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Recent Advances in Ageing and Sexing Animal Bones

For Vasili and Marilena

*Proceedings of the 9th Conference of the International Council
of Archaeozoology, Durham, August 2002*

Series Editors: Umberto Albarella, Keith Dobney and Peter Rowley-Conwy

Recent Advances in Ageing and Sexing Animal Bones

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Preface

Umberto Albarella, Keith Dobney and Peter Rowley-Conwy

This book is one of several volumes which form the published proceedings of the 9th meeting of the International Council of Archaeozoology (ICAZ), which was held in Durham (UK) 23rd–28th August 2002. ICAZ was founded in the early '70s and has ever since acted as the main international organisation for the study of animal remains from archaeological sites. The main international conferences are held every four years, and the Durham meeting – the largest ever – follows those in Hungary, the Netherlands, Poland, England (London), France, USA, Germany and Canada. The next meeting will be held in Mexico in 2006. The Durham conference – which was attended by about 500 delegates from 46 countries – was organised in 23 thematic sessions, which attracted, in addition to zooarchaeologists, scholars from related disciplines such as palaeoanthropology, archaeobotany, bone chemistry, genetics, mainstream archaeology etc.

The publication structure reflects that of the conference, each volume dealing with a different topic, be it methodological, ecological, palaeoeconomic, sociological, historical or anthropological (or a combination of these). This organisation by theme rather than by chronology or region, was chosen for two main reasons. The first is that we wanted to take the opportunity presented by such a large gathering of researchers from across the world to encourage international communication, and we thought that this could more easily be achieved through themes with world-wide relevance. The second is that we thought that, by tackling broad questions, zooarchaeologists would be more inclined to take a holistic approach and integrate their information with other sources of evidence. This also had the potential of attracting other specialists who shared an interest in that particular topic. We believe that our choice turned out to be correct for the conference, and helped substantially towards its success. For the publication there is the added benefit of having a series of volumes that will be of interest far beyond the restricted circle of specialists on faunal remains. Readers from many different backgrounds, ranging from history to zoology,

will certainly be interested in many of the 14 volumes that will be published.

Due to the large number of sessions it would have been impractical to publish each as a separate volume, so some that had a common theme have been combined. Far from losing their main thematic focus, these volumes have the potential to attract a particularly wide and diverse readership. Because of these combinations (and because two other sessions will be published outside this series) it was therefore possible to reduce the original 24 sessions to 14 volumes. Publication of such a series is a remarkable undertaking, and we are very grateful to David Brown and Oxbow Books for agreeing to produce the volumes.

We would also like to take this opportunity to thank the University of Durham and the ICAZ Executive Committee for their support during the preparation of the conference, and all session organisers – now book editors – for all their hard work. Some of the conference administrative costs were covered by a generous grant provided by the British Academy. Further financial help came from the following sources: English Heritage, Rijksdienst voor het Oudheidkundig Bodemonderzoek (ROB), County Durham Development Office, University College Durham, Palaeoecology Research Services, Northern Archaeological Associates, Archaeological Services University of Durham (ASUD), and NYS Corporate Travel. Finally we are extremely grateful for the continued support of the Wellcome Trust and Arts and Humanities Research Board (AHRB) who, through their provision of Research Fellowships for Keith Dobney and Umberto Albarella, enabled us to undertake such a challenge.

The present volume publishes the proceedings of the session 'Ageing and Sexing', which was among the first to be proposed for ICAZ 2002 and ended up being one of the strongest and best attended. This was in large part due to Deborah Ruscillo's excellent organisational skills, but also to the inherent interest and appropriateness of this subject for an ICAZ conference. Whether we study material from Argentina or Japan, from the Palaeolithic or the medieval

period, we still need to deal with the issue of ageing and sexing animal bones. A methodological session may be of little interest outside the field of zooarchaeology, but this is compensated for by the fact that *all* animal bone specialists will be interested in it. Initially Deborah wanted simply to find the best venue to present her interesting new method of sexing mammal bones through shape analysis. However, here was an opportunity to be more ambitious and organise a whole session dedicated to sexing and ageing studies. Things went ahead as planned and this book represents the culmination of almost three years of work, begun with a cosy conversation in the warm environment of the Ruscillo/Cosmopoulos home in Winnipeg (as the external temperature approached *minus* 30°C!).

The publication in 1982 of the volume “Ageing and sexing animal bones from archaeological sites”, edited by Bob Wilson, Caroline Grigson and Sebastian Payne, represented a milestone in the development of zooarchaeological studies, and the book is, unsurprisingly, one of the most cited publications in zooarchaeology. Since then, as Terry O’Connor highlights in his introduction to the present

volume, much more work has been done in refining ageing and sexing methods and in improving our understanding of body development and sexual variation in the vertebrate skeleton. However, so far zooarchaeologists are still by and large adopting ageing and sexing methods that are pre- rather than post- 1982. The challenge of this book is therefore not just to add more information, but also to persuade zooarchaeologists that the time is ripe for experimenting with new methods and for analysing data by taking into account the substantial new advances that this discipline has produced in more recent years. Only time will tell if this volume will have achieved this ambitious goal, but whatever the case, we have little doubt that it will represent an indispensable tool for zooarchaeologists worldwide.

Final special thanks must go to Vasili and Marilena Cosmopoulos (Deborah’s son and daughter), who had the good grace to be born during the final stages of the editing of this volume. We could not have expected a better omen for the success of the book.

Acknowledgments

These proceedings are a direct result of the teamwork and collegiality of the authors involved. Always polite and accommodating, the participants of the Ageing and Sexing Session were a pleasure to work with, and I thank them for their cooperation and their contributions to methodology in zooarchaeology. The participants of the session also acted as referees of the published proceedings; each participant reviewed two papers submitted for publication to ensure the quality and accuracy of the information presented herein. For the sake of keeping costs low, raw data for the various studies presented in this volume could not be published. The authors are happy to provide raw data from their research upon request (addresses provided at the end of each chapter).

The session would not have been such a success were it not for the tireless support and direction of the conference organizers. This publication was made possible by these same individuals who also bravely took on the series

editing and organization after the conference ended. On behalf of all the participants of the Ageing and Sexing Session, I wish to express our appreciation for the commitment of Umberto Albarella, Keith Dobney, Peter Rowley-Conwy and Deborah Jaques for the conference preparations and publication series organization. I would also like to thank Simon Davis and Caroline Grigson for chairing the morning and afternoon sections of the ageing and sexing colloquium, and also for acting as referees for some papers submitted here.

Travel and accommodation grants for the participants were supplied thanks to generous funding from the Institute for Aegean Prehistory (INSTAP). We are grateful for their support and their broad vision of archaeological research. INSTAP is one of the few organizations that realize the potential of zooarchaeological studies in the quest of studying ancient peoples.

6. Reconciling Rates of Long Bone Fusion and Tooth Eruption and Wear in Sheep (*Ovis*) and Goat (*Capra*)

Melinda A. Zeder

Age determination by long bone fusion and tooth eruption and wear patterns are methods used by zooarchaeologists around the world to build mortality profiles of archaeofaunas. These profiles, in turn, are used to reconstruct hunting and herding strategies fundamental to understanding the lifeways of people of the past. However, the empirical grounding for these techniques is shaky at best. Base-line studies rates of long bone fusion and tooth eruption and wear in caprines are generally based on known age populations of domestic breeds of sheep and goats that may not be an entirely appropriate model of ancient wild and early domestic animals. In this study, a large collection of mostly wild modern sheep and goats from Iran and Iraq is examined with the aim of addressing a number of core questions about the comparability of these methods for constructing mortality profiles in ancient caprines. The study helps to resolve open questions about the sequence and timing of epiphyseal long bone fusion in sheep and goats, and both confirms and refines widely used tooth eruption and wear sequences. It also finds systematic differences in the reconciliation of fusion and dental based aging sequences between sheep and goats and males and females that are likely related to differences in the rate of tooth attrition.

Introduction

The reconstruction of mortality profiles of animal remains from archaeological sites is a fundamental tool in zooarchaeological analysis. Sheep and goat mortality profiles, in particular, play a central role in the examination of a wide range of problems, ranging from the transition from hunting to herding to the development of specialized pastoral economies. As a result there is a special premium placed trying to achieve the greatest amount of verisimilitude possible when developing methods for the reconstruction of caprine mortality profiles. The literature is replete with studies aimed at providing a firm empirical basis for fixing age at death of sheep and goat from remains they leave behind in archaeological sites, whether they be teeth or post-cranial bones. For years zooarchaeologists have been peering into the mouths of living sheep and goats, rummaging through out-of-the-way collections of modern caprine skeletons, even scouring obscure 18th century records to determine the precise sequence and timing of long bone fusion and tooth eruption and wear

in order to provide a more accurate standard for the reconstruction of mortality profiles of ancient sheep and goats.

This study represents one more contribution to this general effort. Like other studies of this nature it is based on a large collection of modern skeletal remains of sheep and goats. Unlike earlier work that used skeletal material from domestic breeds or so called feral animals of domestic ancestry, this study focuses on a collection comprised primarily of wild animals from Iran and Iraq, the general region where initial domestication of these animals took place. As a result, this unique collection offers information on the sequence of bone fusion and the patterns of tooth eruption and wear in caprines closer to their natural state, before the development of genetically improved breeds raised under conditions far removed from those of ancient wild and domestic sheep and goats. Specific questions asked of this collection are: 1. What is the sequence of long bone fusion in these wild caprines, are there systematic differences between sheep and goat

fusion patterns, and how do the patterns derived for this study compare with both the sequence and age class groupings of long bone fusion of previous studies; 2. What is the sequence of tooth eruption and wear in these animals, are there differences between sheep and goat in these patterns, and how do these patterns relate to previous work; and, finally, 3. What is the correlation between long bone fusion patterns and tooth eruption and wear sequences in both sheep and goats and are there any systematic differences between these two key species, between different sexes of sheep and goats, or between animals from different collecting localities.

The Sample

The sample of sheep and goat remains studied is curated by the Zoology Department of the Field Museum of Natural History in Chicago and was examined over five different research visits between 1996 and 2003. Many of these animals were collected from wild herds during several expeditions to Iran headed by then FMNH curator Douglas Lay (Lay 1967). Other specimens, including all the domestic specimens, were donated to the museum by Charles Reed, who collected these animals while a member of the Braidwood archaeological expeditions to north western Iraq and north eastern Iran (Fig. 1). A total of 39 goat specimens are included in this study, 37 of which are identified as wild bezoar goat (*Capra aegagrus*, species names follow the new rulings of the International Council for Zoological Nomenclature (2003)), and two of which represent unimproved domestic breeds of goats (*Capra hircus*) kept by local villagers. The goat sample includes 22 males and 17 females from six different collecting localities running from north to south along the spine of the Zagros, from the Caspian Sea to the Persian Gulf (Fig. 2).

The sheep sample consists of 61 animals, including 41 Asiatic mouflons (*Ovis orientalis*) and 15 urials (*Ovis vignei*) (Fig. 3), a more eastward member of the great arc of wild sheep (Clark 1964) collected around the shores of the Caspian Sea where they are known to readily hybridize with mouflons (Valdez *et al.* 1978). Five of the sheep specimens belong to a domestic fat tailed breed (*Ovis aries*) raised throughout the region by both nomadic and village herders. There are 30 females and 31 males in the sample. Six of the sheep collecting localities overlap with those for the goats. Four wild sheep specimens were collected in Baluchistan in far southeastern Iran (Fig. 1).

No estimate of age at death was made for any of the wild hunted specimens. Nor was there information recorded on the age at death of any of the domestic caprines included in the sample. There were no castrates in the sample. Pathologies were noted on four of the specimens.

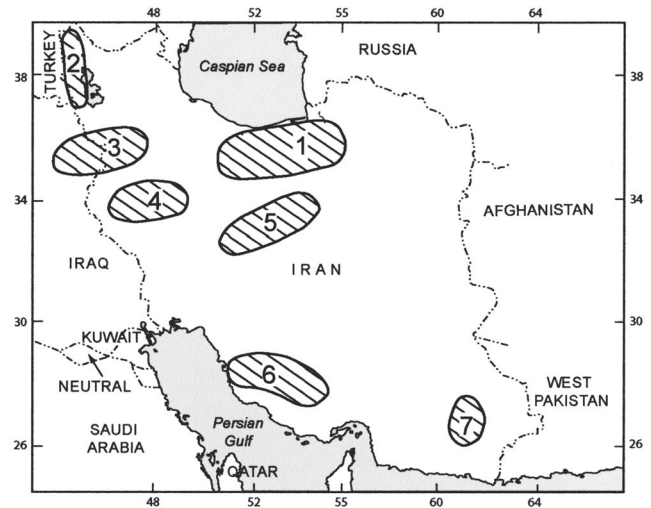


Fig. 1. Collecting localities of sheep and goats used in this study.

Long Bone Fusion

Previous studies

A number of previous studies have focused on trying to determine the sequence and timing of long bone fusion in sheep and goats (Figs 4 and 5; also see Moran and O'Connor 1994, 272–275 for a comprehensive summary of previous studies of epiphyseal fusion and tooth eruption and wear in sheep). Perhaps the best known and most widely used of these is included in the landmark article by Silver (1969). Silver based his work on a variety of sources, including 18th and 19th century records. No sample sizes or raw data are provided in this work that might allow for an assessment of the empirical robustness of this sequence. Other studies of epiphyseal fusion in domestic sheep include Garcia-Gonzalez's (1983) examination of Aragon sheep and Hattling's (1981) study of Gotland sheep. In a more recent study, Moran and O'Connor (1994) examined more than 150 animals, representing mixture of breeds from 'primitive' to modern crossbreeds housed in skeletal collections in Britain and Denmark. Males, females, and castrates were included in the sample. Data from castrates were excluded in compiling the fusion sequences and ages shown in Figs 4 and 5 since castration is known to have a profound impact on epiphyseal fusion in sheep and goats (Moran and O'Connor 1994; Davis 2000). Studies of goat epiphyseal fusion include Noddle's (1974) study of 54 domestic goats of mixed breeds and 20 feral goats culled from flocks in Britain, and Bullock and Rackham's (1982) study of 25 British feral goats.

