. I try to provide answers for the history of the study of ornithopod dinosaurs by collecting bibliographic data from the second edition of *The Dinosauria*. The resulting publication curves were examined for 10 intrinsic factors, nearly all of which increase through the first decade of the twenty-first century. These measures are used to take stock of present-day ornithopod studies and, finally, to try to predict our future as ornithopod researchers in this historically contingent world.

INTRODUCTION

From a historical perspective, knowledge about a taxonomic group can be judged by its publication rate. A zero rate may indicate a momentarily stalled interest in the group or a cessation of interest in it altogether (e.g., Kalodontidae Nopcsa, 1901), while a low rate suggests less than vigorous or meager research activity focused on the group (say, during a war or when there are few publishing scientists). Finally, a high publication rate may have many reasons, including new discoveries and new taxonomic recognition, and evolutionary controversy, to name a few.

Compilations of taxa are not new to studies of dinosaurs, or even tetrapods or invertebrates (Sepkoski et al., 1981; Benton, 1985, 1998; Dodson, 1990; Weishampel, 1996; Sepkoski, 2002; Fastovsky et al., 2004; Wang and Dodson, 2004). However, this present compilation and survey differs from previous varieties in that it focuses on the number of papers published and the research areas those papers address.

For Ornithopoda—the most abundant and diverse of which are hadrosaurids—the record of publication begins in 1825 with the publication of Mantell's *Iguanodon*, and finishes with the numerous papers, some being issued via conventional journals as well as online-only journals, with no hard copies, of the present day. What this record looks like is presented in Figure 1.1. How it was obtained and how it is interpreted are the subjects of this chapter.

Caveat: although this volume is the product of a symposium dedicated predominantly to hadrosaurs, which includes hadrosaurids proper as well as hadrosauroids, it has been extended by the organizers to include iguanodontians as well. By stretching it slightly more to include iguanodontians, we are practically down to the base of Ornithopoda. Hence, this chapter is about hadrosaurs—and more.

MATERIALS AND METHODS

In order to evaluate the rate of publication of papers dealing with ornithopod dinosaurs, the number of papers was tabulated on a per-decade basis from 1820–2010 from the bibliography of *The Dinosauria*, second edition (Weishampel et al., 2004). Containing 90 published pages of references on all dinosaurian taxa, this book is likely to be comprehensive enough for our current purposes. Because the decade of 2000–2010 was incomplete in that volume, the remainder of this decade was filled in proportionally based on the approximate representation during the first three and one-half years of the decade. That is, the 2000–2010 decadal numbers are projections based on tabulations from the first three and one-half years. Total papers and papers for each research category (see below) were adjusted by multiplying the raw totals for the first three and one-half years of the 2000–2010 decade by a factor of 2.86 to yield a total proportionally equivalent to other decades. This kind of correction was judged preferable to changing data sources (e.g., Web of Science), which would have resulted in an under-sampling of the more obscure literature.

In addition to the total curve, I have attempted to characterize the papers that went into this total by identifying nine categories of research (Table 1.1). I provide general description of these categories, denoted in boldface text, below. These categories were usually assessed by title alone, but occasionally it was necessary to consult the paper itself to determine to which category it belonged. I made no account of footprints and eggshell papers, because it was often impossible to assess affinities of the tracks or shell beyond *Dinosauria* from the title of the paper.

Table 1.1. Categories of Ornithopod Research Identified in This Survey

General taxonomy
Functional morphology
Phylogeny
Biostratigraphy and taphonomy
Biogeography
Paleoecology
Soft tissue
Growth
Faunistics

General taxonomy refers to those publications announcing new specific or generic taxa, or new taxonomic revisions that do not come under the heading of phylogeny (see below). For example, Gilmore’s (1913) announcement of *Thescelosaurus neglectus* is here considered a work of general taxonomy.

Functional morphology is the category for papers involving a biomechanical or functional interpretation of an ornithopod anatomical system. An example of a functional morphology study is Alexander’s (1985) work on stance and gait in ornithopods among other dinosaurs.

Phylogeny refers to those studies that attempt to portray the evolutionary history, or phylogeny, of the group. In recent years, these studies have emphasized cladistics in phylogenetic reconstruction (e.g., Prieto-Márquez, 2010), but also include a number of pre-Hennigian analyses (e.g., Galton, 1972).

Biostratigraphy and taphonomy papers involve the geologic disposition of ornithopod specimens, whether within or among rock units. Rogers (1990) provided an example of how bonebed taphonomy can provide evidence for drought-related mortality in dinosaurs that include hadrosaurs.

Biogeography includes studies that examine the geographic distribution of ornithopods either from a dispersal or vicariant perspective, or both. For example, Casanovas et al. (1999) examined the global distribution of lambeosaurine hadrosaurids, whereas Upchurch et al. (2002) considered the full spectrum of controls on dinosaur diversity, including that of ornithopods, as a function of biogeography and biostratigraphy.

Paleoecology papers include those of Carrano et al. (1999) on convergence—or lack thereof—among ornithopods and ungulate mammals, and Varricchio and Horner (1993) on the significance of bonebeds in paleoecological interpretations, and are intended to address the reconstruction of particular taxonomically bound or free ecosystems of the past.

Soft tissue studies have been generally limited to skin impressions. Examples include Osborn (1912) on the “mummy” of *Edmontosaurus annectens* in the American Museum of Natural History.

Growth includes papers associated with aspects of ontogenetic development. The impact of growth on ornithopod studies is relatively recent. Here I note Dodson (1975) on the taxonomic significance of growth in *Lambeosaurus* and *Corythosaurus*, as well as various studies by Horner and colleagues (e.g., Horner et al., 1999, 2000) focused on the cellular basis of bone growth.

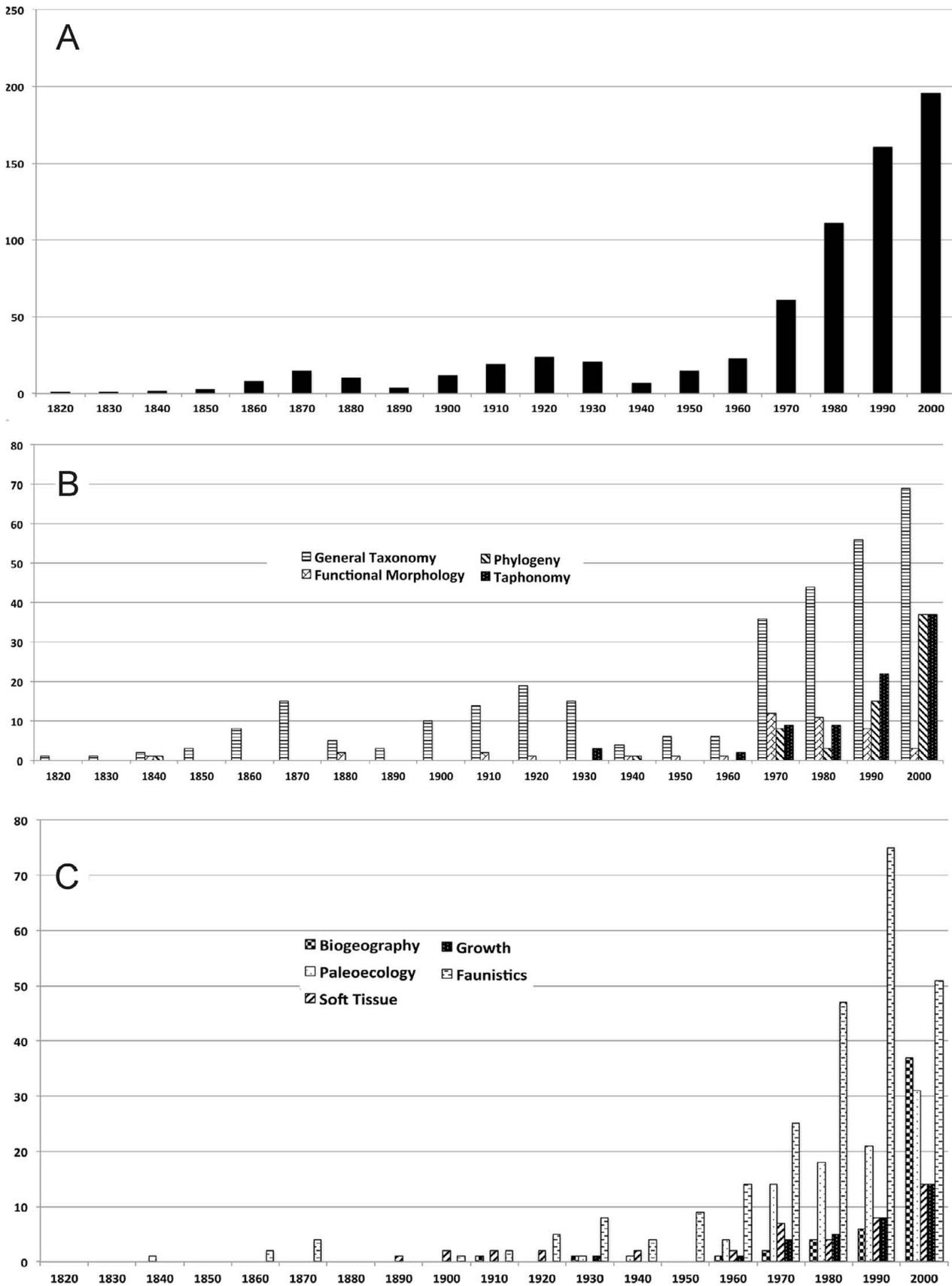
Faunistics includes papers whose principal purpose is to establish or review fossil assemblages that include ornithopods. For example, Lapparent (1960) reviewed the dinosaurs, including many ornithopods, from the “Continental intercalaire” of northern Africa.

Usually contributions were entered once in a category. However, a study can contribute here to several categories. For instance, Ostrom (1961) included discussion of general taxonomy, functional morphology, phylogeny, and other subjects in his major review of North American hadrosaurs, and so it was added to each of these categories.

WHERE HAVE WE BEEN?

Where we have been can be determined by looking at the total curve of ornithopod publications (Fig. 1.1A). Beginning in the 1820s, the number of papers published per decade rises to a high of 15 in the 1870s. It then declines to 4 in the 1890s, and increases again, to 24, in the 1920s. The 1940s see a drop to 7, followed by a persistent, long-term increase to the decade of the 2000s, which is characterized by nearly 200 papers, amounting to almost 2 papers per month!

Before turning to several intrinsic factors, I want to examine three kinds of extrinsic events that may have influenced these numbers and patterns. For possible influences due to world events, the European revolutions of 1848, the American Civil War, World War I, the Russian Revolution, the fall of communism, and the combined Iraq and Afghan wars appear to have no substantial influence on rate of publication, whereas the 1929 stock market crash and the subsequent worldwide financial depression followed by World War II are likely factors in the decline of publication rates in the 1930s and 1940s. Regarding technological influences, there are no great fluctuations in rate of publication for technological events, except for the last two events. It is probably safe to say that the invention of personal computers, particularly laptops (1970s), in combination with the development of the World Wide Web and internet (1990s) made a huge impact on the rate of ornithopod publications. With the initiation of web publishing, this trend is certain to continue. Finally, scientific influences probably account for smaller perturbations in the total curve. For example, the discovery of the *Iguanodon* assemblage from Bernissart probably accounts for the rise in ornithopod publications during the 1870s and 1880s. The



1.1. Publication trends on ornithomimid dinosaurs. (A) Total publication record of ornithomimid dinosaurs from 1820 to 2000 tabulated by decade; (B) Total publications of general taxonomy, functional morphology, phylogeny, and biostratigraphy and taphonomy, tabulated by decade; (C) Total publications in biogeography, paleoecology, soft tissue, growth, and faunistics, tabulated by decade.

rise in publication rates during the 1910s, 1920s, and 1930s can certainly be attributed to the Great Canadian Dinosaur Rush in Alberta. Finally, as a personal homage, I consider John H. Ostrom's first monographic publication—his 1961 treatment of the hadrosaurids of North America—to signal the beginning of what has turned out to be a plethora of ornithopod publications to the present day.

Intrinsic factors, on the other hand, are some of the subjects that I am interested in, which also have given Ornithopoda pride of place in the world of dinosaur publishing. General taxonomy and faunistics are the largest contributors to the total sample, whereas the rest have relatively low influence.

General taxonomy (Fig. 1.1B) has as long a history, beginning with the first publication on *Iguanodon* by Mantell (1825) and early on encompassing the first publication on *Hadrosaurus* by Leidy (1858). Furthermore, it mirrors fairly well the total publication curve, with a high point of 69 publications during the decade of 2000–2010.

Functional morphology (Fig. 1.1B) has a long, but patchy history, beginning with the publication of Mantell (1848) on the teeth and jaws of *Iguanodon*. It has never been common, but increases significantly in the 1970s and 1980s, with renewed interest in ornithopod jaw mechanics. Functional morphology has been in decline since this time.

Phylogeny (Fig. 1.1B) also has a long and equally patchy history, beginning with Owen's (1842) christening of Dinosauria. Thereafter, there is a long hiatus until the 1970s, when we see an irregular publication record reflecting the large impact of cladistics on phylogeny estimates. The 1990s and 2000s indicate an important increase in cladistic studies, peaking near 40 publications.

Biostratigraphy and taphonomy (Fig. 1.1B) have a relatively short history, confined to the period of the 1930s to the present, and within this span only relatively abundant since the 1970s, with the publications of Dodson (1971), Rogers (1990), and Varricchio and Horner (1993). There is a steady increase in biostratigraphic and taphonomic publications from the 1980s to the 2000s, indicative of increased interest in the sedimentological aspects of ornithopod fossils.

Biogeography (Fig. 1.1C) is in its infancy, with its concentration of publications only evident from the 1960s onward. This is roughly the same time as the scientific ascendancy of plate tectonics and phylogenetic systematics, and thus, may be a direct product of these two revolutions in the natural sciences (Serenó, 1997, 1999a, 1999b; Upchurch et al., 2002). Biogeography reaches its zenith in the decade of 2000; in all likelihood it will continue to increase.

Paleoecology (Fig. 1.1C) has a relatively short history. With a few notable exceptions (Mantell, 1844; Nopcsa, 1934), the history of paleoecology papers really began in the 1960s.

There has been a steady increase in the number of paleoecology publications since then, to a high of more than 30 publications in the decade of 2000–2010.

Soft tissue (Fig. 1.1C), consisting almost entirely of the study of integumentary impressions, has a reasonable steady and long history, increasing steadily since the 1970s. It is presently on a very large upswing, in large part because of the discovery of exceptionally well preserved specimens (particularly in northeastern China) and a more focused evaluation of variation in integumentary patterns (Bell, this volume).

Growth (Fig. 1.1C) has a very modest history. It has been common only since the 1970s, and appears to be on a steep upswing to nearly a dozen papers for the decade of 2000–2010. This increase probably represents the rise in fossil bone histology studies in ornithopods (e.g., Chinsamy, 1995; Horner et al., 2000).

Finally, **faunistics** (Fig. 1.1C) has a long history, approximately paralleling general taxonomy and the total curve, at least since the 1860s. Faunistics seems to drop off during the decade of the 2000s, but this downturn should be treated with skepticism because it is almost certainly an artifact of sampling extrapolation. Examples taken from the 1990s and 2000s include Csiki (1997), Ryan and Russell (2001), López-Martínez et al. (2001), and Zhou et al. (2003).

WHERE ARE WE NOW?

Before we all assembled for the International Hadrosaur Symposium, we all probably thought we knew where our science was. At a minimum, that was what we came to Drumheller to report on. It was hadrosaur taxonomy, North American, Asian, South American, and European hadrosaurs, and ornithopod brains. It was also hadrosaur gigantism and age, hadrosaur jaws and herbivory, locomotor mechanics, taphonomy, integument, tracks, and various aspects of development. This was where we thought our discipline was as we began the symposium.

Eighty-eight percent of the symposium talks ($n = 34$ talks, 16 posters) fall within the categories discussed here (Braman et al., 2011). Most are taxonomic, phylogenetic, or biogeographic in scope. Another half-dozen or more pertain to functional morphology, growth, and taphonomy—a good sampling of the categories examined here (an acclaim delivered independently twice over—the organizers and I both got it right!).

Symposium percentages are all the same order of magnitude compared to those obtained for the decade of 2000–2010, but there are several differences. General taxonomic presentations at the symposium were nearly 25% fewer than from 2000–2010, phylogeny was 19% fewer, taphonomy was 15% fewer, biogeography was 28% fewer, paleoecology was

19% fewer, and faunistics was 13% fewer. Soft tissue remained approximately the same. Interestingly, functional morphology was 14% more and growth was 6% more than from the decade of 2000–2010. While it is tempting to assign significance to individual percentages, they are probably no more than sampling errors when comparing a very small number of symposium talks with the projected breakdown of categories for an entire decade.

WHERE ARE WE GOING?

I am certainly no prognosticator, even about my own research field. Like all historical sciences, our ability to predict the future is fraught with the kinds of unpredictability that derives from historical contingency. There is little inevitability that guides us in the progress of our science—just as there is little that links the hand-cranked ice-cream maker (1840s) to the electron microscope (1930s), a transition that happened in only nine decades. What about going from the invention of the Band-Aid (1930s) to the home computer in five decades? Who would have predicted these changes?

But the contents of this volume give an inkling of where we are headed, at least in the short run. I see continued fieldwork, the wellspring of our science. Its direct consequences—new species and taxonomic revisions—are likely to be accompanied by a healthy continuance of studies focused on comparative anatomy, both bony and inferred soft tissue. To do so requires a healthy dose of phylogenetic systematics, which now should be part of everyone’s toolkit.

In functional morphology, finite element analyses and tooth-wear studies have appeared on the horizon and I hope these will be coupled with cladistic analyses to produce even more outstanding work. Finally, growth studies are very likely to continue in the future: the small bit of bone given up for a thin-section is bound to yield disproportionately much more subtle and profound information than if it were left with the rest of the bone.

Still, things do not always work out that way. Contingency makes history messy. Things come out of left field and WHAM! Someone discovers the most amazing specimen or means by which colors can be inferred from skin impressions. All of a sudden, with no way of predicting, we are all scrambling to do research on the melanosomes of what could turn out to be red-, green-, and yellow-striped ornithopods!

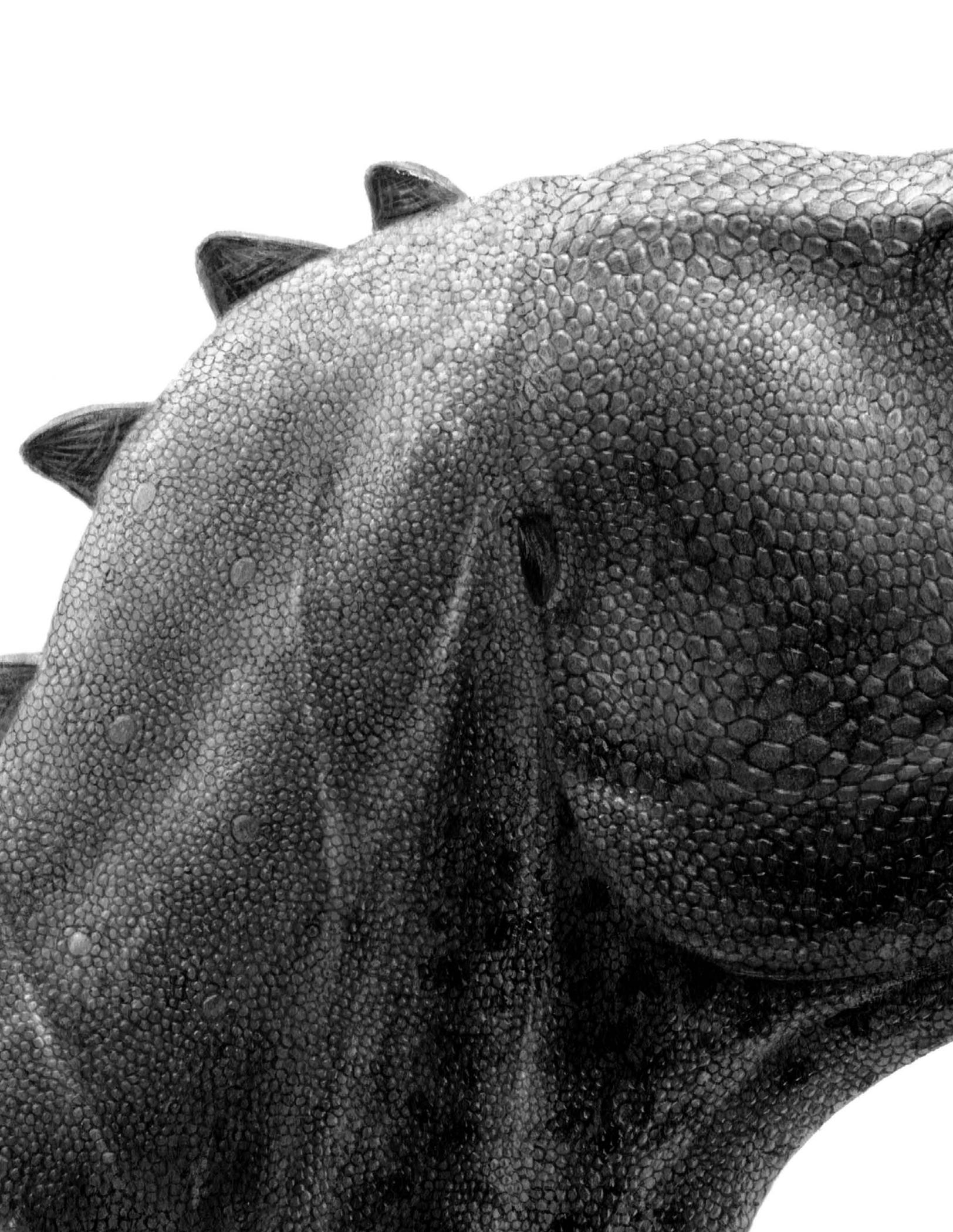
ACKNOWLEDGMENTS

I thank David Eberth and David Evans for their kind invitation to join them at their fantastic first International Hadrosaur Symposium in Drumheller, Alberta, Canada. Their generosity and that of François Therrien and the other hosts at the Royal Tyrrell Museum of Palaeontology are most commendable. And to throw in a bronze plaque of *Corythosaurus intermedius* (ROM 845); well, I sure had a good time! I also thank Ali Nabavizadeh and Cat Sartin for their help on and reading of this manuscript and Jack Horner, Cora Jianu, and Pilar Yagüe for their own individual inspirations.

LITERATURE CITED

- Alexander, R. McN. 1985. Mechanics of posture and gait of some large dinosaurs. *Zoological Journal of the Linnean Society* 83:1–25.
- Bell, P. 2014. A review of hadrosaurid skin impressions; Chapter 25 in D. A. Eberth, and D. C. Evans (eds.), *Hadrosaurs*. Indiana University Press, Bloomington, Indiana.
- Benton, M. J. 1985. Mass extinction among non-marine tetrapods. *Nature* 316:811–814.
- Benton, M. J. 1998. The quality of the fossil record of the vertebrates; pp. 269–303 in S. K. Donovan and C. R. C. Paul (eds.), *The Adequacy of the Fossil Record*. John Wiley & Sons, New York.
- Braman, D., D. A. Eberth, D. C. Evans, and W. Taylor (compilers). 2011. *International Hadrosaur Symposium Abstract Volume*. Royal Tyrrell Museum, Drumheller, Alberta. 171 pp.
- Carrano, M. T., C. M. Janis, and J. J. Sepkoski. 1999. Hadrosaurs as ungulate parallels: lost lifestyles and deficient data. *Acta Palaeontologica Polonica* 44:237–261.
- Casanovas, M. L., X. Pereda-Suberbiola, and D. B. Weishampel. 1999. First lambeosaurine hadrosaurid from Europe: palaeobiogeographical implications. *Geological Magazine* 136:205–211.
- Chinsamy, A. 1995. Ontogenetic changes in the bone histology of the Late Jurassic ornithopod *Dryosaurus lettowvorbecki*. *Journal of Vertebrate Paleontology* 15:96–104.
- Csiki, Z. 1997. Legături paleobiogeografice ale faunei de vertebrate continentale Maastrichtian superioare din Bazinul Hațeg. *Nymphaea* 23–25:45–68.
- Dodson, P. 1971. Sedimentology and taphonomy of the Oldman Formation (Campanian), Dinosaur Provincial Park, Alberta (Canada). *Palaeogeography, Palaeoclimatology, Palaeoecology* 10:21–74.
- Dodson, P. 1975. Taxonomic implications of relative growth in lambeosaurine hadrosaurs. *Systematic Zoology* 24:37–44.
- Dodson, P. 1990. China reaches the top. *American Paleontologist* 17: online supplement. Available at www.museumoftheearth.org/files/pubtext/supplements/suppl_557c.pdf. Accessed summer 2012.
- Fastovsky, D. E., Y. Huang, J. Hsu, J. Martin-McNaughton, P. M. Sheehan, and D. B. Weishampel. 2004. Shape of Mesozoic dinosaur richness. *Geology* 32:877–880.
- Galton, P. M. 1972. Classification and evolution of ornithopod dinosaurs. *Nature* 239:464–466.
- Gilmore, C. W. 1913. A new dinosaur from the Lance Formation of Wyoming. *Smithsonian Miscellaneous Collections* 61:1–5.
- Horner, J. R., A. de Ricqlès, and K. Padian. 1999. Variation in skeletochronological indicators of the hadrosaurid dinosaur *Hypacrosaurus*: implications for age assessment of dinosaurs. *Paleobiology* 25:295–304.
- Horner, J. R., A. de Ricqlès, and K. Padian. 2000. The bone histology of the hadrosaurid dinosaur *Maiaosaurus peeblesorum*: growth dynamics and physiology based on an ontogenetic series of skeletal elements. *Journal of Vertebrate Paleontology* 20:109–123.
- de Lapparent, A. F. 1960. Les dinosauriens du “Continental intercalaire” du Sahara central. *Memoire de la Société géologique de France* 88A:1–57.
- Leidy, J. 1858. *Hadrosaurus foulkii*, a new saurian from the Cretaceous of New Jersey. *Proceedings of the Academy of Natural Science of Philadelphia* 1859:215–218.
- López-Martínez, N., J. I. Canudo, L. Ardèvol, X. Pereda-Suberbiola, X. Orue-Etxebarria, G. Cuenca-Bescós, J. I. Ruiz-Omeñaca, X. Murilaga, and M. Feist. 2001. New dinosaur sites correlated with upper Maastrichtian pelagic

- deposits in the Spanish Pyrenees: implications for the dinosaur extinction pattern in Europe. *Cretaceous Research* 22:41–61.
- Mantell, G. A. 1825. Notice on the *Iguanodon*, a newly discovered fossil reptile, from the sandstone of the Tilgate Forest, in Sussex. *Philosophical Transactions of the Royal Society of London* 115:179–186.
- Mantell, G. A. 1844. *Medals of Creation*. H. G. Bohn, London, U.K., 289 pp.
- Mantell, G. A. 1848. On the structure of the jaws and teeth of the *Iguanodon*. *Philosophical Transactions of the Royal Society of London* 138:183–202.
- Nopcsa, F. 1901. Synopsis und Abstammung der Dinosaurier. *Földtani Közlöny* 31:247–288.
- Nopcsa, F. 1934. The influence of geological and climatological factors on the distribution of non-marine fossil reptiles and Stegocephalia. *Quarterly Journal of the Geological Society of London* 90:76–140.
- Osborn, H. F. 1912. Integument of the iguanodont dinosaur *Trachodon*. *Memoirs of the American Museum of Natural History* 1:33–54.
- Ostrom, J. H. 1961. Cranial morphology of the hadrosaurian dinosaurs of North America. *Bulletin of the American Museum of Natural History* 122:33–186.
- Owen, R. 1842. Report on British fossil reptiles. Part II. Report of the British Association for the Advancement of Science 1841:60–204.
- Prieto-Márquez, A. 2010. Global phylogeny of Hadrosauridae (Dinosauria: Ornithischia) using parsimony and Bayesian methods. *Zoological Journal of the Linnean Society* 159:435–502.
- Rogers, R. R. 1990. Taphonomy of three dinosaur bone beds in the Upper Cretaceous Two Medicine Formation, northwestern Montana: evidence for drought-related mortality. *Palaios* 5:394–413.
- Ryan, M. J., and A. P. Russell. 2001. Dinosaurs of Alberta (exclusive of Aves); pp. 279–297 in D. H. Tanke, and K. Carpenter (eds.), *Mesozoic Vertebrate Life*. Indiana University Press, Bloomington, Indiana.
- Sepkoski, J. J., Jr. 2002. A compendium of fossil marine animal genera; pp. 1–560 in D. Jablon-ski, and M. Foote (eds.), *Bulletins of American Paleontology*, No. 363. Paleontological Research Institution, Ithaca, New York.
- Sepkoski, J. J., Jr., R. K. Bambach, D. M. Raup, and J. W. Valentine. 1981. Phanerozoic marine diversity and the fossil record. *Nature* 293:435–437.
- Sereno, P. C. 1997. The origin and evolution of dinosaurs. *Annual Review of Earth and Planetary Sciences* 25:435–489.
- Sereno, P. C. 1999a. The evolution of dinosaurs. *Science* 284:2137–2147.
- Sereno, P. C. 1999b. Dinosaurian biogeography: vicariance, dispersal and regional extinction. *National Science Museum of Tokyo Monographs* 15:249–257.
- Upchurch, P., C. A. Hunn, and D. B. Norman. 2002. An analysis of dinosaurian biogeography: evidence for the existence of vicariance and dispersal patterns caused by geological events. *Proceedings of the Royal Society of London* B269:613–621.
- Varricchio, D. J., and J. R. Horner. 1993. Hadrosaurid and lambeosaurid bone beds from the Upper Cretaceous Two Medicine Formation of Montana: taphonomic and biological implications. *Canadian Journal of Earth Sciences* 30:997–1006.
- Wang, S. C., and P. Dodson. 2004. Estimating the diversity of dinosaurs. *Proceedings of the National Academy of Science* 103:13601–13605.
- Weishampel, D. B. 1996. Fossils, phylogeny, and discovery: a cladistic study of the history of tree topologies and ghost lineage durations. *Journal of Vertebrate Paleontology* 16:191–197.
- Weishampel, D. B., P. Dodson, and H. Osmólska (eds.). 2004. *The Dinosauria*, Second Edition. University of California, Berkeley, California, 861 pp.
- Zhou Z., P. R. Barrett, and J. Hilton. 2003. An exceptionally preserved Lower Cretaceous ecosystem. *Nature* 421:807–814.





