Ageing the beaver (*Castor fiber* L.):
A skeletal development and life history calendar based on epiphyseal fusion

ANDERS FANDÉN

Historical osteology. Department of Archaeology and Ancient History lund University

ABSTRACT: The skeletal development of 51 recent beavers (*Castor fiber* L.) from Sweden has been studied, with the purpose to put forward a method for ageing individuals from this species. The study of the epiphyseal fusion in 45 epiphyses allowed for the establishment of a calendar. The results indicate that the skeletal maturation of the beaver occurs as late as 12 years. It is suggested that such prolonged epiphyseal fusion is due to the aquatic mode of life of the beaver. The skeletal development additionally allows for the creation of five skeletally defined cohorts namely: juveniles, subadults, young adults, middle aged adults and old adults. It is suggested that this system be used when ageing skeletal remains of beaver from zooarchaeological assemblages and in wildlife management studies.

KEYWORDS: BEAVER, *Castor fiber*, EPIPHYSEAL FUSION, PROLONGED SKELETAL DEVELOPMENT, AQUATIC MODE OF LIFE, LIFE HISTORY

RESUMEN: El desarrollo esquelético de 51 castores (*Castor fiber* L.) recientes de Suecia ha sido estudiado al objeto de obtener un método para evaluar la edad de los individuos de esta especie. El grado de fusión epifisaria en 45 epífisis ha sido estudiado para establecer un calendario que clarificase la secuencia de fusión de estos elementos. Los resultados demuestran que la maduración esquelética del castor se prolonga hasta los 12 años. Se sugiere que este desarrollo esquelético prolongado del castor es debido a su modo de vida acuático. El calendario de fusiones permite asimismo la creación de cinco cohortes definidas esqueléticamente: juveniles, subadultos, adultos jóvenes, adultos y adultos viejos. Se pretende que este sistema sea utilizado cuando se quiera establecer la edad de restos de castores de yacimientos arqueológicos y en los estudios de manejo de poblaciones actuales.

PALABRAS CLAVE: CASTOR, *Castor fiber*, FUSIÓN EPIFISARIA, DESARROLLO ESQUELÉTICO PROLONGADO, MODO DE VIDA ACUÁTICO, ONTOGENIA

INTRODUCTION

Methods for ageing wild animals are important in archaeozoology since mortality profiles shed light on a number of important issues including seasonality studies, hunting strategies and depletion of animal populations.

Compared to domestic animals, methods for ageing wild animals are scarcer in the literature due to the difficulties of obtaining animals whose absolute age is known with precision. Still, one should be able to obtain coarser grain calendars where a species' ontogenetic development could be subdivided into meaningful age classes (cohorts) whose temporal ranges could be in excess of the errors implied by any particular relative ageing technique.

Methods for ageing domesticated animals based on the analysis of epiphyseal fusion date back to the nineteenth century (i.e., Lesbre, 1897/8) and have been thoroughly improved during the twentieth century with the incorporation of many species of wild mammals (e.g. Habermehl, 1961, 1975; Iregren, 1975; Iregren &

Stenflo, 1982; Wilson *et al.,* 1982; Hufthammer, 1995; Storå, 2001).

Wildlife researchers have developed various methods for ageing beavers (*Castor fiber* and *C.canadensis*) in the past. The most reliable of these deal with the development of annuli in both the cementum and the dentine of the molars (Van Nostrand & Stephenson, 1964; Larson & Van Nostrand, 1968; Klevezal & Kleinenberg, 1969; Boyce, 1974). These methods have been widely used by wildlife researchers. Additional ageing techniques had to do with body weight and skull measurements (Hodgdon, 1978; Lancia, 1979). Despite the large errors implied, these two methods have been used in many other studies as well (Larson & van Nostrand, 1968; Hartman, 1992). Based on the X-ray analysis of the development of the root of the second mandibular molar, Hartman improved on a previous method for ageing beavers (Hartman, 1994). This method can be applied to both living and dead beavers and covers age assignments for animals anywhere between 1-7 years of life.

Within zooarchaeological research only one study on the issue of ageing beaver has been presented (Iregren & Stenflo, 1982). A total of 40 modern beavers, from the collections of the NRM (the Swedish National Museum of Natural History), were used. The beavers were all individuals of unknown age but their dates of death were known. Because of it, the authors managed to come up with a sequence of epiphyseal fusion for beavers during their first 2.5 years of life (Iregren & Stenflo, 1982). The establishment of this sequence of epiphyseal fusion in that investigation was based on body weight data of the specimens in that reference collection, their dates of death, and the assumption put forward by Hatting that all of the epiphyses in the extremities of the skeleton of the beaver were completely fused by the age of 2 years (Hatting, 1969).

The purpose of this study is to provide an operative method to age skeletal remains of beaver (*Castor fiber* L.) by means of a calendar based on the sequence of fusion of selected postcranial bones that complements these previous methods. To this end, the skeletal development of a sample of recent beavers from southern Sweden has been contrasted with their previously assigned age and later compared with the life history of the species.

Introducing the beaver (Castor fiber L.)

A brief presentation of the beaver, as it is described in the Scandinavian wildlife literature (Wilsson, 1971; Hartman, 1994; Rosell & Pedersen, 1999), will be given here. The European beaver (*Castor fiber* L.) is the sole representative of the family *Castoridae* (Order Rodentia) on the Eurasian continent. The similar species *Castor canadensis* is found in North America. Most of the beaver's body characteristics are adaptations to its aquatic mode of life. An adult European beaver normally weighs 18-25 Kg, and the full growth body length is approximately 100 cm, without the tail. The beaver is a highly social and territorial animal. A colony has usually 4-5 members, consisting of three different generations: one adult pair, two to three beavers in their first year of life, and a number of subadult individuals of 1-2 (3) years of age . At the age of approximately 2 years the majority of the subadult beavers become sexually mature. Most of the beavers then disperse from their natal colonies. At the age of 3/4 years beavers normally breed for their first time. In the wild, the beaver normally survives to an age of 7-8 years. Some beavers can reach an age of 10-20 years, although individuals older than 15 years of age are scarce.

Beavers in Scandinavia live in a lodge, which they build with sticks and mud. Lodges may have one or several underwater entrances, and one or more living chambers. In the lodge the beavers have virtually complete protection against predators like the wolf, bear, wolverine and lynx. The beaver collects winter food and keeps it submerged in the water near the lodge. They also build dams, using the same material they use for building lodges. These dams, which can transform a small creek into a series of ponds, are usually constructed in shallow waters less than 10 m wide. Transport channels are built, in order to carry food and construction material to the lodge and the beaver dams.

MATERIAL

The beaver became extinct in Sweden at the end of the nineteenth century. The present day population consists of individuals that were reintroduced to the country in the 1920-1940's from Norway (Wilsson, 1971; Hartman, 1994; Rosell & Pedersen, 1999). Beavers from Sweden, killed or

found dead in the 1960-1970's, have been used in the present study. A total of 41 beaver skeletons in the collections of Lund University Zoological Museum (LUZM), and 10 skeletons in the collections of the Swedish Museum of Natural History (NRM) are included. The beavers in the collections of LUZM originate from the Ramsele area (situated on the 63.5° northern latitude) in the county of Ångermanland, and the Filipstad area (60° northern latitude) in the county of Värmland. The Swedish University of Agricultural Sciences (SLU) captured these beavers during 1973-1977 (Hartman, 1992, 1994). The beavers in the LUZM collection were mainly killed during April-May (Table 1), those from the collections of NRM during the months of August, September, October, November, February and March in the period 1960-1972 (Table 2). The NRM beavers originate from the counties of Ångermanland and Jämtland (approximately 63° northern latitude), Värmland (60° northern latitude) and Södermanland (59° northern latitude).

For the beavers in the collections of LUZM, comprehensive data have been collected. These include body weight, body length, sex, kill site, date of death and the estimated age of the individuals (Table 1). The age estimation of these beavers was performed by Hartman and the staff at SLU (Hartman pers. communication), and was based on two methods: 1) analysis of the annuli in the cementum of the molar roots and, 2) X-ray examination of the tooth root development in the second mandibular molar (Hartman, 1992). The beavers in the LUZM collection have not been marked and recaptured. Due to this, their absolute ages are not known with 100% certainty. In fact, it cannot be excluded that some of the beavers in the LUZM collection are one year older or younger than the chronological ages presented in Table 1.