While there is rough agreement in the sequence and, less so, in the timing of epiphyseal fusion reported in these various sources, there are also significant differences

FMNH Number	Species	Sex	Region ¹	Fusion Group	Fusion Rank ²	Dental Group	Dental Rank ²
97911	<i>C. aegagrus</i>	F	1	B	3	IV	5
97912	<i>C. aegagrus</i>	F	1	B	4	IV	4
58018	<i>C. aegagrus</i>	M	1	G	35	XI	35
97908	<i>C. aegagrus</i>	M	1	E	21	V	7
97910	<i>C. aegagrus</i>	M	1	C	9	V	10
97931	<i>C. aegagrus</i>	M	1	G	39	nd	nd
112505 ³	<i>C. aegagrus</i>	F	2	D	18	I	1
99029	<i>C. aegagrus</i>	F	2	G	38	X	34
97913	<i>C. aegagrus</i>	M	2	D	14	VI	16
97914	<i>C. aegagrus</i>	M	2	C	7	V	8
44472	<i>C. aegagrus</i>	F	3	E	28	VII	19
84483	<i>C. hircus</i>	F	3	D	15	V	12
84486	<i>C. aegagrus</i>	F	3	G	34	nd	nd
35676	<i>C. aegagrus</i>	M	3	G	37	X	32
44466	<i>C. aegagrus</i>	M	3	F	33	nd	nd
57253	<i>C. hircus</i>	M	3	D	12	V	15
84485	<i>C. aegagrus</i>	M	3	C	8	V	14
92920	<i>C. hircus</i>	F	4	E	26	IX	30
92921	<i>C. aegagrus</i>	F	4	E	25	VII	22
92922	<i>C. aegagrus</i>	F	4	D	17	V	11
92923	<i>C. aegagrus</i>	F	4	E	29	VII	23
92924	<i>C. aegagrus</i>	M	4	C	6	IV	6
92925	<i>C. aegagrus</i>	M	4	E	22	VIII	29
97919	<i>C. aegagrus</i>	F	5	E	23	VII	18
97930	<i>C. aegagrus</i>	F	5	D	20	VIII	27
97916	<i>C. aegagrus</i>	M	5	A	2	III	2
97917	<i>C. aegagrus</i>	M	5	D	11	V	9
97920	<i>C. aegagrus</i>	M	5	A	1	III	3
97929	<i>C. aegagrus</i>	M	5	D	16	VIII	26
57949	<i>C. aegagrus</i>	F	6	E	27	VII	24
97921	<i>C. aegagrus</i>	F	6	F	31	VII	21
97925	<i>C. aegagrus</i>	F	6	G	36	VII	20
97926	<i>C. aegagrus</i>	F	6	F	30	VIII	28
57935	<i>C. aegagrus</i>	M	6	D	19	VII	25
57937	<i>C. aegagrus</i>	M	6	D	13	VI	17
57938	<i>C. aegagrus</i>	M	6	C	5	V	13
57943	<i>C. aegagrus</i>	M	6	E	24	X	33
97924	<i>C. aegagrus</i>	M	6	F	32	IX	31
97927	<i>C. aegagrus</i>	M	6	D	10	nd	nd

Fig. 2. FMNH Goat Sample (*Capra* sp.). ¹ = Collecting localities are shown in fig. 1, ² = Age order from youngest to oldest, ³ = Mismatch between mandible and post-cranial.

among them. All fusion schemes suggest that there are generally four general stages of epiphyseal fusion that roughly correspond to the first four years of life. However, the sequence, timing, and sometimes even the bones included in each of the four fusion groups vary. The earliest group of fusing bones in all schemes (Fusion Group A in Figs 4 and 5) is comprised of bones that fuse in the first year of life. In most sources, Group A includes the proximal radius, the glenoid process of the scapula, the acetabulum of the pelvis, and the distal humerus, but the sequence of fusion varies from study to study. Moreover, while all sources agree that these bone fuse sometime in the first year of life, both Hatting and Garcia-Gonzalez set the fusion of these bones within the first six months of life, while Silver places fusion of all of these elements in the second six months. In the fusion schemes of Moran and O'Connor and in Noddle, the proximal radius is the earliest fusing bone, fusing within the first

six months of life, while the remaining elements in this group fuse in the second six months.

The second general fusion group (B) usually includes the first and second phalanx, although Noddle also includes the scapula and the distal humerus in this group. Most authors put the fusion age of these bones at between about 11 to 16 months. Once again, however, both Hatting and Garcia-Gonzalez cite earlier ages of fusion for these bones (between five to nine months), while Bullock and Rackham give the oldest ages of fusion at somewhere between 12 and 35 months of age.

Group C in most schemes contains the distal tibia and both distal metapodials, although there is variation in bones included in this group, as well as in the sequence and timing of their fusion. Most authors place the fusion of the distal tibia somewhat earlier than the distal metapodials. However, Silver maintains that the distal tibia and the distal metacarpal both fuse at about the

FMNH Number	Species	Sex	Region ¹	Fusion Group	Fusion Rank ²	Dental Group	Dental Rank ²
58015	<i>O. vigne</i>	F	1	G	55	XI	53
58019	<i>O. vigne</i>	F	1	F	43	VI	32
58020	<i>O. vigne</i>	F	1	C	9	IV	8
58024	<i>O. vigne</i>	F	1	D	18	IV	12
58063	<i>O. vigne</i>	F	1	E	28	V	14
58091	<i>O. vigne</i>	F	1	E	26	V	19
152003	<i>O. vigne</i>	F	1	E	23	V	21
58014	<i>O. vigne</i>	M	1	D	17	V	18
58021	<i>O. vigne</i>	M	1	D	12	V	15
58022	<i>O. vigne</i>	M	1	C	10	IV	11
58062	<i>O. vigne</i>	M	1	G	61	IX	46
58064	<i>O. vigne</i>	M	1	G	51	X	50
58089	<i>O. vigne</i>	M	1	G	52	VII	36
152002	<i>O. vigne</i>	M	1	G	49	nd	nd
152004	<i>O. vigne</i>	M	1	G	53	nd	nd
58039	<i>O. orientalis</i>	F	2	D	13	IV	6
58045	<i>O. orientalis</i>	F	2	G	60	X	51
58047	<i>O. orientalis</i>	F	2	E	29	V	20
58048	<i>O. orientalis</i>	F	2	F	34	VII	37
58057	<i>O. orientalis</i>	F	2	B	3	II	1
58058	<i>O. orientalis</i>	F	2	F	32	V	22
58065	<i>O. orientalis</i>	F	2	F	39	V	16
58069	<i>O. orientalis</i>	F	2	B	2	II	2
58070	<i>O. orientalis</i>	F	2	G	54	VII	40
58071	<i>O. orientalis</i>	F	2	G	44	IX	47
152006	<i>O. orientalis</i>	F	2	F	35	nd	nd
152008	<i>O. orientalis</i>	F	2	D	14	nd	nd
58035	<i>O. orientalis</i>	M	2	F	37	VII	42
58036	<i>O. orientalis</i>	M	2	G	50	IX	48
58037	<i>O. orientalis</i>	M	2	E	30	VI	33
58038	<i>O. orientalis</i>	M	2	D	15	V	17
58040	<i>O. orientalis</i>	M	2	D	20	V	13
58041	<i>O. orientalis</i>	M	2	G	58	XII	54
58042	<i>O. orientalis</i>	M	2	G	46	VII	39
58043	<i>O. orientalis</i>	M	2	F	36	VII	43
58044	<i>O. orientalis</i>	M	2	D	16	VI	26
58046	<i>O. orientalis</i>	M	2	G	57	nd	nd
58072	<i>O. orientalis</i>	M	2	A	1	II	3
152007	<i>O. orientalis</i>	M	2	F	40	nd	nd
58031	<i>O. orientalis</i>	F	3	G	56	IX	49
58033	<i>O. orientalis</i>	F	3	F	33	V	23
58034	<i>O. orientalis</i>	F	3	G	43	VII	38
152005	<i>O. orientalis</i>	F	3	G	47	VIII	44
57254	<i>O. aries</i>	M	3	C	6	IV	9
57255	<i>O. aries</i>	M	3	E	24	VI	28
58032	<i>O. orientalis</i>	M	3	E	25	VI	31
58094	<i>O. aries</i>	M	3	C	5	IV	7
84488	<i>O. orientalis</i>	M	3	C	8	IV	10
92927	<i>O. aries</i>	F	4	D	22	nd	nd
92928	<i>O. aries</i>	F	4	G	59	X	52
98161	<i>O. orientalis</i>	M	4	F	38	VI	34
98162	<i>O. orientalis</i>	M	4	D	19	VI	29
97957	<i>O. orientalis</i>	F	5	G	48	VI	35
97958	<i>O. orientalis</i>	F	5	E	31	VI	27
97959	<i>O. orientalis</i>	F	5	C	7	III	5
97960	<i>O. orientalis</i>	M	5	D	21	VI	25
97973	<i>O. orientalis</i>	M	6	G	45	VIII	45
97985	<i>O. orientalis</i>	F	7	E	27	VI	30
97986	<i>O. orientalis</i>	F	7	B	4	III	4
97983	<i>O. orientalis</i>	M	7	F	41	VII	41
97984	<i>O. orientalis</i>	M	7	D	11	VI	24

Fig. 3. FMNH Sheep Sample (*Ovis* sp.). ¹ = Collecting localities are shown in fig. 1, ² = Age order from youngest to oldest.

Silver (1969) Sheep				Hatting (1981) Gotland Sheep				Garcia-Gonzalez (1983) Aragon Sheep				Moran and O'Connor (1994) Various European Sheep Breeds			
Group	Bone ¹	Order ²	Age ³	Group	Bone	Order	Age	Group	Bone	Order	Age	Group	Bone	Order	Age
A	Scap	1	6–8	A	P.Rad	1	2–4	A	P.Rad	1	1.5–3	A	P.Rad	1	4.5–6
A	Pelvis	2	6–10	A	D.Hum	1	2–4	A	D.Hum	2	2–4	A	Scap	2	6–9
A	P.Rad	3	10	B	1 Phl	2	6–9	A	Scap	3	3–4	A	D.Hum	3	6–10.5
A	D.Hum	3	10	C	D. Tib	3	13–15	B	2 Phl	4	5–7	B	2 Phl	4	11–12
B	1 Phl	4	13–16	C	Calc	4	15–17	B	1 Phl	5	6–8	B	1 Phl	4	11–12
B	2 Phl	4	13–16	C	D.Mc	5	15–22	C	D.Tib	6	12–15	C	D.Tib	5	13–23
C	D. Tib	5	18–24	C	D.Mt	6	15–23	C	D.Mc	7	12–18	C	Calc	6	13–30
C	D. Mc	5	18–24	C	P.Fem	6	15–23	C	D.Mt	7	12–18	C	D.Mc	7	15–24
C	D. Mt	6	20–28	C	D.Fem	6	15–23	C	Calc	7	12–18	C	P.Ulna	8	15–30
D	Calc	7	30–36	D	D.Rad	7	15–30	D	P.Ulna	8	18–30	C	D.Mt	8	15–30
D	P. Ulna	8	36	D	P.Tib	7	15–30	D	P.Fmr	9	18–36	D	P.Fmr	9	23–36
D	P. Fmr	8	36	D	P.Hum	8	24–30	D	D.Rad	9	18–36	D	D.Rad	10	23–40
D	D.Rad	8	36	–	Scap	nd	nd	D	P.Tib	10	24–36	D	D.Fmr	11	24–40
D	P.Tib	9	36–42	–	Pelvis	nd	nd	D	D.Fmr	10	24–36	D	P.Hum	12	36–42
D	D.Fmr	9	36–42	–	2 Phl	nd	nd	D	P.Hum	11	30–42	D	P.Tib	13	36–45
D	P.Hum	9	36–42	–	P.Ulna	nd	nd	–	Pelvis	nd	nd	–	Pelvis	nd	nd

Fig. 4. Fusion sequences and ages of fusion from previous studies on sheep. ¹ = Abbreviations for elements, Scap – scapula, P.Rad – proximal radius, D.Hum – distal humerus, 1 Phl – first phalanx, 2Phl – second phalanx, D.Tib – distal tibia, D.Mc – distal metacarpal, D.Mt – distal metatarsal, P.Ulna – proximal ulna, Calc – calcaneus, P.Fmr – proximal femur, D.Rad – distal radius, P.Tib – proximal tibia, D.Fmr – distal femur, P.Hum – proximal humerus; ² = Order of fusion from earliest to latest, ³ = Age in months.

Noddle (1974) British Breeds and Feral Goats				Bullock and Rackham (1982) British Breeds and Feral Goats			
Group	Bone	Order	Age	Group	Bone	Order	Age
A	P.Rad	1	4–9	A	P.Rad	1	< 12
B	Scap	2	9–11	A	D.Hum	1	< 12
B	2 Phl	3	9–12	A	Scap	2	~ 12
B	1 Phl	4	11–12	A	Pelvis	2	~ 12
B	D.Hum	5	11–13	B	1 Phl	3	> 12 < 35
C	D.Tib	6	19–24	B	2 Phl	3	> 12 < 35
C	D.Mc	7	23–24	C	D.Tib	4	~ 36
C	D.Mt	7	23–24	C	D.Mc	5	~ 48
D	P.Fmr	8	23–36	C	D.Mt	5	~ 48
D	P.Tib	8	23–36	C	P.Fmr	5	~ 48
D	Calc	9	23–48	C	D.Fmr	5	~ 48
D	D.Fmr	9	23–48	D	Calc	6	> 48 < 60
D	P.Hum	9	23–48	D	D.Rad	7	> 47 < 71
D	D.Rad	10	33–48	D	P.Tib	7	> 47 < 71
–	Pelvis	nd	nd	D	P.Hum	8	> 47 < 83
–	P. Ulna	nd	nd	D	P.Ulna	9	~ 71

Fig. 5. Fusion sequences and ages of fusion from previous studies on goats. (Abbreviations concur with fig. 4).

same time, slightly earlier than the metatarsal. Both studies by Hatting and Moran and O'Connor place the fusion of the tuber calis of the calcaneus between the fusion of the distal tibia and the distal metacarpal. Moran and O'Connor also include the proximal ulna in this group, while others place it with later fusing bones. Hatting and Bullock and Rackham include the proximal and distal femur in this group, fusing at about the same time as the distal metapodials.

While all sources put the fusion of Group C bones at greater than 12 months of age, there is considerable variation in the start and end ages given for the fusion of these bones. Once again, Garcia-Gonzalez reports some

of the youngest ages, maintaining that all bones in this group fuse between 12 to 18 months of age. Hatting also reports an early start date for the fusion of bones in this group, with fusion beginning between 13 to 15 months for the distal tibia and calcaneus and completed by 23 months for the distal metapodials and the proximal and distal femur. Moran and O'Connor also put the start date for fusion of these bones at about 13 to 15 months, but give a later completion date of between 24 to 30 months. Silver and Noddle place the fusion of the bones in this stage at between about 18 to 28 months. Once again Bullock and Rackham report the oldest ages of fusion for the bones in this group, maintaining that distal tibia

fuses at about 36 months, and the metapodials and the proximal and distal femur at about 48 months.