Iguanodonts from the Wealden of England: Do They Contribute to the Discussion Concerning Hadrosaur Origins?

2

David B. Norman

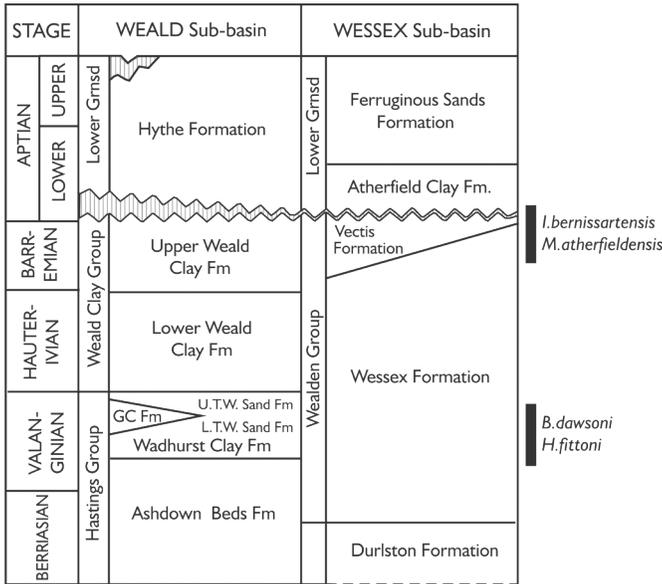
ABSTRACT

The earliest known hadrosaur-like ornithopod is represented by a tooth from the early Cenomanian (Cambridge Greensand) of England. The Wealden outcrops (late Berriasian–early Aptian) of England include a range and variety of iguanodonts that, in many anatomical respects, presage the structures seen in a succession of Albian–Maastrichtian, hadrosaur-like neoiguanodontians, hadrosauromorphans, and euhadrosaurians. The anatomy and taxonomic assignments applicable to known Wealden iguanodonts are reviewed, albeit briefly, and the recently published proposition that Wealden taxonomic diversity was far higher than previously supposed is regarded as unfounded. A new systematic analysis has generated a consistent topological framework that provides the basis for a consideration of the general pattern of assembly of anatomical features, within the neoiguanodontian lineage, that culminated in the appearance of true hadrosaurs (euhadrosaurians) during the Late Cretaceous. The general topology generated by the present analysis largely conforms to previous analyses. However, the primary region of inconsistency is located across a range of taxa that appear to form a plexus of late Early and early Late Cretaceous age; they are widely distributed geographically, vary in their degrees of preservation, and have been described mostly in the last two decades. A revised classification is proposed, based upon the new topology, and generalized phylogenetic inferences have also been drawn from the successional pattern and its associated character distributions. The systematic pattern and therefore the phylogenetic (evolutionary) origin of euhadrosaurians from within the plexus of derived neoiguanodontians is potentially tractable. However, questions focused upon the geographic (area of) origin of hadrosaurs are unlikely to be resolved satisfactorily because of definitional instability (an inherent problem of fossil-based systematic analyses), compounded by the more or less constant flow of new discoveries.

INTRODUCTION

The zenith of ornithopod evolution is represented by the Late Cretaceous duck-billed, or hadrosaurian dinosaurs (e.g., Lull and Wright, 1942; Ostrom, 1961; Horner et al., 2004; Prieto-Márquez, 2010), which were highly speciose, geographically widespread, and anatomically (and probably behaviorally) complex herbivores. However, the details governing the evolutionary transition from derived (neoiguanodontian) to the definitive hadrosaurian state, although understood in general terms, have proved elusive. Initially (encompassing the time between the 1870s and 1970s) the fossil record was comparatively mute on the subject: “middle” Cretaceous (Albian–Cenomanian) ornithopods were extremely rare and poorly described, as well as unreliably dated. As a consequence, evolutionary hypotheses were necessarily speculative (e.g., Gilmore, 1933; Ostrom, 1961; Rozhdestvensky, 1966; Taquet, 1975). The closing decades of the twentieth century and the opening decade of the twenty-first century mark a turning point during which a considerable number of new ornithopod taxa have been identified from both the older and established fossil hunting grounds as well as many new geographic locations. However, it seems that the abundant new data has increased ambiguity, rather than creating the expected resolution or increasing levels of consensus concerning the ancestry of the clade referred to herein as Euhadrosauria (Weishampel, Norman, and Grigorescu, 1993 [= Hadrosauridae sensu lato, e.g., Lull and Wright, 1942; Horner et al., 2004; Prieto-Márquez, 2010]).

Hadrosaur origins can be explored through a number of independent, yet correlated, lines of investigation: the chrono-geographical evidence suggestive of their first appearance in the fossil record; the study of ornithopod taxa that are positioned adjacent to the clade Euhadrosauria; the construction of parsimony-based and Bayesian likelihood trees (Evans, 2010; Prieto-Márquez, 2010); and the evaluation of the anatomical transformations (and phylogenetics) implied by the topology of such trees. In combination, these approaches should be able to reveal when, where, and how hadrosaurian anatomy was assembled (and, by implication,



2.1. Stratigraphy of the Wealden of southern England. Abbreviations: Fm, Formation; GC Fm, Grinstead Clay Formation; L.T.W. Sand Fm, Lower Tunbridge Wells Sand Formation; U.T.W. Sand Fm, Upper Tunbridge Wells Sand Formation; Lower Grnsd, Lower Greensand. Derived from Batten (2011). The vertical bars on the right-hand side indicate the approximate stratigraphic distribution of the four principal Wealden neoiguanodontian taxa.

utilized by these animals in a biological sense) in the lineage(s) ancestral to the first diagnosable members of the clade Euhadrosauria.

This contribution concerns itself with updating our current understanding of the anatomy, taxonomy and systematics of an Early Cretaceous group of neoiguanodontians from the Wealden of northwest Europe (Fig. 2.1). Given their older chronostratigraphic occurrence relative to hadrosaurids, these taxa contribute to an analysis of taxa that are considered topologically basal to hadrosaurids. This review probes our understanding of an important phase in ornithomimid evolution, and highlights areas where more research is needed.

Institutional abbreviations MIWG, Museum of the Isle of Wight Geology, Sandown, Isle of Wight, U.K.; NHMUK, Natural History Museum, London, U.K.; RBINS [formerly IRSNB], Royal Belgian Institute of Natural Sciences, Brussels, Belgium.

A REVIEW OF WEALDEN IGUANODONTIANS

A large number of names have become associated with medium-to-large-bodied Wealden-aged *Iguanodon*-like ornithomimids, or iguanodonts (Fig. 2.2); these include historical names such as *Vectisaurus valdensis* Hulke, 1879 (Norman, 1990); *Sphenospondylus gracilis* Lydekker, 1888; and *Iguanodon seelyi* Hulke, 1882. However, renewed scientific interest in the Wealden since 2008 has resulted in a proliferation of

WEALDEN TAXA (Norman/McDonald)	WEALDEN TAXA (Paul, Carpenter & Ishida, Hulke, Lydekker)
Barremian/Aptian	Barremian/Aptian
<i>Iguanodon bernissartensis</i> Boulenger, 1881 [v]	<i>I. bernissartensis</i> [v]
	<i>I. seelyi</i> Hulke, 1882 [jss]
	<i>Dollodon seelyi</i> (Carpenter & Ishida, 2010) [nd-jss]
<i>Mantellisaurus atherfieldensis</i> (Hooley, 1925) [v]	<i>M. atherfieldensis</i> [v]
	<i>Vectisaurus valdensis</i> Hulke, 1879 [nd]
	<i>Sphenospondylus gracilis</i> (Lydekker, 1888) [nd]
	<i>Proplanicoxa galtoni</i> Carpenter & Ishida, 2010 [nd-jss]
	<i>Dollodon bampingi</i> Paul, 2008 [nd-jss]
	* <i>Mantellodon carpenteri</i> Paul, 2012 [nd-jss]
Valanginian	Valanginian
<i>Barilium dawsoni</i> (Lydekker, 1888) [v]	<i>B. dawsoni</i> [v]
<i>Iguanodon anglicus</i> Holl, 1829 [servo statua]	<i>Kukufeldia tilgatensis</i> McDonald, Barrett & Chapman, 2010 [nd-jss]
	<i>Torilion dawsoni</i> Carpenter & Ishida, 2010 [jos]
	<i>Sellacoxa pauli</i> Carpenter & Ishida, 2010 [nd-jss]
<i>Hypselospinus fittoni</i> (Lydekker, 1889) [v]	<i>H. fittoni</i> [v]
	<i>Wadhurstia fittoni</i> Carpenter & Ishida, 2010 [jos]
	<i>Huxleysaurus hollingtoniensis</i> Paul, 2012 [nd-jss]
	<i>Darwinsaurus evolutionis</i> Paul, 2012 [nd-jss]

2.2. The taxonomy of Wealden iguanodontian dinosaurs tabulated according to (in the left column) the interpretation of Norman (2010, 2011a, 2011b, 2012, 2013, in press; McDonald, pers. comm., 2012), compared with the taxonomy (in the right column) introduced by Paul (2008); Carpenter and Ishida (2010); and McDonald, Barrett, and Chapman (2010). Asterisk indicates non-Wealden taxon. Abbreviations: nd, nomen dubium; jos, junior objective synonym; jss, junior subjective synonym; v, valid taxon.

additional taxa that have been recognized on the morphological variation present in the sample. Recently proposed taxa include *Dollodon bampingi* (Paul, 2008); *Barilium dawsoni* (Norman, 2010); *Hypselospinus fittoni* (Norman, 2010); *Kukufeldia tilgatensis* (McDonald, Barrett, and Chapman, 2010); *Torilion dawsoni* (Carpenter and Ishida, 2010); *Wadhurstia fittoni* (Carpenter and Ishida, 2010); *Sellacoxa pauli* (Carpenter and Ishida, 2010); *Proplanicoxa galtoni* (Carpenter and Ishida, 2010); *Dollodon seelyi* (Carpenter and Ishida, 2010); *Huxleysaurus hollingtoniensis* (Paul, 2012); *Darwinsaurus evolutionis* (Paul, 2012); and *Mantellodon carpenteri* (Paul, 2012).

This proliferation of Wealden taxa suggests that there was considerable taxonomic diversity among these animals during Wealden time (Fig. 2.2). Recognition of this diversity is significant, because phylogenetic analyses suggest these taxa provide insights into the morphological changes that occurred in the evolutionary transition to early hadrosauroids

from more primitive iguanodonts. However, the validity of a number of these recently named taxa has been questioned (Norman, 2013). The taxa erected by Paul, and Carpenter and Ishida are poorly–or incorrectly–diagnosed. Based on detailed study of the original material, many of these new taxa have been considered nomina dubia that are either unambiguously or subjectively synonymous with one of just four osteologically distinct Wealden-aged iguanodont taxa: *Barilium*, *Hypselospinus*, *Iguanodon*, and *Mantellisaurus* (Norman, 2011a, 2011b, 2012, 2013, in press; McDonald, 2012a). In addition, it appears that these novel, but dubious, taxa were proposed (and, in part, justified) on the basis of a fundamental lack of understanding of the stratigraphy of the Wealden and the provenance of the taxa that have been collected from Wealden exposures (Norman, 2013). The anatomy and spatio-temporal distribution of the iguanodonts from the Weald is reviewed below.

SYSTEMATIC PALEONTOLOGY

ORNITHISCHIA Seeley, 1887

ORNITHOPODA Marsh, 1881

DRYOMORPHA Sereno, 1986

ANKYLOPOLLEXIA Sereno, 1986

BARILIUM Norman, 2010

BARILIUM DAWSONI (Lydekker, 1888)

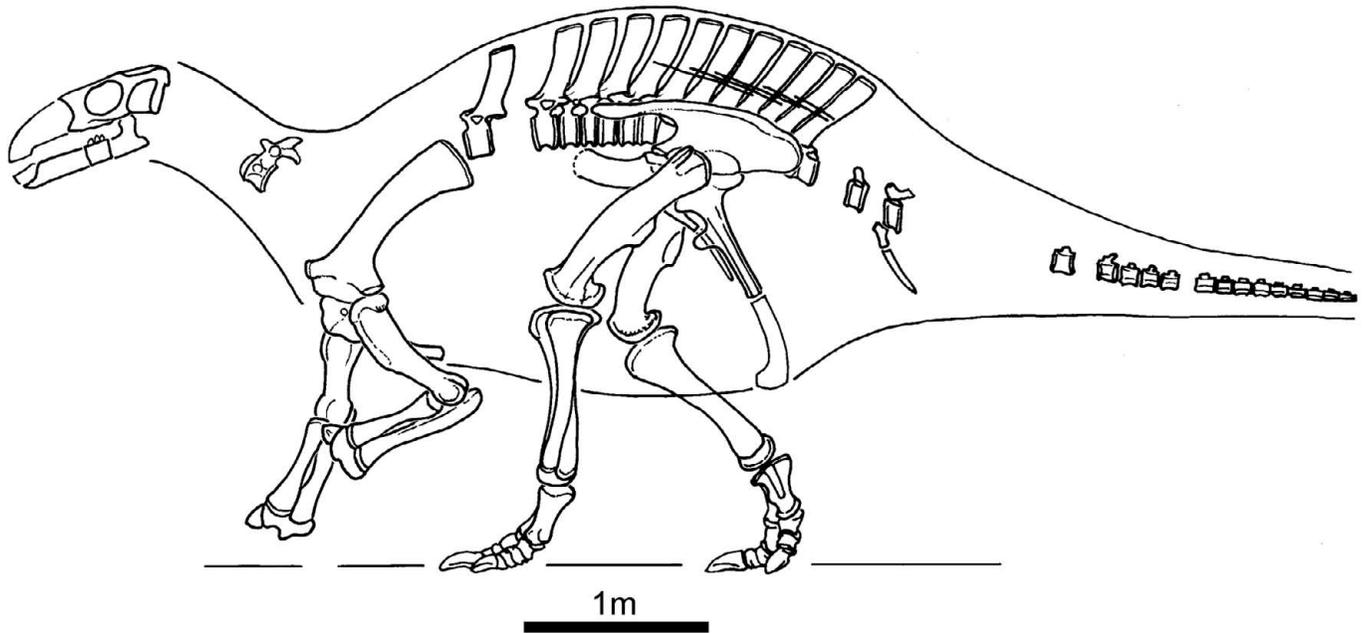
Lydekker (1888) described the partial skeleton of a large iguanodont that had been recovered during quarrying through ferruginous sandstones at Shornden, an open-cast quarry on an area of land about 1.5 km north of Hastings town center (Norman, 2011a). The material included dorsal and caudal vertebrae, portions of the pelvis, and parts of the hindlimb. The ilium was regarded as sufficiently distinct from anything previously described as pertaining to *Iguanodon* that it merited the establishment of a new taxonomic name, *I. dawsoni*. Norman (2010, 2011a) redescribed the type material, presented a formal diagnosis, and proposed the new combination *Barilium dawsoni* (Lydekker, 1888).

Taxonomic Discussion

McDonald et al. (2010) proposed that an isolated, nearly complete dentary of large size with two embedded dentary crowns (NHMUK OR28660), collected from one of the quarries at Whiteman's Green, Cuckfield, can be diagnosed as a new taxon of Valanginian neoiguanodontian: *Kukufeldia tilgatensis* McDonald, Barrett, and Chapman, 2010. This specimen is of considerable historical interest, because it was first studied and described by Mantell (1848) and later by Owen (1855). Their diagnosis currently rests upon one

character: an apparently unique pattern of vascular foramina on the outer surface near the anterior tip of the jaw, and this is supported by some subsidiary evidence concerning the comparative straightness of the anterior part of the dentary ramus. The distribution of vascular foramina on the external surface of the dentary is a character of dubious validity, given the variation in the pattern of vascular openings that may be seen between the left and right jaws of single individuals, let alone that which may be seen in different individuals (pers. obs.).

Apart from the pattern of dentary foramina, the distinction concerning the straightness of the dentary ramus relies upon an alleged association of another partial skeleton (NHMUK R1834) to the taxon *B. dawsoni*. The latter includes the anterior portion of an eroded dentary that appears to be arched, rather than straight. Unfortunately, NHMUK R1834 was incorrectly assigned to the taxon *B. dawsoni* by McDonald et al. (2010); it can be referred, quite unambiguously (Norman, 2010, in press), to the Valanginian taxon *Hypselospinus fittoni* (Lydekker, 1889) on the basis of detailed shared similarities between the ilium of the holotype of *H. fittoni* and that of NHMUK R1834 (Norman, in press). At present, *K. tilgatensis* comprises just the dentary of a large neoiguanodontian that is considered to be a nomen dubium and to be potentially referable to the contemporary large, robust neoiguanodontian taxon *Barilium dawsoni*. Furthermore, the dentary teeth are very similar in form to those of NHMUK R2358, which have been referred to *B. dawsoni*. Carpenter and Ishida (2010) proposed, in October of that year, a new taxonomic combination *Torilion dawsoni* (Fig. 2.2) for the holotype material named *Iguanodon dawsoni*; this proposal can be suppressed, because it is a junior objective synonym of *Barilium dawsoni* (Lydekker, 1888). Furthermore, Carpenter and Ishida proposed a new genus and species (*Sellacoxa pauli*) on the basis of a photograph of the right side of a large partial skeleton (NHMUK R3788) collected by Charles Dawson from Old Roar Quarry, near Hastings (Norman, 2011a). Naish and Martill (2008), using appropriately cautious remarks, suggested that its anatomy was unusual and perhaps indicative of a new species. The description by Carpenter and Ishida (2010) is erroneous (Norman, 2011a, 2011b) because these authors had evidently not examined the specimen closely and therefore failed to recognize preservational anomalies, missing pieces, or additional anatomical features visible on the other (left) side of the specimen (Norman, 2011a). *Sellacoxa pauli* (NHMUK R3788) is considered to be a nomen dubium (its diagnosis is incorrect), and this articulated partial skeleton is considered to be referable to the hypodigm of *B. dawsoni* (as originally argued by Norman, 1977, 2010, 2011a; Blows, 1998). The taxon *Sellacoxa pauli* Carpenter and Ishida, 2010, has been proposed to be a nomen dubium and that it can



2.3. *Barilium dawsoni*. Preliminary skeletal reconstruction based upon the holotype and referred material (from Norman, 2011a).

be relegated into synonym with *Barilium dawsoni* (Norman, 2011a; Fig. 2.2).

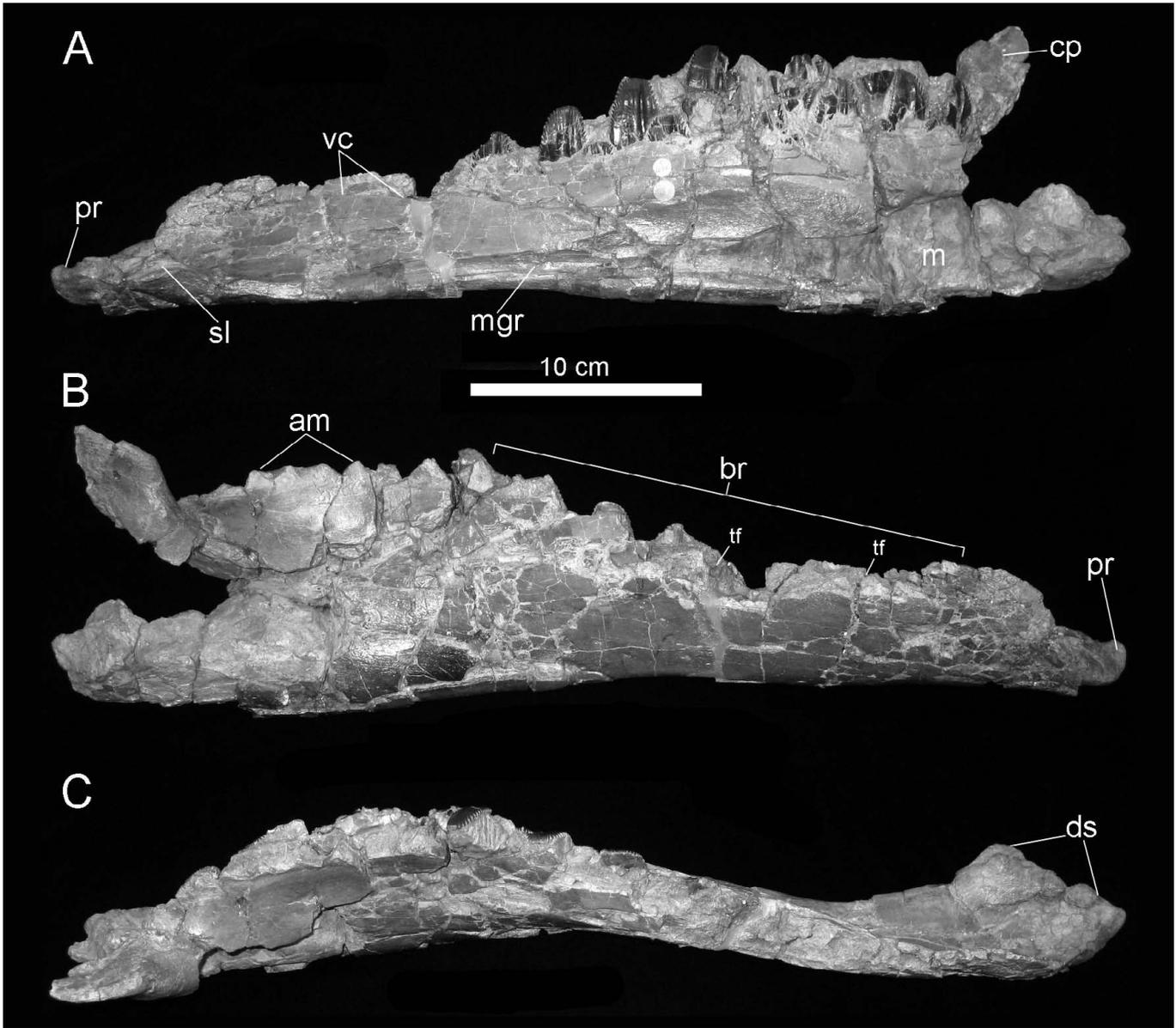
Description

Craniodental Anatomy The dentary is robust and has parallel upper and lower edges and an elevated coronoid process that arises from a shelf lateral to the most posterior alveoli. The large, and visibly crushed, replacement dentary tooth crown preserved in NHMUK OR28660 generally resembles those seen in another referred specimen (NHMUK R2358) that comprises part of a robust dentary with three embedded teeth; these are of additional interest because they resemble the morphology seen in the lectotype tooth (*I. anglicus*; Norman, 2011b:fig. 27.23A).

Vertebrae Dorsal vertebrae are notable for having very tall, deep, and slightly inclined spines; anterior dorsals have slightly waisted, cylindrical vertebral centra; posterior dorsals become more axially compressed and develop everted edges. Sacrals are very poorly known, while the caudals are distinctive: those nearest the sacrum are squat, subrectangular in axial view, and somewhat inclined forward (Norman, 2011a:fig. 6); these are succeeded by deeper-bodied, hexagonal (more typical iguanodont) caudals, whereas the caudals toward the tip of the tail tend to have very angular sides and their articular faces tend to be deeply concave (Norman, 2011a:fig. 7).

Girdles and Limbs The pectoral (shoulder) girdle and forelimb are robust. The scapula (based upon the referred specimen NHMUK R2848) is long, curved, and expands

towards its upper end. The coracoid is notably broad and dished, and has a prominent and completely enclosed coracoid foramen near the suture with the scapula (Norman, 2011a:fig. 17A). One specimen (NHMUK R2357) includes the “handle” portion of a hatchet-shaped sternal bone (Norman, 2011a:fig. 17B). The principal forearm bones (radius and ulna) are very robust; the carpals and metacarpal I cap the ends of the ulna and radius and are fused into a solid block that supports a fused, squat pollex. The form of the remaining bones of the hand is unknown. The hip (pelvic) bones include a very distinctive ilium, which has a long, robust, preacetabular process that is twisted along its length and bears a large rib facet near its base. The main body of the ilium is slab sided, thick along its dorsal edge with minimal lateral swelling and an inflection along its upper edge (posterodorsal to the ischiadic peduncle). The postacetabular process is deep and rounded in profile, and does not develop a ventrolateral ridge that delimits a vaulted brevis fossa; a well-developed brevis fossa is present in all other Wealden iguanodonts. The shape of the shaft of the ischium is unknown, but proximally the external surface of the shaft adjacent to the obturator process displays a pronounced vertical ridge that runs along the ischial shaft (NHMUK R2357) rather than forming a flat, rugose facet seen typically in this area in specimens attributable to *H. fittoni*; and the pubis appears to develop a thick, deep, and slightly upwardly curved prepubic process and the dorsoventrally compressed (strap-like) pubic shaft is unlikely to have extended to the end of the ischial shaft. The hindlimb is poorly known (Norman, 2011a).



2.4. *Hypselospinus* cf. *fittoni*, NHMUK R1831. Dentary (right) with teeth preserved in situ. (A) medial; (B) lateral; (C) dorsal views. Abbreviations: am, alveolar margin; br, badly broken portion of the dentary; cp, coronoid process; ds, dentary symphysis; m, matrix; mgr, Meckelian groove; pr, anterior lateral process of the dentary; sl, "slot-and-lip" portion of the dentary symphysis; tf, tooth fragments in alveolar bone; vc, vascular channel. Scale bar equals 10 cm (from Norman, in press).

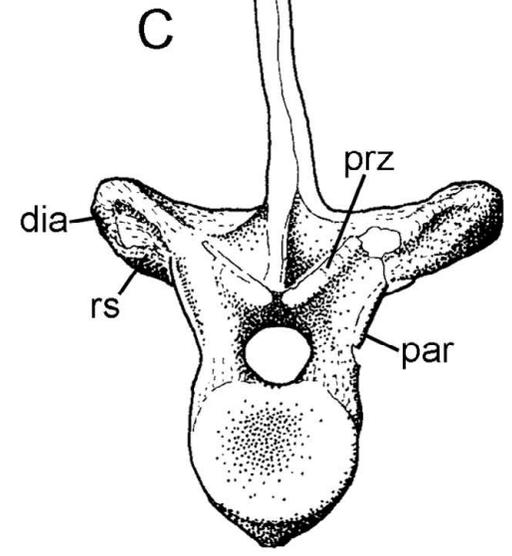
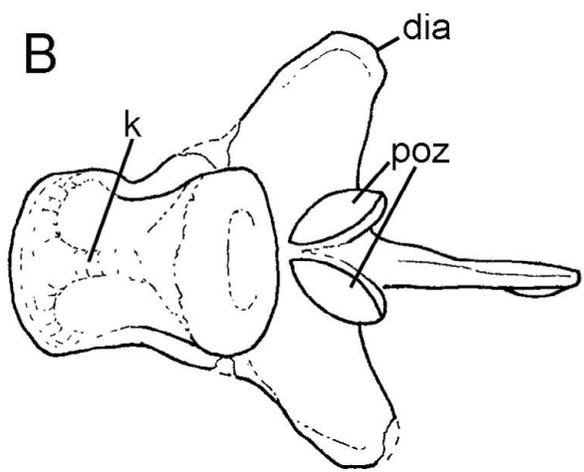
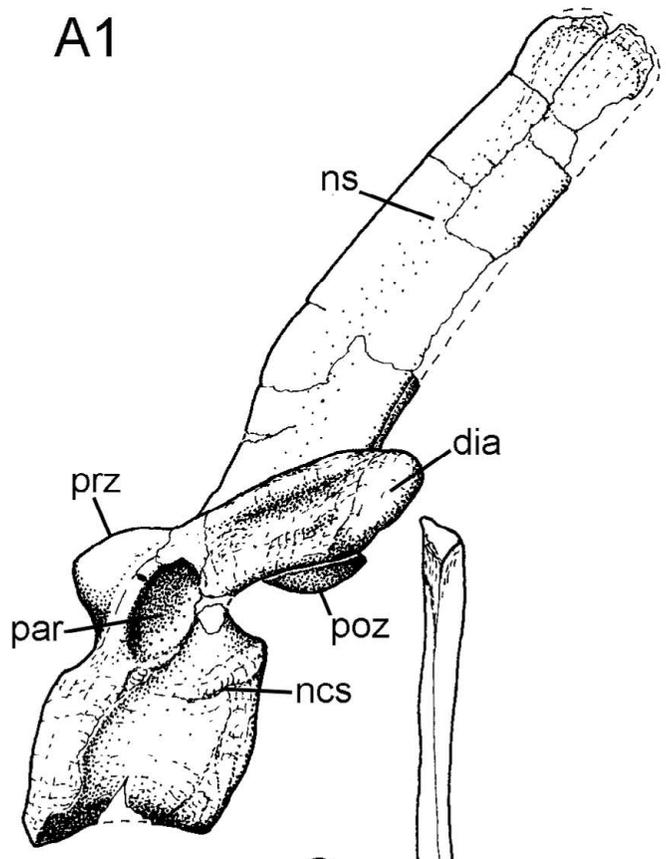
Reconstruction of *Barilium*

The composite reconstruction of the skeleton (Fig. 2.3) suggests that this dinosaur was likely to have been at least facultatively quadrupedal, and it may in fact have been an obligate quadruped.