The skeletons of beaver in the NRM collection come from individuals of unknown age (Table 2). However, as these 10 beavers were collected during different seasons, they greatly complement the data set for the present study. Our own age estimations of these animals, presented in Table 2, are based on an analysis of their skeletal development.

A total of 40 epiphyses and bone growth centres of the postcranial skeleton have been studied (Table 3). Five bone elements (phalanges), which show evidence of the formation of epiphyseal surfaces on the joints of the bone have been further investigated. These epiphyseal surfaces are presented separately in Table 3 since they cannot be

Estim. age	Date of death	Locality	Body weight	Body length	Sex	Reg. nr.
5 m	19761007	Ramsele	3.4	63	M	75445
1 y	19740414	Ramsele	7.0	74	M	74615
1 y	19750415	Ramsele	6.1	75	F	74610
1 y	19750422	Ramsele	6.0	76	F	74616
1 y	19760428	Ramsele	5.2	70	M	75415
1 y	19750411	Ramsele	5.8	76	F	74607
1 y	19750412	Ramsele	7.0	76	F	74609
1 y	19760513	Ramsele	5.8	76	M	75431
1 y	19770511	Filipstad	6.2	79	M	10322
1 y	19770513	Filipstad	7.2	81	F	10329
1 y	19750510	Filipstad	5.6	75	F	10321
2 y	19760515	Ramsele	10.8	89	F	75439
2 y	19760515	Ramsele	8.0	82	M	75441
2 y	19760515	Ramsele	10.8	94	M	75438
2 y	19760510	Ramsele	10.8	93	M	75423
2 y	19770511	Filipstad	12.4	94	M	10325
2 y	19770511	Filipstad	11.6	94	M	10323
2.3 y	19760911	Ramsele	11.4	102	-	75443
2 y	19770428	Filipstad	16.3	105	M	10312
2 y	19770425	Filipstad	10.8	85	M	10308
2 y	19750509	Ramsele	14.1	102	M	74619
3 y	19750509	Ramsele	17.5	103	M	74621
3 y	19750509	Ramsele	15.0	105	M	74622
3 y	19750512	Ramsele	16.4	107	F	75426
3 y	19750513	Ramsele	13.1	95	M	74629
3 y	19760507	Ramsele	12.2	105	F	75418
3 y	19770425	Filipstad	19.8	101	F	10307
3 y	19770510	Filipstad	16.5	108.5	F	10320
4 y	19770423	Filipstad	16.2	105	M	10304
5 y	19770423	Filipstad	18.2	-	F	10305
5 y	19760515	Ramsele	17.9	105	M	75440
6 y	19760424	Ramsele	16.1	107	F	75408
6.4 y	19761013	Ramsele	20.7	109	M	75447
7 y	19750512	Ramsele	16.2	105	M	74626
8 y	19750418	Ramsele	19.4	106	F	74612
9 y	19760401	Ramsele	18.9	107	F	75406
10 y	19770426	Filipstad	17.8	108	M	10324
12 y	19770429	Filipstad	17.8	109	M	10315
13 y	19750412	Ramsele	15.7	99	F	74608
15 y	19750423	Ramsele	18.6	110	M	74617
17 y	19770426	Filipstad	18.2	107	F	10310

TABLE 1

Beaver skeletons in the collection of the LUZM. (Captures by SLU in Filipstad in the county of Värmland and Ramsele in the county of Ångermanland during 1974-1977).

Estim. age	Date of death	Loca-lity	Body weight	Body length	Sex	Reg. nr.
3 m	**19650804	Söder	-	-	M	586920
3 m	*19600807	-	3.0	60	F	615226
4 m	*19690921	Värm	-	-	-	690148
10 m	**19700331	Värm	5.1	78,5	-	700038
1.5 y	*19601118	Äng	-	-	M	587888
2.5 y	*19601118	Äng	12.3	98	F	627886
2.5 y	**19701111	Äng	13.0	91.5	-	700131
2.5 y	*19601118	Äng	11.7	90	F	627891
2.75 y	***19700216	Jämt	12.0	97.0	M	700030
3.4 y	*19721003	Jämt	-	-	M	720108

TABLE 2

Beaver skeletons in the collection of the NRM. (The beavers were killed or found dead 1960-1972 in the counties of Södermanland, Värmland, Ångermanland and Jämtland).

Legend; m = months, y = years. The ages of the beavers are unknown. I have estimated the chronological ages by using the date of death data in combination with an analysis of the skeletal development. * = Killing date, ** = Found dead, *** = Killed in bad condition. Body weight (kg), Body length (cm), M = male, F= female. The registration numbers presented are NRM's numbers.

defined as true epiphyses. However, in order to make the text and tables in this paper consistent throughout, we will only use the term "epiphyses" from here onwards. The list of the 45 epiphyses with their Latin terminology and abbreviations appears in Table 3.

Epiphyses/bone growth centres	Abbreviations
Scapula tuberculum supraglenoidale	Sca tub sup
Scapula processus coracoideus	Sca pro co
Scapula margo dorsalis	Sca ma dor
Costae caput	Cost cap
Vetrebrae cervicales	Ve ce
Vetrebrae thoracicae	Ve tho
Vetrebrae lumbales	Ve lu
Vetrebrae caudales	Ve ca
Humerus proximal epiphysis	Hu px
Humerus distal epiphysis	Hu di
Ulna proximal epiphysis	Ul px
Ulna distal epiphysis	Ul di
Radius proximal epiphysis	Ra px
Radius distal epiphysis	Ra di
Os Carpi accessorium	Ca ac
Metacarpale 1 proximal epiphysis	Mc 1 px
Metacarpalia 2-5 distal epiphyses	Mc 2-5 di
Phalanx 1 anterior proximal	Ph 1 ant px
Phalanx 2 anterior proximal	Ph 2 ant px
Coxae: Os pubis-Os ischium	Cox pub-isch
Coxae: Os ilium-Os pubis	Cox il-pub
Coxae: Os ilium-Os pubis	Cox il-isch
Coxae crista iliaca	Cox cri il
Coxae tuber ischiadicum	Cox tub isch
Coxae: Pubis dexter-Pubis sinister	Cox pub-pub
Femur caput femoris	Fe cap fem
Femur trochanter major	Fe tro maj
Femur trochanter minor	Fe tro min
Femur distal epiphysis	Fe di
Tibia proximal epiphysis	Ti px
Tibia distal epiphysis	Ti di
Fibula proximal epiphysis	Fi px
Fibula distal epiphysis	Fi di
Calcaneus tuber calcaneus	Calc tub cal
Os Tarsi centrale	Tc
Metatarsale 1 distal epiphysis	Mt 1 di
Metatarsale 1 proximal epiphysis	Mt 1 px
Metatarsalia 2-5 distal epiphyses	Mt 2-5 di
Phalanx 1 posterior proximal	Ph 1 post px
Phalanx 2 posterior proximal	Ph 2 post px
Epiphyseal surfaces on the joints	**Abbreviations**
Phalanx 3 anterior proximal part	Ph 3 ant px p
Calcaneus facies articularis	Calc fac art
Talus distal part	Ta di p
Metatarsalia 2-5 proximal part	Mt 2-5 px p
Phalanx 3 posterior proximal part	Ph 3 post px p

TABLE 3

List of epiphyses.

METHODS

All the skeletons were examined in dry condition. The epiphyses of both the left and the right sides were studied. The degree of fusion was divided into three categories.

1. *Unfused epiphyses*: the epiphysis is loose/independent from the diaphysis, meaning that it can be separated from the diaphysis without damaging the bone tissue.

2. *Fusing epiphyses*: when fusion is under progress there exists a fissure between the epiphysis and diaphysis, which means that the epiphysis cannot be separated from the diaphysis without damaging the bone tissue.

3. *Fused epiphyses*: epiphysis and diaphysis become one. The epiphyseal suture line might, however, still be visible.