The latest fusion group, Group D, is also the largest and most variable. Bones included in the latest fusion stage are generally the calcaneus, the proximal and distal femur, the distal radius, the proximal tibia, and the proximal humerus. In some sources this group might be further sub-divided into slightly earlier and slightly later fusing elements, although there is little agreement over the bones included in these sub-groups or their age at fusion. There is also a considerable amount of overlap in start and end dates of fusion among these later fusing bones. In Silver's scheme, the proximal ulna, calcaneus, proximal femur, and distal radius fuse between about 30 to 36 months of age, while the proximal tibia, distal femur, and proximal humerus are the latest fusing bones, at about 36 to 42 months. In Hatting, the distal radius and proximal tibia fuse between 15 to 30 months, while the latest fusing bone is the proximal humerus, which fuses between 24 and 30 months. Garcia-Gonzalez's scheme places the fusion of the proximal ulna, the proximal femur, and the distal radius between 18 to 36 months, while the start point for fusion of the proximal tibia and the distal femur is put at 24 months and the end date at 36 months. As in Hatting, Garcia-Gonzalez's scheme has the proximal humerus as the latest fusing bone, with fusion set at 30 to 42 months. In Moran and O'Connor, the earlier fusing bones in this final stage are the proximal femur, the distal radius, and the distal femur, which fuse between about 23 to 42 months. The latest fusing bones in this fusion scheme are the proximal humerus and proximal tibia, which are reported to fuse between 36 to 45 months.

Among Noddle's goats (Fig. 5) the earlier fusing bones in this final stage are the proximal femur and the proximal tibia, both of which are said to fuse between 23 to 36 months. The calcaneus, distal femur, and the proximal humerus are next with fusion ages set between 23 to 48 months and the latest fusing bones is the distal radius, which is reported to fuse between 33 and 48 months. Bones included in this final fusion stage in Bullock and Rackham's scheme are the calcaneus, distal radius, proximal tibia, and proximal humerus, all of which are said to fuse sometime after about 47 months of age. Fusion of the proximal ulna is said to occur at about 71 months, while the proximal humerus fuses sometime between 48 to 83 months.

Given the mix of different samples on which these different fusion schemes are based, it is difficult to pinpoint the source of variability in the sequence and timing of epiphyseal fusion among them. There are several factors that might be at work here. Genotypic differences between different taxa (sheep and goats) and breeds of animals might be expected to affect both the sequence and, to a large degree, the timing of bone fusion. Phenotypic factors are also likely to have some impact on epiphyseal fusion. In particular, variation in nutrition,

either resulting from differences in pasture and fodder quality or variations in the age at weaning (or both), are especially likely to have an effect on the rate or timing of bone fusion. In addition, while castrates were excluded from the data presented here, differences in the sex of animals included in the various samples may have played some role in the ages of fusion (Moran and O'Connor 1994, 273). It is also possible that pure stochastic variation between these samples, which are of widely varying size and composition, may play some role here.

A more superficial examination of these data might suggest that taxon plays the major role in the timing, if not the sequence, of bone fusion, with goats tending to have more delayed epiphyseal fusion than sheep. However, it is important to note that a number of the goats in both Noddle's sample and all the goats studied by Bullock and Rackham were feral animals that probably had a much lower plane of nutrition than the improved breeds of Gotland and Aragon sheep used in the Hatting and the Garcia-Gonzalez samples. Nutritional deficiencies, especially those early in life, are known to result in delays in epiphyseal fusion (Palsson and Verges 1952, cited in Moran and O'Connor 1994, 274). In this light, the somewhat older ages of fusion given for the sheep on which the Silver and the Moran and O'Connor schemes are based may stem from the inclusion of 'semi-wild' and 'primitive' breeds of animals in both these samples that might be expected to have a somewhat lower plane of nutrition.

The FMNH caprines

For a number of reasons, the sheep and goats included in the Field Museum of Natural History's collections provide a more directly comparable modern analog for the ancient populations of caprines that are of interest to archaeologists. First, even the 'primitive' breeds and feral animals included in other studies of this nature represent the end-point of millennia of selective breeding by humans. This is not a problem with the FMNH sample, which is largely comprised of wild animals. Second, while progressive degradation of the natural habitat of these wild caprines has undoubtedly had some nutritional impact, the feeding regimes of these animals are still more likely to be closer to those of ancient wild and early domestic animals from this region. Even the handful of domestic animals in the sample were derived from unimproved breeds, raised by local villagers or by migrating nomadic tribesmen, that occupied the same general region and roughly the same kinds of pasture as the wild animals in the sample. In contrast, modern European breeds are likely to receive improved fodder or other nutritional supplements, or be subject to accelerated weaning schedules, that can have a profound impact on rates of bone fusion (Moran and O'Connor 1994, 274). Third, comparisons between sheep and goat are also easier

to make with this sample given the general overlap in the collecting localities for these animals. Finally, the almost even representation of males and females in both the sheep and goat samples allows for control of any sex-linked bias. There are no castrates in either the wild or the domestic specimens eliminating any concern over resultant delays in fusion in castrated animals. The major limitation of the sample is the lack of independent information on the age of death of the different animals.

Fusion data for the FMNH goats and sheep are presented by specimens in Fig. 6 (for goats) and Fig. 7 (for sheep) in the Appendix. Four different possible fusion states were identified. Bones were scored as unfused (*U*) if the epiphysis was clearly separate from the diaphysis, even if remaining tendons and tissue held the two together. They were scored as early fusion (*J*) if there were signs of fusion but the junction between the epiphysis and the diaphysis was still partly open. Bones were scored as in late fusion (*L*) if the epiphysis and diaphysis were tightly joined, but there was still a faint line of fusion evident, and as fused (*F*) if the epiphysis and diaphysis were tightly joined and the line of fusion no longer apparent. Specimens were ranked and ordered from youngest to oldest on the basis of the number of unfused elements and the status of the fusing and fused bones. General fusion stages were then determined for both the goat and the sheep samples based on an assessment of the patterning seen in the individual specimens (Figs 6–14 in Appendix).

Although there is some variability, especially in later fusing bones, the same seven general fusion groups were evident in both sheep and goats. Group A (Fig. 8) is reserved for specimens in which the proximal radius is in early fusion. The acetabulum of the pelvis was also in early fusion in one of the goat specimens placed in Group A and the distal humerus was in early fusion in the sheep specimen. However, these bones were also undergoing early fusion in other specimens of sheep and goats in which the proximal radius was in late fusion, indicating that the proximal radius fuses at a slightly earlier point than these other bones and merits being placed in its own fusion group.

In Group B (Fig. 9), the proximal radius is in late fusion while the pelvis, the glenoid process of the scapula, and distal humerus are generally in early fusion. All other elements are unfused. In Group C (Fig. 10) the second and first phalanges come into play, while earlier fusing bones are mostly in either late fusion or fully fused. All other bones are unfused, save for three goat specimens where the radius and ulna were identified as fusing together, although it is sometime difficult to assess the state of fusion of these bones in less cleaned specimens. The phalanges were grouped together into a single fusion stage because they seem to fuse at a distinctly different time than all other bones. When these two bones are fusing, all other earlier fusing bones are either in late fusion or fused, and all later fusing bones are unfused.

However for both the goats and sheep, it is clear that the second phalanx fuses before the first phalanx.

Group D (Fig. 11) centers on the fusion of the distal tibia, distal metacarpal, and the distal metatarsal. Once again, while the fusion of these three bones seems to happen in a distinct period of time between both earlier and later fusing bones, they do not all fuse at the same time. In both sheep and goats the distal tibia fuses slightly earlier than the metapodials, which fuse at about the same time. In some of the goats the radius and the ulna were also beginning to fuse together at this point, though in other specimens these bones fused at the same time as bones included in age class C, and in still others, the fusion of the ulna to the radius happened at the same time as the fusion of other later fusing bones. The radius and the ulna were never fused in any of the sheep examined, regardless of age. Given the longer period of time over which these bones fuse together in goats, and the fact that they never seem to fuse in sheep, the fusion of the radius and ulna is not included in the fusion scheme presented here. It is important to note, however, that in most goats the radius and the ulna only really begin to fuse at about Stage D or E. Therefore, using the lack of fusion of a radius to an ulna as a means of distinguishing sheep from goat bones is not acceptable. A radius or ulna that is found unfused to its companion bone might as easily be a goat killed before it reached these later fusion stages as a sheep.

Fusion patterns are a little less clear cut in Group E (Fig. 12), which includes the tuber calis of the calcaneus, the proximal and distal femur, the proximal ulna, the distal radius, and the distal tibia. As was done for earlier fusion groups, these bones were grouped together because they come into fusion after all other earlier fusing bones are either fully fused or in late fusion. Among the goats there is little apparent consistency in the sequence in which these bones fuse, although there is some suggestion that the calcaneus tends to fuse a bit earlier than the other bones included in Group E. Among the sheep the calcaneus is clearly the first in this group to fuse, followed by the proximal femur (both the caput and the trochanter), distal femur, and the proximal ulna, with the distal radius and the proximal tibia the last to fuse among this group of bones. It is not clear if the difference between sheep and goats in the sequence of fusion of bones included in this fusion stage is an artifact of the FMNH sample (i.e. there is a great range of ages in the sheep that fall into this general stage, while the goats in the sample are all closer in age), or a real difference in the sequence of epiphyseal fusion of sheep and goats. Regardless, what is clear is that in both sheep and goats the fusion of these bones occurs at a distinct phase of an animal's life.

Group F (Fig. 13) is reserved for specimens whose proximal humerus is entering early fusion. The fusion of the proximal humerus is separated from the other later fusing bones because its fusion seems to be somewhat delayed. In both sheep and goat there are a number of

specimens in which all the bones included in the earlier age class E are either in early or late fusion, while the proximal humerus remains unfused. Once the proximal humerus enters early fusion, the bones included in Group E are generally either in early or late fusion, and all other earlier fusing bones are fully fused.

The final fusion stage, Group G (Fig. 14), is reached when the proximal humerus is in either late fusion or fully fused. Once the proximal humerus reaches this advanced phase of fusion, the bones included in Fusion Group E are also either in late fusion or fully fused, while all other earlier fusing elements are fully fused.

Fig. 15 presents the revised fusion sequence for sheep and goats based on the FMNH collections. This fusion scheme varies from earlier ones primarily in the details of the order of bone fusion and the number of fusion groups defined. While earlier fusion schemes all seemed to recognize four general fusion groups, there are seven groups evident in the FMNH data. The extra groups are gained by splitting the earliest fusion group in other schemes into two separate groups (A and B), with Group A based on the fusion of the proximal radius and Group B based on the fusion of the scapula, pelvis, and distal humerus. The large group of late fusing bones that constitute Group D in most sources is divided into three groups with the addition of two final age classes based on the fusion of the proximal humerus (F and G).

The sequence of fusion of these different elements is remarkably consistent across this large sample of animals with no apparent variation between male and female caprines or between animals from different collecting localities. The few domestic specimens in the sample also show no variation in sequence of epiphyseal fusion from the wild ones. Moreover, with the exception of the large group of bones in Group E, the sequence of bone fusion is remarkably consistent in both sheep and goats. And even this later fusion group includes the same suite of bones. The only possible difference here is that in sheep the distal radius and the proximal tibia seem to enter early fusion slightly earlier than the proximal and distal femur and the proximal ulna. In goats these bones seem to fuse as a group in no particular order. But again this may be more an artifact of the sample used than real difference in the sequence of late fusing bones in sheep and goats.

Without independent information on the age of the FMNH caprines, the age ranges of the different fusion stages identified here cannot be determined with any certainty. Using earlier studies based on domestic sheep and goats is problematic for reasons discussed above. However, if one extrapolates from these earlier studies based on known age specimens, a rough hypothetical aging scheme can be offered and used as grounds for comparison to ages derived from the analysis of tooth eruption and wear of the same specimens. The ages offered in Fig. 15 for the various fusion stages identified in the FMNH collection draw principally from Silver,

Moran and O'Connor, and Noddle. Hatting and Garcia-Gonzalez's aging schemes are given less weight since both seem quite young compared to other sources, perhaps because both are based exclusively on single breeds of sheep that may have a higher plane of nutrition than the mixed and feral animals included in other studies. By the same token, Bullock and Rackham's aging scheme is also given less weight in drawing the age estimates presented in Fig. 15. Age estimates provided by Bullock and Rackham are quite broad, probably a result of the spotty coverage of different age classes in their sample. In particular, the very late ages given for the later fusing bones are almost certainly an artifact of the sample on which the study was based. Given the lack of an unimpeachable empirical tether for these age estimates, and the range of ages given in the sources used, the ages assigned here are based on the half year increments which best correspond to the ages given in other sources. No attempt is made to assign ages for the final two fusion stages based on the degree of fusion for the proximal humerus. Group F is simply listed as older than the 48 month end point set for epiphyseal fusion of the bones in Stage E. Group G is similarly said to be older than Group F, with no attempt to fix a specific age range for point in which the proximal humerus enters late fusion or is at last fully fused.

Tooth Eruption and Wear

Previous studies

Dental aging systems for sheep and goats are based on a combination of genotypic and phenotypic factors that drive the eruption and wear of teeth. As with epiphyseal fusion, the sequence and timing of tooth eruption in sheep and goats are hard wired within the genetic code for each species, although variations in nutrition likely play some role in the timing of tooth eruption. By the same token, although there are likely genetically controlled factors that determine the pattern and rate of tooth attrition (i.e. tooth morphology and bio-mechanics of mastication), the primary factors determining tooth attrition are the types of pasturage and fodder consumed and, especially, the ingestion of soil along with pasturage (Moran and O'Connor 1994, 270). Constructing a reliable dental system for determining age at death, then, requires combining tooth eruption sequences that might be expected to be more universally found across closely related taxa, with attritional patterns more likely to vary among even closely related taxa raised under different conditions. Despite this somewhat awkward marriage of convenience, there is a surprising degree of agreement between dental aging systems that combine dental eruption and wear. Ages for the eruption of cheek teeth of sheep and goats cited in most studies of known age populations of sheep and goat are in remarkably close agreement (Fig. 16). As

was the case for epiphyseal fusion, differences in the timing of tooth eruption are most likely linked to differences in nutrition, with feral, 'rough', or 'semi-wild' animals with delayed eruption rates when compared to carefully tended 'improved' breeds. Even so, the overall agreement on the sequence and timing of tooth eruption is quite good. Even North American wild dall sheep (*Ovis dalli*) and the much more distantly related mountain goat (*Oreamnos americanus*) have eruption schedules that closely mirror domestic breeds of sheep and goat. An almost identical eruption schedule is documented in Himalayan Thar (*Hemitragus jemlahicus*) a species of wild goat introduced to the Southern Alps of New Zealand (Caughley 1965).

There are two commonly used systems for noting tooth wear in sheep and goats, that developed by Grant and the system devised by Payne. Grant's (1982) method is essentially a "floating" system that determines relative stages of wear of individual teeth, but does not provide the estimated ages at which these various stages are reached. In contrast, Payne's system (Payne 1973, Deniz and Payne 1982) looks at eruption and wear patterns across the mandible and is linked directly to age classes derived from studies of modern sheep from a village herd in central Turkey and, most significantly, on observations of tooth wear in living animals from an experimental herds of Angora goats under the care of the Turkish Ministry of Agriculture.