HYPSELOSPINUS Norman, 2010
HYPSELOSPINUS FITTONI (Lydekker, 1889)

Taxonomic Discussion

Lydekker (1889) described some portions of a skeleton recovered from the same quarry near Hastings that produced the type material of *Barilium dawsoni*. The type material was redescribed by Norman (2010, 2011b, in press) and on the basis of distinctive features of the holotype ilium, which was supplemented by better-preserved referred material – including specimens that were previously attributed to *Iguanodon hollingtoniensis* Lydekker, 1889. *I. hollingtoniensis* is now regarded as a junior subjective synonym of *Hypselospinus fittoni* (Norman,



2.5. *Hypselospinus* cf. *fittoni*, NHMUK R604. Third dorsal. (A, A1) Lateral ([A] is a reversed image of the right side); (B) ventral; (C) anterior. Abbreviations: dia, diapophysis; k, midline keel; ncs, neurocentral suture; ns, neural spine; par, parapophysis; poz, posterior zygapophysis; prz, anterior zygapophysis; rs, rugose surface for ligamentous attachment of the neck of the rib. Scale bar equals 10 cm (from Norman, in press).

2010). *Iguanodon fittoni* was rediagnosed and renamed as a new nomenclatural combination: *Hypselospinus fittoni*. This iguanodont appears to be generally somewhat smaller (body length ~6 m) and less robustly built than specimens typical of *B. dawsoni*. A number of unsupportable claims concerning the osteology, taxonomic status, and affinities of material referable

to this renamed taxon have been made by Paul (2008), as outlined in Norman (2010). Carpenter and Ishida (2010: October), subsequent to Norman (2010: May), published an alternative name for the type material of *I. fittoni*: *Wadhurstia fittoni*. The latter can safely be suppressed because it is a junior objective synonym of *Hypselospinus fittoni*.

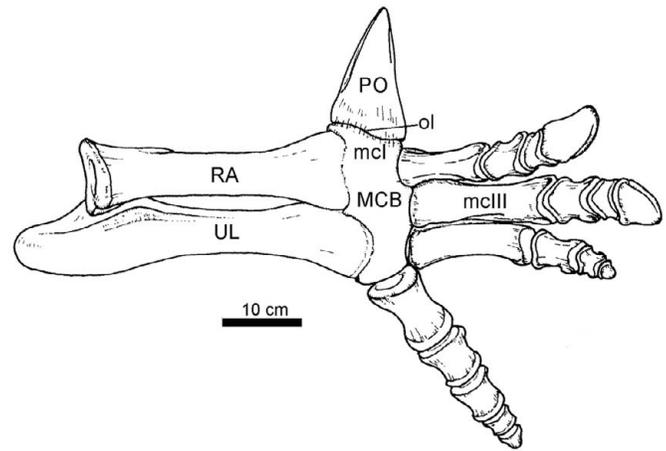
Description

This taxon has a body form that is distinct from its sympatric contemporary *B. dawsoni*: it is smaller in body length overall, less robust, and has a much more lightly built vertebral column with slender, tall neural spines along the dorsal, sacral, and caudal regions.

Craniodental Anatomy A crushed and distorted, yet almost complete, dentary (NHMUK R1831; Fig. 2.4) demonstrates that this bone was more slender than the specimen (NHMUK OR28660) that can be attributed to *B. dawsoni*, and another referred specimen (NHMUK R1834; Norman, in press) indicates that the anterior part of the dentary is deflected ventrally (contra McDonald et al., 2010). Several tooth crowns are preserved in NHMUK R1831 (Norman, 2010, 2011b, in press) and are quite distinct in surface details from those referred to *B. dawsoni*. Whereas the enameled face of the crown is shield shaped and fringed with mammillate, ledge-shaped denticles (as in *B. dawsoni*), the ridge pattern seen on the lingual face of the crown differs considerably. There is a prominent primary ridge running the length of the crown distal (posterior) to the midline, and mesial (anterior) to this is a series of strand-like minor ridges that extend down the remainder of the crown for varying distances.

Vertebrae Most characteristically, the dorsals develop remarkably long, backwardly inclined, narrow spines that in life should have given the appearance of a tall midline ridge (Fig. 2.5). The dorsals differ markedly from those of *B. dawsoni*. The caudals do not exhibit the low (squat), inclined angular form seen in *B. dawsoni*; in contrast, they appear to have compressed, tall centra and support equally elongate, narrow spines. Middle and posterior caudals display the gradual loss of the caudal rib and become lower and more apparently elongate, eventually developing angular (hexagonal) cross sections; they do not seem to show the deeply concave articular surfaces seen in *B. dawsoni*.

Girdles and Limbs The pectoral girdle differs only in size from that of *B. dawsoni*: most of the elements appear similar in general shape and the sternals are hatchet shaped. The forelimb resembles that of *B. dawsoni* in the shape of each element of upper and lower arm, but there is a clear difference in the shape of the characteristic pollex spine (thumb-spike). Whereas in *B. dawsoni* the pollex is short, laterally compressed and bluntly truncated, that of *H. fittoni* appears to be tall, laterally compressed and pointed (triangular in lateral aspect; Fig. 2.6); this thumb-spike resembles Mantell's (1827) classic "nasal horn." The manus (Fig. 2.6) resembles that described in *Iguanodon bernissartensis* (Norman, 1980) in the relative shape and proportions of each digit, although overall it seems to have rather shorter digits

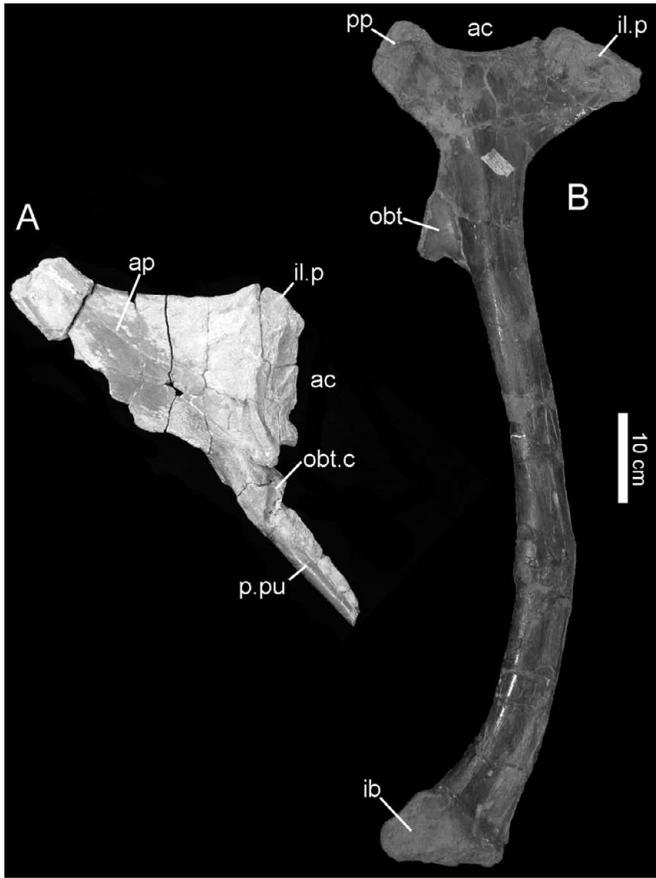


2.6. *Hypselospinus cf. fittoni*, NHMUK R1831 (R1832/R1833). Reconstructed antebrachium and manus in lateral view. Abbreviations: mcl/mclIII, metacarpals; MCB, metacarpocarpal block; ol, ossified ligaments; PO, pollex unguis; RA, radius; UL, ulna. Scale bar equals 10 cm (from Norman, in press).

than might have been expected, judged by the dimensions of the associated radius and ulna.

The pelvis comprises an ilium with a narrow, untwisted, elongate preacetabular process with a low, curved medial ridge; the deep, central portion of the ilium is flat and has a relatively compressed dorsal edge (with, at most, a slight lateral expansion on its dorsal margin above and behind the ischiadic peduncle); the postacetabular process tapers (as upper and lower borders converge) to form a blunt, rounded transverse bar; below the latter is a low-vaulted brevis fossa, demarcated laterally by the presence of a ridge (Norman, 2010:fig. 5). This iliac morphology is clearly distinct from that seen in *B. dawsoni* (Norman, 2011b:fig. 8), which has a transversely thick and axially twisted preacetabular process, a broad dorsal edge to the main blade, a deep postacetabular process that is inflected medially toward its ventral edge but has no lateral ridge, and a brevis shelf that is either absent or very reduced in extent (NHMUK R3788). The pubis (Fig. 2.7A) is incomplete but has a deep and slightly upwardly curved, parallel-sided, prepubic process with an anterior tip that appears to be moderately dorsoventrally expanded. In contrast to the pubis of *B. dawsoni*, the pubic shaft is cylindrical. The ischium (Fig. 2.7B) has a robust, curved (J-shaped) shaft that appears to be twisted along its length and ends in an enlarged anteriorly expanded "boot"; the proximal external surface of the shaft bears a flattened, scarred facet adjacent to the flap-like obturator process (obt) is positioned close to the proximal end of the shaft and offered mechanical support to the pubic shaft.

The hindlimb, as in the case of *Barilium*, is not known from good-quality articulated material; it differs little in morphology from what is known in *B. dawsoni* (Fig. 2.8).

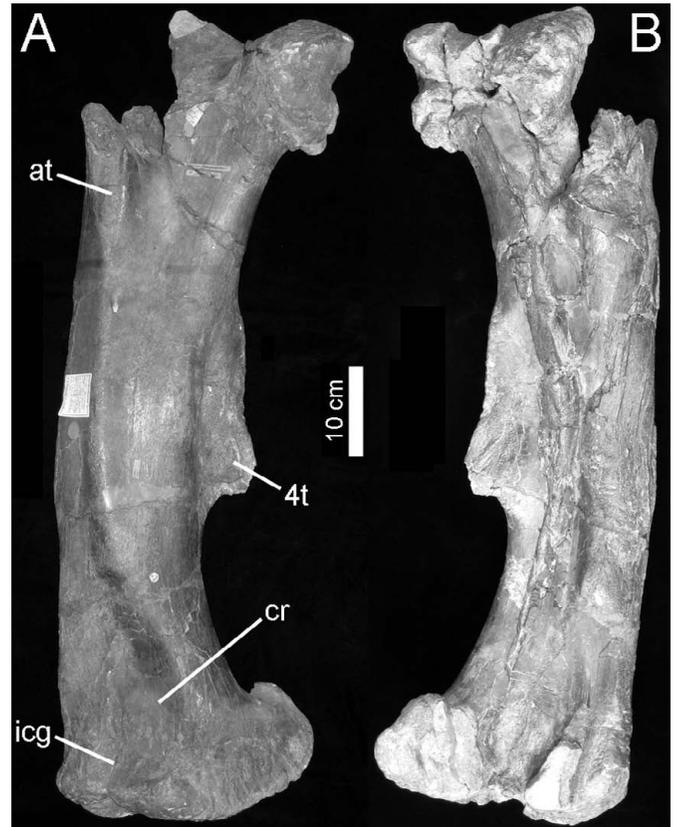


2.7. *Hypselospinus* cf. *fittoni*, NHMUK R811. (A) pubis partial (right, this is a reversed image) in lateral view; (B) ischium complete (left) in lateral view. Abbreviations: ac, acetabular margin; ap, anterior blade of the pubis; ib, ischial "boot"; il.p, iliac peduncle; obt, obturator process; obt.c, obturator channel; pp, pubic peduncle; p.pu, posterior ramus of the pubis. Scale bar equals 10 cm (from Norman, in press).

Hindlimb material of this taxon was first illustrated by Lydekker (1889). There is a prominent crested fourth trochanter that probably terminated in a marginally pendent tip that does not resemble that seen in camptosaurus (contra Lydekker, 1889).

Reconstruction of *Hypselospinus*

A preliminary reconstruction (Fig. 2.9) of *H. fittoni* based on the type and referred material has been described in detail (Norman, in press). The skull was probably more slender and elongate than that of *B. dawsoni* based on the morphology of the lower jaw. The vertebral column is notable for the comparatively small proportions of dorsal centra and the attenuation of the neural spines, which form a sail-like structure reminiscent of the even taller "sail" seen in the gracile neoiguanodontian *Ouranosaurus* (Taquet, 1976). This reconstruction is tentative because it is a composite based on a number of skeletons of individuals of differing size and there

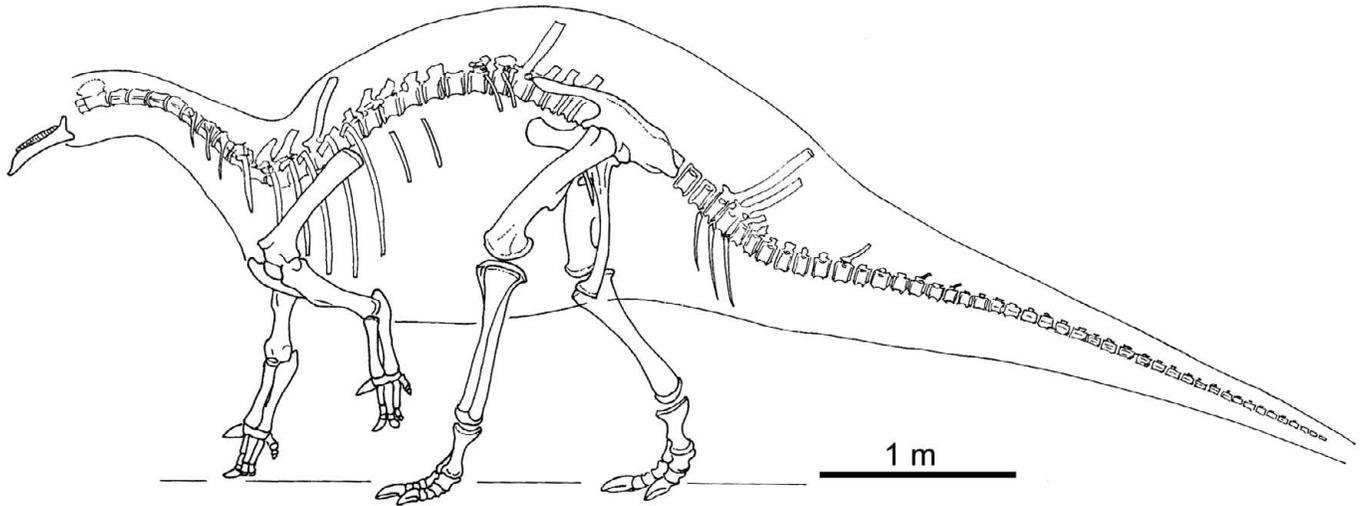


2.8. *Hypselospinus* cf. *fittoni*, holotype of *Iguanodon hollingtoniensis*, NHMUK R1148. (A, B) femur, right, the original specimen as preserved (May 2011) in dorsal and ventral views respectively; the ventral view reveals the extent of longitudinal crushing. Abbreviations: 4t, fourth trochanter; at, anterior (lesser) trochanter; cr, crushing of the dorsal part of the medial condyle; icg, anterior intercondylar groove. Scale bar equals 10 cm (modified from Norman, in press).

are uncertainties about the relative proportions of the fore and hindlimbs (as well as within-limb proportions).

MANTELLISAURUS Paul, 2007 MANTELLISAURUS ATHERFIELDENSIS (Hooley, 1925)

The posthumous work by Hooley (1925) based on a nearly complete skeleton recovered (in 1914) from broken blocks of shale following a cliff collapse near Atherfield Point, Isle of Wight, provided the first detailed anatomical description of any Wealden-aged *Iguanodon*-like ornithopod 100 years after the first *Iguanodon* teeth were described by Mantell. This paper founded a new species: *Iguanodon atherfieldensis* Hooley, 1925. The importance of this discovery and its description cannot be overemphasized, given the previous century of attempts to identify and name new species using material that was often inadequate and compounded by the startling failure to provide detailed descriptions when material was, in fact, available.



2.9. *Hypselospinus fittoni*. Preliminary skeletal reconstruction based upon the holotypes of *Iguanodon fittoni* Lydekker, 1889, and *I. hollingtoniensis* Lydekker, 1889, supplemented by information from several additional referred partial skeletons (from Norman, in press).

Noteworthy, in the latter respect, is the remarkable fully articulated skeletal material collected between 1878 and 1881 from Bernissart in Belgium, which was described only superficially by Louis Dollo (Norman, 1980, 1986, 1987). What became increasingly obvious, with the benefit of hindsight, was that material (notably that collected from the Isle of Wight) described variously under the names *Vectisaurus*, *Sphenospondylus*, or *Iguanodon mantelli*—the latter name usually considered synonymous with the “Mantel-piece” collected from Maidstone in 1834 (Norman, 1993)—would eventually be referred to *I. atherfieldensis* (Norman, 1986, 1990, 2004).

Taxonomic Discussion

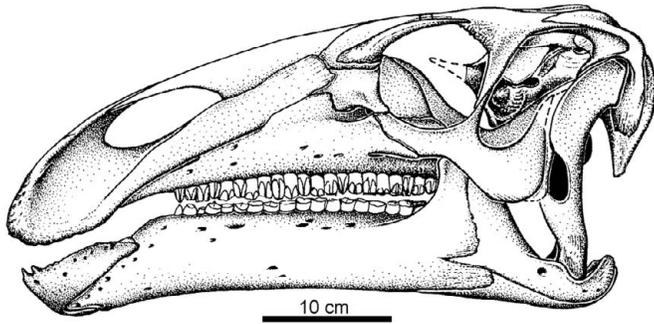
Recently, the taxon *Iguanodon atherfieldensis* has been subjected to revision. Paul (2007) proposed *Mantellisaurus* as a new generic name for *I. atherfieldensis*. The reasoning for this change relied on osteological differences originally regarded as sufficient to distinguish these forms as “osteological species” (Norman, 1986:327). Having proposed the generic name *Mantellisaurus*, Paul (2008) then extended his taxonomic revision of Wealden iguanodonts by creating an entirely new taxon, *Dollodon bampingi* (Fig. 2.2) for the gracile skeleton (RBINS R57 [formerly “IRSNB 1551”]; see Norman, 1986) and referred to, historically, as “*Iguanodon mantelli*” (e.g., Dollo, 1882; Casier, 1960). The first monograph on this specimen (Norman, 1986) referred it to *Iguanodon atherfieldensis*. The case for erecting the new binomial *Dollodon bampingi* was supported by a list of diagnostic characters derived from some simplistic outline drawings, some “fleshed-out” restorations of the heads of these animals and the interpretation of photographs of mounted specimens

(named “technical restorations” by Paul, 2008:202). Norman (2012) evaluated the diagnostic characters proposed by Paul and demonstrated that none could be considered to be valid, and that on that basis alone, the new name should be considered a nomen dubium: a very similar conclusion was reached independently by McDonald (2012a).

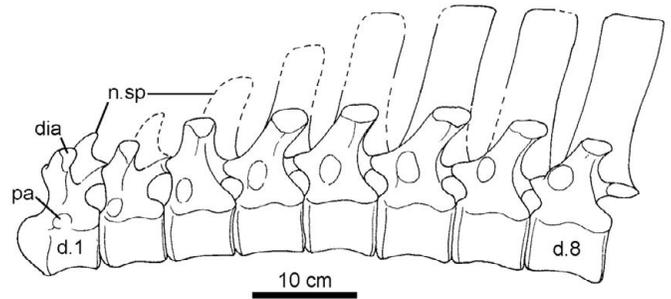
Description

Mantellisaurus atherfieldensis attained a probable adult body length of about 7 m. The type material (NHMUK R5764) represents a disarticulated partial skull and skeleton collected from the Isle of Wight, that is ontogenetically immature and has an estimated body length of approximately 5.5 m; the referred skeleton from Bernissart (RBINS R57) shows some residual features associated with immaturity, and is approximately 6.5 m long; and the length of the “Mantel-piece” individual (Norman, 1993) from Maidstone (NHMUK OR3741) is estimated (based on femoral length) at probably a little in excess of 7 m. Some material collected recently from the Isle of Wight exhibits very interesting anatomical variation (Martill and Naish, 2001:MIWG 6344).

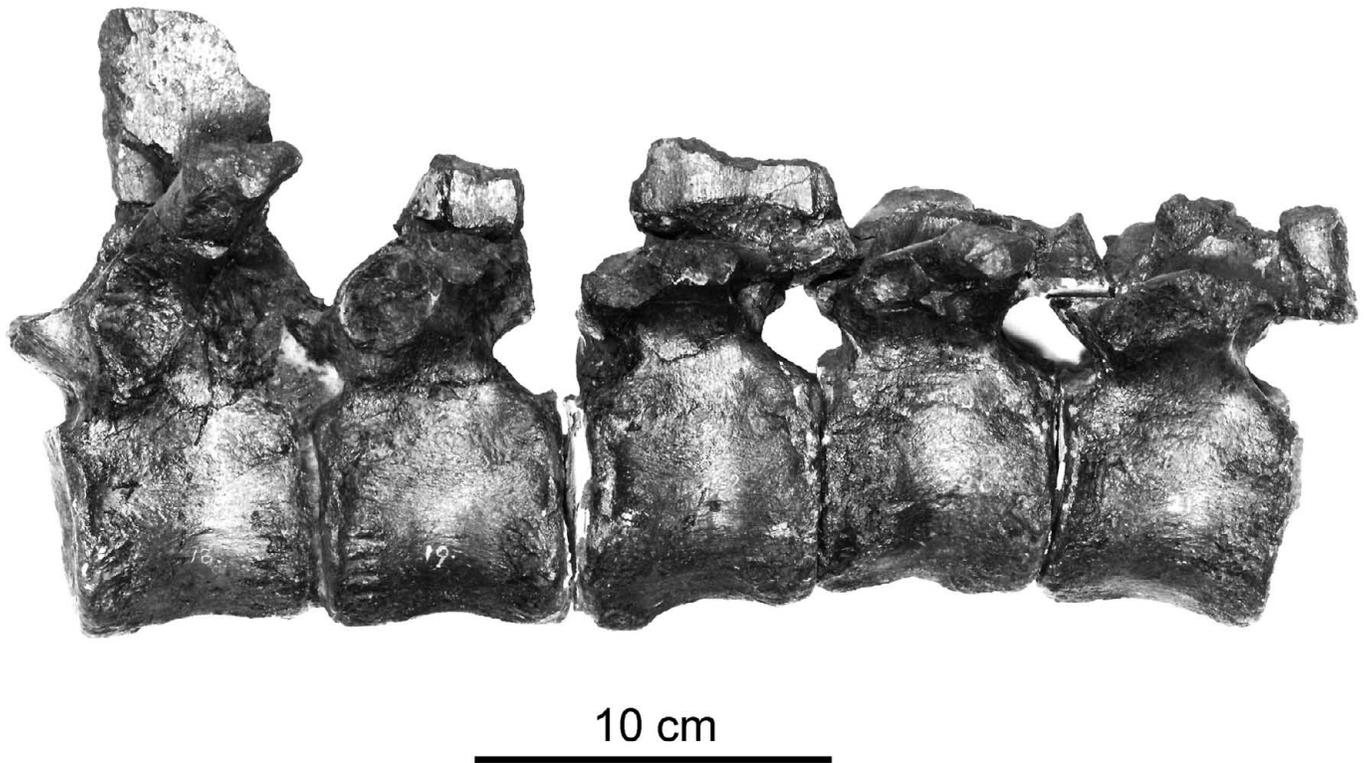
Craniodental Anatomy The skull (Fig. 2.10) of this species is known in considerable detail (Norman, 1986). The lower jaw is elongate and its lower margin is gently arched towards its anterior tip; the coronoid process is comparatively short, vertical and slightly expanded anteriorly at its apex. The posterior end of the lower jaw is marked by a large surangular with a distinct surangular foramen and the angular is visible in lateral aspect. Dentary teeth are comparatively simple in construction with primary and secondary ridges alone on the lingual enameled surface resembling the



2.10. *Mantellisaurus atherfieldensis*. Skull restoration based upon the "Chase skull," NHMUK R11521.



2.11. *Mantellisaurus atherfieldensis*. Anterior dorsal vertebrae, reconstruction in lateral view based upon examination of the original material of RBINS R57 and NHMUK R5764 (the holotype of *I. atherfieldensis*). Abbreviations: d.1–d.8, dorsals numbered in sequence; dia, diapophysis; n.sp, neural spine; pa, parapophysis (after Norman, 1986:fig. 29B).



2.12. *Mantellisaurus atherfieldensis*, holotype of *I. atherfieldensis* Hooley, 1925, NHMUK R5764. Articulated sequence of mid-dorsal vertebrae as preserved (same as Norman, 2011b:fig. 27.42B).

pattern seen in examples of *B. dawsoni*. Maxillary teeth have narrower crowns than dentary teeth and have an extremely prominent distally offset primary ridge.

Vertebrae Cervical vertebrae exhibit the following characteristics: strongly opisthocoelous; low cylinders with ventral keels and a mid-height ridge that is expanded near the anterior condylar margin to form a parapophysis; neural arch develops a small midline spine lateral to which are prominent, stout diapophyses for the attachment of ribs; prezygapophyses are widely spaced and do not project beyond the articular margin of the centrum, whereas the postzygapophyses

are long, arched, and divergent (and overlap the succeeding centrum). The general form of cervical vertebrae is seen in the first dorsal vertebra reconstructed in Figure 2.11.

Mid-dorsal vertebrae develop elongate spines in the articulated skeleton RBINS R57 (Fig. 2.11), but preservation is usually not nearly so good in Wealden specimens: all are broken in the holotype skeleton (Fig. 2.12). Ossified tendons are distributed in the form of a layered lattice across the taller neural spines. The centra are spool shaped and bear a modest ventral keel. The articular faces, which bear remnant opisthocoely across the cervicodorsal transition, have



2.13. The “Sauli Sacrum” illustrated in ventral view, NHMUK OR37685. Specimen referred to *Mantellisaurus* cf. *atherfieldensis*. Scanned from the original lithograph in Owen (1855:pl. 3). This specimen was one of the key specimens that Richard Owen used in order to diagnose his new “sub-order” Dinosauria (Owen, 1842).

predominately amphiplatyan faces. Posterior dorsals develop centra that are broader and deeper than anterior members of the series, and also become slightly opisthocoelous in the region adjacent to the sacrum.

Sacral Vertebrae One specimen (Fig. 2.13) comprises a nearly complete sacrum (lacking the sixth true sacral) with portions of an attached ilium (NHMUK OR37685), which is attributable to this species. The sacrum comprises seven fused vertebrae in mature specimens (fusion is incomplete in immature individuals) and involves the incorporation of a posterior dorsal with a free (non-sacralized) rib. There is a narrow keel present, unlike *I. bernissartensis*, which exhibits a broad, longitudinal midline sulcus.

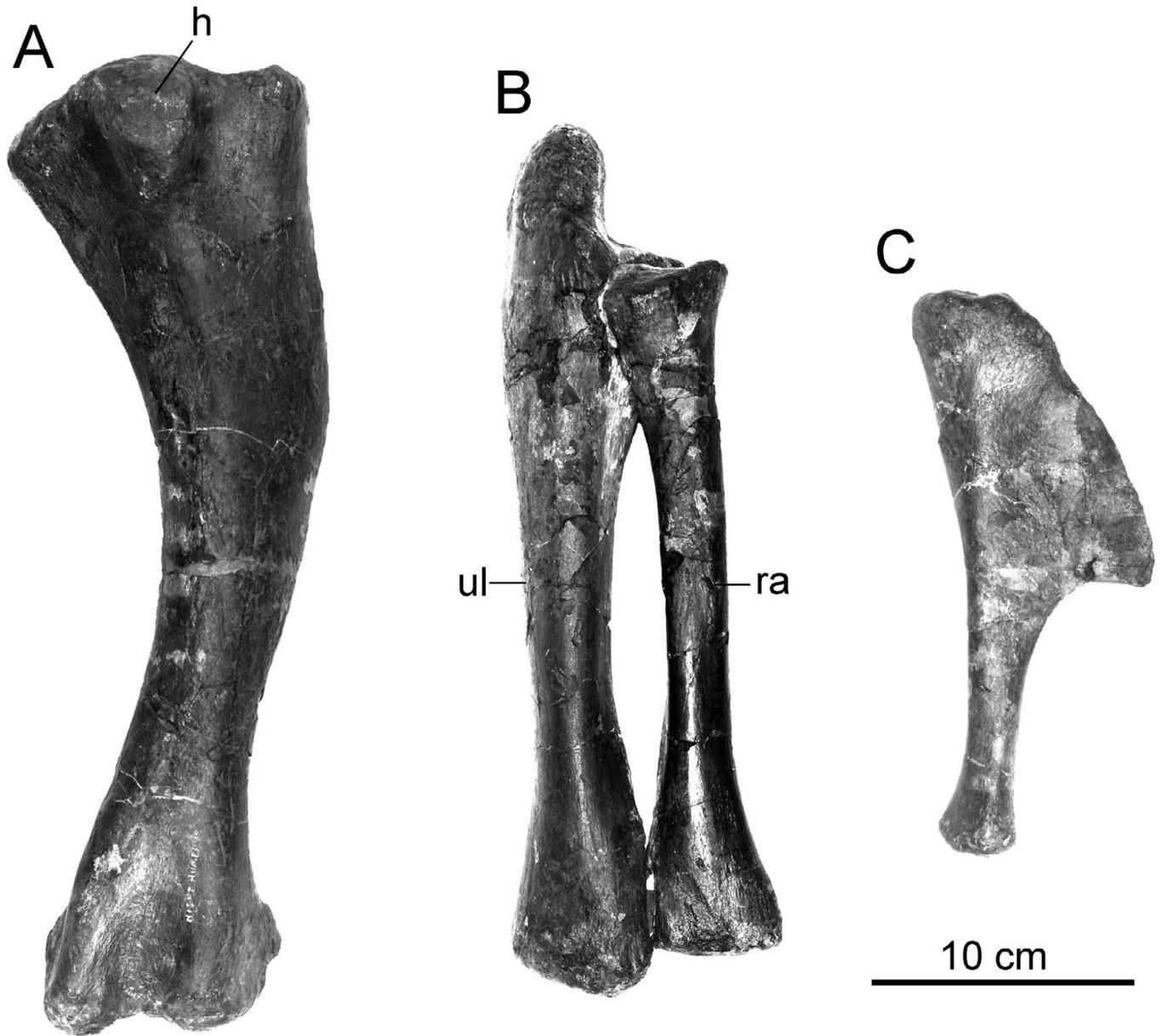
Girdles and Limbs The pectoral girdle and forelimb bones differ little from those described for previous taxa (and the contemporary *I. bernissartensis*) except that they tend to

be smaller and less robust. The blade of the scapula tends to have a narrower shaft and the blade flares distally to a greater extent than in *I. bernissartensis*. The coracoid also exhibits a discrete foramen (cf) externally, which is different from the coracoid “notch” seen in *I. bernissartensis*.