If the degree of fusion has been uncertain, we have checked if it was possible to separate the epiphyses from the diaphyses, in order to distinguish unfused epiphyses from those in progress of fusing. The beavers in the collection of LUZM are better macerated than the beavers in the collection of NRM. A great number of the skeletons in the LUZM collection have been preserved in alcohol for more than 20 years after maceration. Many epiphyses which were originally determined as epiphyses in progress of fusing, could be easily separated from the diaphyses without damaging of bone tissue. The 10 beavers in the collection of the NRM have on the other hand been less thoroughly macerated. These were all boiled in water previous to our analysis. Without this treatment it would not have been possible to make a correct determination of their actual degree of epiphyseal fusion.

The season of birth of the Scandinavian beaver normally occurs between the end of May and the beginning of June, although it starts as early as the middle of April and proceeds till the end of July (Rosell & Pedersen, 1999). In Hartman's studies the date of birth was theoretically calculated to be always on the first of June (Hartman, 1992, 1994). In the present paper we have used the same date of birth in order to establish chronological age groups. As a consequence, a beaver in its first year of life and with the date of death in October has been estimated to be 5 months old, etc. Moreover, the age of the beavers with dates of death in April-May, have been rounded up to the nearest chronological year, in order to standardize the presentation of data.

The date of death data and estimated ages of the beavers in the collection of LUZM were used to establish a sequence of age groups. Thanks to the dental ageing data it was possible to differentiate 16 different chronological age groups. In this way the youngest beaver was estimated to be 5 months old and the oldest individual 17 years (Table 1). The state of fusion in the 45 epiphyses of the 41 aged beavers was then registered. By using this established sequence of the skeletal development as a reference, it was possible to estimate the age of the 10 beavers of unknown age in the NRM collection (Table 2). This resulted in adding 10 beavers with estimated ages of 3-4 months, 10 months, 1.5 years, 2.5 years, 2.75 years and 3.4 years to our previous (i.e., LUZM) data set that had no specimens from these chronological ages.

The distribution of unfused epiphyses, fusing epiphyses and fused epiphyses for each of the 45 studied epiphyses in each chronological age class, has been registered and quantified. The total number of epiphyses of any particular category (eg., right and left *Phalanx 2 anterior proximal* from all of the beavers in the 3 years cohort), has been considered as one analytical unit. The percentage of each of the three different stages of epiphyseal fusion within a particular unit has been quantified by dividing the number within each stage by the total number present within the analytical unit.

RESULTS

The skeletal development of the beaver

The results from the analysis of the skeletal development of the beaver are presented in Table 4 and Figure 1. Table 4, which comprises the epiphyseal fusion data for the 41 epiphyses, refers the percentage distribution of unfused, fusing and fused epiphyses. The epiphyses, are presented in a sequence that clarifies the order of epiphyseal fusion. This sequence, which comprises 19 chronological age groups, begins with the epiphyses that fuse at the age of 5 months and ends with those that fuse at approximately 12 years (Table 4). It is important to note that from the age of 3 years and onwards the number of individuals in the reference collection is low (Tables 1, 2).

In Figure 1 the epiphyses are presented in anatomical order. The age for complete fusion of the epiphyses and the age for the latest observation of

unfused epiphyses are presented. The data on the epiphyseal fusion for the anterior and the posterior limbs appear in Figure 1.1 and 1.2. Note that only 30 epiphyses are included in this Figure.

The results presented in Table 4 and Figure 1.1-1.2 evidence that one epiphysis fuses at 5 months (*Metatarsale 1 distal*). By 10 months five epiphyses have become fused (*Phalanx 3 anterior proximal, Calcaneus facies articularis, Talus distal, Metatarsalia 2-5 proximal* and *Phalanx 3 posterior proximal*). All these elements belong to the paw. There are, however, no skeletons available from the 6-9 months category in the reference collection. For such reason it cannot be excluded that some of these last five epiphyses fuse before 10 months. One should note that these five zones that become fused at 10 months cannot be considered to be true epiphyses (Table 3).

Three epiphyses fuse at the age of 1.5 years (*Scapula tuberculum supraglenoidale, Humerus distal* and *Metacarpus 1 proximal*) and two further ones by 2 years (*Os tarsi centrale* and the three elements of the *Os coxae*). At 2.5 years the *processus coracoideus* of the Scapula is completely fused (Table 4, Figure 1.1-1.2).

At the age of 3 years the *Os carpi accesorium* becomes fused. At 3.4 years the epiphyses of *Phalanx 1-2 anterior proximal, Radius proximal* and *Metacarpalia 2-5 distal* are completely fused. Note that the majority of these four epiphyses are fused already by 3 years (Table 4). It is evident that the distal epiphyses of *Metacarpalia 2-5* and the proximal epiphyses of *Phalanx 1-2 anterior* in the anterior extremity fuse at an earlier age than their equivalents in the posterior extremity (Figure 1.1-1.2). At the age of 4 years the *Ulna proximal, Phalanx 2 posterior proximal* and Femur *trochanter minor* have become fused (Table 4). The fusion of the proximal epiphysis of the Ulna occurs one year later than the fusion of the corresponding proximal epiphysis of the Radius. It is interesting to note that the fusion of the three epiphyses in the elbow occurs markedly earlier than the fusion of the three epiphyses of the knee joint (Figure 1.1-1.2).

Between the ages of 5-6.4 years, *Phalanx 1 posterior proximal, Metatarsale 1 proximal, Metatarsalia 2-5 distal* and *Calcaneus tuber calcaneus* become fused (Table 4). The epiphyses in the lower part of the posterior extremity seem to become fused at a later stage than those in the lower part of the anterior limb (Figure 1.1-1.2).

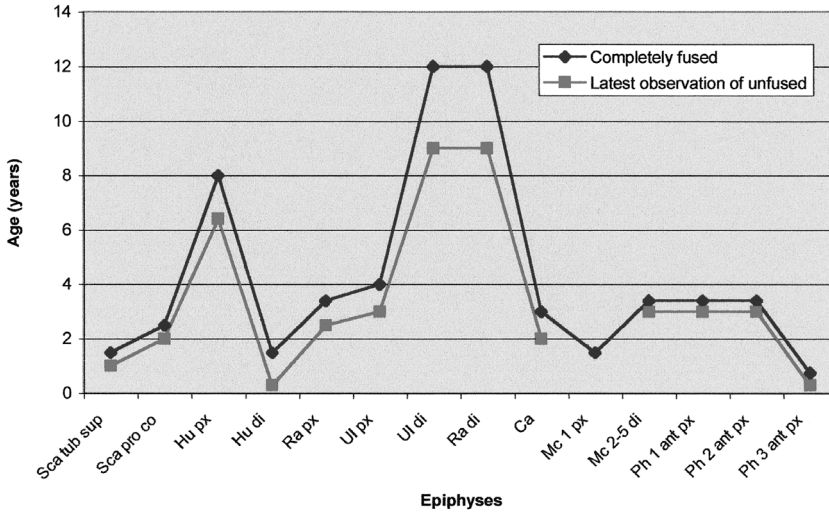The epiphyses *Femur trochanter major, Coxae tuber ischiadicum, Costae caput, Femur caput*

FIGURE 1.1

The ages for completed fusion of the epiphyses, and for the latest observation of unfused epiphyses, in the anterior extremity of the beaver (*Castor fiber* L.). For abbreviations see Table 3.
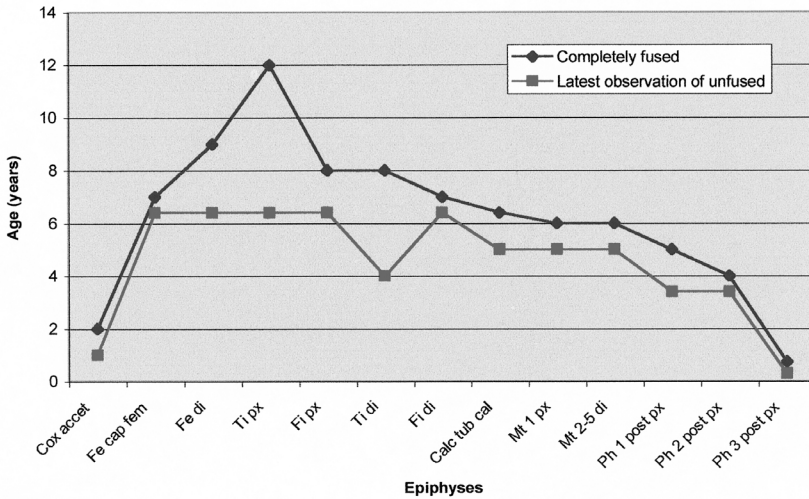

FIGURE 1.2

The ages for completed fusion of the epiphyses, and for the latest observation of unfused epiphyses, in the posterior extremity of the beaver (*Castor fiber* L.). For abbreviations see Table 3.

femoris and the distal epiphysis of the Fibula become fused at the age of 7 years (Table 4). The distal epiphyses of the Tibia, proximal epiphysis of the Humerus and the proximal epiphysis of the Fibula become fused by 8 years. The distal epiphysis of the Femur becomes fused at 9 years of age (Table 4, Figure 1.1-1.2).