Subsequent applications of Payne's system to known age populations have resulted in some refinement of the methods for noting wear patterns (Payne 1987, Zeder 1985 and 1991), adjustment and sharpening of age stages (Jones, this volume), and cautionary notes about the reliability of older age classes (Moran and O'Connor 1994). Overall though, the Payne system has proven quite robust and reliable. In particular, Jones' remarkable work with living British sheep published here goes a long way toward demonstrating the validity of both the sequence of tooth wear patterns identified in this earlier work and the ages at which these stages of wear are generally reached. Fig. 17 presents the age classes defined in Payne's system using the notational system developed by Zeder (1985 and 1991). The correlation between Zeder's notational system and that published by Payne in 1987, as well as its correlation with Grant's system, is provided in Fig. 18.

Unlike Payne's notational system that assigns a different sequence of letters and numbers to the wear patterns for each tooth, Zeder's system assigns the same sequence of numbers to all teeth when they reach equivalent stages of wear. For example, in Zeder's system stage '09' is reserved for teeth when they just begin to show signs of wear, '17' is assigned to teeth worn to the point when either one or two enamel islands (depending on the number of cusps the tooth has) are isolated by dentine from the outer enamel covering of the tooth, and '25' is reserved for teeth where all internal enamel is worn away

and the occlusal surface contains nothing but dentine. In contrast, under Payne's system Zeder's stage '17' would be stage '9A' for the M1 and M2, or 11G for the M3, 14L for the dp4, or 9A, 9S, or 9T for the P4. Although perhaps less familiar, Zeder's system is followed here partly as a matter of convenience since it was the system used in the study of dental wear of the FMNH collections. This system also makes it easier to follow wear patterns across the jaw.

Payne system identifies nine different groups labeled A–I. In Zeder's notational system, the letters used to designate Payne's dental groups are replaced with roman numerals (I–IX). Again while Payne's dental groups may be more familiar, the Zeder system is used here to avoid confusion when contrasting longbone fusion groups with dental groups. In contrast to aging systems based epiphyseal fusion which only cover the first four to five years of life, dental age schema cover a much wider span – up to 10 or more years, which is essentially the entire life span of an animal. The first five dental groups (I–V following Zeder) are defined primarily on the basis of eruption and early wear stages deciduous and permanent teeth. Each of these early dental groups represents an increasingly longer span of time, ranging from 0–2 months for Group I to 2–3 years for Group V. Groups VI–IX are based solely on attrition of permanent premolars and molars. Once again, the age ranges represented by these groups also expand in duration in the later stages. Group V represents 2–3 year old animals, Group VIII represents 6–8 year olds, and the final group, Group IX represents animals in the range of 8–10+ years.

The FMNH caprines

Dental aging was applied to all sheep and goat specimens in the FMNH collection from Iran and Iraq that had both post-cranial and cranial bones. For the goats, this was 35 specimens (Figs 2 and 19), and 54 specimens for the sheep (Figs 3 and 20). Stages of cheek tooth eruption and wear were recorded for the right and left sides of the mandible using Zeder's notations. The system was also adapted for maxillary teeth, but these data are not reported here. As was done for the post-cranial epiphyseal fusion patterns, individual specimens of sheep and goats were ranked and ordered from youngest to oldest based on eruption and wear patterns, and then grouped into general dental age classes (Figs 19, 20 and 21–30).

Figs 21–30 present the FMNH dental data in a way that makes it easier to visualize eruption and wear patterns across the mandible for each dental group in both goats (on the left) and sheep (on the right). The deciduous and permanent cheek teeth are arrayed along the horizontal axis of the table, while the various wear stages are displayed on the vertical axis (Fig. 15, see Zeder 1991, 92 for the definition of these stages). Stages 02 through 08 represent eruption stages before the tooth begins to experience wear. Stage 09, highlighted in bold double

lines, represents the beginning of tooth wear on the mesial cusps. Stages 10 through 12 are early wear stages where enamel is just beginning to wear and dentine is first exposed on various cusps, while stages 13 through 17 represent more active wear stages in which progressive amounts of dentine exposed as individual cusps are joined together. Stage 17, in which central enamel islands are separated from the enamel covering the outside of the teeth by a sea of dentine (equivalent to Payne's long lived stage 9a for the P4, M1, and M2 and his 11G for the M3), is also highlighted by double bolded lines. Stages 18 through 26 represent late wear stages in which the remnants of enamel on the occlusal surfaces of the teeth are eroded away until they disappear altogether (stage 25) and the tooth is worn to the root (stage 26). The number of specimens with teeth in different wear stages is noted, with .5 representing a specimen in which teeth on the right and left of the jaw are in different states of wear. Shading covers the range of wear stages observed for the teeth of the individuals included in each age class. As with epiphyseal fusion patterns, dental eruption and wear patterns for sheep and goats are quite similar to one another. However, there are systematic differences between sheep and goats in all dental groups that suggest differences in mastication in these two species. Group I (Fig. 21) is present in only one very young goat in which the deciduous premolars are just entering early wear stages and the M1 is visible in the crypt but below the surface of the bone. Group II (Fig. 21), found in only three sheep specimens, is typified by deciduous premolars in more active wear, the M1 in later stages of eruption but either unworn or just beginning to wear, and the M2 visible in the crypt but not yet beginning to erupt.

There are both goat and sheep specimens represented in Group III (Fig. 22), which allows an initial look at differences in tooth wear patterns in these two species. Group III is defined by deciduous premolars in late wear stages (after stage 17), the M1 in active wear but before stage 17, and the M2 either just visible in the crypt or beginning to erupt, but still below the surface of the bone. Sheep vary from goats in that the dP2 is also entering late wear stages, while in the goats only the dP3 and dP4 are in these more advanced stages of wear and the dP2 is essentially unworn.

The deciduous premolars are in late or final stages of wear in Group IV (Fig. 23), although in some specimens the permanent premolars can be seen pushing up through the bone under the deciduous premolars. The M1 is in active wear reaching the keystone wear stage 17, the M2 is either erupting but not yet level with the other cheek teeth, or just entering early wear, and the M3 is usually still either only visible in the crypt or just beginning to erupt but still below the top of the surface of the mandible. In two goat specimens the M3 is further along in the eruption process, but still yet to come into wear. Once again the deciduous premolars of the sheep in this age class show more even wear across all teeth, with the dP2

worn in a similar fashion as the dP3 and dP4. In contrast in the goat the dP3 seems to take the brunt of attritional force, while both the dP4 and especially the dP2 are less worn.

Mandibles placed in Group V (Fig. 24) have permanent premolars entering more active wear stages. The M1 remains at stage 17, while the M2 is undergoing active wear but generally has yet to reach this plateau stage. The M3 is either still erupting or just entering early wear stages. In both sheep and goats the M1 seems to be experiencing the greatest degree of wear at this stage. However, as seen in earlier dental groups wear seems to be more evenly spread across the cheek teeth in sheep, while in goats the wear is more narrowly focused.

The majority of cheek teeth reach stage 17 during the subsequent Group VI (Fig. 25), when the P3, P4, M1, and M2 all reach this wear stage. The M3 is entering more active wear stages, with the M3 in sheep more likely to experience more wear than in goats.

The P3, P4, and, to a lesser extent, the M1 all breach this plateau stage of wear and enter later wear stages in Group VII (Fig. 26). The M2 remains at stage 17 and the M3 is still undergoing active wear leading up to stage 17. In sheep the M3 is more likely to reach stage 17, and the M1 is more likely to breach this stage. In goats wear seems more narrowly focused on the P3 and P4.

During Dental Group VIII (Fig. 27) the P3 through M1 reach stage 20 wear in which only a single isolated enamel island remains on the tooth. The M2 remains at stage 17 and the M3 is either at or close to stage 17. In the sheep the P2 might also reach the more advanced wear stage 20. In Group IX mandibles (Fig. 28) the M1 is in final stages of wear and may reach stage 25 in which all internal enamel is eroded from the tooth. The M2 and M3 may be either at stage 17 or beginning to breach this stage and enter the later wear stages. The premolars generally remain at stage 20, although in goats the P2 remains essentially unworn.

The P3 and P4 lose all traces of central enamel (stage 25) in the Group X mandibles (Fig. 29) and the M1 may be worn to the root (stage 26). Although the M2 may remain at stage 17, most are in the final stages of erosion of the central enamel islands. The M3 remains at stage 17. Once again the P2 in sheep is clearly undergoing more wear than in goats.

The final two dental groups (Fig. 30) are distinguished from one another by the wear of the M3. In Group XI all teeth but the M3 are worn to the root, while the M3 is in late wear. The M3s in Group XII mandibles are either devoid of any central enamel or worn to the root.

The dental groups represented in the FMNH caprines are directly analogous to the original Payne system (Figs 31 and 32). The only departure from this system is that two of the original dental groups can now be divided into two younger and older phases of wear. Zeder's old Group IV (Group D in Payne's system) can be divided into earlier and later dental groups (new groups IV and V).

Zeder's original Group VII (Payne's Group G) now becomes new dental groups VIII and IX. Figs 31 and 32 also gives age estimates for these various age classes by retaining the ages assigned to these wear classes by Payne (and subsequently empirically supported by other studies). In the case of the two new dental groups, the age range assigned to the original group is divided evenly. Original Group IV (Payne's D) which covered 12 to 24 months is now divided into Group IV (12–18 months) and Group V (18–24 months), and original Group VII (Payne's G) which covered 4 to 6 years, is divided into groups VIII (4–5 years) and IX (5–6 years).

It is important to remember that the assignment of ages to these dental groups needs to be treated as hypothetical since the true age of the FMNH caprines is not known. While these data strongly suggest that mandibular teeth in both sheep and goats follow regular patterns of eruption and wear, it is entirely possible that the mandibles of different animals will arrive at these different states of eruption and wear at different ages. This is especially true for the later dental groups that are based solely on attritional patterns, (see also Moran and O'Connor 1994, 282).

A particularly interesting result of this examination has been the detection of systematic differences in the patterns of wear in sheep and goat mandibular teeth. While both sheep and goat follow the same general sequence of mandibular tooth wear, there is a consistent tendency for wear to be more evenly spread across the cheek tooth row in sheep. In contrast mandibular tooth wear in goats seems more narrowly focused on one or two teeth, with the primary load of attritional force shifting among different teeth (primarily the P3, P4, and M1) as the mandible undergoes progressive wear. Possible reasons for this difference and its effect on the rates of tooth wear in sheep and goats are discussed below. There is no detectable difference in the sequence of tooth eruption and wear in the few domestic sheep and goats in the sample.

Reconciling Fusion and Dental Groups

One of the outstanding questions in the construction of mortality profiles from archaeological remains centers on how well profiles based on epiphyseal fusion data correspond to those based on dental eruption and wear. Direct comparability between mortality profiles constructed with these different measures of age requires that the estimation of age at death of an individual using epiphyseal fusion be the same as the age estimate based on the individual's state of dental eruption and wear. And yet the correlation between these two different measures has never been adequately tested. While we are hampered by the lack of definitive information on the age at death of the FMNH caprines, we can look at the degree of correspondence between fusion and dental age estimates in a couple of ways.

Comparability within taxa

One measure of the degree of correlation between these two different ways of estimating age is to compare the rank age orders for the FMNH sheep and goats based on fusion and dental data. Matching fusion and dental rank orders of sheep and goats provided in Figs 2 and 3 clearly demonstrates a very close correspondence between these two measures of age. Whether using parametric or non-parametric tests, the correlation between the fusion and dental age orders of both the sheep and goats are highly correlated at better than the .00005 level of probability. Pearson product-moment correlations for fusion and dental rank order for goats is 0.917 and for sheep 0.832. Using Spearman's Rho statistics the correlation between fusion and dental rank order is .831 for goats and .916 for sheep.

But how well do the actual age estimates for the FMNH sheep and goats based on fusion data correspond to those based on tooth eruption and wear? Fig. 33 presents a matrix for goats and sheep that looks at the correspondence between fusion and dental groups. Fusion groups are arranged across the horizontal axis along with estimated age ranges for each group derived from published sources. Dental groups are arrayed along the vertical axis, and are also shown with estimated ages. Cells in the matrix that represent a total overlap between the fusion and dental age estimates are shaded in dark grey, while those that represent overlap with either the start or the end of the age range estimates are shaded in light grey. The number of specimens that fall into each cell is indicated, with goats on the left and sheep on the right.

The correspondence between age estimates for the fusion and the dental groups is generally fairly good. There is total overlap in the age estimates based on fusion and dental data (specimens that fall in the dark grey cells) in 55% of the goat specimens and 57% of the sheep. An additional 33% of the goats and 25% of the sheep specimens fall in the overlap zones for either the beginning or the end of the age ranges given by fusion and dental data (specimens in light grey cells). This means that there is general agreement between these two estimators in 82% of the FMNH sheep and 88% of the goats. To a certain extent, the better degree of overlap between dental and fusion age estimates in goats may be attributable to the fact that dental age ranges are primarily based on Deniz and Payne's study of a known age population of Angora goats.

The agreement between the fusion based age estimates and the dental estimates is closest in the younger groups (A–C fusion groups and I–V dental groups). Older groups show more variability, perhaps because older dental groups are based solely on attritional patterns that are likely to show more variation in the ages at which these different wear states are reached. Without an independent measure of the age of FMNH caprines it is impossible to assess the correspondence between the dental age assignment and fusion age assignment of individuals placed in

the final two open-ended fusion groups (F and G). However, it is promising that in both sheep and goats (with only one exception for each), individuals in Fusion Group F (48+ months) generally fall into younger dental groups than individuals placed in the final Fusion Group G (48++ months).

Comparability between taxa

There is evidence of consistent systematic differences between sheep and goats in the way in which the fusion and dental groups correspond to one another. Age estimates for sheep based on dental data are uniformly younger than those provided by fusion data, while the dental ages for goats are consistently older than age estimates based on fusion data. For example, both of the goats classified in Fusion Group A fall into Dental Group III, but the sheep specimen assigned to Fusion Group A has a dental pattern that places it in Dental Group II. The goat specimens in Fusion Group B both fall into Dental Group IV. In contrast, two of the sheep in Fusion Group B fall into Dental Group II and one falls into Dental Group III. This pattern becomes even more exaggerated in subsequent Fusion Groups C, D, and E.

Moreover, goats in older fusion groups (i.e. D and E) tend to fall into a much wider range of dental groups than do sheep. Goats with fusion patterns that place them in Fusion Group D (18–30 months), for example, have dental patterns that place them in Dental Groups V, VI, and VIII (covering a range of ages from 18 months to 5 years). In contrast, sheep placed in Fusion Group D fall into either Dental Group IV, V, or VI (from 12–36 months). Goats placed in Fusion Group E (30–48 months) may fall into Dental Groups VII–X (from 4–10 years), while sheep classified as belonging to Fusion Group E have dental patterns that place them in Dental Groups V and VI (18–36 months).