The sternal bone (Fig. 2.14C) has the classic “styracosternan” hatchet-like shape. The humerus (Fig. 2.14A) is sinuous. The ulna and radius (Fig. 2.14B) are comparatively slender and bowed, thus suggesting the possibility of some axial rotation between these elements. The wrist and hand are worth mentioning because they are distinctive (Fig. 2.15). The carpals are sutured together, but they are neither as massive nor as tenaciously bound by ossified ligaments as is the case in previous examples (above; Norman, 2011a, in press) or in *I. bernissartensis* (below; Norman, 1980). The first metacarpal is fused to the carpals and forms an oblique, roller-like structure for articulation with the base of the pollex; the latter is relatively diminutive and, unlike the *Barilium* and *Hypselospinus*, is genuinely conical rather than transversely compressed or truncated. In its general shape the pollex of *M. atherfieldensis* echoes, on a smaller scale, the conical pollex of *I. bernissartensis*. The central bones of the hand (metacarpals II–IV) are slender and more elongate than those known in either *Hypselospinus* or *Iguanodon*.

The ilium (Fig. 2.16) has a long, slender, preacetabular process (prp) that is buttressed by a curved medial ridge. The main body of the iliac blade is vertical, but the dorsal edge is thickened and everted so that it overhangs the lateral surface. Farther posteriorly, the dorsal edge thickens and becomes more everted, forming a beveled structure (boss) posterodorsal to the ischiadic peduncle. The dorsal edge of the postacetabular process beyond the iliac boss is inflected downward before terminating in a short transverse bar. Beneath this bar there is a narrow, vaulted brevis fossa (br.f). In overall shape the ilium resembles that of *Hypselospinus fittoni* from the Valanginian of the Weald Sub-basin; however, the preacetabular process is more slender and transversely thicker, whereas the equivalent portion of *H. fittoni* is more strongly compressed laterally and considerably deeper; the central portion of the iliac blade is shallower than in *H. fittoni*; and the postacetabular process differs also in having a far less pronounced brevis fossa than in *H. fittoni* and, as a direct consequence, the posterior bar is also much narrower.

The pubis (Fig. 2.16) has a thin, deep, prepubic process that expands distally, whereas the pubic shaft is narrow and short; there is a massive iliac peduncle, and beneath this a broad cup-shaped depression forms the anterior part of the acetabulum. The proximal part of the pubic shaft has a finger-like dorsal process that nearly encircles the obturator foramen (obt.f); its posterior surface forms a flattened vertical surface for attachment of the adjacent part of the ischium



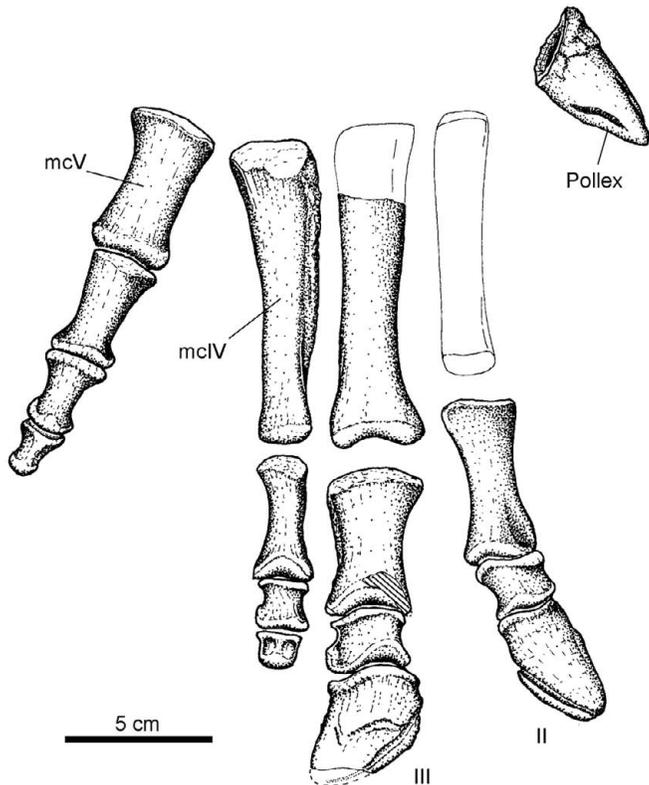
2.14. *Mantellisaurus atherfieldensis*, holotype of *I. atherfieldensis* Hooley, 1925, NHMUK R5764. (A) humerus, right in dorsal view; (B) radius and ulna, right lateral view; (C) right sternal bone in ventral view. Abbreviations: h, articular head of the humerus; ra, radius; ul, ulna (same as Norman, 2011b:fig. 27.43C–E).

and, when articulated, the obturator foramen is completely enclosed. The shaft of the ischium is long, slender, and only slightly arched along its length (the arching is perhaps exaggerated in Figure 2.16, and the distal boot is too large) and has a modest anterodistal expansion.

The hindlimb (Fig. 2.17) is not particularly distinctive, as is true of most similar-sized iguanodonts. The femur (Fig. 2.17A, B) has a shaft that is more slender, less angular-sided, and less curved along its length than that seen in *B. dawsoni* and *H. fittoni* from the Weald Sub-basin (any remaining curvature of the shaft is present only below the fourth trochanter [4t]); and the anterior trochanter (at) is narrower, less robust,

more laterally compressed, and more closely appressed to the lateral surface of the greater trochanter, when compared to the latter taxa. The lower leg elements (Fig. 2.16C, D) are not distinctive, except insofar as they are more slender and lightly built than in the contemporaneous taxon *I. bernissartensis*, and the proximal tarsals are firmly attached (but not fused) to the crus (Fig. 2.17: ast, cal).

The pes (Fig. 2.18A, B) is slender and functionally three toed. Neither the holotype (NHMUK R5764) nor the referred specimen (RBINS R57) have metatarsal I preserved. A well-preserved and articulated pes that is commensurate and that is the same stratigraphic age has been referred to



2.15. *Mantellisaurus atherfieldensis*, holotype of *I. atherfieldensis* Hooley, 1925, NHMUK R5764. The associated elements of the right manus in dorsal view. Abbreviation: mc, metacarpal (from Norman, 1977).

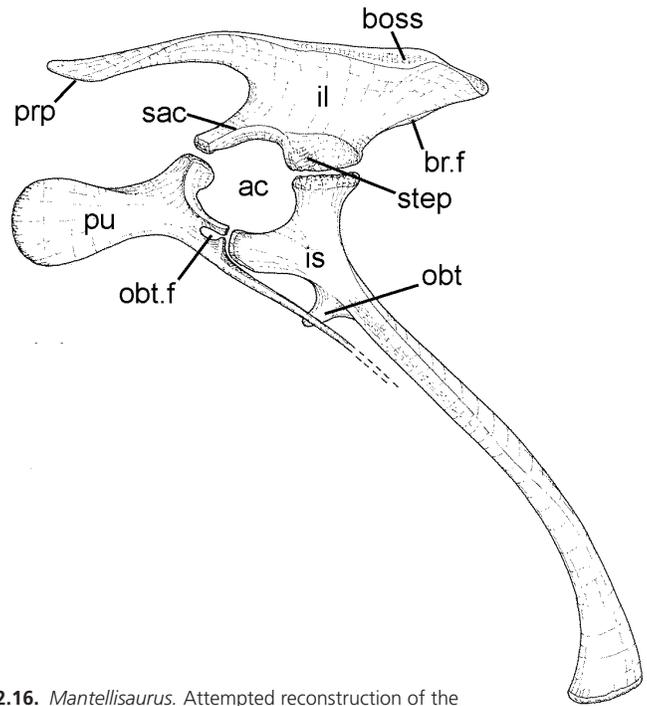
M. atherfieldensis (Norman, 1986; NHMUK R1829) exhibits a narrow, splint-like metatarsal I. The sympatric contemporary *I. bernissartensis* has a small, laterally compressed metatarsal I (Norman, 1980).

Reconstruction of *Mantellisaurus*

The reconstruction in a bipedal pose (Fig. 2.19) is based primarily upon the proportions of the holotype skeleton (NHMUK R5764) and that of the referred skeleton (RBINS R57). The pectoral girdle and forelimb are notably less robust than those seen in either of the Valanginian taxa.

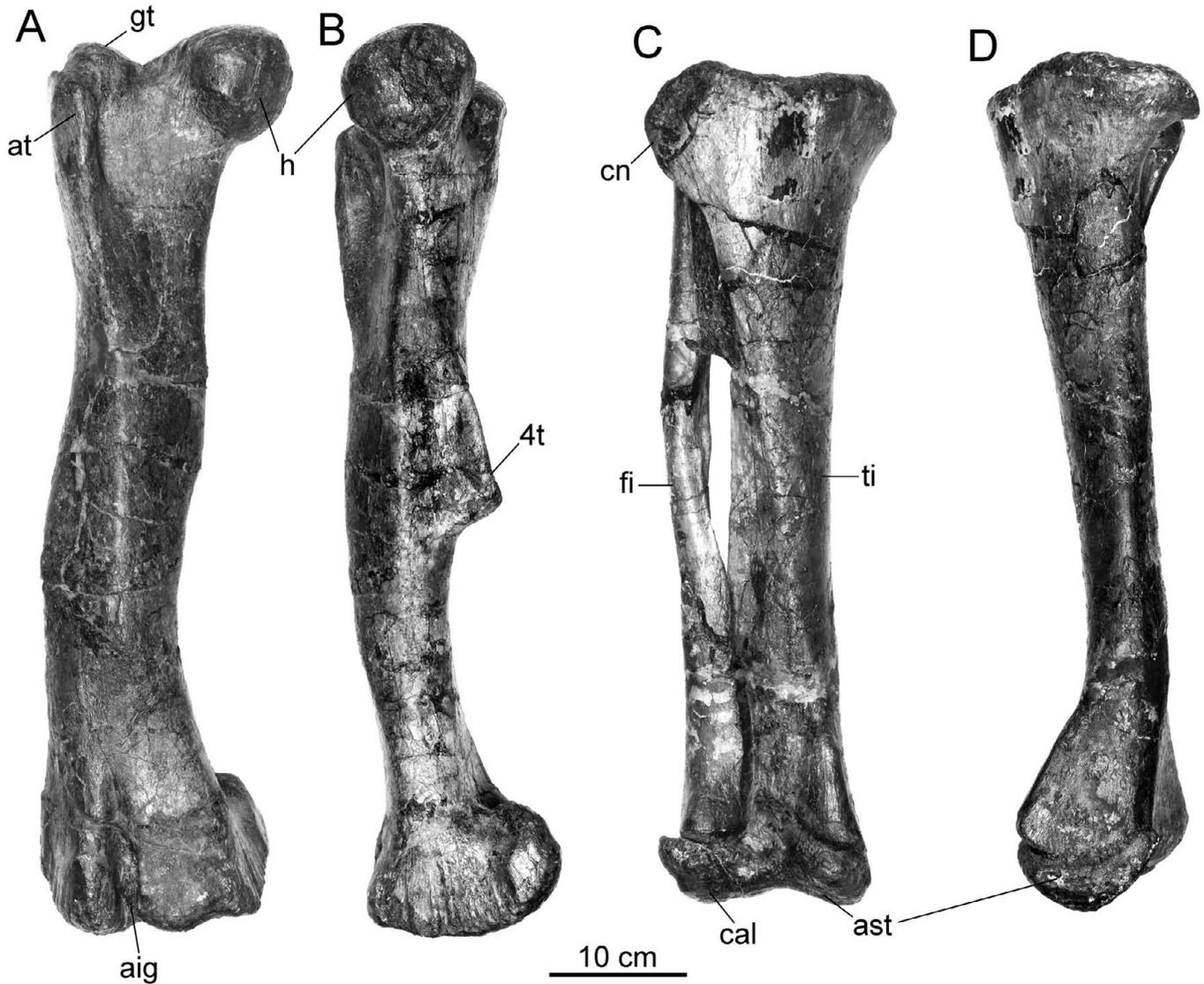
IGUANODON Mantell, 1825
IGUANODON BERNISSARTENSIS Boulenger
(in Beneden, 1881)

Although extremely well known in mainland Europe, where more than 30 complete and partial skeletons have been recovered in Belgium, Germany, France, and Spain, *Iguanodon bernissartensis* is comparatively rare in Britain. The first occurrence of this morphotype was a hindlimb, pelvis, and some caudal vertebrae of large size collected in 1870 by



2.16. *Mantellisaurus*. Attempted reconstruction of the articulated pelvic bones in left lateral view. The curvature of the ischial shaft is exaggerated; the shaft is typically straighter, more angular-sided proximally, and has a smaller distal "boot" (from Norman, 1977, 2011b). Abbreviations: ac, acetabulum; boss, faceted dorsal margin of the iliac blade; br.f, brevis fossa; il, ilium; is, ischium; obt, obturator process; obt.f, obturator foramen; prp, preacetabular process of the ilium; pu, pubis; sac, supra-acetabular crest; step, beveled external surface of the ischiadic peduncle.

John Whitaker Hulke at Brook Chine, Isle of Wight (late Barremian: NHMUK R2501-R2514; associated bones of an almost complete ilium and hindlimb that were given separate registered numbers). This material was eventually described and illustrated as *Iguanodon seelyi* Hulke, 1882 (Norman, 2012). Rather interestingly, from a purely historical perspective, this paper appeared shortly after Hulke had spent time studying the newly excavated Bernissart material in Brussels. Hulke was informed (as he quite candidly reported in this article) that formal description of the Belgian remains was not expected for a number of years; however, he must have been aware of the strong anatomical similarity between the material that he had discovered earlier and that of the large iguanodont skeletons from Bernissart. Hulke's specimen consisted of the ilium, portions of both hindlimbs (including an almost complete pes), a major portion of a humerus, and a small number of caudal vertebrae (Norman, 2012); it should be noted there are also a number of additional complementary skeletal elements that are commensurate with the holotype that were also recovered from Brook Chine by Hulke and Rev. William Fox. Although these specimens were recovered at about the same time, they were not recorded in the same series of accession numbers. Dollo (1882) synonymized



2.17. *Mantellisaurus atherfieldensis*, holotype of *I. atherfieldensis* Hooley, 1925, NHMUK R5764. The principal bones of the hindlimb. (A, B) femur in anterior (dorsal) and medial views, respectively; (C, D) the crus in anterior (dorsal) and medial views, respectively. Abbreviations: 4t, fourth trochanter; aig, anterior intercondylar groove; ast, astragalus; at, anterior (lesser) trochanter; cal, calcaneum; cn, cnemial crest; fi, fibula; gt, greater trochanter; h, femoral articular head; ti, tibia (same as Norman, 2011b:fig.27.46).

Hulke's material with *Iguanodon bernissartensis* Boulenger, which had been named within the text of a critical report by P.-J. van Beneden (1881).

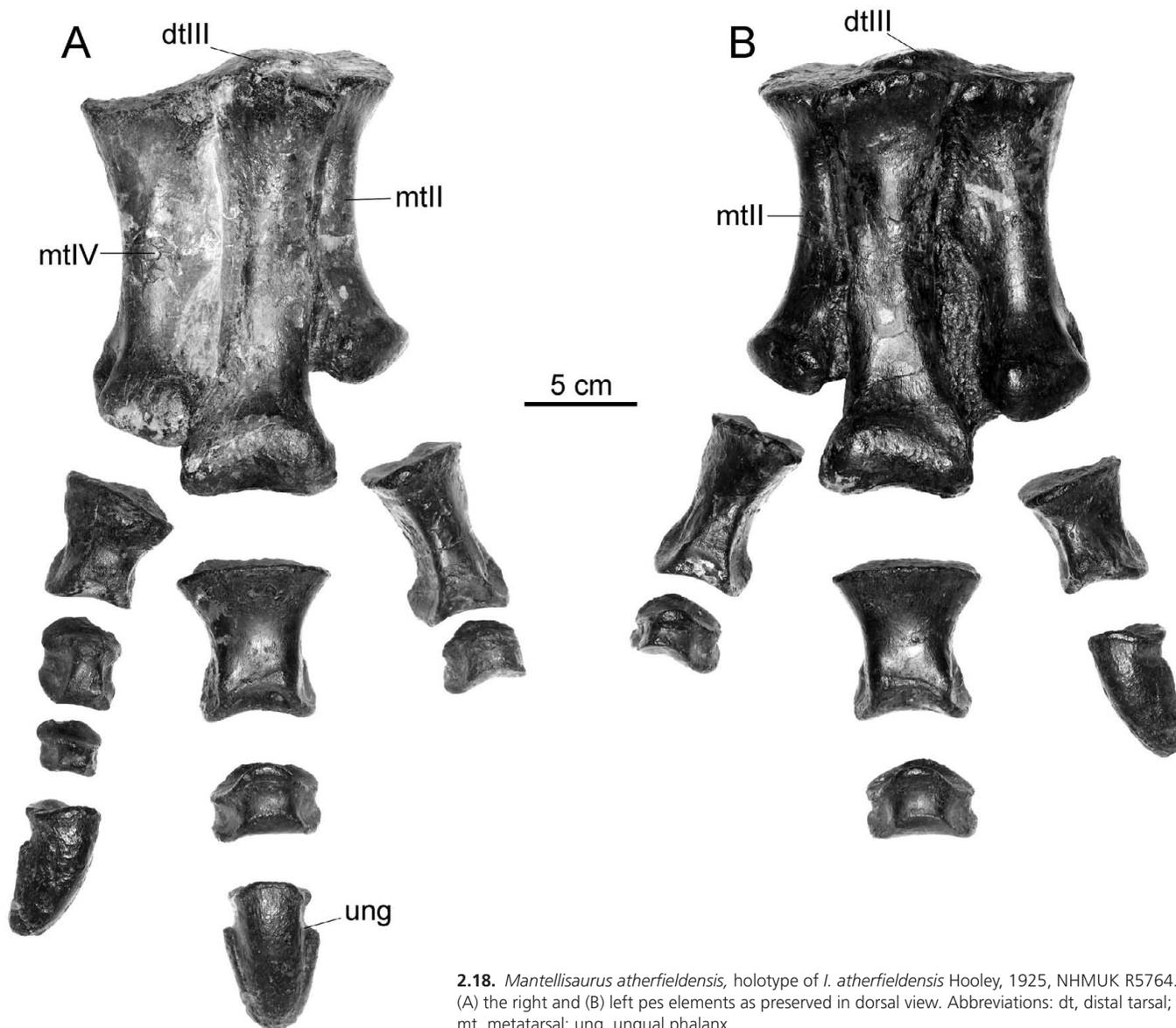
Taxonomic Discussion

Despite some lingering concerns about the status of *Iguanodon seelyi*, the iconic taxon *I. bernissartensis* has remained largely unaffected by recent taxonomic revisions. However, an entirely unnecessary confusion concerns a new taxonomic combination, *Dollodon seelyi* (Fig. 2.2). Carpenter and Ishida (2010:148) consider the ilia of RBINS R57 that were renamed *Dollodon bampingi* by Paul (2008) to be “practically

indistinguishable from that of *Iguanodon seelyi* Hulke, 1882 and therefore the species *seelyi* has priority over *bampingi*.” However, the two ilia are distinguishable. *Dollodon* is an invalid taxon (see above, *D. bampingi*) and referring another specimen to this genus by creating a new species without reference to diagnostic characters is logically and taxonomically unacceptable (McDonald, 2012a).

Description

Mature specimens of *I. bernissartensis* attained a body length in the range 10–13 m (*I. seelyi* being at the top end of the range) and, by virtue of their size and robustness, these remains are

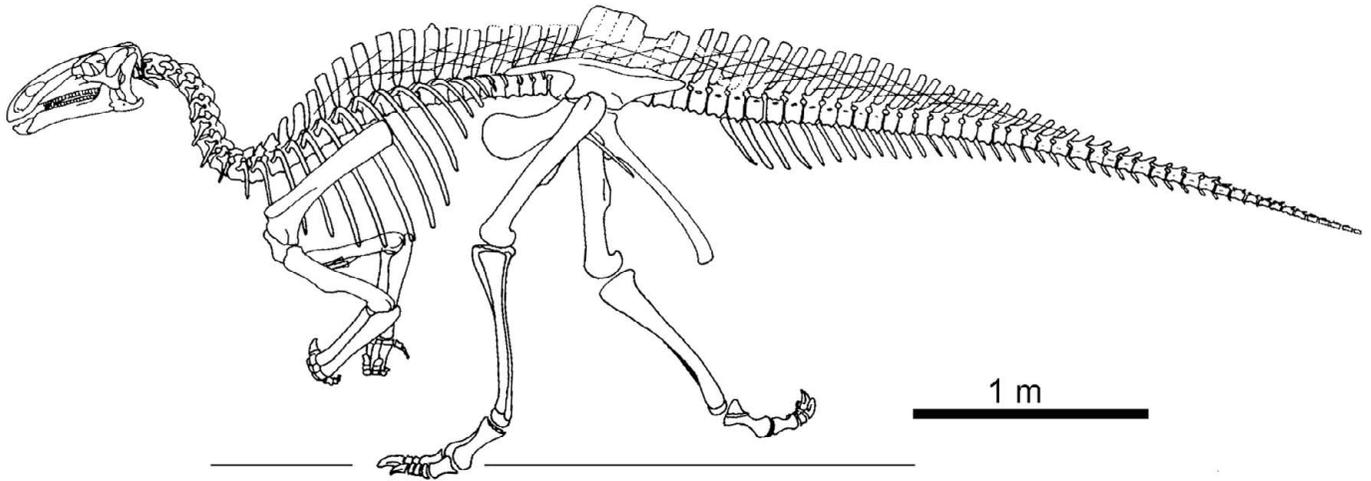


2.18. *Mantellisaurus atherfieldensis*, holotype of *I. atherfieldensis* Hooley, 1925, NHMUK R5764. (A) the right and (B) left pes elements as preserved in dorsal view. Abbreviations: dt, distal tarsal; mt, metatarsal; ung, ungual phalanx.

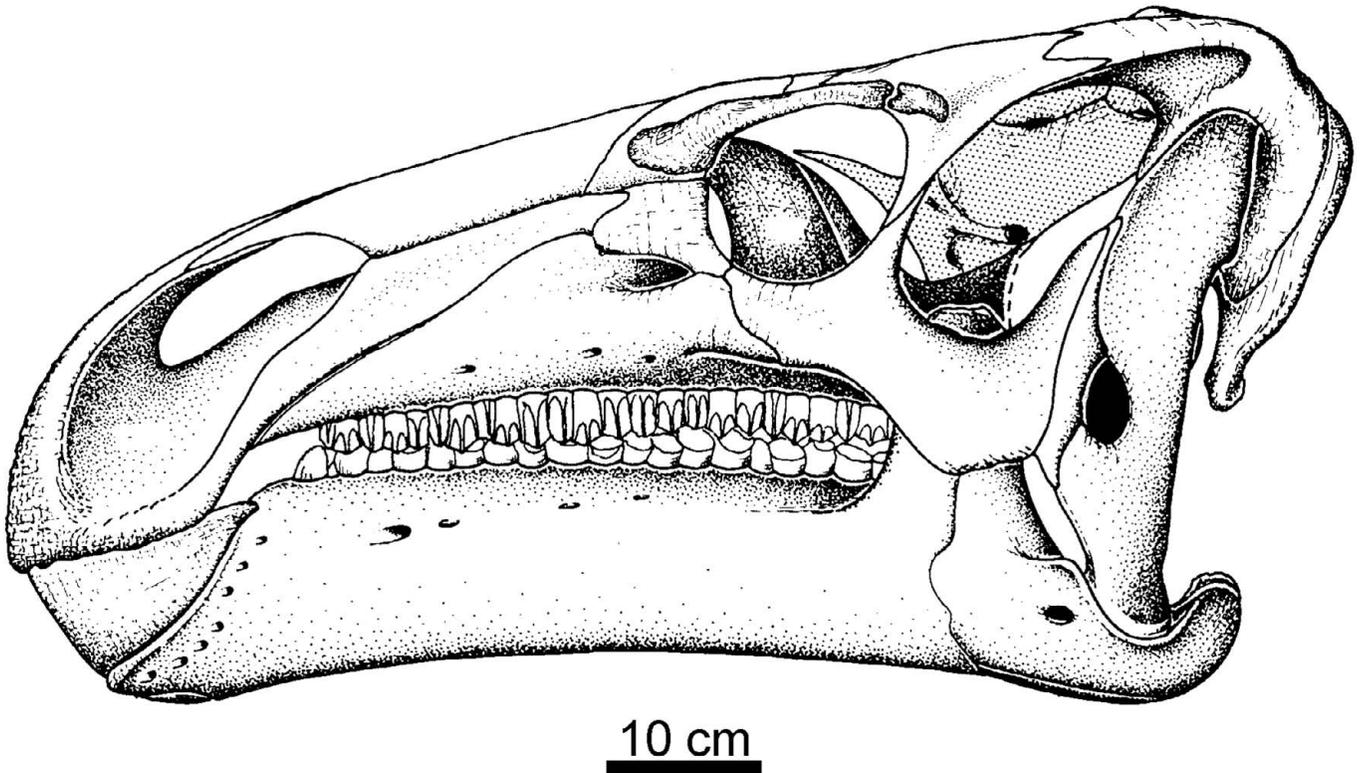
readily distinguished from those of the contemporaneous taxon *Mantellisaurus*. Subadult remains overlap the size range of *Mantellisaurus* (Norman, 1980), but can generally be distinguished anatomically without too much difficulty.

Craniodental Anatomy The skull of *I. bernissartensis* (Fig. 2.20) has been described in detail (Norman, 1980) and is distinctive in both its proportions and osteology. Compared to that of *Mantellisaurus* (Fig. 2.10) the skull is taller and less elongate rostrally. The lower jaw is deep and robust, parallel sided, and is less arched along its ventral margin. The other notable feature of the skull of *I. bernissartensis* compared to that of *M. atherfieldensis* is the double palpebral. Apart from their generally larger size, maxillary and dentary teeth are very similar in appearance to those described for *Mantellisaurus*.

Vertebrae The large size of the cervical and dorsal vertebrae (Fig. 2.21) are distinctive, and the spines of the dorsals are not as tall, relative to centrum height, as in *Mantellisaurus*; the form of the dorsal centra also shows an exaggerated change in shape from anterior to posterior along the series. Anterior dorsals tend to have comparatively narrow, tall centra, whereas posterior dorsals have centra that are broad and short with everted articular margins; the posterior articular surfaces (initially flat with a slight depression at the center) also become increasingly concave nearer the sacrum. The sacrum typically comprises eight fused vertebrae (including the sacrodorsal) and examples with nine fused caudals (by incorporation of the first caudal) are known (Norman, 1980), and there is typically a broad ventral sulcus on the posterior sacra. Caudal vertebrae form slightly taller than broad subrectangular bodies



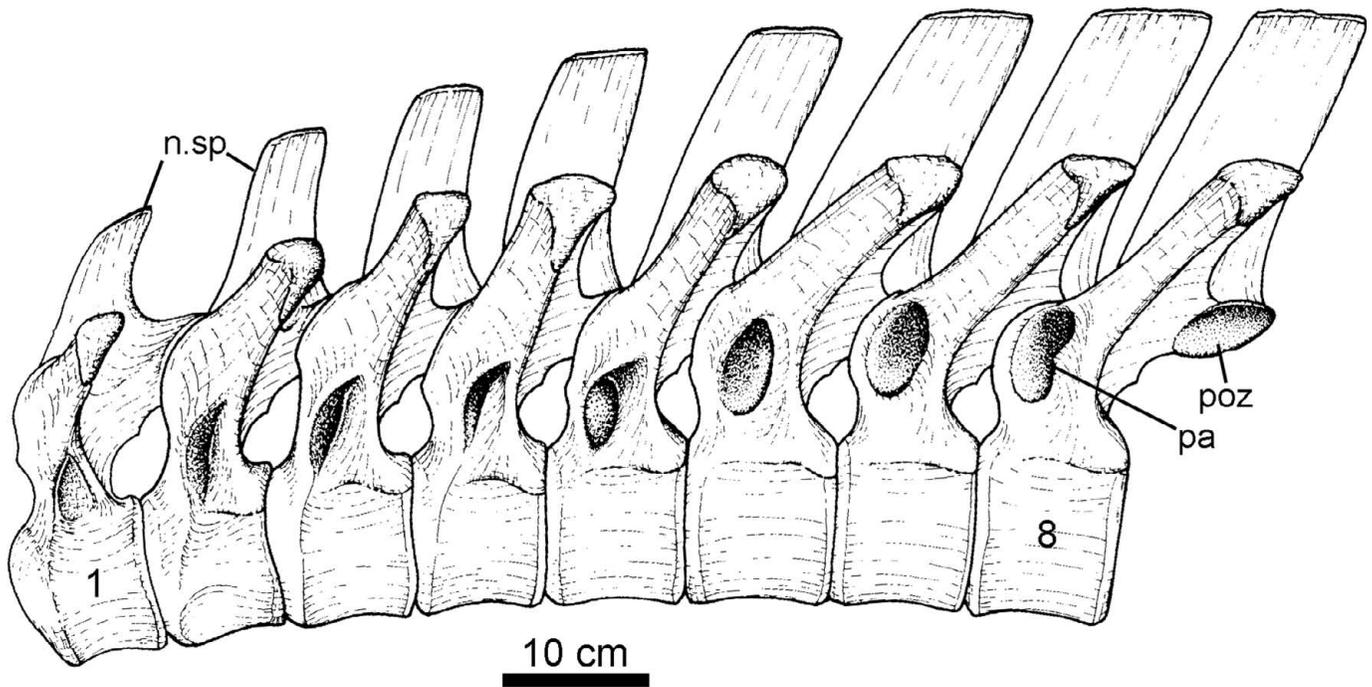
2.19. *Mantellisaurus*. Skeletal reconstruction based primarily upon the articulated, albeit crushed and distorted, skeleton from Bernissart, RBINS R57 (formerly IRSNB 1551 [after Norman, 1986]).