At approximately 12 years six further epiphyses fuse (i.e., *Tibia proximal, Coxae crista illiaca, Coxae pubis dexter - pubis sinister, Scapula margo dorsalis, Radius distal,* and *Ulna distal*). All of these are completely fused in beavers of 13, 15 and 17 years respectively. However, as there is no beaver in the age class of 11 years in our refe-

rence collection it cannot be excluded that some of these epiphyses could fuse earlier (Table 4, Figure 1.1-1.2).

The skeletal development of the beaver is prolonged, the "maturation" of the skeleton being only accomplished at an age of more than 10 years. Also peculiar are the significant differences between the ages for epiphyseal fusion in the anterior and posterior extremity. The data also evidences that a number of ten epiphyses in the anterior extremity become completely fused between 1.5-4 years (Figure 1.1) whereas nine in the posterior extremity only do so in the 5-9 years range (Figure 1.2).

Epiphyseal fusion of the Vertebrae

Data that clarifies the epiphyseal fusion of the *Vertebrae* (the vertebral discs) is presented in Table 5, where it can be seen that there is a very large variability in the epiphyseal fusion. Due to this, the *Vertebrae* are difficult to use for ageing beavers. The majority of the vertebral discs are, at any rate, still unfused at the age of 3-4 years. The first observation of fused vertebral discs occurs at the age of 5 years for the cervical and thoracic vertebrae, and at 7 years in the lumbar and caudal vertebrae. Some vertebral discs can be in progress of fusion already by the age of 3 years, whereas a few are still in progress of fusion between 13-15 years.

Variation in the skeletal development

For the majority of the age groups there are only few individuals in the reference collection. As a consequence, evidence of variation in the skeletal development can only be studied with some degree of certainty in a few cohorts only.

At the age of 1 year, there is evidence of variation in the degree of fusion of the *Os pubis* to *Os ischium*. The data presented in Table 6 show that in 30% of the beavers the *Os pubis* and *Os ischium* are unfused, in 40% the left side is unfused and the right side is in progress of fusion and in 20% both the left and right side are in progress of fusion. We have investigated if there is any correlation between the variation in the fusion of the *Os pubis* to the *Os ischium*, with the sex and the localities the beavers originated from. The data, presented in Table 1 and Table 6, evidences that no such correlation exists.

In the age groups of 2-2.3 and 3 years there is also variation in the skeletal development. In order

Epiphyses	Unfused epiphyses	Fusing epiphyses	Fused epiphyses
Mt 1 di	3 – 4 m		5 m
Ph 3 ant px	3-4 m		10 m
Calc di	3-4 m		10 m
Ta d px	3-4 m		10 m
Mt 2-5 px	3-4 m		10 m
Ph 3 post px	3-4 m		10 m
Sca tub sup	3 m – 1 y		1.5 y
Hu di	3 – 4 m	5 m – 1 y	1.5 y
Mc 1 px	-	3 m – 1 y	1.5 y
Tc	3 m – 1.5 y		2 – 2.3 y
Cox pub-isch	3 m – 10 m 1 y (60 %)	1 y (40 %) 1.5 y	2 – 2.3 y
Cox il-isch	3 m – 1 y	1.5 y	2 – 2.3 y
Cox pub-il	3 m – 1.5 y		2 –2.3 y
Sca pro co	3 m – 1 y 2 – 2.3 y (10%)	1.5 y 2 – 2.3 y (10%)	2 – 2.3 y (80 %) 2.5 y
Ca ac	3 m – 1.5 y 2 – 2.3 y (70%)	2.5 – 2.75 y	2 –2.3 y (30%) 3 y
Ph 1 ant px	3 m – 1.5 y 2 – 2.3 y (90%) 2.5 – 2.75 y 3 y (14 %)	2 – 2.3 y (2%)	2 – 2.3 y (8%) 3 y (86%) 3.4 y
Ph 2 ant px	3 m – 1.5 y 2 – 2.3 y (70%) 2.5 y 3 y (7%)	2 – 2.3 y (10%) 3 y (9 %)	2 – 2.3 y (20%) 3 y (84 %) 3.4 y
Ra px	3 m – 1.5 y 2 – 2.3 y (70%) 2.5 y (66 %)	2 – 2.3 y (20%) 2.5 y (33%) 2.75 y (100%) 3 y (29%)	2 – 2.3 y (10%) 3 y (71%), 3.4 y
Mc 2-5 di	3 m – 1.5 y 2 – 2.3 y (97%) 2.5 – 2.75 y 3 y (18%)	2 – 2.3 y (3%) 3 y (16%)	 3 y (66%), 3.4 y
Ph 2 post px	3 m – 1.5 y 2 – 2.3 y (99%) 2,5 – 2.75 y 3 y (29%) 3.4 y (15 %)	2 – 2.3 y (1%) 3 y (10%)	 3 y (61%), 3.4 y (85 %) 4 y
Ul px	3 m – 2.75 y 3 y (50%)	3 y (29%) 3.4 y (100 %)	3 y (21%) 4 y
Fe tro min	3 m – 2.75 y 3 y (33%)	3 y (33%)	3 y (33%) 4 y
Ph 1 post px	3 m – 2.75 y 3 y (86%) 3.4 y (100%)	3 y (8%) 4 y (44%)	3 y (6 %) 4 y (56%) 5 y
Mt 1 px	3 m – 4 y 5 y (50%)	-	5 y (50%) 6 y
Mt 2-5 di	3 m – 4 y 5 y (50%)	-	5 y (50 %) 6 y
Calc tub cal	3 m – 4 y 5 y (25%)	5 y (50 %) 6 y	5 y (25%) 6.4 y
Fe tro maj	3 m – 3.4 y	3 – 5 y, 6.4 y	6 y 7 y
Cost f a c c	3 m – 3.4 y	4 – 6.4 y	7 y
Cox tub isch	3 m – 3.4 y	4 – 6.4 y	7 y
Fe cap fem	3 m – 5 y 6.4 y	6 y	7 y
Fi di	3 m – 6.4 y	-	7 y
Ti di	3 m – 4 y	5 – 7 y	8 y
Hu px	3 m – 5 y 6.4 y	6 y, 7 y	8 y
Fi px	3 m – 6.4 y	7 y	8 y
Fe di	3 m – 5 y 6.4 y	6 y, 7 – 8 y	9 y
Ti px	3 m – 6.4 y	7 – 10 y	12 y
Sca ma med	3 m – 6.4 y	7 – 10 y	12 y
Cox cri il	3 m – 6.4 y	7 – 10 y	12 y
Cox pub-pub	3 m – 6.4 y	7 – 10 y	12 y
Ra di	3 m – 9 y	10 y	12 y
Ul di	3 m – 9 y	10 y	12 y

TABLE 4

Sequence of epiphyseal fusion in the postcranial skeleton of the beaver (*Castor fiber* L.). The ages and the corresponding distribution of unfused epiphyses, fusing epiphyses and fused epiphyses are given in their rough sequence of fusion.