Both of these patterns suggest that there are systematic differences between sheep and goat in either the timing of epiphyseal fusion or in the rate of tooth eruption and wear. Specifically, the FMNH data indicates that either sheep teeth erupt and wear at a slower rate than goat teeth (and conversely that goat teeth erupt and wear faster than sheep teeth), or that the long bones of sheep fuse earlier than in goats (and conversely that goat long bones fuse later than in sheep). Again the lack of independent data on age at death of the FMNH caprines means that this question cannot be definitively resolved. But there are indications from the review of previous literature and from data provided by this study of the FMNH caprines that may help distinguish between these two options.

It is difficult to attribute these patterns to differences in fusion schedules of sheep and goat long bones. Previous studies of fusion rates in known age animals suggest generally close correspondence between sheep and goats in the ages at which bones fuse. And while Noddle's (1974) and Bullock and Rackham's (1982) studies suggest

some delay in epiphyseal fusion in goats compared to sheep, these differences are more likely attributable to differences in nutritional intake between feral goats and closely tended improved breeds of sheep. The nearly identical sequence of bone fusion in the FMNH goats and sheep is also suggestive of close correspondence in the timing of fusion. In fact, the only potential differences in epiphyseal fusion sequence detected in the FMNH sheep and goats occur in the late fusion stages represented by the bones included in Fusion Group E. Yet the mismatch in the fusion and dental groups between sheep and goats is evident across all groups, not just in this late stage of development.

As with epiphyseal fusion, most studies indicate that schedules of tooth eruption in sheep and goats are quite similar (see Fig. 16). This means that if the source of the disparity lies in the dental age estimates, it is most likely attributable to differences in rates of tooth wear – specifically that sheep teeth wear more slowly than goat teeth. Yet on the surface this conclusion would seem somewhat counterintuitive. Sheep are much more committed grazers, while goats utilize a much higher proportion of browse in their diets (Redding 1981, 47–49). As a result, sheep teeth are subjected to a higher degree of attritional agents, both in the form of the silica bodies derived from pasture grasses that typically have a very high silica content (Delores Piperno, personal communication 2003), and from the higher proportion of soil that is likely to be ingested along with graze. Goats also move more quickly between feeding localities than sheep, while sheep are more likely to stay in one spot cropping all grasses and forbs as close to the ground as possible and thereby taking in more soil as they graze (Redding 1981, 48). The amount of soil ingested with graze is known to be a primary agent in differential tooth wear in caprines (Moran and O'Connor 1994, 270). There may also be differences in the amount of rumination needed to break down higher silica content pasturage, which would also subject sheep teeth to more wear. Therefore, one might think that sheep teeth should wear faster than goats, not slower as suggested here.

However, there is some reason to believe that the greater potential for tooth attrition in the feeding ecology of sheep selected for both structural and behavioral features that serve to slow the rate of tooth wear in these animals. First, sheep teeth in general are said to show greater hypsodonty than goats (Payne 1985, 143), an adaptation aimed at prolonging the use life of teeth that make it seem as if sheep teeth wear more slowly. There is simply more tooth that must be worn down to progress between various wear stages. Second, patterns of mandibular tooth wear observed in the FMNH caprines suggest differences in the mechanics of mastication in sheep and goat that may also be an adaptation of different feeding ecologies. Whether deciduous or permanent teeth, tooth wear in sheep was more even across all cheek teeth, from the P2 (or dP2) to the M3. In goats, primary wear

was more narrowly focused on central cheek teeth, with attritional load shifting across these teeth as the mandible undergo progressive wear. Distributing the load more evenly across the tooth row would likely lessen the attrition of individual teeth and therefore slow the rate of tooth wear in sheep.

These differences in feeding ecology, degree of hypsodonty, and chewing mechanics may also contribute to the tendency for goats to show a wider range of dental groups associated with older fusion groups. Redding (1981, 49) reports that goats will vary their diets depending on the nature and the quality of pasturage available, mixing variable amounts of graze and browse plants depending on local conditions. While they prefer to graze on grasses and forbs if available, they will also browse on a wide array of other plants and plant parts if adequate graze is not available. As a result, goats in regions with better quality pasturage may have a higher intake of graze, exposing their teeth to more silica and soil ingested while grazing which both cause teeth to wear more quickly. Goats in regions with poorer pasture may consume a higher proportion of browse with less potential for tooth attrition. The amount of graze and browse that any one goat consumes over its lifetime will also likely vary seasonally or perhaps over years with variable amounts of rainfall. The effect of the variable intake of attrition causing agents in goats might be exacerbated by their masticatory mechanics, which tend to focus load more narrowly across the tooth row. Moreover, if indeed goat teeth show less hypsodonty than sheep teeth, they will also be more likely to reflect variable rates of wear more dramatically than sheep. Sheep, on the other hand are more obligate grazers and will live off of stored body fat when adequate graze is not available (Redding 1981, 49). Thus the more consistent, tighter correlation between fusion and dental groups in sheep may be the result of their more exclusive commitment to grazing on a narrower range of plants, their higher crowned teeth, and the more even spread of load across the cheek teeth in sheep. There are no detectable differences in wear patterns between wild and domestic sheep and goats.

Comparability between sexes

Figs 34 and 35 look at the correlation between fusion and dental age estimates for male and female specimens with goats in Fig. 34 and sheep in Fig. 35. In both sheep and goats, male specimens consistently fall into older dental groups than females. This pattern is especially clear in the larger sample of sheep examined. For example, there are eight male sheep with fusion patterns that place them in Fusion Group D (18–30 months). Four of these animals have dental patterns that place them in Dental Group V (18–24 months) and four fall into Dental Group VI (24–36 months). In contrast, the two female sheep in Fusion Group D have dental patterns that place them in Dental Group IV (12–18 months). In goats, six males in Fusion

Group D range in dental age between Dental Group V to Dental Group VIII (18 months to 5 years), while two female goats in Fusion Group D fall into Dental Group V (18–24 months).

Once again, the most likely source of this difference lies in rates of dental attrition rather than in the timing of epiphyseal fusion. While there is some indication of delayed fusion in the long bones of male sheep, the data are somewhat contradictory. Hatting reports earlier fusion in females for eight of fourteen epiphyses examined and earlier fusion in males for the remaining six epiphyses (Hatting 1981, cited in Moran and O'Connor 1994, 273). These results are similar to those of Moran and O'Connor (1994, 280) who found slightly earlier fusion in females in bones that fuse before about 24 to 30 months of age, while males show slightly earlier fusion in bones that fuse at about 36 months or later. The difference in fusion age between males and females noted by Moran and O'Connor, however, is never more than seven months and usually less than three.

In contrast, Deniz and Payne (1982, 187) found clear differences in rates of tooth wear in male and female Angora goats. While rates of wear in males and females were about the same in animals in their first year, there was a tendency toward more rapid wear in males at about two years that seemed to increase with age. Deniz and Payne attribute this difference to the larger body size of males that becomes more marked after one year and to higher levels of activity in males which probably requires more intake to sustain.

Comparability between collecting localities

It is also possible that differences in pasture quality will affect rates of epiphyseal fusion and tooth eruption schedules in sheep and goats. Differences in pasture plants and in local soil conditions (i.e. the hardness and amount of grit inclusions in soil), in particular, are often mentioned as a potential factor in the rate of tooth wear attrition in these animals. Therefore, it is not unreasonable to expect some differences in the rates of epiphyseal fusion and tooth eruption and wear in FMNH sheep and goats from different collecting localities.

Regrettably, it is difficult to directly test this possibility with the FMNH caprines, since the sample animals from any one collecting locality is quite small (Figs 2 and 3). However judging from this limited sample, there do not appear to be any marked differences between animals from different collecting localities. In all localities, the dental age estimates for the sheep are consistently younger than the fusion age estimates and the dental age estimates for the goats for are consistently older than fusion age estimates. The patterning observed for males and females also holds true across all localities. Both larger samples and better information on local pasture conditions are needed before this question can be adequately addressed.

Conclusions

At its outset this paper raised a number of questions about the sequence and timing of epiphyseal fusion and tooth eruption and wear and the correlation between these measures of age. The study of the FMNH caprines has shed a significant amount of light on these questions. First, it has established a clear sequence of bone fusion that is consistently found in both sheep and goats. Regardless of the ages at which these various bones fuse, the order of fusion from youngest (proximal radius) to oldest (proximal humerus) is firmly established here (see Figs 8–15). This new sequence based on this large population of wild animals will hopefully resolve open questions about the precise sequence of epiphyseal fusion in early hunted and herded sheep and goats. Whether put together in fusion groups (A–G) or singly as individual bones, this should be the sequence used when ordering elements in an archaeological assemblage in the process of constructing mortality profiles for sheep, goats, or sheep and goats as a combined sample.

Similarly, this study establishes a progressive pattern of tooth eruption and wear in caprines. Even with the clear differences noted between sheep and goats, the general phases of eruption and wear identified here are consistently seen in both. Once again, regardless of age assignment, these stages can be used to provide a rank order of specimens (see Figs 21–32). One of the innovations of this study is that it looks at wear patterns across the mandible rather than in individual teeth. Most other studies of dental eruption and wear, even those that make age assignments based on eruption and wear states of a number of different cheek teeth, tend to look at eruption and, especially, wear patterns of individual teeth in isolation (i.e. Deniz and Payne 1982, Moran and O'Connor 1994, Jones this volume). While much valuable effort has been devoted to refining and attempting to calibrate individual stages of tooth wear of individual teeth, to some extent some of this very tight focus may lose sight of important mandible wide patterns with direct relevance to the reconstruction of reliable dental mortality profiles. Specifically what one misses in this approach is an understanding of the overall mechanics of wear across a mandible over the course of an animal's life. Looking at wear across the mandible has made it possible to detect subtle but, I believe, important patterns of wear that represent new dental groups that provide greater resolution to sequence of dental eruption and wear in these animals. Most importantly, this study highlighted hitherto unnoticed differences in the wear patterns of sheep and goat teeth that may have a significant impact on the use of dental patterns in the construction of mortality profiles in sheep and goats.

As to the correlation between fusion and dental aging techniques, clearly there is a high degree of correlation between the ranked age order of specimens using these two methods. Moreover, there is reasonable consistency

in the placement of both sheep and goats in the various fusion and dental groups. With some exceptions in older animals, the majority of goats whose fusion patterns place them in certain fusion groups are consistently placed in the same dental groups. The same is true for sheep, although the correspondence between groups varies. Even in the later fusion groups with defined end points (D and E) where there is more variability in corresponding dental group assignments, the majority of specimens fall into one or two adjacent groups.

The problem comes in reconciling which fusion groups correspond to which dental groups. There are clear systematic differences in the correspondence between fusion and dental groups in sheep and goats that have been attributed primarily to differential rates of tooth wear related to differences in feeding ecology, tooth morphology, and chewing mechanics in sheep and goats. There are also differences in the correspondence between these age estimators in males and females which have similarly been linked primarily to differential rates of wear. These species and sex-linked differences in rates of tooth wear raise serious questions about the application of dental based age estimates to samples which contain both sheep and goats, as well as a mixture of males and females. If, for example, one accepts that all sheep and goats classified in Fusion Group D actually fall within the same closely defined age range (18–30 months), these animals have a range of dental patterns that place them in dental groups spanning an estimated age range of four years (from 1–5 years). Sheep and goat specimens classified in Fusion Group E (estimated to range from 30–48 months) fall into 6 different dental groups that are estimated to range from 18 months to 8 years.

Until recently the only criteria for distinguishing between the teeth of sheep and goat were those presented by Payne (1985) developed for certain milk teeth and unworn M1s, useful only in classification of young individuals. A recent article by Halstead and Collins (2002) presents criteria for adult teeth, both premolars and molars, as well as for the mandible. However, in both studies there are few unambiguous criteria that can be used to reliably distinguish between the teeth and mandible of goats and sheep. Most of the criteria presented in these papers will only distinguish specimens that are clearly goats from specimens that are either sheep or goat. Thus, we are still lacking definitive criteria that allow secure separation of sheep and goat mandibles and mandibular teeth that can then be used to devise species-specific dentally based mortality profiles. There are no methods I know of for distinguishing males from females on the basis of tooth or mandibular morphology.

In contrast, there are a number of solid criteria for distinguishing between the long bones of sheep and goat that make it possible to compute species-specific fusion based age profiles with some confidence (Zeder and Lapham, in preparation). Moreover, in goats (and to a certain extent in sheep) marked sex-linked dimorphism

in the size of skeletal elements can be used to reliably separate male from female animals (at least in wild assemblages and those dating to the earlier phases of the domestication process). Thus, with large assemblages it is possible to construct mortality profiles that are both species and sex-specific (see Zeder 2001). If fusion sequences and timing are indeed reasonably consistent across taxa and sexes as concluded here, then even fusion-based mortality profiles based on mixed samples of sheep and goats, males and females may be more likely to reflect the actual age order sequence of the mixed population than a dental profile based on a mixed sample.

This is not to say that dental-based mortality profiles are not useful. Indeed they are, especially in looking at ages that fall outside the upper limit of fusion data. However, profiles based on these data need to be considered as rough approximates of mortality, especially in the later ages when variations in rates of attrition have the greatest impact. Attempts to affix precisely defined age estimates to these older groups are out of line with the fact that different animals will reach these different stages of dental wear at somewhat different ages.

As to the calibration of the fusion and the dental groups defined here, for the moment the age ranges drawn from previous studies of known age populations will have to suffice. A planned study of annual increments in the horn sheaths of the FMNH sheep and goats will provide another estimate of the ages of these animals that may help with the calibration of the fusion and dental groups defined in this study. It may also help to test some of the conclusions drawn here about the reliability of fusion and dental criteria and the mortality profiles based on them. But for now these age estimates should be taken as rough proxies of age and age order that can be used for comparison between samples, rather than a firm empirically grounded estimates of the actual age at death.