2.20. *Iguanodon bernissartensis* Boulenger, 1881. Skull reconstruction, in lateral view, based on several of the Bernissart specimens (from Norman, 1980:fig. 2).

anteriorly, with prominent horizontal caudal ribs and large chevron facets. More posteriorly in the caudal series, the loss of the caudal ribs and diminution of size often result in a change of centrum morphology from hexagonal cylinders to elongate, round cylinders. Ossified tendons are present as a latticelike array along the sides of the neural spines of the entire

dorsal series, across the sacrum, and along the anterior third of the tail; they may also form what appear to be collapsed bundles lying in the longitudinal recess formed between the base of the neural spines and the adjacent transverse processes, either as preservational artifact or reflecting their involvement in different parts of the epaxial musculature.



2.21. *Iguanodon bernissartensis*. Anterior dorsal series based upon an articulated series of vertebrae preserved in the Conservatoire Collections of the RBINS [individual "S"]. Abbreviations: 1–8, serial arrangement of dorsals; n.sp, neural spine; pa, parapophysis; poz, posterior zygapophysis (after Norman, 1980).

Girdles and Limbs Size and robustness are key features that distinguish these elements from those of the contemporary *Mantellisaurus*. The scapula tends to be generally less curved along its length and less expanded towards the distal end of the blade than in *Mantellisaurus*, although there is variation in both curvature and distal expansion among the individuals collected at Bernissart (pers. obs., 2009). The coracoid has a well-developed coracoid notch (co.n) rather than the discrete coracoid foramen seen in the much smaller *Mantellisaurus*. The sternal bones are comparatively very large and the handle of the hatchet tends to be more curved; and associated with these in some individuals there is also an unusual, somewhat irregular mass of bony material located in the center of the chest and referred to as an "intersternal ossification" (Norman, 1980:fig. 56). The humerus is very robust and nearly straight rather than strongly sigmoid (obscured by crushing), and has a massively thickened deltopectoral crest. The forearm bones are equally massive and parallel, with very little gap between the shafts of the two bones, which supports the contention that this dinosaur used its forelimbs for walking and body-weight support. The carpals and metacarpal I are fused into a large block (Norman, 1980:fig. 59); the metacarpal has a roller-like articular surface for articulation of the large, conical, and slightly curved pollex. Unlike the condition seen in Hastings Group taxa (*B. dawsoni* and *H. fittoni*), the pollex does not become fused to the carpometacarpal

block in mature specimens and remained freely mobile at its base. A small, flattened phalanx is occasionally seen lodged in the base of the pollex ungual. The central metacarpals are more massive, and in proportion shorter, than those of *Mantellisaurus* (Fig. 2.15).

The pelvis (Fig. 2.22) is distinct from that seen in *Mantellisaurus* (Fig. 2.16). The ilium has a very robust, thick, preacetabular process, which is supported by an enlarged medial ridge (note the shape of its cross section in silhouette; Fig. 2.22). The main part of the iliac blade is vertical, but the upper edge is thick and posteriorly it becomes more so—so that it forms a somewhat everted and curved ledge that overhangs the ischiadic peduncle; there is no abrupt inflection along the upper margin of the postacetabular process that characterizes the ilium of *Mantellisaurus*. The dorsal margin of the posterior ilium is elongate and pointed in profile and its ventral surface forms a broad, shallowly vaulted brevis fossa (br.f) bounded laterally by a prominent ridge (Fig. 2.22). The ischiadic peduncle does not exhibit the prominent lateral and stepped expansion typical of all other Wealden iguanodontians. The prepubic process forms an elongate anterior blade that is transversely thick (Fig. 2.22, silhouette), but dorsoventrally narrow along much of its length, before expanding distally; this is distinct from the thinner and deeper blade that is typical of *Mantellisaurus* (Fig. 2.16). The pubic shaft forms a tapering rod that is much shorter than the shaft of the ischium. The ischium has a shaft that is elongate

and stout, with a generally rounded, rather than angular, cross section; the shaft is curved along its length (J-shaped) and ends in a prominent, anteriorly expanded “boot.” This structure is distinct from the narrower, angular-sided, and far straighter ischial shaft with a small boot that characterizes *Mantellisaurus*.

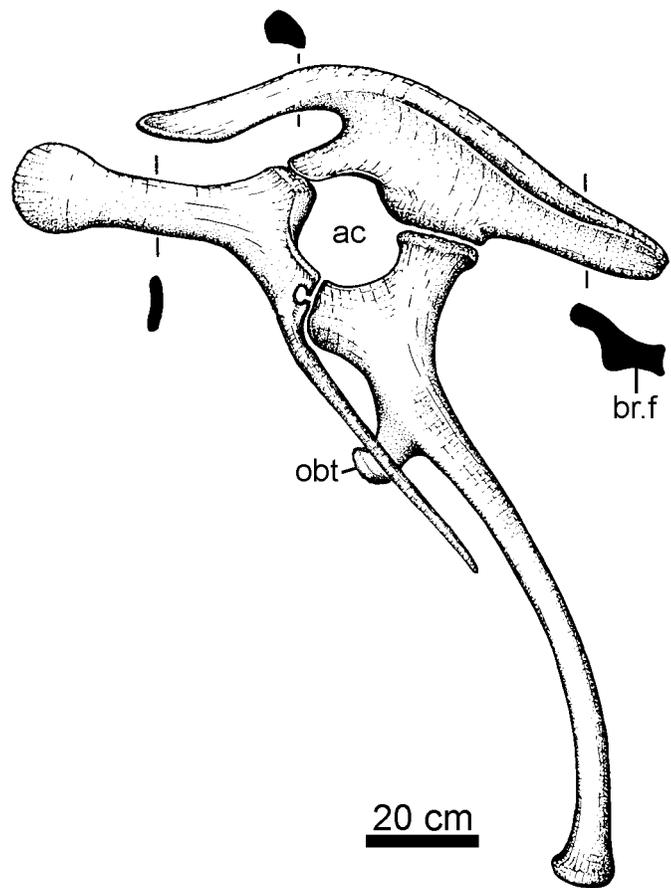
In the hindlimb the femur is large and very stout compared to that of *Mantellisaurus*; the fourth trochanter is very elongate and forms a very thick crested blade along the postero-interior edge of the mid-shaft. The shin or lower half of the limb is similar in overall shape in the two taxa, but the difference in robustness is notable; this is especially so in the massive construction of the pes. The first metatarsal of the foot in *I. bernissartensis* forms a small, oblique, flattened spatula-shaped splint bone that is distinct from the thin, pencil-like, metatarsal that lies parallel to the shaft of metatarsal II in one articulated example of *Mantellisaurus* from the Isle of Wight.

Reconstruction of Iguanodon bernissartensis

The reconstruction of *I. bernissartensis* presented here is modified from an often-published version created originally by the artist Gregory Paul (e.g., Brett-Surman, 1997; Fig. 2.23). Changes introduced are as follows: the joint between the forelimb and manus has been straightened; mammal-style scapular rotation against the ribcage has been removed (this was physically impossible judged by the anatomy of the pectoral girdle); and a lattice of ossified tendons has been added. The overall impression of an *Iguanodon* in a hurry depicted in the earlier reconstruction is potentially misleading in an animal that attained a body length of 12 m and probably weighed in excess of 5 metric tons.

SYSTEMATIC ANALYSIS

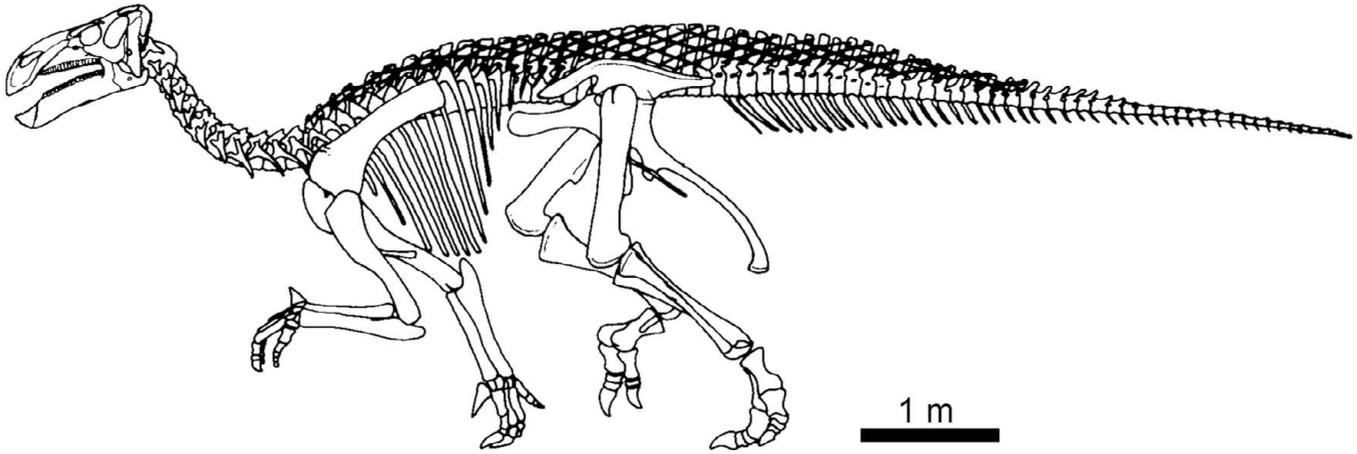
The brief anatomical survey of these Wealden taxa provides an opportunity to align them, systematically, with other reasonably well-known taxa from younger stratigraphic stages, with the intention of exploring their phylogenetic relationships generally, as well as exploring the origin of euhadrosaurids. Numerous phylogenetic hypotheses have been proposed (e.g., Norman 2002, 2004, in press; Weishampel et al., 2003; Horner et al., 2004; Prieto-Márquez, Gaete, et al., 2006; Dalla Vecchia, 2009; McDonald et al., 2010; Prieto-Márquez, 2010; McDonald, 2012b). These analyses have either directly or indirectly addressed the relationships of those animals that are proximate to the clade most commonly referred to as Hadrosauridae (= Euhadrosauria, Weishampel et al. 1993), but have resulted in little general consensus on the relationships of individual taxa.



2.22. *Iguanodon bernissartensis* Boulenger. Holotype pelvis partially restored, RBINS R51. Abbreviations: ac, acetabulum; br.f, brevis fossa; obt, obturator process. Cross-sectional views shown as solid black (after Norman, 1980).

Data and Methodological Framework

A new systematic analysis is presented here for the explicit purpose of exploring the nature of putative phylogenetic relationships between a range of more derived non-hadrosaurian ornithomorphs. Twenty-four taxa (Appendix 2.1) were selected for this analysis because they are known from generally well preserved skulls and/or skeletons, and have been reasonably well described. A significant number of additional taxa have been named in very recent years but these are, on the whole, more fragmentary, and their addition to the analyses materially affects the resolution and stability of tree topology. These have been removed a priori. More comprehensive analyses incorporating these additional taxa, as well as more basal ornithomorphs, are being considered in more detail elsewhere (Norman, in press). *Lesothosaurus* (based on the descriptions of Thulborn [1970, 1972], and the supplementary information from Sereno [1991]) is used as the outgroup taxon (Butler et al., 2008) in order to polarize character-states. The character-states and their codings are presented in Appendix 2.2, and these comprise a suite of 92 characters that have

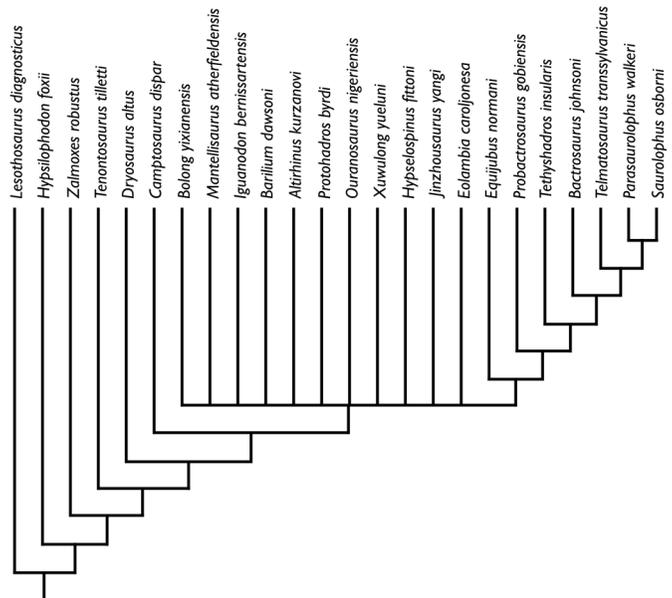


2.23. *Iguanodon bernissartensis*. Reconstruction of the skeleton, modified from an earlier original drawing by Gregory S. Paul (from Brett-Surman, 1997).

been generated after reassessment and revision of previously published character lists (e.g., Norman, 2004; McDonald et al., 2010; Prieto-Márquez, 2010; Wu and Godefroit, 2012). Unusually, compared to the general trend in the literature, the number of characters used is fewer rather than greater. The data matrix was constructed in MacClade 4.06 (Maddison and Maddison, 2003), and the analysis was undertaken using PAUP* 4.0b10 (Swofford, 2002). All characters were equally weighted, and were first analyzed as “unordered” using the Branch and Bound search option (and the analysis was run twice using ACCTRAN and DELTRAN optimizations). Because a substantial number of characters used in this analysis are multistate in nature, a second run was undertaken using the “ordered” character option. The matrix was again analysed using Branch and Bound search option and was run under both ACCTRAN and DELTRAN optimization protocols.

Results

Running the data matrix with characters unordered produced a fairly well resolved topology in the strict consensus tree. Twelve most-parsimonious trees (MPTs) were produced, each with a tree length of 262 steps (Consistency Index [CI]: 0.56, Retention Index [RI]: 0.74). The strict consensus tree based on these analyses is represented in Figure 2.24. The lack of resolution revolves around the character distributions seen in the 11 taxa that fall across the center of the cladogram. The 50% majority rule tree (Fig. 2.25, top) and Adams consensus tree (Fig. 2.25, bottom) derived from the 12 MPTs produce a measure of resolution (as expected) within this taxon plexus. A second search of the data matrix using the same protocols, but with the characters run as “ordered,” generated a well-resolved topology represented by three MPTs of 267 steps, a CI of 0.55, and a RI of 0.75. The strict consensus

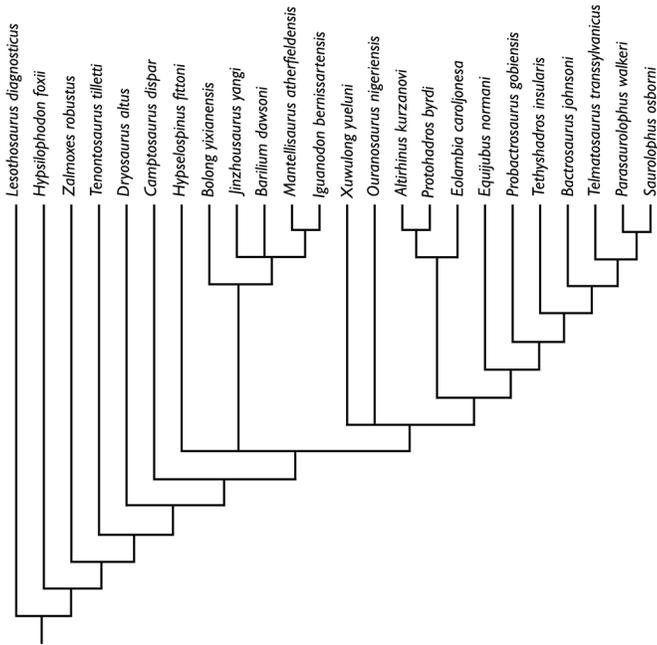


2.24. The strict consensus tree (based on 12 MPTs) generated by running the data matrix with characters unweighted and coded as unordered.

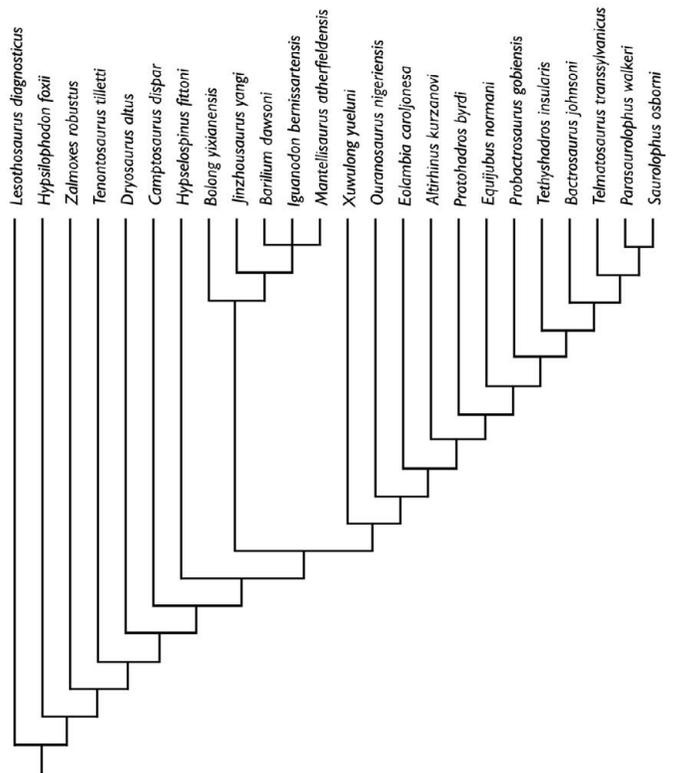
tree shown in Figure 2.26 is identical to the 50% majority rule tree (Fig. 2.25, top) generated from the first analysis. The strict consensus tree reveals an unresolved trichotomy between *Barilium*, *Iguanodon*, and *Mantellisaurus* within a clade (= Iguanodontidae) containing the additional taxa *Bolong* and *Jinzhousaurus*.

CHARACTER DISTRIBUTION AND PHYLOGENETIC IMPLICATIONS

The degree of resolution seen in the tree generated through this analysis (Fig. 2.26) provides a topology that is available



2.25. (Left) Adams consensus tree based upon 12 MPTs generated using characters coded as unordered; (right) The 50% majority rule tree resulting from analysis of the same 12 MPTs.



for morpho-phylogenetic interpretation within this taxonomic subset of the ornithopod lineage, and forms a framework that highlights the anatomical acquisitions that resulted in the attainment of true hadrosaurian morphology (represented by the clade Euhadrosauria [sensu Weishampel et al., 1993]).

Basal Ornithopod Taxa

Basal, or “hypsilophodontian-grade” ornithopods sensu lato (Norman et al., 2004; see also Butler et al., 2008), are generally small–medium sized (1–3 m long), bipedal cursors with simple leaf-shaped teeth in both upper and lower jaws; their dental morphology is similar in morphology to that described by Thulborn (1970) and is typical of all basal ornithischians. At the base of the tree, the outgroup is polarized (in this analysis, crudely) against what appear to be more derived taxa in the absence of a consideration of the substantially greater diversity of hypsilophodontian-grade ornithopods (see Butler et al., 2008).

Clypeodonta clade nov.

Phylogenetic Definition The stem-based definition of Clypeodonta (“shield-teeth”) is *Parasaurolophus walkeri* and all taxa positioned more closely to *P. walkeri* than to *Thescelosaurus neglectus*. However, the topology of more

basal stem taxa falls outside the scope of this account, and Clypeodonta in this analysis occurs at the node that includes *Hypsilophodon foxii*, *Parasaurolophus walkeri*, their common ancestor, and all of its descendants.

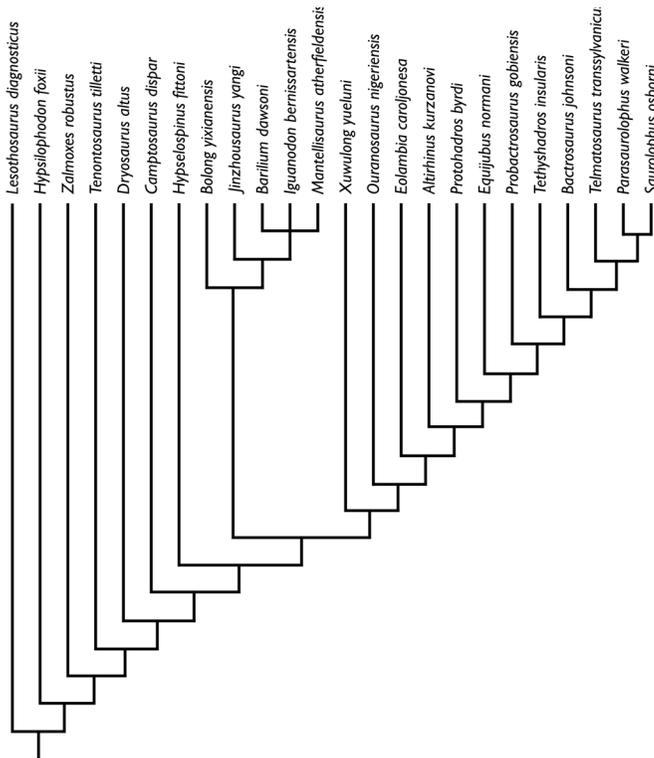
Character Acquisition at This Node

ACCTRAN: 19, 20, 45, 47, 50, 52, 53, 54, 55, 56, 59, 60, 65, 79, 80, 85.

DELTRAN: 20, 45, 47, 50, 52, 53, 54, 55, 56, 59, 60, 79, 80.

Condensed Diagnosis

1. Dentary crowns laterally compressed, asymmetrical, and shield shaped in lingual aspect only. The lingual surface of the crown is demarcated from the root by an oblique cingulum.
2. Dentary teeth are curved apicobasally along their length and describe an arc (a convexity lingually) as they emerge from the alveolus during growth.
3. Crowns of dentary and maxillary teeth display an asymmetrical distribution of enamel (dentary crowns have thicker enamel lingually, and maxillary crowns have thicker enamel labially).
4. Dentary crowns bear a prominent primary ridge on the lingual surface that is flanked by a variable number of less prominent subsidiary (accessory, or tertiary) ridges.



2.26. The strict consensus tree (based upon three MPTs) generated by running the data matrix with characters unweighted and coded as ordered.

5. Maxillary crowns are transversely compressed, asymmetrical and shield shaped, but their thickly enameled labial surface bears a variable number of subsidiary ridges, and a prominent primary ridge is not present.

Comments Clypeodontans (and more basal ornithopods)—*Hypsilophodon*, rhabdodontids (*Zalmoxes* spp., *Rhabdodon*, *Mochlodon*), and tenontosaurus—are skeletally conservative. However, the specialized modifications seen in clypeodontan teeth exclude a substantial diversity of basal ornithopod taxa—including *Jeholosaurus*, *Othnielia*, *Gasparinisaura*, *Orodromeus*, *Parksosaurus*, *Thescelosaurus*, and *Bu-genasaura* (Butler et al., 2008). Tenontosaurus exhibit larger size and some graviportal adaptations that converge upon those seen in more derived taxa such as *Camptosaurus*, but the latter taxon and more derived forms exhibit a fundamentally different dental morphology.

Clypeodontan dentary crowns are laterally compressed, are inclined labially, and have denticulate margins; the crowns sit upon curved roots and, as a consequence, the teeth move along a lingual-to-labial arc as they emerge from the dental alveolus, instead of rising vertically from the alveolus as is the case in basal ornithopods, and basal ornithischians

more generally. When viewed lingually, dentary crowns are broad and exhibit a clearly defined (“shield-like” surface), and are more thickly enameled than on their labial surfaces (Norman et al., 2004:fig. 18.3). The lingual crown surface exhibits incomplete, oblique ledges (sometimes referred to as a “cingulum”) that define a V-shaped junction between crown and root. The enameled crown surface bears a prominent primary ridge flanked by a variable number of much less prominent subsidiary ridges. Maxillary teeth are also transversely compressed, but it is the labial surface of the crown that is more thickly enameled and traversed (apicobasally) by a variable number of low ridges; a primary ridge is not present. The roots of maxillary teeth do not appear to display the lengthwise curvature seen in dentary teeth.

It may also be noted that the singular combination of a prominent primary ridge on the dentary crown and no primary ridge on the maxillary crown may contribute to character combinations that define a more restrictively defined clypeodontan clade—which includes *Rhabdodon*, *Zalmoxes* spp., *Mochlodon*, and *Tenontosaurus* spp.—and that this clade represents a sister clade to the Dryomorpha. In addition, the unusually specialized basal ornithischians known as heterodontosaurids (Butler et al., 2008) and most notably *Heterodontosaurus tucki* (Norman et al., 2011) homoplasticly exhibit specialized, superficially shield-like dentary and maxillary tooth crown morphologies, with asymmetrical enamel distribution and prominent enamel ridges. However, these teeth are straight rooted, and the detailed structure of these teeth is quite distinct from that described in clypeodontans. Conventional usage of the name Iguanodontia (sensu Sereno, 1986, 2005) is becoming increasingly problematic because it recognizes a clade that includes *Tenontosaurus tilletti* and all taxa positioned closer to hadrosaurs (e.g., *Parasaurolophus walkeri*) and yet excludes *Hypsilophodon* and *Thescelosaurus*. The conventional node Iguanodontia (sensu Sereno, 2005) occurs immediately above the node here named Clypeodonta (see also discussion in Norman, in press).

Dryomorpha

Phylogenetic Definition This node-based clade is defined as *Parasaurolophus walkeri*, *Dryosaurus altus*, their common ancestor, and all of its descendants.

Character Acquisition at This Node

ACCTRAN: 4, 20, 53, 54, 58, 59, 61, 65, 68, 81, 85, 89, 91.

DELTRAN: 12, 20, 33, 53, 54, 58, 59, 82, 83, 85.

1. Maxillary tooth crowns are apicobasally elongate and characterized by the possession of a narrow, elevated primary ridge on the labial surface of the crown that is positioned slightly distal to the midline.
2. Dentary tooth crowns exhibit a clearly defined, but low, primary ridge that is offset distally to the midline.
3. In lingual view a shoulder-like edge is formed between the denticle that marks the tip of the primary ridge and the point of inflection that marks the start of the subvertical mesial margin of the crown.
4. The quadrate bears a well-defined semicircular notch on the central portion of the anterior margin of the jugal wing that is spanned anteriorly by the quadratojugal. With the quadratojugal in articulation a fully enclosed quadrate (paraquadratic) foramen is formed.
5. Prementary with divergent, ventrolateral processes.
6. The obturator process of the ischium is positioned proximally (separated by an embayment from the pubic peduncle of the ischium) on the anteromedial edge of the shaft of the ischium.
7. The ischial shaft has a subcircular cross section along almost its entire length and there is a small anterior expansion of the distal tip of the ischial shaft that forms a “boot.”
8. The femoral shaft displays an anterior intercondylar groove that is defined by a pair of ridges that form on the adjacent edges of the dorsal part of the distal articular condyles.

Comments There is a marked contrast between the style of morphological differentiation of the dentition in basal clypeodontans and that in dryomorphans, which suggests that a new morpho-functional trajectory (probably linked to oral food processing) had emerged. Additional characters, such as the development of a bilobate posteroventral processes on the prementary, probably served to reinforce a structurally weak dentary symphysis and may reflect alterations to jaw function. A ventrally bilobate prementary also appears sporadically in basal clypeodonts (rhabdodontids), but this is interpreted as an example of convergence (homoplasy) in the larger-bodied tenontosaurus and the very late appearing (Maastrichtian) rhabdodontids. The ischial characters (such as the positioning of the obturator process and curvature of the ischial shaft) also appear sporadically and probably convergently in Maastrichtian rhabdodontids.

Phylogenetic Definition This node-based clade (Fig. 2.26) can be defined as *Parasaurolophus walkeri*, *Camptosaurus dispar*, their common ancestor, and all of its descendants.

Character Acquisition at This Node

ACCTRAN: 2, 15, 46, 51, 57, 69, 72.

DELTRAN: 2, 4, 15, 30, 45, 51, 57, 64, 68, 69, 72.

Condensed Diagnosis

1. Conical pollex unguis.
2. Short, block-shaped metacarpal I is sutured at an oblique angle against the radiale and carpal 2.
3. Carpo-metacarpal block formed by suturing of the individual elements.
4. Manus digit IV bears an unguis phalanx that is small and shows no obvious grooves for attachment and growth of a claw or hoof.
5. Occlusal plane of the premaxilla and prementary deflected ventrally.
6. Ventral margin of the jugal is arched and forms a prominently angled projection posteriorly.
7. Acromion process of the scapula curved anteriorly at its proximal end.

Comment It is unfortunate that the structure of the carpus and manus is presently unknown among dryosaurs, since this might have a significant bearing on the status of the ankylopollexian clade.

Neoiguanodontia (“New Iguanodonts”)

Phylogenetic Definition The node-based clade can be defined as *Parasaurolophus walkeri*, *Hypselospinus fittoni*, their common ancestor, and all of its descendants.