Bone elements	Unfused epiphyses	Fusing epiphyses	Fused epiphyses
Ve ce	3 m – 5 y	3 y - 13	5 – 17 y
Ve tho	3 m – 5 y	3 y – 15 y	5 – 17 y
Ve lu	3 m – 6 y	(3) 5-15 y	7 – 17 y
Ve ca	3 m – 6 y	4 – 7 y	7 – 17 y

TABLE 5

Epiphyseal fusion of the vertebral discs.

to shed light on it, the skeletal development in these two ages classes is presented in Table 7. Data on the epiphyseal fusion in a number of ten epiphyses is presented. The progress in skeletal development has been quantified on an individual basis by scoring the distribution of fused epiphyses (0 = 0-25 % fused; 1 = 26-75 % fused; 2 = 76-100 % fused). The scoring of fused epiphyses for each beaver is presented in Table 7. Data on the localities, the sex, and the body weights and lengths of the animals are presented in order to investigate whether a possible correlation between some of these variables and variation in the timing of fusion occurred (Table 7).

The data presented in Table 7 indicates that three beavers, aged at 2 years have reached a more advanced degree of epiphyseal fusion than the remaining seven from this age class. One of the outliers (10312) has a more advanced skeletal development than two of the beavers in the follo-wing age class (3 years; numbers 74629, 74618).

Reg. numb.	Sex	Local-ity	Unfused epiphyses	Fusing epiphyses
74616	F	Äng.	Sin / Dx	
75415	M	Äng.	Sin / Dx	
10329	F	Värml.	Sin / Dx	
74610	F	Äng.	Sin	Dx
75431	M	Äng.	Sin	Dx
10321	F	Värml.	Sin	Dx
74607	F	Äng.	Sin	Dx
10322	M	Värml.		Sin / Dx
74609	F	Äng.		Sin / Dx
74615	M	Äng.		- / Dx

TABLE 6

The distribution of unfused and fusing epiphyses, in the *Os pubis – Os ischium,* at the age of 1 year. The stage of fusion in the left side (Sin) and the right side (Dx) are given.

Likewise, two beavers from age class 2 (75441, 75423) exhibited a significantly less advanced degree of skeletal fusion than the outliers in this age class. The differences in the progress of skele-tal development between the outliers and the other seven beavers at the age of 2-2.3 years, would have been more significant if data on the epiphy-ses in progress of fusion would have been inclu-ded. In age class 2-2.3 there is only one female present. Due to this it was not possible to evaluate whether a correlation between the sex and the ske-letal development existed. The evaluation of a correlation between variation in skeletal develop-

Reg. Nr.	Estimated age	Sex	Locality	Body weight	Body lenght	Sca pr co	Ca ac	Ph 2 ant	Ph 1 ant	Ra px	Mc 2-5 di	Ph 2 post	Ul px	Ph 1 post	Total score
75441	2 y	M	Äng	8	82	0	0	0	0	0	0	0	0	0	0
75423	2 y	M	Äng	10.8	93	0	0	0	0	0	0	0	0	0	0
75438	2 y	M	Äng	10.8	94	2	0	0	0	0	0	0	0	0	2
10325	2 y	M	Värm	12.4	94	2	0	0	0	0	0	0	0	0	2
10323	2 y	M	Värm	11.6	94	2	0	0	0	0	0	0	0	0	2
75439	2 y	F	Äng	10.8	89	2	0	0	0	0	0	0	0	0	2
75443	2.3 y	-	Äng	11.4	102	2	0	0	0	0	0	0	0	0	2
10308	2 y	M	Värm	10.8	85	**2**	**2**	0	0	0	0	0	0	0	**4**
74619	2 y	M	Äng	14.1	102	**2**	**2**	**2**	0	0	0	0	0	0	**6**
10312	2 y	M	Äng	16.3	105	**2**	**2**	**2**	**2**	**2**	0	0	0	0	**10**
74629	3 y	M	Äng	13.1	95	**2**	**2**	0	0	0	0	0	0	0	**4**
75418	3 y	F	Äng	12.2	105	2	2	2	2	0	0	0	0	0	8
75426	3 y	F	Äng	16.4	107	2	2	2	2	2	1	1	0	0	12
74621	3 y	M	Äng	17.5	103	2	2	2	2	2	2	2	1	0	15
10320	3 y	F	Värm	16.5	108.5	2	2	2	2	2	2	2	0	1	15
74622	3 y	M	Äng	15	105	2	2	2	2	2	2	2	2	0	16
10307	3 y	F	Värm	19.8	101	2	2	2	2	2	2	2	2	0	16

TABLE 7

Skeletal development beavers in age classes 2 years and 3 years by means of scoring the percentage of fused epiphyses.

Legend: Reg. nr = Registration number, Estimated age in chronological years, M = male, F = female, Äng = captured in the county of Ångermanland, Värm = captured in the county of Värmland, Body weight (kg), Body length (cm), Score 0 = 0–25% fused, Score 1 =26–75% fused, Score 2 = 76–100% fused. The outliers are marked with bold text.

ment and the localities was hampered by the fact that seven out of the ten beavers originated from the county of Ångermanland. However, on first sight, there does not seem to exist any significant correlation between these two variables. On the other hand, it seems evident that body weight and body length in two out of the three outliers differ markedly from the other beavers in the 2 years cohort. In this way, body weight and body length of these two outliers (74619, 10312) correspond rather to beavers from the 3 years cohort (Table 7).

One of the 3-year-old beavers exhibited a slower skeletal development than the other six beavers in this age class. This additional outlier (74629) has reached a degree of skeletal development, which is similar to one of the outliers from the 2 years cohort (10308). Another 3-year-old beaver (75418) exhibited a somewhat less advanced degree of skeletal development than one of the outliers (10312) from the 2 years cohort. Five beavers in the age class 3 years have a more advanced skeletal development than the other two beavers from this same cohort. Both females and males, which originate from the two localities, represent the four individuals with the most advanced degree of skeletal development in age class 3 years. As a consequence, there does not seem to exist any correlation between an advanced skeletal development, the sex of the animal, and the localities where the beavers originate. Both females and males have representatives with a less or somewhat less advanced degree of skeletal development. There are, however, no individuals from the county of Värmland among the beavers with a less advanced skeletal development. This is probably due to the fact that there are only two beavers from the county of Värmland in the age class 3 years. A significant correlation has been, on the other hand, detected, between a less advanced degree of skeletal development, and a low body length and body weight. The outlier (74629) has a body weight and body length that corresponds with beavers in age class 2 years rather than individuals from age class 3 years.

In the light of the data presented in Table 7 it is possible to conclude that there is variation in the skeletal development of the beavers in the age classes of 2-2.3 and 3 years. This variation in the degree of progress in skeletal development probably reflects a natural variation in the skeletal development of the beaver. It cannot, however, be excluded that there might errors in the dental age estimation of some of these outliers (i.e. 10320, 74629). Moreover, for age classes 1, 2-2.3 and 3

years no significant correlation between the degree of progress in skeletal development, sex and locality could be demonstrated. It is therefore possible to conclude that beavers of both sexes and from both the county of Ångermanland and that of Värmland share a similar skeletal development. For such reason, the ageing method presented can most probably be applied to beavers of both sexes irrespectively of their geographical area of origin in Scandinavia. A final test to see whether a possible correlation existed between the different years (1974-1977) that the beavers were killed (Table 1) and the variation in their skeletal development (Tables 6, 7) evidenced no correlation between these variables.

Due to the sample size of the reference collection, it was not possible to clarify if similar variation in the skeletal development exists for beavers in the older age classes. For such reason one cannot exclude that the 100% of the fusions of certain epiphyses occurs at a different chronological age than those presented in Table 4.

DISCUSSION

Skeletal development in the beaver: previous studies

The results from our analysis indicate that the skeletal maturation of the beaver occurs at a much later date (ie. approximately 12 years) than hitherto postulated. Due to the much reduced number of specimens in the older cohorts one can not exclude that this maturation could take place slightly earlier than those 12 years but, at the same time, one should not forget the data referring to the vertebral epiphyses. In this way, even though there exists great variation in the time of fusion of these elements, rendering them inadequate as age estimators, vertebral discs fuse in 100% of the specimens only as late as 13-15 years of age.