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Appendix

Fusion Group	FMNH #	P. Rad ¹	Pelvis	Scap	D. Hum	2 Phl	1 Phl	D. Tib	D. Mc	D. Mt	Rad & Ulna	Calc	P. Fmr (ball)	P. Fmr (troch) ²	D. Fmr	P. Ulna	D. Rad	P. Tib	P. Hum
A	97920	J	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
A	97916	J	J	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
B	97911	L	U	J	J	–	U	U	U	U	U	U	U	U	U	U	U	U	U
B	97912	L	J	J	J	–	U	U	U	U	U	U	U	U	U	U	U	U	U
C	57938	F	L	J	L	–	U	U	U	U	U	U	U	U	U	U	U	U	U
C	92924	F	F	L	F	J	U	U	U	U	U	U	U	U	U	U	U	U	U
C	97914	F	F	F	F	F	U	U	U	U	U	U	U	U	U	U	U	U	U
C	84485	F	F	F	F	L	J	U	U	U	J	U	U	U	U	U	U	U	U
C	97910	F	F	F	L	–	L	U	U	–	J	U	U	U	U	U	U	U	U
D	97927	F	F	F	F	F	F	U	U	U	U	U	U	U	U	U	U	U	U
D	97917	F	F	F	F	F	J	U	J	U	U	U	U	U	U	U	U	U	U
D	57253	F	F	F	F	F	L	J	U	U	U	U	U	U	U	U	U	U	U
D	57937	F	F	F	F	–	F	L	J	J	U	U	U	U	U	U	U	U	U
D	97913	F	F	F	F	F	F	J	U	U	U	U	U	U	U	U	U	U	U
D	84483	F	F	F	F	F	F	F	U	U	J	U	U	U	U	U	U	U	U
D	97929	F	F	F	F	F	F	L	J	L	J	U	U	J	U	U	U	U	U
D	92922	F	F	F	F	F	F	L	L	L	U	U	U	U	U	U	U	U	U
D	112505	F	F	F	F	–	F	L	L	L	U	U	U	U	U	U	U	U	U
D	57935	F	F	F	F	–	F	F	L	L	U	U	U	U	U	U	U	U	U
D	97930	F	F	F	F	F	F	L	L	L	J	U	U	U	U	U	U	U	U
D	97908	F	F	F	F	F	F	F	F	F	U	U	U	U	U	U	U	U	U
E	92925	F	F	F	F	F	F	L	F	F	J	L	J	J	U	U	U	U	U
E	97919	F	F	F	F	F	F	L	L	F	J	U	J	J	J	J	J	J	U
E	57943	F	F	F	F	–	F	F	F	F	L	F	J	J	J	J	J	J	U
E	92921	F	F	F	F	F	F	F	F	F	L	F	J	J	J	J	J	J	U
E	92920	F	F	F	F	F	F	F	F	F	L	F	J	J	J	J	L	J	U
E	57949	F	F	F	F	–	F	F	F	F	L	L	L	L	L	L	J	J	U
E	44472	F	F	F	F	F	F	F	F	F	J	L	L	L	L	J	J	J	U
E	92923	F	F	F	F	F	F	F	F	F	L	L	L	L	L	U	L	J	U
F	97926	F	F	F	F	F	F	F	F	F	J	L	J	L	J	J	J	J	J
F	97921	F	F	F	F	F	F	F	F	F	F	F	L	L	L	L	J	J	J
F	97924	F	F	F	F	F	F	F	F	F	L	F	J	L	L	L	L	L	J
F	44466	F	F	F	F	F	F	F	F	F	F	F	L	L	L	L	L	L	J
G	84486	F	F	F	F	F	F	F	F	F	L	F	J	L	L	L	L	L	L
G	58018	F	F	F	F	F	F	F	F	F	L	F	L	F	F	L	L	L	L
G	97925	F	F	F	F	F	F	F	F	F	L	F	L	L	F	F	L	L	L
G	35676	F	–	F	F	–	–	L	F	F	F	F	L	F	F	F	F	F	L
G	99029	F	F	F	F	F	F	F	F	F	F	F	L	F	F	F	F	F	F
G	97931	F	F	F	F	–	–	F	F	F	F	F	L	F	F	F	F	F	F

Fig. 6. Epiphyseal fusion in FMNH goats in rank order from youngest to oldest (U – unfused, J – early fusion, L – late fusion, F – fully fused, see text for explanation). ¹ – see fig. 4 for element abbreviations, ² – Troch – trochanter.

Age Class	FMNH #	P. Rad ¹	Pelvis	Scap	D. Hum	2 Phl	1 Phl	D. Tib	D. Mc	D. Mt	Rad & Ulna	Calc	P. Fmr (ball)	P. Fmr (troch) ²	D. Fmr	P. Ulna	D. Rad	P. Tib	P. Hum
A	58072	J	U	U	J	–	U	U	U	U	U	U	U	U	U	U	U	U	U
B	58069	L	U	U	J	U	U	U	U	U	U	U	U	U	U	U	U	U	U
B	58057	L	J	J	J	–	U	U	U	U	U	U	U	U	U	U	U	U	U
B	97986	L	J	J	J	U	U	U	U	U	U	U	U	U	U	U	U	U	U
C	58094	F	J	L	L	J	U	U	U	U	U	U	U	U	U	–	U	U	U
C	57254	F	L	L	L	J	U	U	U	U	U	U	U	U	U	U	U	U	U
C	97959	L	J	L	L	J	U	U	U	U	U	U	U	U	U	U	U	U	U
C	84488	F	F	F	F	J	U	U	U	U	U	U	U	U	U	U	U	U	U
C	58020	F	F	F	F	–	L	U	U	U	U	U	U	U	U	U	U	U	U
C	58022	F	F	F	F	F	L	U	U	U	U	U	U	U	U	U	U	U	U
D	97984	F	F	F	F	L	L	J	U	U	U	U	U	U	U	U	U	U	U
D	58021	F	F	F	F	–	F	J	U	U	U	U	U	U	U	U	U	U	U
D	58039	L	F	F	F	F	L	L	U	U	U	U	–	–	U	U	U	U	U
D	152008	F	F	F	F	–	L	L	U	U	U	U	U	U	U	U	U	U	U
D	58038	F	F	F	F	F	F	L	U	U	U	U	U	U	U	U	U	U	U
D	58044	F	F	F	F	–	F	L	U	U	U	U	U	U	U	U	U	U	U
D	58014	F	F	F	F	–	F	F	U	U	U	U	U	U	U	U	U	U	U
D	58024	F	F	F	F	–	F	L	J	J	U	U	–	–	U	U	U	U	U
D	98162	F	F	F	F	F	L	L	J	J	U	U	U	U	U	U	U	U	U
D	58040	F	F	F	F	–	F	L	J	J	U	U	U	U	U	U	U	U	U
D	97960	F	F	F	F	F	F	F	L	L	U	U	U	U	U	U	U	U	U
D	92927	F	F	F	F	F	F	L	F	F	U	U	U	U	U	U	U	U	U
E	152003	F	F	F	F	–	F	F	F	F	U	J	U	U	U	U	U	U	U
E	57255	F	F	F	F	F	F	L	L	L	U	L	U	U	U	U	U	U	U
E	58032	F	F	F	F	F	F	F	L	L	U	J	J	U	U	U	U	U	U
E	58091	F	F	F	F	–	F	F	F	F	U	J	J	J	U	U	U	U	U
E	97985	F	F	F	F	F	F	F	L	L	U	L	J	J	U	U	U	U	U
E	58063	F	F	F	F	F	F	L	F	F	U	J	J	J	U	U	U	U	U
E	58047	F	F	F	F	–	F	L	L	L	U	J	L	J	J	L	U	U	U
E	58037	F	F	F	F	–	F	F	F	F	U	L	J	J	J	L	J	J	U
E	97958	F	F	F	F	F	F	F	F	F	U	L	L	L	J	L	J	J	U
F	58058	F	F	F	F	–	F	F	F	F	U	L	L	L	J	J	J	J	J
F	58033	F	F	F	–	–	F	F	F	F	U	L	J	L	J	L	J	J	J
F	58048	F	F	F	F	–	L	F	L	L	U	L	J	L	J	L	L	J	J
F	152006	F	F	F	F	F	F	L	L	L	U	L	L	J	J	L	L	J	J
F	58043	F	F	F	F	–	F	F	F	F	U	F	L	L	J	L	L	J	J
F	58035	F	F	F	F	F	F	F	F	F	U	F	L	L	J	L	F	J	J
F	98161	F	F	F	F	–	F	F	F	F	U	F	L	F	J	L	L	L	J
F	58065	F	F	F	F	–	F	F	F	F	U	F	L	F	L	L	L	J	J
F	152007	F	F	F	F	–	F	F	F	F	J	F	J	F	F	F	F	F	J
F	97983	F	F	F	F	F	F	F	F	F	U	F	L	F	L	F	L	L	J
F	58019	F	F	F	F	F	F	F	F	F	U	F	L	F	L	L	F	L	J
G	58034	F	F	F	F	–	F	F	F	F	U	F	J	F	L	F	F	F	L
G	58071	F	F	F	F	–	F	F	F	F	U	F	L	F	L	L	L	J	L
G	97973	F	F	F	F	F	F	F	F	F	U	F	J	L	L	F	F	L	L
G	58042	F	F	F	F	–	F	F	F	F	U	F	L	L	L	L	L	L	L
G	152005	F	F	F	F	–	F	F	F	F	J	F	L	F	L	L	L	L	L
G	97957	F	F	F	F	F	F	F	F	F	U	F	L	F	L	F	L	L	L
G	152002	F	F	F	F	–	F	F	F	F	U	F	L	F	F	F	L	L	L
G	58036	F	F	F	F	F	F	F	F	F	U	F	L	F	F	L	L	F	L
G	58064	F	F	F	F	F	F	F	F	F	J	F	L	F	L	F	F	L	L
G	58089	F	F	F	F	F	F	F	F	F	U	L	L	L	L	L	L	L	L
G	152004	F	F	F	F	–	F	F	F	F	J	F	L	F	L	F	F	F	L
G	58070	F	F	F	F	–	F	F	F	F	U	F	L	F	F	F	F	L	L
G	58015	F	F	F	F	F	F	F	F	F	J	F	L	F	F	F	F	F	L
G	58031	F	F	F	F	F	F	F	F	F	U	F	L	F	F	F	F	F	L
G	58046	F	F	F	F	–	F	F	F	F	U	F	L	F	F	F	F	F	L
G	58041	F	F	F	F	–	F	F	F	F	U	F	F	F	F	F	F	F	L
G	92928	F	F	F	F	F	F	F	F	F	J	F	L	F	L	F	L	L	F
G	58045	F	F	F	F	–	F	F	F	F	U	F	L	F	F	F	F	F	F
G	58062	F	F	F	F	F	F	F	F	F	U	F	F	F	F	F	F	F	F

Fig. 7. Epiphyseal fusion in FMNH sheep in rank order from youngest to oldest (U – unfused, J – early fusion, L – late fusion, F – fully fused, see text for explanation). ¹ – see fig. 4 for element abbreviations, ² – Troch – trochanter.

	Goats n=2					Sheep n=1			
	Unfused	Early Fusing	Late Fusing	Fully Fused		Unfused	Early Fusing	Late Fusing	Fully Fused
P.Rad		2			P.Rad		1		
Pelvis	1	1			Pelvis	1			
Scap	2				Scap	1			
D.Hum	2				D.Hum		1		
2Phl	2				2Phl				
1Phl	2				1Phl	1			
D.Tib	2				D.Tib	1			
D.Mc	2				D.Mc	1			
D.Mt	2				D.Mt	1			
Rad/Ulna	2				Rad/Ulna	1			
Calc	2				Calc	1			
P.Fmr(b)	2				P.Fmr(b)	1			
P.Fmr(t)	2				P.Fmr(t)	1			
D.Fmr	2				D.Fmr	1			
P.Ulna	2				P.Ulna	1			
D. Rad	2				D. Rad	1			
P. Tib	2				P. Tib	1			
P. Hum	2				P. Hum	1			

Fig. 8. Fusion groups for goats and sheep – Group A.

	Goats n=2					Sheep n=3			
	Unfused	Early Fusing	Late Fusing	Fully Fused		Unfused	Early Fusing	Late Fusing	Fully Fused
P.Rad			2		P.Rad			3	
Pelvis	1	1			Pelvis	1	2		
Scap		2			Scap	1	2		
D.Hum		2			D.Hum		3		
2Phl					2Phl	2			
1Phl	2				1Phl	3			
D.Tib	2				D.Tib	3			
D.Mc	2				D.Mc	3			
D.Mt	2				D.Mt	3			
Rad/Ulna	2				Rad/Ulna	3			
Calc	2				Calc	3			
P.Fmr(b)	2				P.Fmr(b)	3			
P.Fmr(t)	2				P.Fmr(t)	3			
D.Fmr	2				D.Fmr	3			
P.Ulna	2				P.Ulna	3			
D. Rad	2				D. Rad	3			
P. Tib	2				P. Tib	3			
P. Hum	2				P. Hum	3			

Fig. 9. Fusion groups for goats and sheep – Group B.

	Goats n=5					Sheep n=6			
	Unfused	Early Fusing	Late Fusing	Fully Fused		Unfused	Early Fusing	Late Fusing	Fully Fused
P.Rad				5	P.Rad			1	5
Pelvis			1	4	Pelvis		2	1	3
Scap		1	1	3	Scap			3	3
D.Hum			2	3	D.Hum			3	3
2Phl		1	1	1	2Phl		4		1
1Phl	2	1	1		1Phl	4			1
D.Tib	5				D.Tib	6			
D.Mc	5				D.Mc	6			
D.Mt	5				D.Mt	6			
Rad/Ulna	3	2			Rad/Ulna	6			
Calc	5				Calc	6			
P.Fmr(b)	5				P.Fmr(b)	6			
P.Fmr(t)	5				P.Fmr(t)	6			
D.Fmr	5				D.Fmr	6			
P.Ulna	5				P.Ulna	5			
D. Rad	5				D. Rad	6			
P. Tib	5				P. Tib	6			
P. Hum	5				P. Hum	6			

Fig. 10. Fusion groups for goats and sheep – Group C.

	Goats n=12					Sheep n=12			
	Unfused	Early Fusing	Late Fusing	Fully Fused		Unfused	Early Fusing	Late Fusing	Fully Fused
P.Rad				12	P.Rad				11
Pelvis				12	Pelvis				12
Scap				12	Scap				12
D.Hum				12	D.Hum				12
2Phl				12	2Phl			1	5
1Phl		1	1	10	1Phl			4	8
D.Tib	2	2	5	3	D.Tib		2	8	2
D.Mc	4	3	4	1	D.Mc	7	3	1	1
D.Mt	5	1	5	1	D.Mt	7	3	1	1
Rad/Ulna	9	3			Rad/Ulna	12			
Calc	12				Calc	12			
P.Fmr(b)	12				P.Fmr(b)	10			
P.Fmr(t)	11	1			P.Fmr(t)	10			
D.Fmr	12				D.Fmr	12			
P.Ulna	12				P.Ulna	12			
D. Rad	12				D. Rad	12			
P. Tib	12				P. Tib	12			
P. Hum	12				P. Hum	12			

Fig. 11. Fusion groups for goats and sheep – Group D.