Character Acquisition at This Node

ACCTRAN: 9, 13, 27, 34, 40, 48, 61, 62, 66, 67, 70, 73, 80, 81, 87, 88, 89, 90, 92.

DELTRAN: 40, 48, 62, 66, 67, 70, 73, 80, 81, 87, 88, 89, 90, 92.

Condensed Diagnosis

1. The marginal denticles on the mesial and distal margins of maxillary and dentary tooth crowns form curved ledges that are ornamented with mammillae/papillae.

2. The posterodistal corner of dentary crowns, when viewed lingually, exhibit inrolling of the marginal denticulate edge to form an oblique ledge-like structure (sometimes referred to as a cingulum).
3. Posterior dentary dentition extends medial to the coronoid process, and from which the dentition is separated by a narrow, horizontal ledge that represents a posterior extension of the lateral cheek recess.
4. Coronoid process elevated and its axis lies perpendicular to the long axis of the dentary ramus.
5. Antorbital fenestra (and fossa) reduced in size and forms an oblique channel between the maxilla and lacrimal.
6. The articulation between the jugal and maxilla comprises an oblique, finger-like posterolateral projection from the maxilla that fits into a complementary elongate slot on the anteroventral surface of the jugal.
7. The supraoccipital is excluded from the posterodorsal margin of the foramen magnum by a shelf-like structure formed by dorsomedial processes of the exoccipitals that meet in the midline.
8. Sternal bones develop an oblique, posterolateral, rod-like extension that ends in an articular boss.
9. Metacarpals II–IV of the manus are elongate, bundled together and held in place by development of collateral ligaments that are sometimes ossified.
10. Manus unguals II and III are dorsoventrally flattened, asymmetrical and generally hoof-like.
11. Posterior pubic ramus is slender and significantly shorter than the shaft of the ischium (this character is homoplastic in rhabdodontids and tenontosaurids).
12. Pedal ungual phalanges are dorsoventrally flattened and bluntly truncated distally, but retain well-developed claw grooves bilaterally.

Comments The position of *Hypselospinus* with respect to the sister clade comprising *Bolong*, *Jinzhousaurus*, *Barilium*, *Iguanodon*, and *Mantellisaurus* (= Iguanodontidae) and Hadrosauriidea needs to be more accurately determined (Norman, in press). It is also clear, following the systematic review above that the anatomies of the contemporary taxa *Bolong* and *Jinzhousaurus* are very similar. A range (plexus, as in Figure 2.24) of neoiguanodontian taxa forms a cluster between *Hypselospinus* and Hadrosauromorpha. These taxa have proved difficult to arrange consistently in any published phylogeny, and this may well reflect anatomical incompleteness and/or a phase of comparatively rapid evolution (and

possibly disparate character acquisition) among and between ornithopods during the early Late Cretaceous.

Hadrosauromorpha clade nov.

Phylogenetic Definition This stem-based clade is defined as *Parasaurolophus walkeri* and all taxa positioned more closely to *P. walkeri* than to *Probactrosaurus gobiensis*.

Character Acquisition between *Probactrosaurus* and the Succeeding Node

ACCTTRAN: 1, 4, 16, 20, 41, 43, 48, 54, 55, 56, 60, 68, 69, 71, 72, 77, 78, 87, 88.

DELTRAN: 1, 9, 10, 19, 20, 41, 43, 48, 54, 55, 68, 69, 71, 72, 77, 87.

Condensed Diagnosis

1. Dentary dentition with small, diamond-shaped crowns integrated into a closely packed dental magazine.
2. Dentary and maxillary crowns bear a single median primary ridge (carina) on their labial or lingual surfaces, respectively.
3. Surangular foramen absent.
4. A shallow embayment in the jugal wing of the quadrate to accommodate a disc-shaped quadratojugal that completely occludes the quadrate (paraquadratic) foramen.
5. Modification of the acromion process to form a pendant promontory orientated along the long-axis of the scapular blade.
6. Carpus represented by no more than two small discoidal elements.
7. Phalanges of digit I of the manus absent.
8. Metacarpal I absent.
9. Ilium has a region of the dorsal margin, posterodorsal to the ischiadic peduncle, that forms a discrete everted lip (pendule, see below) that overhangs the ischiadic peduncle of the ilium.
10. Postacetabular ramus of the ilium forms a laterally flattened bar-like structure.
11. Pedal ungual phalanges are strongly dorsoventrally compressed, short proximodistally, and very broad with a rounded anterior margin; distinct claw grooves on the lateral margins are absent, and are therefore truly hoof-shaped when compared to those seen in more basal taxa.

Note here that the term “pendule” is suggested for the everted and downturned tongue-shaped structure that projects lateroventrally from the dorsal margin of the ilium. This word is proposed for two reasons. First, it obviates the need for repeated complex descriptive phraseology to describe the feature. Second, this structure has been mistakenly referred to as an “antitrochanter” (e.g., Lull and Wright, 1942). The true antitrochanter is an articular facet located on the posterior margin of the acetabulum and is not topographically similar or anatomically homologous to the development of the dorsal margin of the ilium. Similarly, the term “supra-acetabular crest” has been proposed more recently for this structure (Prieto-Márquez, 2011); unfortunately this latter usage creates a homonym with the anatomically distinct supra-acetabular crest (a specialized feature derived from the supra-acetabular buttress of tetrapods [as per Romer, 1956]) that forms a prominent ridge located on the acetabular margin of the ilium in derived archosaurs (e.g., Charig, 1972).

Comments The sister taxon to this clade, *Probactrosaurus gobiensis*, displays important anatomical differences that distinguish this and all non-hadrosauromorphan taxa from hadrosauromorphans: dentary crowns are comparatively small, and almost diamond-shaped, but they retain an asymmetrical aspect when viewed lingually, and bear accessory ridges running parallel to the distally offset primary ridge. In addition, a surangular foramen is present, and the quadrate has a semicircular embayment in the jugal wing rather than the shallow embayment seen in *Tethyshadros* (Dalla Vecchia, 2009) and more derived hadrosauromorphans. The acromion process of the scapula curves forward (rather than forming an overhanging promontory-like structure that lies parallel to the main axis of the scapular blade as in hadrosauromorphans).

In the forelimb, the radius, ulna, and metacarpals are elongate and slender in *Probactrosaurus* and hadrosauromorphans, which is suggestive of a general trend toward gracility in this part of the skeleton. However, *Probactrosaurus* retains a small, spike-like pollex, which implies the presence of an at least partially competent and ossified carpus (Norman, 2002). The ilium of *Probactrosaurus* has a modestly everted dorsal margin (Norman, 2002), but there is no evidence of either strong eversion or development of a tongue-shaped pendule, as described in *Tethyshadros*. The unguals of the pes of *Probactrosaurus* are comparatively elongate and truncated at their tips (Norman, 2002).

Bactrosaurus and *Telmatosaurus* retain a consistent topology in many different analyses (Prieto-Márquez, 2010, 2011; Wang et al., 2010; McDonald, 2012b; Wu and Godefroit, 2012), as, respectively, successive outgroup taxa to the well-established node-based clade (Euhadrosauria) represented in this analysis by the sister taxa *Parasaurolophus* and *Saurolophus*.

By tradition, these latter taxa are placed within the clade Hadrosauridae. The clade Euhadrosauria was originally proposed by Weishampel et al. (1993) and was diagnosed at that time on the basis of five unambiguous and two ambiguous synapomorphies. This node-based clade may be defined using phylogenetic nomenclature protocol as *Saurolophus* and *Parasaurolophus*, their most common ancestor, and all of its descendants.

Abbreviated Diagnosis

1. Loss of all but the primary ridge on dentary and maxillary tooth crowns.
2. Ilium with its posterodorsal margin everted and ventrally deflected forming a pendule positioned dorsal to the posteroventral margin of the lateral expansion of the ischiadic peduncle.
3. Pendule on the ilium anteroposteriorly shorter than deep.
4. No lateral expansion of the ischiadic peduncle, so that this area is flush with the lateral wall of the ilium.
5. See Prieto-Márquez (2010:457–461) for an extended consideration of the character states that may be used to diagnose Hadrosauridae (= Euhadrosauria, this account).

Comments Prieto-Márquez (2010:456) argued that the clade Euhadrosauria was not “defined” (the implication being that it lacked a phylogenetic definition, although it should be recognized that such definitions did not come into practice until later than 1993) and he thus considered it to be ambiguous; he also objected to its usage because he claimed that it violated recommendations in the ICZN (1999) concerning the naming of “family group” taxa by not having as its root the name of a nominal taxon. Invoking the ICZN “family group” concept to derived iguanodontians implies a degree of stability of taxon relationships that is not consistent with the type of accumulative science practiced by paleontologists. The recent history of systematic evaluations of hadrosaurians and their near relatives typifies this problem. Consistency is not the general rule, even though it is an obvious aspiration (cf., Horner, 1985, 1990, 1992; Sereno, 1986, 1998; Weishampel and Horner, 1990; Weishampel et al., 1993; Head, 1998; Norman, 2002, 2004; Horner et al., 2004; Prieto-Márquez, Weishampel, and Horner, 2006; Gates and Sampson, 2007; Evans and Reisz, 2007; Godefroit et al., 2008; Dalla Vecchia, 2009;

Evans, 2010; Prieto-Márquez, 2010, 2011; Wang et al., 2010; McDonald, 2012b; Wu and Godefroit, 2012).

Prieto-Márquez's suggestion that the stem of the family group name (Euhadrosauria) does not derive from the nominal taxon name *Hadrosaurus*, is at best specious: the origin of the name is self-evident and the use of the prefix serves a specific role by polarizing the nomenclature in order to reflect one aspect of tree topology. It can also be observed that a logical extension of Prieto-Márquez's concerns about the validity of the family group name Hadrosauridae is that the nominal taxon Hadrosauridae is based upon a taxon that has in the past been considered a nomen dubium (Prieto-Márquez, Weishampel, and Horner, 2006), whose position within any topology is probabilistic (Prieto-Márquez, 2010), and could be considered *sedes mutabilis*—especially considering the fragmentary and incomplete nature of its remains.

More recently Prieto-Márquez (2011) has contradicted previous work by proposing that *Hadrosaurus foulkii* is indeed a valid taxon, which he assigns (on its own) to the subfamily Hadrosaurinae (as in Prieto-Márquez, 2010). In addition he now defines the node-based clade Hadrosauridae as “the clade stemming from the the most recent common ancestor of *Hadrosaurus foulkii* and *Parasaurolophus walkeri*” (Prieto-Márquez, 2011:67). His clade Saurolophidae (= Euhadrosauria in this account) is given a node-based definition: “the last common ancestor of *Saurolophus osborni*, *Lambeosaurus lambei*, and all its descendants” (Prieto-Márquez, 2011:67; it is not made explicit why he has abandoned the use of *Parasaurolophus* in favour of *Lambeosaurus* as one specifier in this instance) and he concludes with the proposition that this latter clade (Saurolophidae = Euhadrosauria in this account) includes “the two major hadrosaurid clades: Saurolophinae and Lambeosaurinae” (Prieto-Márquez, 2011:67). Phylogenetic definition of the taxonomic scheme proposed by Weishampel et al. (1993) with respect to Hadrosauridae (the least inclusive, node-based clade containing *Telmatosaurus transsylvanicus* and *Parasaurolophus walkeri*) and Euhadrosauria (see above) solves a number of problems put forward by Prieto-Márquez (2011), and necessitates only adopting Saurolophinae for the clade traditionally recognized as Hadrosaurinae. However, if future phylogenetic analyses recover *Hadrosaurus foulkii* as a member of this clade, Hadrosaurinae would have precedence.

A DISCUSSION: THE ORIGIN OF HADROSAURS

The topology generated by this analysis provides an interpretative framework for exploring the morphological transition from derived neoiguanodontian ornithopod to

euhadrosaurian and can be compared directly to those that have been produced more recently.

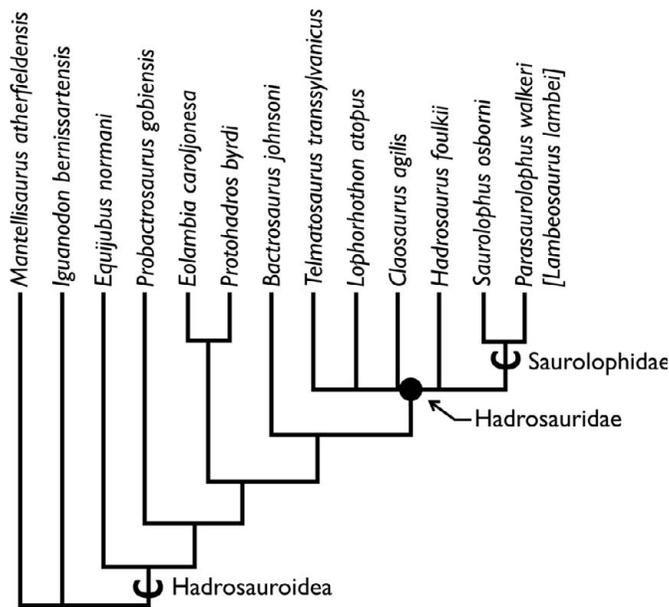
Topological Variation

Prieto-Márquez (2010) offered a detailed analysis of the systematics of hadrosaurians and included a consideration of a few of the more basal forms considered herein (Fig. 2.27). The stem-based clade Hadrosauroidae was redefined as comprising *Hadrosaurus foulkii* and all taxa more closely related to it than to *Iguanodon bernissartensis*, including Hadrosaurinae (represented solely by *H. foulkii*) and Saurolophidae (Prieto-Márquez, 2011:67). *Equijubus* and *Probactrosaurus* occupy significantly more basal positions in this topology than in the resolved tree generated by the latest analyses (compare Figs. 2.26 and 2.30). However, the relative positions of *Eolambia*, *Protohadros*, and *Bactrosaurus* are topologically more consistent.

McDonald (2012b) produced an alternative tree depicting ornithopod relationships (Fig. 2.28), which incorporated a greater proportion of the taxa considered herein and is therefore more truly comparable to the one generated in this account (Figs. 2.26, 2.30). The topology shows substantial similarity to that which has been proposed in this account. Basal taxa appear with the same topology as seen in Figure 2.30, and all the topological variation is to be found within a range of what might be termed “intermediate” taxa leading to *Tethyshadros* (in this particular instance *Altirhinus*, *Equijubus*, *Xuwulong*, *Eolambia*, *Probactrosaurus*, and *Protohadros*). Above *Tethyshadros*, the topology of the two trees is again identical. The node-group names follow conventional usage and amplify those outlined by Prieto-Márquez (2010, 2011). It should also be noted that Hadrosauroidae has a different composition to that suggested by Prieto-Márquez (compare Fig. 2.27).

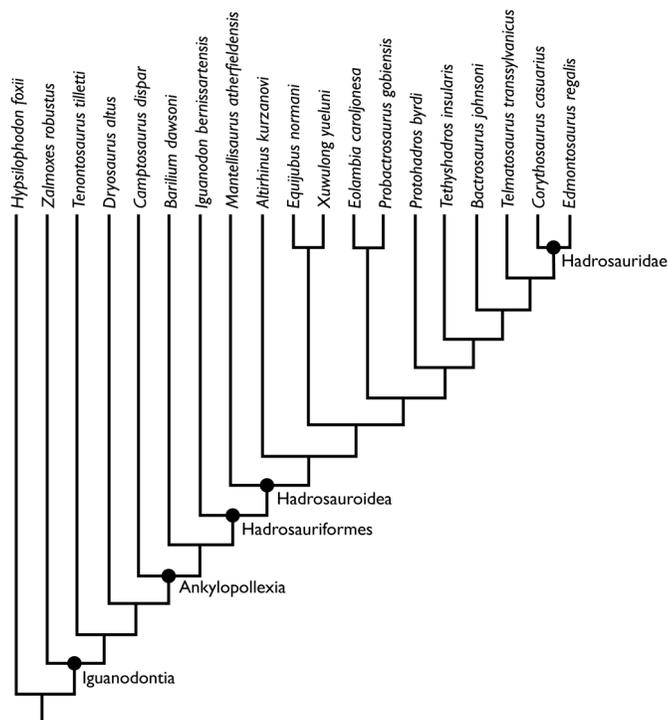
Wu and Godefroit (2012) provided another analysis that is pertinent to this review (Fig. 2.29). Basal relationships are consistent with those shown in Figure 2.26. *Iguanodon* and *Mantellisaurus* plus *Ouranosaurus* are recognized as a clade (Iguanodontidae), although this node is weakly supported. More derived taxa show differences in relative position, the most notable of which is the comparatively basal positions of *Equijubus* and *Probactrosaurus*. Clade names were placed at nodes, and it is notable that Hadrosauridae incorporates *Bactrosaurus* as well as *Tethyshadros*, *Telmatosaurus*, and Euhadrosauria, and that the latter conforms to the concept of this clade created by Weishampel et al. (1993).

The latest contribution to this on-going debate focused on hadrosaur origins is presented in summary form in Figure 2.30. Although this topology was resolved from three MPTs, the topology is not entirely unambiguous. The clade



2.27. Cladogram generated by the analysis of Prieto-Márquez (2010, 2011). Modified in order to present the topology that reflects (with a few exceptions) the taxa considered in this account. Clade names and positions indicated as in the original version.

Clypeodonta is recognized in order to differentiate those ornithopods that specialize their teeth in order to create an integrated dentition of distinctively shield-shaped teeth, from those that retain a simpler set of non-imbricating, straight, leaf-shaped teeth that do not develop interdentally continuous wear surfaces. Basal clypeodonts (hypsilophodonts, rhabdodonts, and tenontosaurus) have a distinct set of tooth morphologies that may eventually prove to unite them into a sister clade to more derived dryomorphans, although that is not recovered here. The node-based clade Neoiguanodontia recognizes a range of taxa that demonstrate the acquisition of the definitive *Iguanodon*-like tooth morphology (notably mammillate denticles along mesial and distal crown margins; dentary crowns with a shouldered crown edge, inrolled enameled ledges, and crown subdivision by primary and secondary ridges) as well as a subsidiary set of postcranial features. Five taxa (*Bolong*, *Jinzhousaurus*, *Barilium*, *Iguanodon*, and *Mantellisaurus*) form a relatively poorly supported clade (= Iguanodontidae), but this is not formally defined at this stage. Succeeding taxa demonstrate the gradual acquisition of hadrosaur-like anatomical features, and this inconsistency reflects the wide geographic spread of these taxa and the difficulties inherent in trying to resolve phylogenetic relationships among groups of taxa that were evidently evolving relatively rapidly during the early Late Cretaceous. This evolutionary “plexus” (see Fig. 2.24) is succeeded by more derived taxa such as *Probactrosaurus* that exhibit a number of hadrosaur-like characteristics. Here,

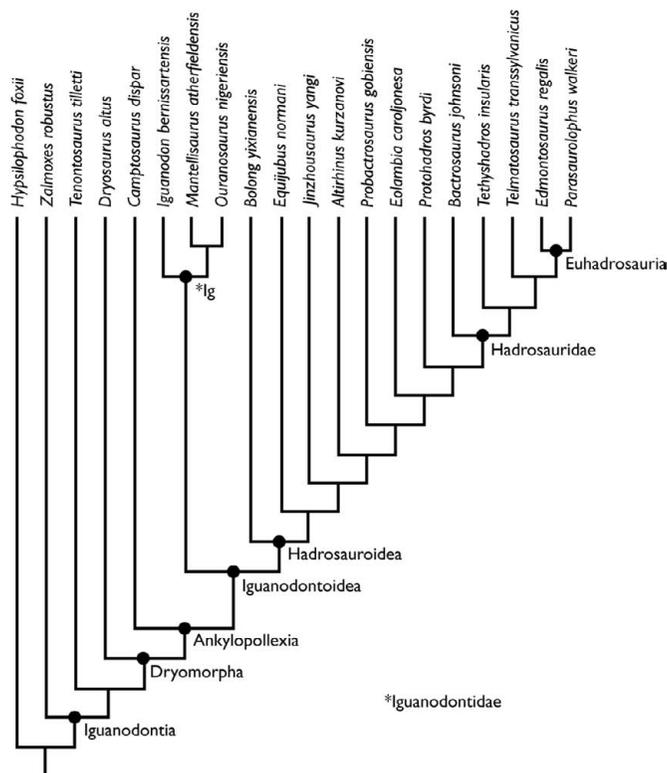


2.28. Cladogram generated by the analysis of McDonald (2012b). Modified in order to present the topology that reflects the taxa considered in this account. Clade names and positions indicated as in the original version.

the term Hadrosauromorpha encompasses taxa that are more derived than the pollex-spike-bearing *Probactrosaurus*. Hadrosauromorpha comprise *Tethyshadros*, *Bactrosaurus*, and *Telmatosaurus*, as well as the potential non-euhadrosaurians (non-saurolophids sensu Prieto-Márquez, 2010, 2011) such as *Hadrosaurus foulkii*, *Claosaurus agilis*, and *Lophorhothon atopus*.

An Evolutionary Narrative of Hadrosaur Origins

Clypeodonta Clypeodontans exhibit a unique combination of features involved in the differentiation of the dentary and maxillary dentitions (partially integrated opposing occlusal surfaces and the creation of incipient dental magazines of smaller teeth). Dryomorphans link these dental modifications with others that stabilize the anterior end of the lower jaw (the ventrally bilobed prementary). The restructuring of the pelvis, notably through the development of a structurally dominant, J-shaped ischium (functionally replacing the elongate, but slender, posterior pubic ramus) suggests the need to support a more massive and by implication more complex gut, which reflects the increasing dietary sophistication implied from the structure of the jaws and teeth. Furthermore, the specialization of the knee joint, through the development of a defined anterior intercondylar groove, may



2.29. Cladogram generated by the analysis of Wu and Godefroit (2012). Modified in order to present the topology that reflects the taxa considered in this account. Clade names and positions indicated as in the original version.

be correlated with increasing strength of the joint (to cope with the more massive gut) and at the same time maintaining or even improving joint mechanics and locomotor ability.

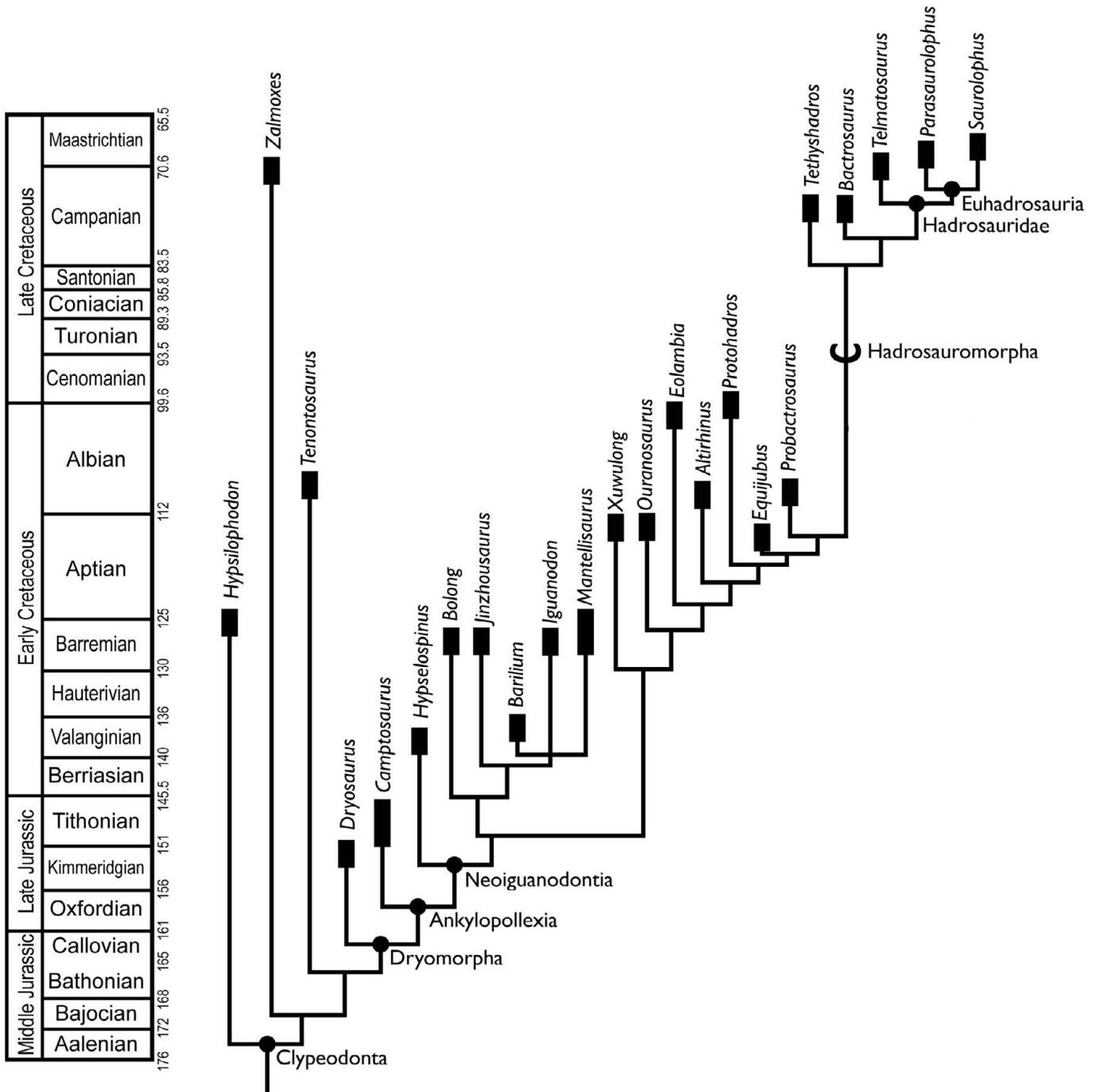
Neoiguanodontia Neoiguanodontians are notable for the development of larger and longer (jaw-dominated) skulls with larger and increasingly structurally sophisticated teeth. Teeth form incipient dental magazines that show increasing signs of integration into mutually supportive arrangements, creating the equivalent of single functional megatooth in each jaw. The leverage exerted by the jaw muscles is augmented by the development of a tall, perpendicular coronoid process, and there are a number of lineages that appear to experiment with the functional separation and specialization of food gathering (the premaxillary and predentary beak) and food processing (cheek teeth) through the development of a diastema. It is very notable that some of the more derived taxa tend to develop a broader, down-turned snout (*Altirhinus*, *Protohadros*, *Probactrosaurus*), which anticipates a feature seen among euhadrosaurids and suggests that these animals were functionally modifying their food gathering abilities. Whether this trend can be linked to vegetational changes is uncertain at present. The skeletons of neoiguanodontians are generally large (6–12 m in body length), their guts are clearly very large and heavy, and their limbs become

increasingly stout and graviportally adapted. Linked to the generally pedestrian build of their bodies, these forms develop a specialized spike-like pollex that is anchored to an enlarged and fused, or partially fused, set of carpometacarpals. These anatomical features correlate with stoutly constructed pectoral and forelimb skeletons that were evidently adapted for weight support and locomotion. The pollex may have had multiple functions, but as a potential stilleto-like weapon of defense, wielded at close quarters, this may well have proved advantageous in animals that lacked obvious cursorial abilities.

Hadrosauromorpha Rather unexpectedly, the taxa that form successional sister taxa to the clade Euhadrosauria exhibit relatively conservative anatomies, insofar as their skulls are concerned. Within their jaws, the fully integrated and interdental cemented dentary magazine (megatooth) with interlocked, diamond-shaped dentary teeth and multiple successional crowns is firmly established. The coronoid process is both tall and expanded apically, suggesting that both the volume of musculature that can be recruited to jaw closure and its lever-arm mechanics have been augmented. The dental magazine also begins to migrate distally along the jaw, medial to the coronoid process. Counterintuitively, given the recognition (above) of a diffuse trend focusing upon elaboration of the shape and proportions of the lower jaw in derived neoiguanodontians, there is little evidence for elongation, deepening, or curvature of the dentary. The diastema is comparatively abbreviated and the specialized functional separation between the cropping (beak) and food processing (dental battery) regions in the jaw that had become apparent in (for example) *Mantellisaurus*, *Ouranosaurus*, *Altirhinus*, and *Protohadros* is far less evident.

The most derived non-hadrosauromorphan neoiguanodontian in this analysis (*Probactrosaurus*) exhibits the onset of a trend that culminates in the loss of both the substantial carpometacarpus and manus digit I (the latter taxon being still characterized by its offset, small conical pollex unguis). As a functionally linked consequence, hadrosauromorphans show a reduction in robustness of the antibrachium and manus, which had previously been associated with the specialized locomotor and weight-supporting structures, consistently seen in more basally positioned neoiguanodontians.

No hadrosauromorphan exhibits a pollex spine or the heavily co-ossified carpus (even though modest-sized hoof-like unguals are present on digits II and III of the manus), and the forelimb and manus when considered as a whole present comparatively gracile proportions combining a short, sinuous humerus with elongation and slenderness in the more distal elements (antibrachium and metacarpals). The pectoral girdle shows a reduction in the size of the coracoid and modification to the structure of the scapular



2.30. Summary cladogram calibrated against the geological timescale (Ma ages listed along right side of timescale). New clade names discussed in the text.

acromion that appears to correlate with the gracility of the forelimb. The pelvis is modified primarily by the elaboration of the dorsal margin of the ilium to create a discrete pendule and a postacetabular process that is bar-like and laterally compressed. Since the dorsal margin of the ilium and the brevis shelf of the postacetabular process are areas for the origin of significant hindlimb musculature (Norman, 1986; Maidment et al., this volume), these anatomical changes

are suggestive of changes in hindlimb functionality. The hindlimb is characterized by a columnar (straight) femoral shaft, a globular femoral head (which lacks the femoral head notch seen in more basal forms), and a completely enclosed (tunnel-like) anterior intercondylar groove. The pedal unguals become short and remarkably hoof shaped, rather than elongate with truncated tips and claw grooves as seen in more basally positioned neoiguanodontians.