In the light of these results it is evident that the epiphyseal calendar fusion in the beaver is much delayed by comparison with that of terrestrial mammals of much larger size, such as the ungulates (Amorosi, 1989; Hufthammer, 1995). At the same time there exists conflict between the fusion dates offered by our study and two previous ones made by Hatting (1969) and Iregeren & Stenflo (1982) (Table 8).

Table 8 evidences a large discrepancy between the latter of these two studies and our own that not

Epiphyses	Anders Fandén (table 4)			Iregren & Stenflo (1982: table 2)		
	Unfused	**Fusing**	**Fused**	**Unfused**	**Fusing**	**Fused**
Hu di	3 – 4 m	5 m – 1 y	**1.5 y**	3 m	4 m – 1 y	**2 m - 1 y**
Cox acet	3 m – 1.5 y	1 – 1.5 y	**2 – 2.3 y**	2 m – 1,2	1 – 1.3 y	**1,2 – 1,5**
Ph 1 ant px	3 m – 3 y	2 – 2.3 y	**2–3.4 y**	2 m – 2.2 y	2 – 2.1 y	**2 – 2.3 y**
Ca ac	3 m – 2.3 y	2 - 2.75 y	**2 - 3 y**	2 m – 1.5 y	1 – 1.5 y	**1,5 – 2 y**
Ph 2 ant px	3 m – 3 y	2 – 3 y	**2 – 3.4 y**	2 m – 1.5 y	2 – 2.2 y	**2 – 2.3 y**
Ra px	3 m – 2.5 y	2.5 – 3 y	**2 – 3.4 y**	2 m – 2.2 y	1 y – 2.2 y	**2 – 2.3 y**
Mc 2-5 di	3 m – 3 y	2 – 3 y	**2 – 3.4 y**	2 m – 1.5 y	2 – 2.2 y	**2 – 2.3 y**
Ph 2 post px	3 m – 3.4 y	2 – 3 y	**3 – 4 y**	2 m – 2.2 y	2 – 2.2 y	**2.1 – 2.3 y**
Ul px	3 m – 3 y	3 – 3.4 y	**3 – 4 y**	2 m – 2.2 y	1 – 2.4 y	**2 – 2.5 y**
Ph 1 post px	3 m – 3.4 y	3 - 4 y	**3 - 5 y**	2 m – 2.4 y	2 – 2.2 y	**2.1 – 2.5 y**
Mt 1 px	3 m – 5 y	-	**5 – 6 y**	2 m – 2.5 y	2 – 2.2 y	**2.3 y**
Mt 2-5 di	3 m – 5 y	-	**5 – 6 y**	2 m – 2.4 y	2 – 2.5 y	**2.3 y**
Calc tub cal	3 m – 5 y	5 – 6 y	**5–6.4 y**	2 m – 2.4 y	2 – 2.5 y	
Fe cap fem	3 m – 6.4 y	6 y	**7 y**	2 m – 2.4 y	2 – 2.5 y	
Fi di	3 m – 6.4 y	-	**7 y**	2 m – 2.4 y	2 – 2.5 y	**2 y**
Ti di	3 m – 4 y	5 – 7 y	**8 y**	2 m – 2.4 y	2 – 2.5 y	
Hu px	3 m – 6.4 y	6 – 7 y	**8 y**	2 m – 2.5 y	1,5 – 2.3 y	
Fe di	3 m – 6.4 y	7 – 8 y	**9 y**	2 m – 2.5 y	2 – 2.1 y	
Ti px	3 m – 6.4 y	7 – 10 y	**12 y**	2 m – 2.5 y	2.1 y	
Ra di	3 m – 9 y	10 y	**12 y**	2 m – 2.5 y		
Ul di	3 m – 9 y	10 y	**12 y**	2 m – 2.5 y		

TABLE 8

A comparison between the sequence of epiphyseal fusion in the skeleton of the beaver presented in this paper with that of Iregren & Stenflo (1982).

only relates to the actual time of fusion of specific epiphyses but also to the sequence of fusion. Thus, even though there seems to exist an overall coincidence on the sequence offered by Iregren and our own (Table 9) there are three epiphyses (bold letters in Table 9) that occur at an earlier time and a further three (underlined in Table 9) that take place at a latter time.

In relation to the discrepancies recorded in the time of fusion of specific epiphyses, we believe that these can be essentially explained on account of two factors: (1) Iregren & Stenflo's analysis was based on the untested assumption put forward by Hatting (1969) that all of the epiphyses in the limbs of beavers were completely fused at two years of age. More important, (2) Iregren & Stenflo's analysis was carried out on specimens of unknown age. For these reasons, we consider that the ages of the majority of beavers in Iregren & Stenflo specimens are heavily underestimated. As a corollary of this, we believe that our study, based on aged animals that cover a sequence of 3 months-17years, is, despite its limitations, a much more reliable data set on which to age beavers, whether complete skeletons or isolated bones.

Skeletal development and mode of life

As was previously stated, in terrestrial mammals of far lager size, such as the domestic and wild ungulates, the completion of epiphyseal fusions takes place at a much earlier time, often in the range of 3.5-4 years for the limb bones (Amorosi, 1987; Hufthammer, 1994). It is only within aquatic mammals, seals in particular, that a similar delayed process of fusion is to be found (Storå, 2001). There thus seems to exist a connection between an aquatic mode of life that places less pressure on the limbs of mammals to fuse resulting in a delayed calendar of epiphyseal fusions. This general phenomenon should not be taken as the complete explanation for there are also details that have to do with the specific locomotor needs of the different groups, and also leave their imprint on the calendar of epiphyseal fusions.

Fandén table 4	Iregren & Stenflo 1982: table 2
Hu di	Hu di
Sca tub sup	Cox acet
Cox acet	Sca tub sup
Sca pro co	Sca pro co
Ca ac	Ra px
Ph 1 ant px	**Ul px**
Ph 2 ant px	Ph 2 ant px
Ra px	Ph 1 ant px
Mc 2-5 di	Mc 2-5 di
Ph 2 post px	**Ca ac**
Ul px	**Fe px**
Ph 1 post px	Calc tub cal
Mt 1 px	Ph 2 post px
Mt 2-5 di	Ph 1 post px
Calc tub cal	Mt 1 px
Fe px	Mt 2-5 di
Fi di	Hu px
Ti di	Ti di
Hu px	Fi di
Fe di	Ra di
Ti px	Ul di
Ra di	Fe di
Ul di	Ti px

TABLE 9

A comparison between the order of epiphyseal fusion in the skeleton of the beaver presented in this paper with that of Iregren & Stenflo (1982).

When one compares the skeletal development of the beaver with that of the smallest of the seals studied by Storå, the ringed seal (*Phoca hispida botnica*), differences appear that seem to be more important than the overall coincidences due to the phenomenon of delayed fusion (compare our Table 4 with Storå's Tables 5-7).

Figure 2 compares the earliest observations of complete epiphyseal fusion for both species (It would have been statistically more relevant to compare the ages when 100% of a particular epiphysis becomes fused for all the individuals within a specific cohort but such data have not been presented by Storå, 2001).

The data presented in Figure 2.1 evidence that the fusion of the epiphyses in the elbow of the beaver occur two years earlier than is the case for the ringed seal. In addition, the fusion of the epiphysis of the *Metacarpale I* that in the beaver

occurs at the age of 1.5 years, in the ringed seal takes place at the age of 7.25 years. Likewise, the fusion of the distal epiphyses of *Metacarpalia 2-5* and proximal epiphyses of *Phalanx 1-2 anterior* take place four an three years earlier respectively in the beaver than in the ringed seal (Figure 2.1). These figures become even more significant when data from Table 4 are analyzed in detail with Tables 5-7 of Storå (2001) indicating that, notwithstanding the overall delayed fusion when compared to terrestrial mammals, higher pressures exist for the beaver to complete the epiphyseal fusion of its upper limb than appear in the ringed seal.