	Goats n=8					Sheep n=9			
	Unfused	Early Fusing	Late Fusing	Fully Fused		Unfused	Early Fusing	Late Fusing	Fully Fused
P.Rad				8	P.Rad				9
Pelvis				8	Pelvis				9
Scap				8	Scap				9
D.Hum				8	D.Hum				9
2Phl				7	2Phl				5
1Phl				8	1Phl				9
D.Tib			2	6	D.Tib			3	6
D.Mc			1	7	D.Mc			4	5
D.Mt				8	D.Mt			4	5
Rad/Ulna	0	3	5		Rad/Ulna	9			
Calc	1		4	3	Calc		5	4	
P.Fmr(b)	0	5	3		P.Fmr(b)	2	5	2	
P.Fmr(t)	0	5	3		P.Fmr(t)	3	5	1	
D.Fmr	1	4	3		D.Fmr	6	3		
P.Ulna	2	5	1		P.Ulna	6	0	3	
D. Rad	1	5	2		D. Rad	7	2		
P. Tib	2	6			P. Tib	7	2		
P. Hum	8				P. Hum	9			

Fig. 12. Fusion groups for goats and sheep – Group E.

	Goats n=4					Sheep n=11			
	Unfused	Early Fusing	Late Fusing	Fully Fused		Unfused	Early Fusing	Late Fusing	Fully Fused
P.Rad				4	P.Rad				11
Pelvis				4	Pelvis				11
Scap				4	Scap				11
D.Hum				4	D.Hum				10
2Phl				4	2Phl				4
1Phl				4	1Phl			1	10
D.Tib				4	D.Tib			1	10
D.Mc				4	D.Mc			2	9
D.Mt				4	D.Mt			2	9
Rad/Ulna			1	3	Rad/Ulna	10	1		
Calc			1	3	Calc			4	7
P.Fmr(b)		2	2		P.Fmr(b)		3	8	
P.Fmr(t)			4		P.Fmr(t)		1	5	5
D.Fmr		1	3		D.Fmr		7	3	1
P.Ulna		1	3		P.Ulna		1	8	2
D. Rad		2	2		D. Rad		2	6	3
P. Tib		2	2		P. Tib		7	3	1
P. Hum		4			P. Hum		11		

Fig. 13. Fusion groups for goats and sheep – Group F.

	Goats n=6					Sheep n=19			
	Unfused	Early Fusing	Late Fusing	Fully Fused		Unfused	Early Fusing	Late Fusing	Fully Fused
P.Rad				6	P.Rad				19
Pelvis				5	Pelvis				19
Scap				6	Scap				19
D.Hum				6	D.Hum				19
2Phl				4	2Phl				9
1Phl				4	1Phl				19
D.Tib			1	5	D.Tib				19
D.Mc				6	D.Mc				19
D.Mt				6	D.Mt				19
Rad/Ulna			3	3	Rad/Ulna	14	5		
Calc				6	Calc			1	18
P.Fmr(b)		1	5		P.Fmr(b)		2	15	2
P.Fmr(t)			2	4	P.Fmr(t)			3	16
D.Fmr			1	5	D.Fmr			10	9
P.Ulna			3	3	P.Ulna			5	14
D. Rad			3	3	D. Rad			8	11
P. Tib			2	4	P. Tib		1	9	9
P. Hum			4	2	P. Hum			16	3

Fig. 14. Fusion groups for goats and sheep – Group G.

Goats				Sheep			
Group	Bone	Order	Estimated Age ¹	Group	Bone	Order	Estimated Age
A	P. Rad ²	1	0–6	A	P. Rad	1	0–6
B	D. Hum	2	6–12	B	D. Hum	2	6–12
B	Pelvis	2	6–12	B	Pelvis	2	6–12
B	Scap	2	6–12	B	Scap	2	6–12
C	2Phl	3	12–18	C	2Phl	3	12–18
C	1Phla	4	12–18	C	1Phla	4	12–18
D	D.Tib	5	18–30	D	D.Tib	5	18–30
D	D.Mc	6	18–30	D	D.Mc	6	18–30
D	D..Mtl	6	18–30	D	D..Mtl	6	18–30
E	Calc	7	30–48	E	Calc	7	30–48
E	P.Fmr	8	30–48	E	P.Fmr	8	30–48
E	D.Fmr	8	30–48	E	D.Fmr	8	30–48
E	P.Ulna	8	30–48	E	P.Ulna	8	30–48
E	D.Rad	8	30–48	E	D.Rad	9	30–48
E	P.Tib	8	30–48	E	P.Tib	9	30–48
F	P. Hum ³	9	48+	F	P. Hum	10	48+
G	P. Hum ⁴	10	48++	G	P. Hum	11	48++

Fig. 15. Revised fusion sequence and ages for sheep and goats. ¹ – Age in months, ² – See fig. 4 for element abbreviations, ³ – Early fusion, ⁴ – Late fusion or fully fused.

Species	Source	P4	M1	M2	M3
'Modern' Sheep	Silver 1969	21–24	3	9–12	18–24
'Semi-Wild' Sheep	Silver 1969	40	6	18	36–48
Mixed Breeds of Sheep	Jones this volume	24	3	10–11	21
Mixed Breeds of Sheep	Moran and O'Connor 1974	23	2–4	7–12	17
Angora Goats	Deniz and Payne 1982	22	3	11	25
'Rough' Goats	Silver 1969	30	–	12	30
Dall Sheep (<i>Ovis dalli</i>)	Taber 1971	23	4	10	22–33
Mt Goats (<i>Oreamnos americanus</i>)	Taber 1971	24	6	10–16	16–29
Himalayan Thar (<i>Hemitragus juemlahicus</i>)	Caughley 1965	30	2.5	11.5	26

Fig. 16. Tooth eruption schedules for permanent teeth in months from previous studies.

Zeder Group	Payne Group	Age	Tooth Eruption and Wear Stages						
			dp2–3	dp4	P2–3	P4	M1	M2	M3
I	A	0–2m	02–07	02–08	U ¹	U	02–03	U	U
II	B	2–6m	nd	09–19	U	U	04–09	U	U
III	C	6–12m	16–20	16–20	U	U	10–14	02–09	U
IV	D	1–2y	25	19–25	02–08	02–08	13–17	11–14	02–08
V	E	2–3y	25	25	02–08	02–17	17–19	11–17	02–11
VI	F	3–4y	S ²	S	nd	16–20	17–25	14317	12–16
VII	G	4–6y	S	S	nd	20–25	18–26	17	12–17
VIII	H	6–8y	S	S	nd	20–25	20–26	18–25	16–17
IX	I	8–10+y	S	S	nd	25–26	25–26	25	18–26

Fig. 17. Dental groups from previous studies (Payne 1973, Deniz and Payne 1982, and Zeder 1985 and 1991). ¹ = U – unerupted, ² = S – shed.

General Wear	Zeder 1991	Payne (1986)				Grant (1982)			
		dP4	P4	M1&M2	M3	dP4	P4	M1&M2	M3
Eruption Stages	02	nye	nye	nye	nye	C	C	C	C
	03					V	V	V	V
	04	E	E	E	E	E	E	E	E
	05	½	½	½	½	H	H	H	H
	06	U	U	U	U	U	U	U	U
	07	J	J	J	J				
	08	0	0	0	0	a	a	a	a
Early Wear	09	2A	2A	2A	2A			b	b
	10		4A	4A	4A	b			
	11	5A	5A	5A	5A			c	c
	12	8L			6G	d			d
Active Wear	13			6A	7G			d	
	14		7A	7A	8G		e	e	e
	15				9G				
	16	13L	8A	8A	10G	f	f	f	f
	17	14L	9A	9A	11G	g	g	g,h	g,h
	18			10A	12G				
Late Wear	19	16L		11A	13G	h		j	j
	20	17L	12S	12A	14G	j,k	h,j	k	k
	21	18L		13A	15G				
	22			14A	16G			l	l
	23	20L							
	24	22L				m			
	25	23L	15A	15A	17G	n	l	m,n	m
Final Wear	26	23L	1618	1618	1820	n		o	

Fig. 18. Correlation between tooth wear stages developed by Payne, Grant and Zeder.

Dental Group	FMNH #	Side	dP2	dP3	dP4	P2	P3	P4	M1	M2	M3
I	112505	L	08	10	12				03		
	112505	R	08	10	12				03		
III	97916	L	10	20	19				11	02	
	97916	R	10	20	19				11	02	
III	97920	L	10	25	19				13	02	
	97920	R	10	25	20				13	02	
IV	97912	L	17	20	19				14	07	02
	97912	R	17	20	19				14	07	02
IV	97911	L	10	25	19				16	05	02
	97911	R	10	25	19				16	05	02
IV	92924	L	10	25	19	03	03	03	16	11	06
	92924	R	10	20	19	03	03	03	17	11	03
V	97908	L				05	06	10	17	16	03
	97908	R				06	07	10	17	11	04
V	97914	L				09	10	11	17	13	04
	97914	R				09	10	11	17	13	04
V	97917	L				09	10	11	17	14	04
	97917	R				09	10	11	17	14	04
V	97910	L				08	09	09	17	14	05
	97910	R				–	09	09	17	14	05
V	92922	L				09	10	10	17	14	07
	92922	R				–	10	10	17	14	07
V	84483	L				09	10	14	17	16	05
	84483	R				09	10	14	17	16	05
V	57938	L				08	10	11	17	14	07
	57938	R				08	10	11	17	16	07
V	84485	L				08	10	16	17	14	07
	84485	R				08	10	16	17	14	07
V	57253	L				09	09	11	17	17	09
	57253	R				09	09	11	17	17	09
VI	97913	L				08	17	17	17	16	10
	97913	R				08	17	17	17	14	10
VI	57937	L				09	17	17	17	17	10
	57937	R				09	17	17	17	17	10
VII	97919	L				09	17	20	17	17	11
	97919	R				09	17	20	17	17	11
VII	44472	L				09	17	20	17	17	11
	44472	R				09	17	20	17	17	11
VII	97925	L				10	20	20	17	16	11
	97925	R				10	20	20	17	16	11
VII	97921	L				10	17	20	17	17	13
	97921	R				10	17	20	17	17	13
VII	92921	L				08	17	20	17	17	12
	92921	R				08	17	20	17	17	12
VII	92923	L				10	20	20	17	17	12
	92923	R				10	20	20	17	17	12
VII	57949	L				09	20	20	18	17	13
	57949	R				09	20	20	18	17	13
VII	57935	L				09	20	20	17	17	15
	57935	R				09	20	20	17	17	15
VIII	97929	L				09	20	20	20	17	15
	97929	R				09	20	20	20	17	15
VIII	97930	L				10	20	20	20	17	15
	97930	R				10	20	20	20	17	15
VIII	97926	L				10	20	20	19	17	17
	97926	R				10	20	20	20	17	17
VIII	92925	L				08	20	20	20	17	17
	92925	R				08	20	20	20	17	17
IX	92920	L				09	20	20	25	17	17
	92920	R				09	20	20	25	17	17
IX	97924	L				09	20	20	25	18	17
	97924	R				09	20	20	25	19	17
X	35676	L				17	20	25	25	17	17
	35676	R				17	20	25	25	17	17
X	57943	L				10	20	25	25	17	17
	57943	R				10	20	20	25	18	17
X	99029	L				10	25	25	26	19	17
	99029	R				10	25	25	26	22	17
XI	58018	L				25	–	26	26	26	22
	58018	R				25	26	26	26	26	20

Fig. 19. Dental eruption and wear in FMNH goats in rank order from youngest to oldest.

Dental Group	FMNH #	Side	dP2	dP3	dP4	P2	P3	P4	M1	M2	M3
II	58057	L	10	10	16				05	02	
	58057	R	10	10	16				05	02	
II	58069	L	10	17	16				09	02	
	58069	R	10	17	16				09	02	
II	58072	L	10	20	17				07		
	58072	R	10	20	17				07		
III	97986	L	17	25	19				11	02	
	97986	R	17	25	19				11	02	
III	97959	L	20	25	19				14	03	
	97959	R	20	25	19				14	03	
IV	58039	L	17	20	19				13	08	02
	58039	R	17	20	17				11	08	02
IV	58094	L	17	25	17				16	05	02
	58094	R	17	25	17				16	05	02
IV	58020	L	20	25	21				14	09	02
	58020	R	20	25	21				14	09	02
IV	57254	L	20	25	19				16	07	02
	57254	R	20	25	19				17	07	02
IV	84488	L	25	26	19				16	05	02
	84488	R	–	26	19				16	05	02
IV	58022	L	20	25	19				17	08	02
	58022	R	–	25	19				17	09	02
IV	58024	L	10	25	25				17	11	02
	58024	R	10	25	25				17	11	02
V	58040	L				–	10	10	17	13	07
	58040	R				–	10	10	17	13	07
V	58063	L				09	10	11	17	14	09
	58063	R				09	10	11	17	14	09
V	58021	R				08	08	09	17	16	07
V	58065	L				09	10	16	17	14	10
	58065	R				09	10	14	17	14	10
V	58038	L				08	10	10	17	14	05
	58038	R				08	10	10	17	14	05
V	58014	L				–	10	16	17	14	05
	58014	R				–	–	16	17	16	05
V	58091	L				09	10	11	17	14	10
	58091	R				09	10	11	17	14	10
V	58047	L				09	09	11	17	16	09
	58047	R				09	09	11	17	16	09
V	152003	L				08	09	10	17	16	09
	152003	R				08	10	10	17	16	10
V	58058	L				08	09	11	17	16	10
	58058	R				08	09	11	17	16	10
V	58033	L				08	17	14	17	16	07
	58033	R				08	16	14	17	16	07
VI	97984	L				08	17	17	17	14	09
	97984	R				08	10	17	17	14	09
VI	97960	L				08	10	17	17	14	10
	97960	R				08	10	17	17	14	10
VI	58044	L				10	17	17	17	16	10
	58044	R				10	17	17	17	14	10
VI	97958	L				09	10	16	17	14	11
	97958	R				09	10	16	17	16	11
VI	57255	L				–	10	16	17	17	11
	57255	R				08	10	16	17	17	11
VI	98162	L				–	10	17	17	17	09
	98162	R				09	10	17	17	17	09
VI	97985	L				08	17	17	17	16	09
	97985	R				08	17	17	17	16	09
VI	58032	L				–	10	17	17	16	11
	58032	R				–	10	17	17	16	11
VI	58019	L				09	17	17	17	17	11
	58019	R				10	17	17	17	16	10
VI	58037	L				–	17	17	17	17	12
	58037	R				09	17	17	17	17	12

Fig. 20. Dental eruption and wear in FMNH sheep in rank order from youngest to oldest.