Euhadrosaurians Derived hadrosauromorphans (euhadrosaurians) represent a culmination of the general trends seen through more primitive neoiguanodontians and hadrosauromorphans. The elongation of upper and lower jaws creates a prominent diastema and an undoubted functional separation between the cropping and food processing components of jaw action. Linked to this functional differentiation, the muzzle/beak (and its ensheathing rhamphotheca) can be seen to become increasingly diverse in morphology (ranging from a droop-tipped and comparatively narrow morphology common among lambeosaurines to extreme transverse expansions bordered by upturned margins seen in some hadrosaurines/saurolophines). These variations in muzzle form are suggestive of ecological separation (niche partitioning) with respect to feeding guilds within euhadrosaurians (Carrano et al., 1999). The dental magazines are highly integrated and migrate distally (posteriorly) along the jaw so that they come to lie partly behind the elevated and anteriorly curved coronoid process; the effect of these changes is to increase the lever-arm mechanics (and hence efficiency) of the jaw muscles by promoting the development of a “bent first-order lever” from the traditional diapsid low-efficiency third-order lever mechanics that are associated with most non-mammalian vertebrate jaws. In addition to the jaw anatomy changes, the architecture of the roof of the skull becomes modified in a variety of ways: the temporal region becomes robust in order to withstand the stresses imposed upon the skull roof by the large and complex jaw adductors, and modifications of the nasal vestibule and dorsally projecting crests have been linked to a variety of biological functions. These include olfaction, sound production, and visual recognition (Ostrom, 1961; Hopson, 1975; Weishampel, 1981) that are suggestive of increasingly complex social interactions between euhadrosaurians. The postcranial skeleton differs little from that seen in hadrosauromorphans, except that the sacrum incorporates many more sacra and produces an extremely strong region to support the stresses generated through weight-support using the hind limbs almost exclusively. It is also worth noting that some euhadrosaurians are the largest of all ornithomorphs (15+ m long) and yet retained a facultatively bipedal locomotor strategy. As noted above, the forelimbs are comparatively slender and distally elongate, but the unguals of digits II and III are hoof shaped. It is presumed their forelimbs were used for support while feeding upon low browse or when moving slowly and cautiously when feeding or moving in, for example, crowded colonial nesting sites, or indulging in nest building and related activities. So it appears that the mechanical efficiency of their hindlimb support and locomotor

system was considerable. In contrast it is the case that among more basal neoiguanodontians an upper size range (~11 m long) is accompanied by a consistent tendency to become specialized by becoming secondarily obligate quadrupeds (Norman, 1980).

The evidence based upon times of occurrence in the fossil record (Prieto-Márquez, 2010:fig. 10) suggests that the pattern of diversification of euhadrosaurians displays a significant lag phase during the Coniacian–Santonian before a log-phase diversification in the Campanian and an equilibration during the Maastrichtian. Whether this pattern is an artifact of preservation in the fossil record, or represents some element of “bottle-necking” associated with the process of assembly of euhadrosaurian anatomy (and implicit biology), cannot yet be resolved satisfactorily.

ACKNOWLEDGMENTS AND DEDICATION

I would like to thank a very old friend, Dave Eberth, for inviting me to attend this symposium. Circumstances dictated that his co-organizer and co-editor, David Evans, had the unenviable task of presenting my talk because a family bereavement prevented me from attending the meeting. I am also indebted to David Weishampel for savagely criticizing another draft manuscript that is of relevance to this contribution (and hence thank him for indirectly contributing to this article). David Evans and Paul Barrett, my formal reviewers, were unstinting in their critical commentaries and made a number of valuable observations and cogent points that helped to turn a far too rapidly produced first draft into a better-structured, and more cogent, revised version. None of the above can take any blame for the remaining errors; the latter will, perforce, fall upon my shoulders.

This chapter is, of course, dedicated to a dear friend whom I first met when he visited me in London and Oxford University in the early 1980s (our having corresponded for some time before over matters relating to ornithomorph jaw mechanisms and their implications). Suffice it to say we saw eye to eye rather than tooth to claw pretty much immediately and became firm friends (we are, after all, both named David Bruce and were born in the same year); and, despite a few ups and downs along the way, we have never lost that core friendship. So it is with pleasure (and a little amusement) that I contribute to a volume on hadrosaurians in Dave’s honor when I know so little about such exotic beasts, especially given that old canard that Dave W. has undoubtedly forgotten more about hadrosaurians than Dave N. will ever know.

LITERATURE CITED

- Batten, D. J. 2011. Wealden geology; pp. 7–14 in D. J. Batten (ed.), *English Wealden Fossils*. The Palaeontological Association, London, U.K.
- Beneden, P. J. van. 1881. Sur l'arc pelvien chez les dinosauriens de Bernissart. *Bulletin de l'Académie des Sciences, Belge* 1:600–608.
- Blows, W. T. 1998. A review of Lower and Middle Cretaceous dinosaurs of England. *New Mexico Museum of Natural History and Science Bulletin* 14:29–38.
- Brett-Surman, M. K. 1997. Ornithopods; pp. 330–346 in J. O. Farlow, and M. K. Brett-Surman (eds.), *The Complete Dinosaur*. Indiana University Press, Bloomington, Indiana.
- Butler, R. J., P. Upchurch, and D. B. Norman. 2008. The phylogeny of the ornithischian dinosaurs. *Journal of Systematic Palaeontology* 6:1–40.
- Carpenter, K., and Y. Ishida. 2010. Early and “middle” Cretaceous Iguanodonts in time and space. *Journal of Iberian Geology* 36:145–164.
- Carrano, M. T., C. M. Janis, and J. J. Sepkoski, Jr. 1999. Hadrosaurs as ungulate parallels: lost lifestyles and deficient data. *Acta Palaeontologica Polonica* 44:237–261.
- Casier, E. 1960. Les Iguanodonts de Bernissart: a la mémoire de Louis Dollo (1857–1931). Editions du patrimoine de l'Institut royal des Sciences naturelles de Belgique, Bruxelles, Belgium, 134 pp.
- Chargé, A. J. 1972. The evolution of the archosaur pelvis and hind limb: an explanation in functional terms; pp. 121–155 in K. A. Joysey, and T. S. Kemp (eds.), *Studies in Vertebrate Evolution*. Oliver and Boyd, Edinburgh, U.K.
- Cope, E. D. 1869. Synopsis of the extinct Batrachia, Reptilia, and Aves of North America. *Transactions of the American Philosophical Society* 14:1–252.
- Dalla Vecchia, F. M. 2009. *Tethyshadros insularis*, a new hadrosaurid dinosaur (Ornithischia) from the Upper Cretaceous of Italy. *Journal of Vertebrate Paleontology* 29:1100–1116.
- Dollo, L. 1882. Première note sur les dinosauriens de Bernissart. *Bulletin de la Musée royale d'Histoire naturelle de Belgique* 1:55–80.
- Evans, D. C. 2010. Cranial anatomy and systematics of *Hypacrosaurus altispinus*, and comparative analysis of skull growth in lambeosaurine hadrosaurids (Dinosauria: Ornithischia). *Zoological Journal of the Linnean Society* 159:398–434.
- Evans, D. C., and R. R. Reisz. 2007. Anatomy and relationships of *Lambeosaurus magnicristatus*, a crested hadrosaurid dinosaur (Ornithischia) from the Dinosaur Park Formation, Alberta. *Journal of Vertebrate Paleontology* 27:373–393.
- Gates, T. A., and S. D. Sampson. 2007. A new species of *Gryposaurus* (Dinosauria: Hadrosauridae) from the Late Campanian Kaiparowits Formation, southern Utah, USA. *Zoological Journal of the Linnean Society* 151:351–376.
- Gilmore, C. W. 1933. On the dinosaurian fauna of the Iren Dabasu Formation. *Bulletin of the American Museum of Natural History* 67:23–78.
- Godefroit, P., S. Hai, T. Yu, and P. Lauters. 2008. New hadrosaurid dinosaurs from the uppermost Cretaceous of northeastern China. *Acta Palaeontologica Polonica* 53:47–74.
- Head, J. J. 1998. A new species of basal hadrosaurid (Dinosauria: Ornithischia) from the Cenomanian of Texas. *Journal of Vertebrate Paleontology* 18:718–738.
- Holl, F. 1829. *Handbuch der Petrefactenkunde Pt 1*. Quedlinberg, Leipzig, pp. 232.
- Hookey, R. W. 1925. On the skeleton of *Iguanodon atherfieldensis* sp. nov., from the Wealden shales of Atherfield (Isle of Wight). *Quarterly Journal of the Geological Society of London* 81:1–61.
- Hopson, J. A. 1975. The evolution of cranial display structures in hadrosaurian dinosaurs. *Paleobiology* 1:21–43.
- Horner, J. R. 1985. Evidence for polyphyletic origin of the Hadrosauridae (Reptilia: Ornithischia). *Proceedings of the Pacific Division of the American Association for the Advancement of Science* 4:31–32.
- Horner, J. R. 1990. Evidence of diphyletic origin of the hadrosaurian (Reptilia: Ornithischia) dinosaurs; pp. 179–187 in K. Carpenter, and P. J. Currie (eds.), *Dinosaur Systematics: Approaches and Perspectives*. Cambridge University Press, Cambridge, U.K.
- Horner, J. R. 1992. Cranial morphology of *Prosaurolophus* (Ornithischia: Hadrosauridae). With descriptions of two new hadrosaurid species and an evaluation of hadrosaurid phylogenetic relationships. *Museum of the Rockies Occasional Paper* 2:1–119.
- Horner, J. R., D. B. Weishampel, and C. Forster. 2004. Hadrosauridae; pp. 438–463 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, Second Edition. University of California Press, Berkeley, California.
- Hulke, J. W. 1879. *Vectisaurus valdensis*, a new Wealden dinosaur. *Quarterly Journal of the Geological Society of London* 35:421–424.
- Hulke, J. W. 1882. Description of some *Iguanodon* remains indicating a new species, *I. seelyi*. *Quarterly Journal of the Geological Society of London* 38:135–144.
- ICZN. 1999. International Code of Zoological Nomenclature, Fourth Edition. International Trust for Zoological Nomenclature, Natural History Museum, London, U.K., 306 pp.
- Lull, R. S., and N. E. Wright. 1942. Hadrosaurian Dinosaur of North America. *Geological Society of America Special Papers* 40. 242 pp.
- Lydekker, R. 1888. Note on a new Wealden iguanodont and other dinosaurs. *Quarterly Journal of the Geological Society of London* 44:46–61.
- Lydekker, R. 1889. Notes on new and other dinosaur remains. *Geological Magazine* VI (Decade III):352–356.
- Maddison, D. R., and W. P. Maddison. 2003. *MacClade: Analysis of Phylogeny and Character Evolution*. Version 4.06. Sinauer Associates, Sunderland, Massachusetts.
- Maidment, S. C. R., K. T. Bates, and P. M. Barrett. 2014. Three-dimensional computational modeling of pelvic locomotor muscle moment arms in *Edmontosaurus* (Dinosauria, Hadrosauridae) and comparisons with other archosaurs; chapter 25 in D. A. Eberth, and D. C. Evans (eds.), *Hadrosaur*. Indiana University Press, Bloomington, Indiana.
- Mantell, G. A. 1825. Notice on the *Iguanodon*, a newly discovered fossil reptile, from the sandstone of Tilgate forest, in Sussex. *Philosophical Transactions of the Royal Society of London* CXV: 179–186.
- Mantell, G. A. 1827. *Illustrations of the Geology of Sussex: With Figures and Descriptions of the Fossils of Tilgate*. Lupton Relfe, London, U.K., 92 pp.
- Mantell, G. A. 1848. On the structure of the jaws and teeth of the *Iguanodon*. *Philosophical Transactions of the Royal Society of London* 138: 183–202.
- Marsh, O. C. 1881. Classification of the Dinosauria. *American Journal of Science* 7: 81–86.
- Martill, D. M., and D. Naish (eds.). 2001. *Dinosaurs of the Isle of Wight*. Palaeontological Association, London, U.K., 433 pp.
- McDonald, A. T. 2012a. The status of *Dollodon* and other basal iguanodonts (Dinosauria: Ornithischia) from the Lower Cretaceous of Europe. *Cretaceous Research* 33:1–6.
- McDonald, A. T. 2012b. Phylogeny of basal iguanodonts (Dinosauria: Ornithischia): an update. *PLoS ONE* 7(5):e36745.
- McDonald, A. T., P. M. Barrett, and S. D. Chapman. 2010. A new basal iguanodont (Dinosauria: Ornithischia) from the Wealden (Lower Cretaceous) of England. *Zootaxa* 2569:1–43.
- Naish, D., and D. M. Martill. 2008. Dinosaurs of Great Britain and the role of the Geological Society of London in their discovery: Ornithischia. *Journal of the Geological Society of London* 165:613–623.
- Norman, D. B. 1977. On the anatomy of the ornithischian dinosaur *Iguanodon*. Ph.D. dissertation, King's College London, London, U.K., 631 pp.
- Norman, D. B. 1980. On the ornithischian dinosaur *Iguanodon bernissartensis* from Belgium. *Mémoires de l'Institut royal des Sciences naturelles de Belgique* 178:1–105.
- Norman, D. B. 1986. On the anatomy of *Iguanodon atherfieldensis* (Ornithischia: Ornithopoda). *Bulletin de l'Institut royal des Sciences naturelles de Belgique* 56:281–372.
- Norman, D. B. 1987. On the discovery of fossils at Bernissart (1878–1921) Belgium. *Archives of Natural History* 13:131–147.
- Norman, D. B. 1990. A review of *Vectisaurus valdensis*, with comments on the family Iguanodontidae; pp. 147–162 in K. Carpenter, and P. J. Currie (eds.), *Dinosaur Systematics: Approaches and Perspectives*. Cambridge University Press, Cambridge, U.K.
- Norman, D. B. 1993. Gideon Mantell's “Mantel-piece”: the earliest well-preserved ornithischian dinosaur. *Modern Geology* 18:225–245.
- Norman, D. B. 2002. On Asian ornithopods (Dinosauria: Ornithischia). 4. Redescription of *Probactrosaurus gobiensis* Rozhdestvensky, 1966. *Zoological Journal of the Linnean Society (London)* 136:113–144.
- Norman, D. B. 2004. Basal Iguanodontia; pp. 413–437 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, Second Edition. University of California Press, Berkeley, California.
- Norman, D. B. 2010. A taxonomy of iguanodontians (Dinosauria: Ornithopoda) from the lower Wealden Group (Valanginian) of southern England. *Zootaxa* 2489:47–66.

- Norman, D. B. 2011a. On the osteology of the lower Wealden Group (Valanginian) ornithopod *Barilium dawsoni* (Iguanodontia: Styracosterna). *Special Papers in Palaeontology* 86:165–194.
- Norman, D. B. 2011b. Ornithopod dinosaurs; pp. 407–475 in D. J. Batten (ed.), *Field Guide to the Wealden of England*. The Palaeontological Association, Oxford, U.K.
- Norman, D. B. 2012. Iguanodontian taxa (Dinosauria: Ornithischia) from the Lower Cretaceous of Britain and Belgium; pp. 174–212 in P. Godefroit (ed.), *Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems*. Indiana University Press, Bloomington, Indiana.
- Norman, D. B. 2013. On the taxonomy and diversity of Wealden euiguanodontian dinosaurs (Ornithischia: Ornithopoda); pp. 385–404 in T. Malvesy (ed.), *Fourth Georges Cuvier Symposium*. *Revue de Paléobiologie*, Genève, Switzerland.
- Norman, D. B. in press. On the osteology, comparative morphology and systematics of *Hypselospinus fittoni* (Ornithopoda: Euiguanodontia) and its bearing on euiguanodontian phylogeny. *Zoological Journal of the Linnean Society*.
- Norman, D. B., A. W. Crompton, R. J. Butler, L. B. Porro, and A. J. Charig. 2011. The Lower Jurassic ornithischian dinosaur *Heterodontosaurus tucki* Crompton and Charig, 1962: cranial anatomy, functional morphology, taxonomy and relationships. *Zoological Journal of the Linnean Society* 163:182–276.
- Norman, D. B., H.-D. Sues, L. Witmer, and R. A. Coria. 2004. Basal Ornithopoda; pp. 393–412 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, Second Edition. University of California Press, Berkeley, California.
- Ostrom, J. H. 1961. Cranial morphology of the hadrosaurian dinosaurs of North America. *Bulletin of the American Museum of Natural History* 122:33–186.
- Owen, R. 1842. Report on British Fossil Reptiles. Part 2. Report of the British Association for the Advancement of Science (Plymouth) 11(1841):60–204.
- Owen, R. 1855. Monograph of the Fossil Reptilia of the Wealden and Purbeck Formations. Part II. Dinosauria (*Iguanodon*). *Palaeontographical Society Monographs* 8:1–54.
- Paul, G. S. 2007. Turning the old into the new: a separate genus for the gracile iguanodont from the Wealden of England; pp. 69–77 in K. Carpenter (ed.), *Horns and Beaks*. Indiana University Press, Bloomington, Indiana.
- Paul, G. S. 2008. A revised taxonomy of the iguanodont dinosaur genera and species. *Cretaceous Research* 29:192–216.
- Paul, G. S. 2012. Notes on the rising diversity of Iguanodont taxa, and Iguanodonts named after Darwin, Huxley, and evolutionary science; pp. 123–133 in P. H. Hurtado, F. T. Fernandez-Baldró, and J. I. C. Sanagustin (eds.), *Actas de V Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno*. Colectivo Arqueológico y Paleontológico de Salas, C.A.S. Salas de Los Infantes, Burgos, Spain.
- Prieto-Márquez, A. 2010. Global phylogeny of Hadrosauridae (Dinosauria: Ornithopoda) using parsimony and Bayesian methods. *Zoological Journal of the Linnean Society* 159:435–502.
- Prieto-Márquez, A. 2011. Revised diagnosis of *Hadrosaurus foulkii* Leidy, 1858 (the type genus and species of Hadrosauridae Cope, 1869) and *Claosaurus agiis* Marsh, 1872 (Dinosauria: Ornithopoda) from the Late Cretaceous of North America. *Zootaxa* 2765:61–68.
- Prieto-Márquez, A., R. Gaete, G. Rivas, A. Galobart, and M. Boada. 2006. Hadrosauroid dinosaurs from the Late Cretaceous of Spain: *Parahabdodon isonensis* revisited and *Koutalisaurus kohlerorum*. *Journal of Vertebrate Paleontology* 26:929–943.
- Prieto-Márquez, A., D. B. Weishampel, and J. R. Horner. 2006. The dinosaur *Hadrosaurus foulkii*, from the Campanian of the East Coast of North America, with a re-evaluation of the genus. *Acta Palaeontologica Polonica* 51:77–98.
- Romer, A. S. 1956. *Osteology of the Reptiles*. University of Chicago Press, Chicago, Illinois, 772 pp.
- Rozhdestvensky, A. K. 1966. [New iguanodonts from Central Asia. Phylogenetic and taxonomic interrelationships of late Iguanodontidae and early Hadrosauridae]. *Palaeontologicheskii Zhurnal* 1966:103–116. [Russian]
- Seeley, H. G. 1887. On the classification of the fossil animals commonly named Dinosauria. *Proceedings of the Royal Society of London* 43:165–171.
- Sereno, P. C. 1986. Phylogeny of the bird-hipped dinosaurs. *National Geographic Research* 2:234–256.
- Sereno, P. C. 1991. *Lesothosaurus*, “Fabrosaurids” and the early evolution of Ornithischia. *Journal of Vertebrate Paleontology* 11:234–256.
- Sereno, P. C. 1998. A rationale for phylogenetic definitions, with application to the higher-level taxonomy of Dinosauria. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 109:41–83.
- Sereno, P. C. 2005. Stem Archosauria version 1.0 website. Available at www.taxonsearch.org/Archive/stem-archosauria-1.0.php. Accessed summer 2012.
- Swofford, D. L. 2002. PAUP*, Phylogenetic Analysis Using Parsimony (*and other methods). Version 4.0b10. Sinauer Associates, Sunderland, Massachusetts.
- Taquet, P. 1975. Remarques sur l'évolution des iguanodontidés et l'origine des hadrosauridés. [Comments on the evolution of Iguanodontids and the origin of Hadrosaurids]: problèmes actuels de paléontologie-évolution des vertébrés [current problems in paleontology-vertebrate evolution]. Paris, Colloque international, Centre national de la Recherche scientifique Paris 218:1–8. [French].
- Taquet, P. 1976. Géologie et paléontologie du gisement de Gadoufaoua (Aptien du Niger). *Cahiers de Paléontologie*. [Geology and paleontology of the Gadoufaoua Locality (Aptian of Niger)]. Centre national de la Recherche scientifique Paris:1–191. [French]
- Thulborn, R. A. 1970. The skull of *Fabrosaurus australis*, a Triassic ornithischian dinosaur. *Palaeontology* 13:414–432.
- Thulborn, R. A. 1972. The postcranial skeleton of the Triassic ornithischian dinosaur *Fabrosaurus australis*. *Palaeontology* 15:29–60.
- Wang, X.-L., R. Pan, R. J. Butler, and P. M. Barrett. 2010. The postcranial skeleton of the iguanodontian ornithopod *Jinzhousaurus yangi* from the Lower Cretaceous Yixian Formation of western Liaoning, China. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 101:135–159.
- Weishampel, D. B. 1981. The nasal cavity of lambeosaurine hadrosaurids (Reptilia: Ornithischia): comparative anatomy and homologies. *Journal of Paleontology* 55:1046–1057.
- Weishampel, D. B., and J. R. Horner. 1990. Hadrosauridae; pp. 534–561 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*. University of California Press, Berkeley, California.
- Weishampel, D. B., C. M. Jianu, Z. Csiki, and D. B. Norman. 2003. Osteology and phylogeny of *Zalmoxes* (n.g.), an unusual euornithopod dinosaur from the latest Cretaceous of Romania. *Journal of Systematic Palaeontology* 1:65–123.
- Weishampel, D. B., D. B. Norman, and D. Grigorescu. 1993. *Telmatosaurus transsylvanicus* from the Late Cretaceous of Romania: the most basal hadrosaurid dinosaur. *Palaeontology* 36:361–385.
- Wu, W.-H., and P. Godefroit. 2012. Anatomy and relationships of *Bolong yixianensis*, an Early Cretaceous iguanodontoid dinosaur from western Liaoning, China; pp. 293–333 in P. Godefroit (ed.), *Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems*. Indiana University Press, Bloomington, Indiana.

Appendix 2.1. Taxon-Character Matrix

<i>Lesothosaurus diagnosticus</i>	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	00
<i>Hypsilophodon foxii</i>	0000000000	0000000111	0000000000	0000000000	0000101001	0111110021	0000100000	0000000011	0000100000	00
<i>Zalmoxes robustus</i>	0010000010	00000?1011	00?10?0001	0112101000	0100111111	1111111021	101??00???	????100111	1111000010	?0
<i>Tenontosaurus tilletti</i>	1010101110	0???'0?0101	100100001?	1100101000	0000101111	1111110021	1011100000	0001000312	1002101010	00
<i>Dryosaurus altus</i>	101?102110	1100000000	0000100001	0101010000	0000010111	1112211011	10000000?0	0?00?000112	0111200020	10
<i>Camptosaurus dispar</i>	1111101010	0?0010001?	0001000011	1110101000	0000111111	2122111111	0011000110	0101000112	0111200010	00
<i>Mantellisaurus atherfieldensis</i>	1111102110	1110100000	0001011011	1110201111	0100111211	2122111111	1111011111	0111101114	1021201131	11
<i>Iguanodon bernissartensis</i>	1111102110	1110100000	1001011111	1110101111	0100111211	2122111111	1111011111	0111112113	1111201131	11
<i>Ouranosaurus nigeriensis</i>	3111111110	0211100000	1001001?11	111?202001	0000111211	2122111111	1121011111	0111001114	11112?1131	??
<i>Altirhinus kurzanovi</i>	211110112?	0211100000	100100?1?1	1111211111	0001212211	2122111111	?????11111	0111001113	101?2?11??	?1
<i>Eolambia caroljonesa</i>	21111011??	??11000000	10?10?10?1	??1?202101	0001112211	2123112111	??1??11111	011?011113	?111211131	?1
<i>Jinzhousaurus yangi</i>	211?102121	1?101?0000	??0111?1?1	11111010?0	000011?2?1	2122111111	1111?11111	0111?01112	?0112?1131	??
<i>Hypselospinus fittoni</i>	?1????????	??????????	??????????	????111001	???'0112211	21221?1111	?121?11111	011?000113	1111201131	?1
<i>Barilium dawsoni</i>	??????????	??????????	??????????	????101111	???'0112211	21221?1111	?111?11111	01??100013	111?201131	?1
<i>Equijubus normani</i>	211?101010	1?101?1000	10?100?1?1	11111011?1	0101102211	1122111111	11??????1	?????0011??	11????????	??
<i>Prothadros byrdi</i>	211010????	??10100010	10?100????	1111212111	0101212211	1123111111	??????????	??????????	??????????	??
<i>Probactrosaurus gobiensis</i>	21101010??	1?1?101??0	00?10??01?	1111101111	0101212211	2122112111	?11??12?22	011?001113	1111201131	21
<i>Bactrosaurus johnsoni</i>	1111101?21	?2111100?1	0011001011	1211112211	1111222321	2123222111	111??12?22	12??002113	1111212231	22
<i>Tethyshadros insularis</i>	1111101021	1?200?1011	000100?1?1	1111?01111	1111?1?321	21232?2112	1111012222	12?1003213	11012?2??1	21
<i>Parasaurolophus walker</i>	2111100021	0222110011	0112111111	1211211212	1112222321	3113222112	1111022222	1211013214	1111212241	22
<i>Saurolophus osborni</i>	3111110021	1221111011	1112011111	121?201212	1112222321	3113222112	1111022222	1211013214	1000212241	22
<i>Telmatosaurus transylvanicus</i>	1111101121	1?211????1	10?100101?	??1?101112	1102222321	3113222112	111??2????	??????????	?????12141	??
<i>Xuwulong yueluni</i>	1111101?21	0??11????0	0?0100?1?1	111?101101	??001?1???	2122111111	?11??1????	?????001113	11112?????	??
<i>Bolong yixianensis</i>	11111011?0	1?0??????0	??0?????11	111?10?001	???'0111211	2122111111	1?1?1?1111	11111022??	?1112?11?1	?1

Appendix 2.2. Character Choice and State Definitions for the Phylogenetic Analysis Conducted in This Study