Such differences have a lot to do with different locomotor habits. Since early life, and, in particular after its first year of life, beavers require a robust upper limb to aid in the stability of the animal when in land but also to allow hands to help with the gathering and transport of food, felling of trees, etc. The intensive use of the hands and arms of the beaver is described in detail in the wildlife literature (Wilsson, 1971: 137-149, 161-164; Richard, 1983: 105-108; Rosell & Pedersen, 1999: 19-22). Although the ringed seal does use its arms during locomotion, it is mainly as stabilizers and thus has not the same need the beaver has for early stability of its upper limbs.

These pressures are reversed when one considers the lower limbs. The legs are much more important organs of locomotion for the ringed seal that requires an early stability at the knee-joint (King, 1983). Such early need is probably not required by beavers which nevertheless use their legs for both swimming and walking on land (Wilsson, 1971: 125-131; Rosell & Pedersen, 1999: 19-22) yet have a very different requirement for stabilisation at their knee joint (Wilsson, 1971; King, 1983; Rosell & Pedersen, 1999). As a result of this, the epiphyses at the knee-joint and posterior limb of the ringed seal become fused anywhere from 1.4-4 years whereas in the beaver the knee-joint's epiphyses fuse from 8-12 years (Figure 2.1). This pattern is reversed, although on a more restricted scale, in the proximal epiphyses of *Phalanx 1-2 posterior* and *Phalanx 3 posterior* that fuse slightly earlier in the beaver than they do in the ringed seal. Again, a greater need for stability when in land probably accounts for this "discrepancy" in the lower limbs of beaver and seal indicating that the fusion calendars are finely tuned to minor details of the locomotor habits of any particular species.
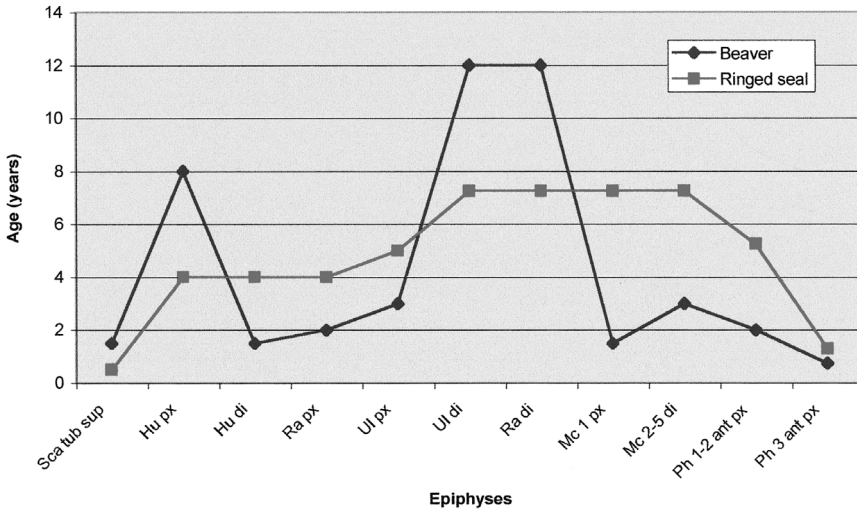
FIGURE 2.1

The earliest observed age of complete fusion of the epiphyses in the anterior extremities of the beaver (*Castor fiber* L.) and the ringed seal (*Phoca hispida botnica*).
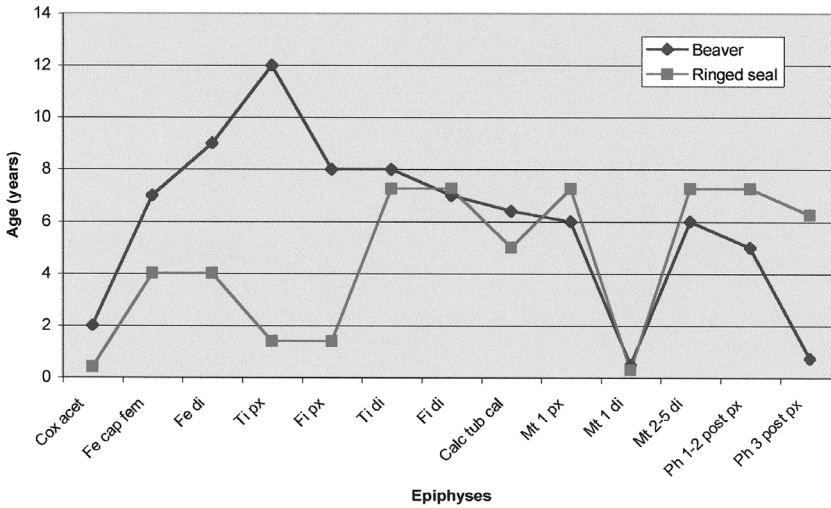

FIGURE 2.2

The earliest observed age of complete fusion of the epiphyses in the posterior extremities of the beaver (*Castor fiber* L.) and the ringed seal (*Phoca hispida botnica*).

A system for ageing beavers combining epiphyseal fusion data with life history traits

   As there probably exists a greater amount of variation in the skeletal development of the beaver than could be demonstrated in this study, translation of epiphyseal fusion times into chronological years involves a certain amount of uncertainty. In order to construct a system of operative cohorts whose ranges would neutralize errors implicit to age assignal based on isolated epiphyses, the skeletal development data will be combined with a series of life history traits of the species. In this way, the epiphyseal fusion data will be related to

five theoretically constructed life history stages of the beaver (Table 10). These stages will be as follows: Juveniles, Subadults, Young adults, Middle aged adults and Old adults. It should be stressed that, in order to avoid confusion, these

names are different from their equivalents used in the wildlife literature. In our case the categories are based on significant changes that have been recorded in the skeletal development. The epiphyses that become completely fused within each stage are presented in Table 10. They are presented in their rough order of complete fusion. Finally it should be remarked that each of these five life history stages comprises two or more of the conventional age classes used by the wildlife biologists (the data on the life history of the beaver is based on the works of Wilsson (1971), Hartman (1994) and Rosell & Pedersen (1999)).

The five categories are identified as follows:

Juveniles. The youngest life history stage corresponds to beavers of less than 1 year. Six epiphyses become completely fused within this stage (Table 10). Beavers stay in their natal colony during the first year of life. At 12 days, the beaver can swim and dive in the underwater entrances of the lodge yet the young beavers spend all of their time within the lodge during their first 2 months of life. The young beavers are able to fetch food, from the store under the water surface, during the first winter. The drive for tree felling does not exist during the beavers´ first year, although the young are able to cut and fell small trees already when they are 2.5 months old.

The first critical period for beavers is the first summer. If the animal survives, it chances of survival rise steeply. The next critical period occurs when the beaver is dispersing from the natal colony. Records of beavers dispersing from their natal colonies previous to 1 year, however, are scarce.

Subadults. The second life history stage corresponds to beavers that are approximately 1 to 2.5 years old. Eight epiphyses become completely fused within this stage (Table 10). Subadults normally stay in their natal colony during the second year of life where they take part in the care of the young. In addition, subadults normally start to fell large trees and collect food during their second autumn. The majority of the beavers become sexually mature at the age of 2 years. The dispersal from the natal colonies normally takes place between 2-2.5 years. Shortly after the ice cap disappears, beavers approaching 2 years of age start to disperse. Some, however, may stay in their natal colonies for one or more years. Records of beavers dispersing during their second summer or

Life history stages	Epiphyses in the rough order of complete fusion	Chronological age for complete fusion of the epiphyses
Juveniles	Mt 1 di	5 m
	Ph 3 ant px	10 m
	Calc di	10 m
	Ta d px	10 m
	Mt 2-5 px	10 m
	Ph 3 post px	10 m
Subadults	Sca tub sup	1.5 y
	Hu di	1.5 y
	Mc 1 px	1.5 y
	Tc	2 – 2.3 y
	Cox pub-isch	2 – 2.3 y
	Cox il-isch	2 – 2.3 y
	Cox pub-il	2 – 2.3 y
	Sca pro co	2.5 y
Young adults	Ca ac	3 y
	Ph 1 ant px	3.4 y
	Ph 2 ant px	3.4 y
	Ra px	3.4 y
	Mc 2-5 di	3.4 y
	Ph 2 post px	4 y
	Ul px	4 y
	Fe tro min	4 y
	Ph 1 post px	5 y
Middle aged adults	Mt 1 px	6 y
	Mt 2-5 di	6 y
	Calc tub cal	6.4 y
	Fe tro maj	7 y
	Cost tub	7 y
	Cox tub isch	7 y
	Fe cap fem	7 y
	Fi di	7 y
	Ti di	8 y
	Hu px	8 y
	Fi px	8 y
	Fe di	9 y
Old adults	Ti px	12 y
	Sca ma med	12 y
	Cox cri il	12 y
	Cox pub-pub	12 y
	Ra di	12 y
	Ul di	12 y

TABLE 10

The sequence of epiphyseal fusion in beaver arranged into a system of five cohorts. Epiphyses that become completely fused within each stage are roughly presented in the sequence of fusion.

autumn are scarcer. The dispersal from the natal colonies implies a fairly high mortality for the subadult beavers.