Dental Group	FMNH #	Side	dP2	dP3	dP4	P2	P3	P4	M1	M2	M3
VI	98161	L				09	17	17	17	17	15
	98161	R				09	17	17	17	17	15
VI	97957	L				10	17	17	17	17	16
	97957	R				10	17	17	17	17	16
VII	58089	L				09	14	14?	17	17	15
	58089	R				09	17	20	17	17	15
VII	58048	L				10	17	20	17	17	14
	58048	R				10	17	20	17	17	14
VII	58034	L				–	17	20	17	17	15
	58034	R				10	17	20	17	17	15
VII	58042	L				09	17	–	17	17	14
	58042	R				–	17	20	17	17	16
VII	58070	L				17	20	20	17	17	17
	58070	R				17	20	20	17	17	17
VII	97983	L				20	20	17	17	17	17
	97983	R				20	20	17	17	17	16
VII	58035	L				17	20	17	18	17	17
	58035	R				17	20	17	18	17	17
VII	58043	L				10	20	20	19	17	17
	58043	R				10	20	17	18	17	17
VIII	152005	L				20	25	20	20	17	16
	152005	R				20	25	17	19	17	15
VIII	97973	L				10	17	20	20	17	17
	97973	R				09	17	20	20	17	17
IX	58062	L				10	17	20	22	17	17
	58062	R				10	17	20	22	17	17
IX	58071	L				10	20	20	25	17	16
	58071	R				10	20	20	25	17	16
IX	58036	L				–	20	20	25	17	17
	58036	R				20	25	20	25	17	17
IX	58031	L				17	20	20	25	18	18
	58031	R				–	20	20	22	18	18
X	58064	L				20	20	22	25	18	17
	58064	R				20	20	22	25	18	17
X	58045	L				–	25	26	26	18	17
	58045	R				20	25	26	26	19	17
X	92928	L				25	25	26	25	22	17
	92928	R				25	25	26	25	18	17
XI	58015	L				25	25	25	25	22	17
	58015	R				25	25	25	25	25	18
XII	58041	L				10	25	20	26	26	26
	58041	R				–	25	20	–	–	26

Fig. 20. continued.

Group I	Goats n=1									Group II	Sheep n=3								
	dP 2	dP 3	dP 4	P 2	P 3	P 4	M 1	M 2	M 3		dP 2	dP 3	dP 4	P 2	P 3	P 4	M 1	M 2	M 3
02										02								2	
03							1			03									
04										04									
05										05							1		
06										06									
07										07							1		
08	1									08									
09										09							1		
10		1								10	3	1							
11			1							11									
12										12									
13										13									
14										14									
15										15									
16										16			1						
17										17		1	1						
18										18									
19										19									
20										20		1							
21										21									
22										22									
23										23									
24										24									
25										25									
26										26									

Fig. 21. Dental groups for FMNH goats and sheep – Groups I and II.

Group III	Goats n=2									Group III	Sheep n=2								
	dP2	dP3	dP4	P2	P3	P4	M1	M2	M3		dP2	dP3	dP4	P2	P3	P4	M1	M2	M3
02								2		02								1	
03										03								1	
04										04									
05										05									
06										06									
07										07									
08										08									
09										09									
10	2									10									
11							1			11							1		
12										12									
13							1			13									
14										14							1		
15										15									
16										16									
17										17	1								
18										18									
19			1							19			2						
20		1	1							20	1								
21										21									
22										22									
23										23									
24										24									
25		1								25		2							
26										26									

Fig. 22. Dental groups for FMNH goats and sheep – Group III.

Group IV	Goats n=3									Group IV	Sheep n=7								
	dP2	dP3	dP4	P2	P3	P4	M1	M2	M3		dP2	dP3	dP4	P2	P3	P4	M1	M2	M3
02									2	02									7
03				1	1	1			1.5	03									
04										04									
05										05								2	
06								1	1.5	06									
07								1		07								1	
08										08								1.5	
09										09								1.5	
10	2									10	1								
11								1		11							.5	1	
12										12									
13										13							.5		
14							1			14							1		
15										15									
16							1.5			16							2.5		
17	1						1.5			17	2		1.5				2.5		
18										18									
19			3							19			3.5						
20		1.5								20	2.5	1							
21										21			1						
22										22									
23										23									
24										24									
25		1.5								25	.5	5	1						
26										26		1							

Fig. 23. Dental groups for FMNH goats and sheep – Group IV.

Group V	Goats n=9									Group V	Sheep n=11								
	dP2	dP3	dP4	P2	P3	P4	M1	M2	M3		dP2	dP3	dP4	P2	P3	P4	M1	M2	M3
02										02									
03									.5	03									
04									2.5	04									
05				.5					2	05								2	
06				.5	.5					06									
07					.5			3		07								2.5	
08				2.5						08				4.5					
09				4.5	2	1			1	09				4		.5			2.5
10					6	2				10					5.5	3			3.5
11						4		.5		11						4			
12								1		12									
13										13								1	
14						1		4.5		14						1.5		4	
15										15									
16						1		2		16					.5	1.5		4	
17							9	1		17					.5		10.5		
18										18									
19										19									
20										20									
21										21									
22										22									
23										23									
24										24									
25										25									
26										26									

Fig. 24. Dental groups for FMNH goats and sheep – Group V.

Group VI	Goats n= 2									Group VI	Sheep n=12								
	dP2	dP3	dP4	P2	P3	P4	M1	M2	M3		dP2	dP3	dP4	P2	P3	P4	M1	M2	M3
02										02									
03										03									
04										04									
05										05									
06										06									
07										07									
08				1						08				3.5					
09				1						09				3.5					3
10									2	10				2.5	5.5				2.5
11										11									3.5
12										12									1
13										13									
14								.5		14							3		
15										15									1
16								.5		16						2		3.5	1
17					2	2	2	1		17					6.5	10	12	5.5	
18										18									
19										19									
20										20									
21										21									
22										22									
23										23									
24										24									
25										25									
26										26									

Fig. 25. Dental groups for FMNH goats and sheep – Group VI.

Group VII	Goats n= 8									Group VII	Sheep n=8									
	dP2	dP3	dP4	P2	P3	P4	M1	M2	M3		dP2	dP3	dP4	P2	P3	P4	M1	M2	M3	
02										02										
03										03										
04										04										
05										05										
06										06										
07										07										
08				1						08										
09				4						09				1.5						
10				3						10				2.5						
11									3	11										
12									2	12										
13									2	13										
14										14				.5	.5				1.5	
15									1	15									2	
16								1		16									1	
17					4		7	7		17					3.5	2.5	6	8	3.5	
18							1			18							1.5			
19										19							.5			
20					4	8				20				4	4.5					
21										21										
22										22										
23										23										
24										24										
25										25										
26										26										

Fig. 26. Dental groups for FMNH goats and sheep – Group VII.

Group VIII	Goats n= 4									Group VIII	Sheep n=2								
	dP2	dP3	dP4	P2	P3	P4	M1	M2	M3		dP2	dP3	dP4	P2	P3	P4	M1	M2	M3
02										02									
03										03									
04										04									
05										05									
06										06									
07										07									
08				1						08									
09				1						09				.5					
10				2						10				.5					
11										11									
12										12									
13										13									
14										14									
15								2		15									.5
16										16									.5
17								4	2	17					1	1		2	1
18										18							.5		
19							.5			19							.5		
20					4	4	3.5			20				1		1	1.5		
21										21									
22										22									
23										23									
24										24									
25										25					1				
26										26									

Fig. 27. Dental groups for FMNH goats and sheep – Group VIII.

Group IX	Goats n= 2									Group IX	Sheep n=4								
	dP2	dP3	dP4	P2	P3	P4	M1	M2	M3		dP2	dP3	dP4	P2	P3	P4	M1	M2	M3
02										02									
03										03									
04										04									
05										05									
06										06									
07										07									
08										08									
09				2						09									
10										10				2					
11										11									
12										12									
13										13									
14										14									
15										15									
16										16									1
17								1	2	17				.5	1			3	2
18								.5		18								1	1
19								.5		19									
20					2	2				20				.5	2.5	4			
21										21									
22										22							1.5		
23										23									
24										24									
25							2			25					.5		2.5		
26										26									

Fig. 28. Dental groups for FMNH goats and sheep – Group IX.

Group X	Goats n= 3									Group X	Sheep n=3								
	dP2	dP3	dP4	P2	P3	P4	M1	M2	M3		dP2	dP3	dP4	P2	P3	P4	M1	M2	M3
02										02									
03										03									
04										04									
05										05									
06										06									
07										07									
08										08									
09				2						09									
10										10									
11										11									
12										12									
13										13									
14										14									
15										15									
16										16									
17				1				1.5	3	17									3
18								.5		18								2	
19								.5		19								.5	
20					2	.5				20				1.5	1				
21										21									
22								.5		22						1			
23										23								.5	
24										24									
25					1	2.5	2			25				1	2		2		
26							1			26						2	1		

Fig. 29. Dental groups for FMNH goats and sheep – Group X.

Group XI	Goats n= 1									Group XI XII	Sheep n=2								
	dP2	dP3	dP4	P2	P3	P4	M1	M2	M3		dP2	dP3	dP4	P2	P3	P4	M1	M2	M3
02										02									
03										03									
04										04									
05										05									
06										06									
07										07									
08										08									
09										09									
10										10									
11										11									
12										12									
13										13									
14										14									
15										15									
16										16									
17										17				.5					.5
18										18									.5
19										19									
20									.5	20						1			
21										21									
22									.5	22								.5	
23										23									
24										24									
25				1						25				1	2	1	1	.5	
26					1	1	1	1									.5	.5	1

Fig. 30. Dental groups for FMNH goats and sheep – Group XI and XII

Revised Group	Zeder Group	Payne Group	Age	Tooth Eruption and Wear Stages								
				dp2	dp3	dp4	P2	P3	P4	M1	M2	M3
I	I	A	0–2m	08	10	11	U	U	U	03	U	U
II	II	B	2–6m	–	–	–	–	3	–	–	–	–
III	III	C	6–12m	10	20–25	19–20	U	U	U	11–13	02	U
IV	IV	D	12–18m	10–17	20–25	19	U–03	U–03	U–03	14–17	06–11	02–06
V	IV	D	18–24m	S	S	S	05–09	06–10	09–16	17	11–17	03–09
VI	V	E	2–3y	S	S	S	08–09	17	17	17	14–17	10
VII	VI	F	3–4y	S	S	S	08–10	17–20	20	17–18	16–17	11–15
VIII	VII	G	4–5y	S	S	S	08–10	20	20	19–20	17	15–17
IX	VII	G	5–6y	S	S	S	09	20	20	25	17–19	17
X	VIII	H	6–8y	S	S	S	09–17	20–25	20–25	25–26	17–22	17
XI	IX	I	8–10y	S	S	S	25	26	26	26	26	20–23
XII	IX	I	10+	–	–	–	–	–	–	–	–	–

Fig. 31. Revised dental groups for goats.

Revised Group	Zeder Group	Payne Group	Age	Tooth Eruption and Wear Stages								
				dp2	dp3	dp4	P2	P3	P4	M1	M2	M3
I	I	A	0–2m	–	–	–	–	–	–	–	–	–
II	II	B	2–6m	10	10–20	16–17	U	U	U	04–09	02	U
III	III	C	6–12m	17–20	25	19	U	U	U	11–14	02–03	U
IV	IV	D	12–18m	10–25	20–26	17–25	U	U	U	11–17	05–10	02
V	IV	D	18–24m	S	S	S	08–09	10–17	09–16	17	13–16	05–10
VI	V	E	2–3y	S	S	S	08–10	10–17	16–17	17	14–17	09–16
VII	VI	F	3–4y	S	S	S	09–10	14–20	14–20	17–19	17	14–17
VIII	VII	G	4–5y	S	S	S	09–20	17–25	17–20	18–20	17	15–17
IX	VII	G	5–6y	S	S	S	10–20	17–25	20	22–25	17–18	16–18
X	VIII	H	6–8y	S	S	S	20–25	20–25	22–26	25–26	18–23	17
XI	IX	I	8–10y	S	S	S	25	25	25	25	22–25	17–18
XII	IX	I	10+y	S	S	S	10	25	20	26	26	26

Fig. 32. Revised dental groups for sheep.

Goats	A 0–6m	B 6–12m	C 12–18m	D 18–30m	E 30–48m	F 48+m	G 18++m	Sheep	A 0–6m	B 6–12m	C 12–18m	D 18–30m	E 30–48m	F 48+m	G 18++m
I 0–2m								I 0–2m							
II 2–6m								II 2–6m	1	2					
III 6–12m	2							III 6–12m		1	1				
IV 12–18m		2	1					IV 12–18m			5	2			
V 18–24m			4	5				V 18–24m				4	4	3	
VI 24–36m				2				VI 24–36m				4	5	2	1
VII 36–48m					5	1	1	VII 36–48m						4	4
VIII 4–5y				2	1	1		VIII 4–5y							2
IX 5–6y					1	1		IX 5–6y							3
X 6–8y					1		2	X 6–8y							3
XI 8–10y							1	XI 8–10y							1
XII 10+y								XII 10+y							1

Fig. 33. Correlation between fusion and dental groups for goats and sheep (dental group dark shading indicates exact overlap in estimated ages, light shading indicates overlap with either the beginning or end of age range).

Males	A 0-6m	B 6-12m	C 12-18m	D 18-30m	E 30-48m	F 48+m	G 18++m	Females	A 0-6m	B 6-12m	C 12-18m	D 18-30m	E 30-48m	F 48+m	G 18++m
I 0-2m								I 0-2m							
II 2-6m								II 2-6m							
III 6-12m	2							III 6-12m		2					
IV 12-18m			1					IV 12-18m							
V 18-24m			4	2				V 18-24m				2			
VI 24-36m				2				VI 24-36m							
VII 36-48m				1				VII 36-48m					5	1	1
VIII 4-5y				1	1			VIII 4-5y				1		1	
IX 5-6y						1		IX 5-6y					1		
X 6-8y					1		1	X 6-8y							1
XI 8-10y								XI 8-10y							
XII 10+y							1	XII 10+y							

Fig. 34. Correlation between fusion and dental groups for male and female goats (dental group dark shading indicates exact overlap in estimated ages, light shading indicates overlap with either the beginning or end of age range).

Males	A 0-6m	B 6-12m	C 12-18m	D 18-30m	E 30-48m	F 48+m	G 18++m	Females	A 0-6m	B 6-12m	C 12-18m	D 18-30m	E 30-48m	F 48+m	G 18++m
I 0-2m								I 0-2m							
II 2-6m	1							II 2-6m		2					
III 6-12m								III 6-12m		1	1				
IV 12-18m			4					IV 12-18m			1	2			
V 18-24m				4				V 18-24m					4	3	
VI 24-36m				4	3	1		VI 24-36m					2	1	1
VII 36-48m						3	2	VII 36-48m						1	2
VIII 4-5y							1	VIII 4-5y							1
IX 5-6y							2	IX 5-6y							2
X 6-8y							1	X 6-8y							2
XI 8-10y								XI 8-10y							1
XII 10+y							1	XII 10+y							

Fig. 35. Correlation between fusion and dental groups for male and female sheep (dental group dark shading indicates exact overlap in estimated ages, light shading indicates overlap with either the beginning or end of age range).