1. Premaxillary rostrum: dorsal aspect. Margins converge to a blunt tip (0), modest rounded expansion (1), occlusal margin is broad and rounded in dorsal view such that its overall width approaches that of the skull roof (2), flared occlusal margins that form a "spoon-bill" structure in dorsal view (3).
2. Premaxilla: level of occlusal margin relative to that of the maxillary tooth row. Not at all (or slightly) ventrally offset from alveolar margin of the maxilla (0), strongly ventrally offset (1).
3. Premaxillary teeth: present (0), absent (1).
4. Premaxillary denticles: absent (0), present (1).
5. External naris: confined to area above oral margin of premaxilla (0), posterior margin extended posteriorly to lie above the maxilla (1).
6. Premaxilla: anterolateral margin of the nasal fossa, above the occlusal edge of the premaxilla is reflected dorsally to form a distinct rim: absent (0), present (1).
7. Premaxilla-lacrimal contact: absent (0), present (1) posterolateral premaxillary process extends posterodorsally to also contact/overlap the prefrontal (2).
8. Premaxillary posterolateral process: tapers to point (0), posterior tip is bluntly truncated (1).
9. Antorbital fenestra shape. Opening when viewed laterally: large and subtriangular (0), small and subcircular (1), absent (2).
10. Antorbital fenestra location: between lacrimal and maxilla (0), on anterodorsal margin (premaxillary suture) of maxilla and not visible in lateral view of the articulated skull (1).
11. Lacrimal-nasal contact: present (0), absent (1).
12. Maxilla: dorsal process morphology. Flattened mound-like structure (0), narrow, finger-like process (1), laterally flattened subtriangular plate (2).
13. Jugal: anterior process. Tapering (0), expanded (1), expanded and truncated anteriorly (2).
14. Jugal-maxilla suture: scarf joint (0), "finger-in-recess" (oblique finger-like process of the maxilla fits into a slot formed in the medioventral surface of the anterior jugal ramus) (1), butt-jointed against a broad facet on the lateral surface of the ascending process of the maxilla (2).
15. Jugal and its free ventral margin: generally strap-like with little undulation along the ventral edge (0), marked sinuous ventral edge with marked ventral deflection posteriorly (1).
16. Jugal-ectopterygoid contact: present (0), absent (1). *Difficult to score in many instances.*
17. Jugal contribution to the margin of the infratemporal fenestra: jugal forms part of the margin (0), jugal forms the entire margin by excluding the quadratojugal (1).
18. Quadratojugal foramen: absent (0), present (1). *Very limited distribution.*
19. Quadrate (paraquadrate) foramen: between quadratojugal and quadrate. Present (0), absent (1).
20. Quadrate: embayment on anterolateral wing. Relatively small and semicircular in outline (0), broad embayment whose edges are marked by a scarf suture for a close-fitting quadratojugal (1).
21. Quadrate: posterior margin of the shaft. Bowed anteriorly and the dorsal portion tilted posteriorly (0), straight (1). *Often difficult to score because of postmortem distortion.*
22. Quadrate-articular condyle: transversely expanded (0), laterally compressed so that it forms (almost) a simple rounded condyle (1).
23. Palpebral (supraorbital) bone(s): present (0), absent or fused to orbital margin (1). *Given the looseness of attachment of this bone to the orbital margin (and therefore the lack of a reliable osteological marker) evidence of absence is subjective.*
24. Frontal: shape. Arched and narrow embayed laterally so that the orbital cavity is exposed dorsally (0), flat and transversely broad plate, roofing the orbital cavity dorsally (1), anteroposteriorly abbreviated (2).
25. Frontal: forms part of the dorsal margin of the orbital cavity. Present (0), absent (1).
26. Postorbital-squamosal contact: postorbital forms a tapering finger-like squamosal process the overlaps the squamosal (0), this process develops a bifurcate tip (1). *McDonald et al. (2010) proposed that this process might be coded in three ways: "blunt," "pointed," or "bifurcate." However, there is variation in this structure as it is illustrated in skull reconstructions, which makes the distinction between "blunt" and "pointed" one that is potentially subjective and risks misinterpretation.*
27. Foramen magnum dorsal margin: supraoccipital in dorsal margin (0), supraoccipital excluded from dorsal margin by exoccipitals (1).
28. Foramen magnum ventral margin: basioccipital in ventral margin (0), basioccipital excluded from ventral margin by the exoccipitals (1). *This character, though commonly used and perhaps of more value at a coarser scale (e.g., across higher-level taxonomic groupings), is often difficult to assess reliably (within individual taxa), and may vary ontogenetically and be subject by taphonomic influence.*
29. Paroccipital wing shape: horizontal and dorsoventrally expanded distally (0), pendant distal tip (1).
30. Basipterygoid process orientation: anteroventral (0), posterolateral (1).
31. Predentary occlusal margin: smooth edged (0), denticulate (1).
32. Predentary shape (in plan view): subtriangular (0), arcuate (1), broad and subrectangular (2).
33. Predentary ventral lobe: median tab sometimes notched in the midline (0), deeply incised in the midline and with strongly bifurcate lobes (1).
34. Predentary rostral surface: smooth (0); bearing a pair of oblique grooves, one on either side of midline (1), midline groove (2).
35. Mandibular diastema (the gap between the posterior end of the predentary and the first dentary alveolus): absent (0), present (1), greater than three crown widths (2). *Difficult to assess in instances in which the predentary is not articulated with the dentary and/or when the anterior part of the dentary is not well preserved.*
36. Dentary ramus shape in lateral view: straight (0), arched along its ventral edge (1).
37. Dentary ramus (tooth-bearing portion) shape: tapers anteriorly (0), parallel dorsal and ventral borders (1), deepens anteriorly (2).
38. Dentary coronoid process profile: axis of coronoid oblique (posterodorsal orientation) (0), perpendicular (1), anteriorly inclined (2).
39. Dentary coronoid process shape: dorsal tip unexpanded (0), expanded (1).
40. Dentary coronoid process position: laterally offset and dentition [alveoli] curves laterally into its base (0), posterior dentition extends medial to the middle of the coronoid process (1), posterior dentition extends posterior to the coronoid process (2).
41. Surangular foramen: present (0), absent (1).
42. Surangular-angular suture: obliquely inclined (0), horizontal (1). *Difficult to score faithfully because this feature may be based upon skull reconstructions which may, or may not, be accurate in this area.*
43. Angular: lateral exposure. Visible laterally (0), not visible (contact with surangular is positioned ventrally or medially) (1).
44. Replacement crowns present: one (0), two (1), three or more (2).
45. Wear facet distribution on dentary and maxillary crowns: irregular and discontinuous distribution on individual crowns (0), wear facets continuous across adjacent crowns, producing a uniformly narrow cutting/grinding surface (1), the oldest and successional crowns contribute to the wear surface to varying degrees to produce a transversely broader cutting/grinding occlusal (2).
46. Relative crown width: maxillary crowns equal in width to dentary crowns (0), narrower than dentary crowns (1), equal in width to dentary crowns, but "miniaturized" (2).
47. Enamel surface distribution on tooth crowns: equally distributed on both sides of crown (0), asymmetrical distribution, thicker on one surface of the crown (1), enamel is restricted to one side of the crown (2).
48. Marginal denticle shape: simple cones (0), tongue-shaped (1), curved ledges with mammillae (2), absent, or reduced to small irregular papillae (3).
49. Tooth roots: tapering cylinders (0), longitudinally grooved to accommodate adjacent, closely packed teeth (1), highly angular sided "prismatic" roots (2).
50. Dentary tooth curvature of long axis: the root-crown axis of the tooth is straight (0), the long axis of the tooth is bowed lingually so that the occlusal portion of the crown becomes directed labiodorsally (1).
51. Dentary teeth, crown shape in lingual view: simple, symmetrical leaf-shaped profile (0), broad, shield-like (1), in unworn examples occlusal margin forms a distinct shoulder mesially (2), mesiodistally compressed and diamond shaped (3).
52. Dentary teeth, presence of oblique, thickened ledges at the base of the enamelled lingual face of the crown: absent (0), present (1).

Appendix 2.2. (continued)

53. Dentary teeth, primary ridge: absent (0), median position (1), distally offset (2).
54. Dentary teeth, ridge pattern: simple median swelling (0), prominent primary ridge with variable number of parallel subsidiary ridges (1), parallel primary and secondary ridge divide crown face into three zones (2), primary ridge alone (3).
55. Dentary teeth, relative size in mandible: large and shield shaped (0), miniaturized (1).
56. Dentary, lateral alveolar wall shape: shaped by dentary crowns (0), narrow, parallel-sided grooves (1).
57. Maxillary teeth shape 1: equal width to dentary crowns (0), narrower and more lanceolate than opposing dentary crowns (1), lanceolate but equal in width to dentary crowns (2).
58. Maxillary teeth shape 2: Root–crown long axis of the tooth straight (0); long axis bowed, convex labially (1).
59. Maxillary teeth, labial ridges 1: simple median swelling (0), very prominent primary ridge (1), several subsidiary ridges and no obvious primary ridge (2).
60. Maxillary teeth, labial ridges 2: simple medial swelling (0), array of primary, secondary, and subsidiary ridges (1), single median primary ridge with no other ridges present (2).
61. Axis vertebra. Neural spine shape: low and sloping (0), tall and expanded (1).
62. Cervical vertebrae. Centrum articular surfaces: amphiplatyan (0), opisthocoelous (1).
63. Dorsal vertebrae. Neural spine shape: low and rectangular (0), tall and narrow (1). Extremely tall, relative to the anteroposterior dimension of spine (2). Dubious. *Biomechanical: small animals have short neural spines. Only two taxa, Ouranosaurus and Hypselospinus, have extremely elongate neural spines—i.e., probable homoplasy.*
64. Epaxial ossified tendons: arranged in linear bundles (0), form a layered lattice against the neural spines (1). Dubious: *reflects the accommodation space available: taller spines enable a lattice-like arrange of tendons to exist.*
65. Ossified tendons form a posterior caudal sheath: absent (0), present (1). *Rarely preserved, and where a sheath of tendons is known, its occurrence seems to be restricted to basal clypeodontans and may be plesiomorphic within cerapodans.*
66. Scapular acromion: prominent on the proximodorsal margin of scapula (0), occupying a median position on the proximal shaft and curved toward the dorsal edge of the proximal scapular blade (1), developed into a promontory that overhangs the proximal end of the scapula and is not curved toward the dorsal border (2).
67. Sternal shape: reniform (0), hatchet shaped with a stout, short “handle” (1), pronounced elongation of the “handle” of the hatchet relative to the “blade” (2).
68. Carpals: fully ossified (0), fused to form a carpometacarpal I block (1), reduced to no more than two small ossicles (2).
69. Metacarpal I: elongate dumbbell shaped (0), short, block-like and fused against carpals (1), absent (2).
70. Metacarpals II–IV: spreading (0), robust, closely appressed (1), slender and elongate (2).
71. Manus digit I: present (0), absent (1).
72. Ungual of manus digit I: claw-like (0), subconical (1), lost (2).
73. Unguals of manus digits II and III: claw-like (0), flattened, twisted and hoof-like (1).
74. Manus digit III: four phalanges (0), three phalanges (1).
75. Ilium, preacetabular process: long, laterally compressed (0), axially twisted so that lateral surface faces dorsolaterally (1).
76. Ilium: profile of dorsal edge. Horizontal to slightly arched, no significant notch in its profile posterodorsal to the ischiadic peduncle (0), sinuous profile created by the presence of a broad saddle-like notch (1).
77. Ilium: dorsal margin development: no transverse thickening of the dorsal edge in the region posterodorsal to the ischiadic peduncle (0), transversely thickened, beveled edge (1), thickened edge developed into a thick rolled edge (2), prominently everted, with a downturned, flap-shaped pendule that overhangs the ischiadic peduncle (3).
78. Ilium: postacetabular process in profile. Vertical plate with rounded edge (0), generally triangular, tapering posteriorly (1), laterally compressed and relatively narrow, rectangular bar (2), upturned plate (3).
79. Pubis: anterior ramus form: short (0), elongate (1).
80. Pubis: anterior ramus shape. Short, deep and blunt (0), rod-shaped (1), laterally compressed parallel-sided blade (2), expanded distally (3), strongly transversely compressed and deeply expanded distal portion (4).
81. Pubis: posterior ramus. Terminates bluntly adjacent to distal end of ischium (0), shorter than ischium, tapers to a point (1).
82. Ischium: shaft morphology 1. Straight (0), bowed (1).
83. Ischium: shaft morphology 2. Compressed and blade-like along length of shaft (0), sub-cylindrical shaft (1), narrow, angular-sided shaft (2).
84. Ischium: shaft morphology 3. Distal end unexpanded (0), distal end expanded into “boot” (1), distal end laterally expanded, rather than expanded anteroposteriorly (2).
85. Ischium: obturator process. Absent (0), positioned near mid-shaft (1), positioned close to pubic peduncle, from which it is separated by an embayment (2).
86. Femoral head grooved posteriorly: present (0), absent (1).
87. Femur: curvature of shaft. Femoral shaft bowed along its length (0), proximal half of the shaft straight, distal half of shaft curved caudally (1), femoral shaft straight (2).
88. Femur: fourth trochanter. Pendant (0), large, triangular (1), curved, laterally compressed eminence (2).
89. Femur: distal extensor groove. Absent (0), very broad trough (1), U-shaped trough (2), partially enclosed by expansion of adjacent anterior condyles (3), edges of trough meet to form a fully-enclosed tunnel (4).
90. Femur: distal condyles. Moderately expanded anteroposteriorly (0), strongly expanded and partly occluding flexor channel (1). *Most probably a size-related mechanical feature.*
91. Metatarsal I: well developed and articulates with proximal phalanx (0), slender and splint-like (1), absent (2). *Difficult to assess in many instances. As in the case of a palpebral bone on the orbital margin, is absence actual evidence of absence, or a biostratigraphic artifact?*
92. Pedal phalanges: shape. Dorsoventrally flattened but elongate and pointed (0), elongate, bluntly truncated tip with prominent claw grooves retained (1), anterior margin broadly rounded in dorsal view, lateral claw grooves absent (2).

Osteology of the Basal Hadrosauroid *Equijubus normani* (Dinosauria, Ornithopoda) from the Early Cretaceous of China

3

Andrew T. McDonald, Susannah C. R. Maidment, Paul M. Barrett, Hai-lu You, and Peter Dodson

ABSTRACT

The basal hadrosauroid *Equijubus normani* is rediagnosed and fully described based upon the holotype and only known specimen, IVPP V 12534, from the Lower Cretaceous Xinminpu Group of Gansu Province, China. *Equijubus* can be diagnosed by a suite of cranial (finger-like process on the maxillary process of the jugal, rostrally elongate lacrimal) and vertebral (epiphyses present on third cervical vertebra, hyposphene present on at least dorsal vertebrae 6–8 and 11–15) autapomorphies, and a unique combination of characters. Comprehensive description of the skull and partial postcranium of IVPP V 12534 allows *Equijubus* to be compared to other iguanodontians from China and elsewhere. A better understanding of the anatomy of *Equijubus* will be useful for assessing the diversity of Asian iguanodonts, and allow it to be more confidently placed in a phylogenetic context.

INTRODUCTION

During much of the nineteenth and twentieth centuries, Europe boasted the richest fossil record of basal (i.e., non-hadrosaurid) iguanodontian dinosaurs in the world (Buffetaut and Le Loeuff, 1991; Weishampel et al., 2003; Norman, 2010, 2011a, this volume; Barrett et al., 2011). However, recent discoveries have revealed an abundance of new taxa from Asia, particularly China; recently named taxa include *Nanyangosaurus zhugeii* (Xu et al., 2000), *Jinzhousaurus yangi* (Wang and Xu, 2001; Barrett et al., 2009; Wang et al., 2010), *Shuangmiaosaurus gilmorei* (You, Ji, et al., 2003), *Equijubus normani* (You, Luo, et al., 2003), *Lanzhousaurus magnidens* (You et al., 2005), *Penelopognathus weishampeli* (Godefroit et al., 2005), *Jintasaurus meniscus* (You and Li, 2009), *Bolong yixianensis* (Wu et al., 2010), and *Xuwulong yueluni* (You et al., 2011). Although it is represented by one of the most complete skeletons known for these taxa, *Equijubus* has received only a brief description (You, Luo, et al., 2003).

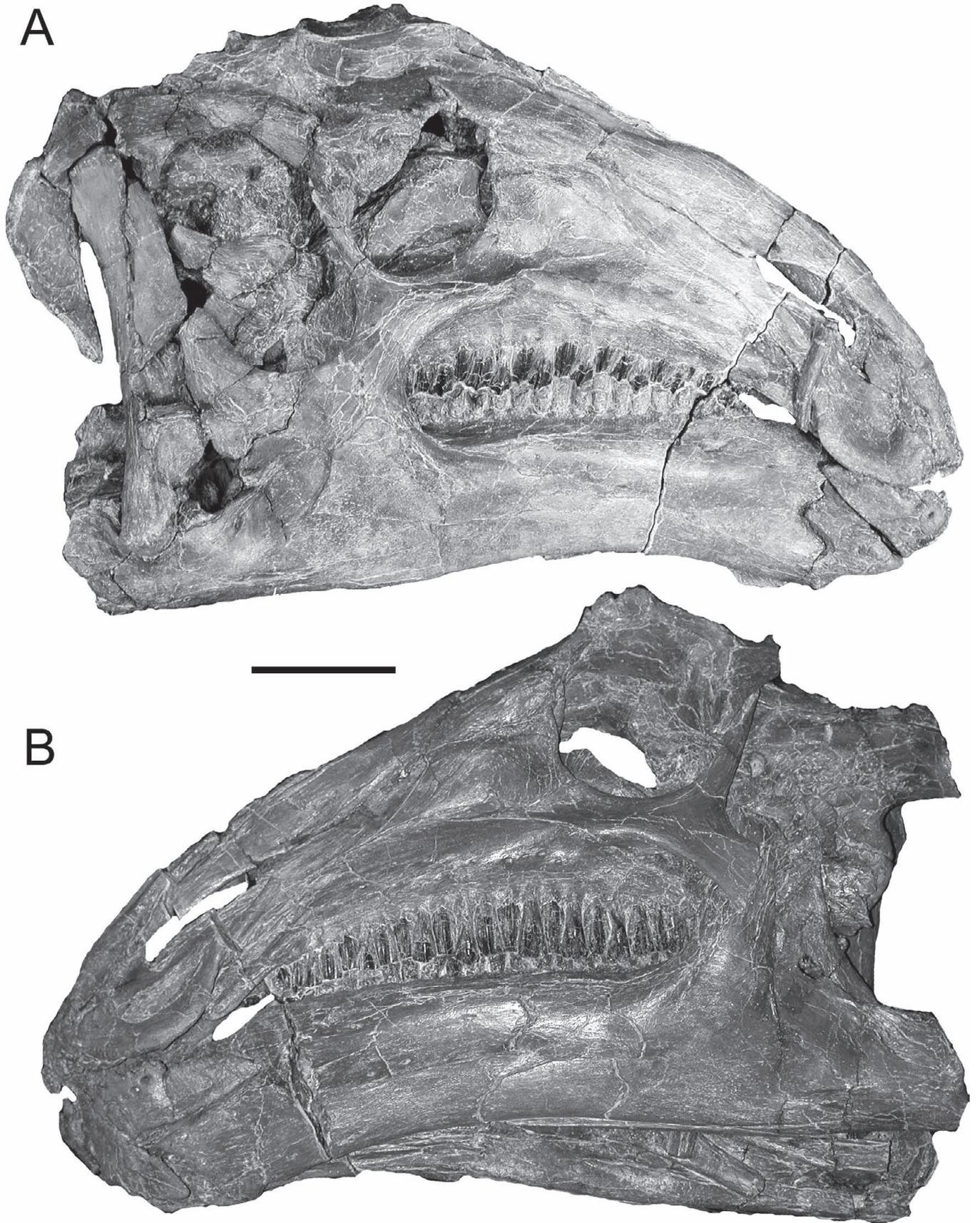
We present herein a complete osteological description of the holotype and only known specimen of *Equijubus*,

including elements that were not described or figured in the original description, and we provide a revised diagnosis for the taxon. The additional information presented on *Equijubus* in this description will facilitate comparison with other basal iguanodonts and allow its phylogenetic affinities to be more adequately tested. As is evident from the long list of taxa above, new Chinese iguanodonts are being discovered at a rapid pace, and it is essential when diagnosing new taxa that full comparisons with other iguanodonts are possible. Detailed descriptions of existing Chinese taxa, such as *Equijubus* and *Jinzhousaurus* (Barrett et al., 2009; Wang et al., 2010), will aid such comparative study.

Institutional Abbreviations AMNH, American Museum of Natural History, New York; CEUM, College of Eastern Utah Prehistoric Museum, Price, Utah; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MB, Museum für Naturkunde, Berlin, Germany; MNHN, Muséum national d'Histoire naturelle, Paris, France; NHMUK, Natural History Museum, London, U.K.; SDSM, South Dakota School of Mines and Technology, Rapid City, South Dakota; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842
ORNITHISCHIA Seeley, 1887
ORNITHOPODA Marsh, 1881
IGUANODONTIA Dollo, 1888, sensu Sereno, 2005
ANKYLOPOLLEXIA Sereno, 1986,
sensu Sereno, 2005
STYRACOSTERNA Sereno, 1986,
sensu Sereno, 2005
HADROSAURIFORMES Sereno, 1997,
sensu Sereno, 1998
HADROSAUROIDEA Cope, 1870,
sensu Sereno, 2005



3.1. Fully assembled skull of IVPP V 12534, holotype of *Equijubus normani*, in (A) right lateral and (B) left lateral views. Scale bar equals 10 cm.

EQUIJUBUS NORMANI You, Luo, Shubin,
Witmer, Tang, and Tang, 2003
(Figs. 3.1–3.20)

Holotype IVPP V 12534, complete skull and partial postcranium of a single individual.

Diagnosis For genus and species by monotypy. Characters derived from the original diagnosis of You, Luo, et al. (2003) are marked with an asterisk (*). Basal hadrosauroid characterized by four autapomorphies: (1), rostr dorsally curved finger-like process that arises from the maxillary process of the jugal at the jugal-lacrimal contact*; (2), elongate rostral ramus of lacrimal that extends along the dorsal margin of the maxilla and terminates rostral to the apex of the ascending process of the maxilla*; (3), epiphyses present on third cervical vertebra; and (4), hyposphene present on at least dorsal vertebrae 6–8 and 11–15. Also distinguished by the following unique combination of characters: rostral ramus of lacrimal tapers to a point, ventrolateral process of premaxilla contacts prefrontal (also noted by Paul, 2008:201, as lack of contact between the lacrimal and nasal); quadrate gradually curves caudally along its entire length in lateral view (also noted by Paul, 2008:201, as “shaft nearly straight”); and convex dorsal margin of ilium (also noted by Carpenter and Ishida, 2010).

Horizon Middle Grey Unit, Xinminpu Group; Albian, Early Cretaceous (Tang et al., 2001).

Type Locality Gongpoquan Basin, Mazongshan area, Gansu Province, China.

DESCRIPTION

Cranium and Mandible

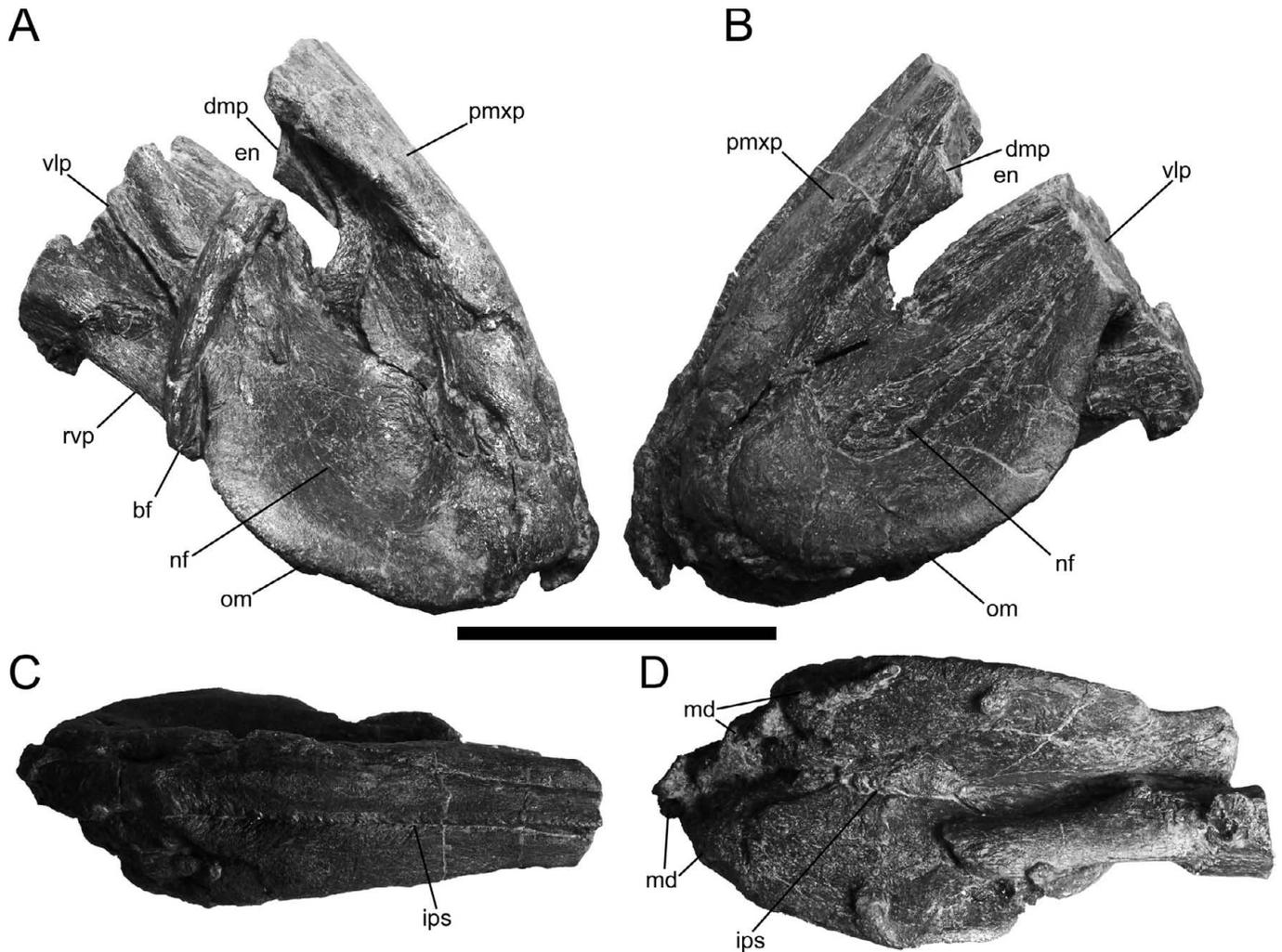
Although it is nearly complete, the skull of IVPP V 12534 is extremely compressed transversely, obscuring the medial surfaces of most of the cranial elements (Fig. 3.1); the dorsal surface of the skull roof is visible in only right lateral view (Fig. 3.1A). Some pieces, including the prefrontal, rostral ramus of the right dentary, rostral ends of both premaxillae, the articulated right postorbital and squamosal, and the left paroccipital process can be separated from the rest of the skull and described in greater detail. See You, Luo, et al. (2003:348–350, fig. 1C) for a reconstruction and measurements of the fully assembled skull. See Appendix 3.1 for additional cranial and postcranial measurements of IVPP V 12534.

Premaxilla and Nasal The oral margin of the premaxilla is gently convex and edentulous (Fig. 3.2A, B). The rostral end of the premaxilla is ventrally inflected relative to the ventral margin of the maxilla, such that the oral margin is

positioned well below the maxilla (Fig. 3.2A, B). The caudolateral corner of the oral margin curves caudodorsally towards the rostroventral process of the maxilla (Fig. 3.2A). The oral margin of each premaxilla expands laterally to form a transversely broad snout (Fig. 3.2C, D). Each premaxilla bears two rostrocaudally elongate denticles on its oral margin (Fig. 3.2D), as in *Mantellisaurus* (NHMUK R5764), *Ouranosaurus* (cast of MNHN GDF 300), and *Eolambia* (CEUM 35635). Caudal to the denticles, the ventral surface of the premaxilla is flat and somewhat rugose along the interpremaxillary suture (Fig. 3.2D). Dorsal to the oral margin, the lateral surface of the premaxilla is concave, forming the rostral end of the narial fossa (Fig. 3.2A, B).

Caudodorsal to the narial fossa, the premaxilla splits into two processes, the dorsomedial and ventrolateral processes; the point at which these processes diverge forms the rostral margin of the external naris (Fig. 3.2A, B). The dorsomedial process is overlapped laterally by the premaxillary process of the nasal, which forms the dorsal margin of the external naris (Figs. 3.2A, B, 3.3, 3.4). The dorsomedial processes of the left and right premaxillae meet along the interpremaxillary suture (Fig. 3.2C). The ventrolateral process forms the ventral margin of the external naris and contacts the maxilla along its ventral margin, curving over the rostroventral process of the maxilla and extending caudally to contact the lacrimal and prefrontal (Figs. 3.2A, 3.3, 3.4). The ventrolateral process also contacts the prefrontal in *Hippodraco* (McDonald, Kirkland, et al., 2010), *Theiophytalia* (Brill and Carpenter, 2006), *Dakotadon* (Weishampel and Bjork, 1989), *Iguanodon bernisartensis* (Norman, 1980), *Mantellisaurus* (Norman, 1986), and *Jinzhouosaurus* (Barrett et al., 2009), but does not in *Altirhinus* (Norman, 1998) or *Xuwulong* (You et al., 2011). The ventrolateral process tapers towards its caudal end, as in *Hippodraco* (McDonald, Kirkland, et al., 2010), *Dakotadon* (Weishampel and Bjork, 1989), *Iguanodon* (Norman, 1980), and *Mantellisaurus* (Norman, 1986) in contrast to the dorsoventrally expanded ventrolateral processes of more derived hadrosauroids such as *Eolambia* (Kirkland, 1998; Head, 2001) and *Probactrosaurus gobiensis* (Norman, 2002) (Figs. 3.3, 3.4). The ventrolateral process contacts the nasal along its dorsal margin (Figs. 3.3, 3.4). The ventrolateral process of the premaxilla and the nasal contribute equally to the caudal margin of the external naris.

The nasal contacts the premaxilla rostrally and ventrally, the prefrontal ventrally, the frontal caudally, and its counterpart medially (Figs. 3.3, 3.4). Rostral to its contact with the ventrolateral process of the premaxilla, the ventral margin of the nasal curves rostr dorsally toward the dorsomedial process of the premaxilla, forming the dorsal margin and part of the caudal margin of the external naris. The sutures



3.2. Articulated premaxillae of IVPP V 12534, holotype of *Equijubus normani*. (A) right premaxilla in lateral view; (B) left premaxilla in lateral view; (C) premaxillae in dorsal view; (D) same in ventral view. Abbreviations: bf, bone fragment; dmp, dorsomedial process; en, external naris; ips, interpremaxillary suture; md, marginal denticles; nf, narial fossa; om, oral margin; pmxp, premaxillary process of nasal; rvp, rostroventral process of right maxilla; vlp, ventrolateral process. Scale bar equals 10 cm.

between the nasals and frontals are difficult to discern due to damage and compression of the skull; their shape is not certain (Figs. 3.3, 3.4).

Maxilla, Palatine, and Pterygoid The rostroventral process of the maxilla curves rostroventrally to contact the ventrolateral process of the premaxilla (Figs. 3.2A, 3.3, 3.4). There is a short diastema between the rostral end of the rostroventral process and the first alveolus. The presence of a rostradorsal process cannot be ascertained due to the articulation of the premaxillae with the maxillae of IVPP V 12534. The ventral margin of the maxilla is gently concave in lateral view (Figs. 3.3, 3.4). The lateral surface of the maxilla is pierced by several deep, irregularly distributed neurovascular foramina dorsal to the tooth row and near the dorsal margin of the maxilla (Figs. 3.3A, 3.4A), as in *Dakotadon* (SDSM 8656; Weishampel and Bjork, 1989).

The ascending process of the maxilla is rostrocaudally broad and triangular, and contacts the ventrolateral process of the premaxilla and the lacrimal along its rostral margin, and the maxillary process of the jugal along its caudal margin (Figs. 3.3, 3.4). The antorbital fossa is not visible in lateral view. The jugal process of the maxilla is finger-like and projects caudolaterally to lock into a recess on the medial surface of the maxillary process of the jugal (Fig. 3.5), as in *Iguanodon bernissartensis* (Norman, 1980), *Mantellisaurus* (Norman, 1986), *Altirhinus* (Norman, 1998), *Probactrosaurus gobiensis* (Norman, 2002), and *Eolambia* (Kirkland, 1998; CEUM 34356).

The right palatine and right and left pterygoids are partially visible through the orbits and infratemporal fenestrae of IVPP V 12534 (Figs. 3.3, 3.4). However, due to damage and the overlap of other cranial elements, little can be determined