The beaver is a monogamous animal and subordinate members in the colony will normally not reach sexual maturity or be sexually active in the presence of a dominant animal of the same sex. If one of the adult beavers in a colony dies, normally a sexually mature beaver, arriving from another territory, becomes the new mating partner. However, it may also occur that one of the subadult individuals in the natal colony becomes the new mating partner.

Young adults. The third life history stage corresponds to beavers aged 3-5 years. Nine epiphyses become completely fused within this stage (Table 10). Our definition of a young adult is based on a number of changes that occur in the life of the beaver. At this age all beavers are sexually mature. A majority of them have reached full body length and size by the age of 3-4 years (Table 1). Moreover, the majority of the dispersed beavers that have survived up to this stage have succeeded in establishing a territory and finding a mating partner. The beaver normally has its first progeny at the age of 3/4 years, although the first parturition can vary anywhere from 2-5 years.

Still, beavers 2.5-3 years old may occasionally return to their natal colonies if they fail to establish territories. Delayed dispersal can be a consequence of the lack of available habitat in dense beaver populations.

Middle aged adults. The fourth life history stage corresponds to beavers 6-9 years old. Twelve epiphyses become completely fused within this stage (Table 10). These beavers share the same life history and behaviour as the majority of beavers from the previous stage. Middle aged adults have reached full body size and body length in all cases. Moreover, these beavers have bred for several times. In the wild, the Scandinavian beaver normally survives to approximately 7-8 years of age. As a consequence of this, mortality is normally rising at the end of this stage.

Old adults. The fifth stage corresponds to beavers aged 12 years or beyond. Within this stage six epiphyses become completely fused (Table 10). Our definition of old adult essentially corresponds to beavers featuring a completely fused skeleton. As previously stated, a few of the vertebral discs may, however, still be in progress of fusion.

This stage is also based on our recording of degenerative changes (i.e. osteoarthritis, on and around the joints are common in the reference collections for all specimens of 12-17 years). One should stress that observations of wild beavers at the ages of 10-20 years are truly scarce: according to Rosell & Pedersen (1999) only 3-6% of the beavers in any population reach to 10 years.

CONCLUSIONS

The skeletal development of a sample of 51 beavers of recent age from two different Swedish localities reveals an epiphyseal calendar that, despite some certain amount of intrinsic variation, does seem to be consistent for the group as a whole irrespective of the sex, geographical origin and year of death of the specimens involved. It is therefore suggested that this method might be of wider application for beavers of the species *Castor fiber*. At the same time, one should keep in mind that the restrictions of the data set presented force one to be cautious about an indiscriminate use of the method and, in particular, for populations temporally and geographically distant from the one that formed the basis of this study. In order to further explore whether discrepancies occur in the skeletal development of beaver, data from other populations both inside and outside Scandinavia should be investigated in the future. Of particular interest would be a comparison of the skeletal development of the European beaver (*Castor fiber*) with that of its North American relative (*Castor canadensis*).

ACKNOWLEDGEMENTS

REFERENCES

AMOROSI, T. 1989: A Postcranial Guide to Domestic Neo-Natal and Juvenile Mammals. The Identification and Ageing of Old World Species. B.A.R. (International Series) 533. Oxford.

BOYCE, M. S. 1974: *Beaver population ecology in interior Alaska.* Ms Thesis, University of Alaska Fairbanks.

HABERMEHL, K. H. 1961: *Die Alterbestimmung bei Haustieren, Pelztieren und beim jagdbaren Wild.* Paul Parey, Berlin-Hamburg.

HABERMEHL, K. H. 1975: *Die Altersbestimmung bei Haus- und Labortieren.* Paul Parey. Berlin.

HARTMAN, G. 1992: Age determination of live beaver by dental X-ray. *Wild Society Bulletin* 20: 107-111.

HARTMAN, G. 1994: *Ecological studies of a reintroduced beaver (Castor fiber) population.* The Swedish University of Agricultural Sciences Rapport 25. Uppsala.

HATTING, T. 1969: Age determination for Subbfossil Beavers (*Castor fiber* L.) (Mammalia) on the Basis of Radiographs of Teeth. *Vidensk. Meddr. Dansk naturh. Foren*. 132: 115-128.

HODGDON, H. E. 1978: *Social dynamics and behaviour within an unexploited beaver (Castor canadensis) population.* Ph D. Thesis, University of Massachusetts.

HUFTHAMMER, A. K. 1995: Age determination of Reindeer (*Rangifer tarandus* L.). *Archaeozoologia* Vol. VII/2: 33-42.

IREGREN, E. 1975: Age-dependent changes in the lower extremities of the elk (*Alces alces*) in Central Sweden. In: Clason, A.T. (ed.): *Archaeozoological studies*: 367-380. North-Holland-American Elsevier, Groningen.

IREGREN, E. & STENFLO, G. 1982: An osteological and statistical attempt to interpret seasonal occupation of dwelling sites in Northern Sweden by studying the beaver (*Castor fiber* L). *PACT 7 part I 1982*: 225-234. Second Nordic Conference On The Application Of Scientific Methods In Archaeology, Helsingor.

KING, J. E. 1983: *Seals of the World*. 2nd edition. British Museum of Natural History, London.

KLEVEZAL, G. A. & KLEINENBERG, S. E. 1969: *Age determination of mammals from annual layers in teeth and bones.* Israel Program for Scientific Translantions, Jerusalem.

LANCIA, R. A. 1979: *Year-long activity patterns of radiomarked beaver (Castor canadensis).* Ph. D. Thesis, University of Massachusetts.

LARSON, J. S. & VAN NOSTRAND, F. C. 1968: An evaluation of beaver ageing techniques. *Journal of Wildlife Management* 32: 99-103.

LESBRE, F. X. 1897/8: Contribution a l'étude de l'ossification du squelette des mammifères domestiques. *Annales de la Societé d'Agriculture, Sciences et Industrie de Lyon*, Sér. 7, 5: 1-106.

RICHARD, P. B. 1983: Mechanisms and adaptation in the constructive behaviour of the beaver (*C. fiber* L.). *Acta Zoologica Fennica* 174: 105-108.

ROSELL, F. & PEDERSEN, K. V. 1999: *Bever*. Landbruksforlaget. Stockholm.

SILVER, I.A. 1969: The ageing of domesticated animals. In: Brothwell, D. & Higgs, E. (eds.): *Science in Archaeology*: 283-302. 2nd edition. Thames and Hudson. London.

STORÅ, J. 2001: Skeletal development in the Grey seal *Halichoerus grypus*, the Ringed seal *Phoca hispida botnica*, the Harbour seal *Phoca vitulina vitulina* and the Harp seal *Phoca groenlandica*. Epiphyseal fusion and life history. *ArchaeoZoologia,* XI: 199-222.

VAN NOSTRAND, F .C. & STEPHENSON, A. B. 1964: Age determination for beavers by tooth development. *Journal of Wildlife Management* 28: 430-434.

WILSON, B.; GRIGSON, C. & PAYNE, S. (eds.) 1982: Ageing and Sexing Animal Bones from Archaeological Sites. B.A.R. (British Series) 109. Oxford.

WILSSON, L. 1971: Observations and experiments on the ethology of the European beaver (*Castor fiber* L.). A study in the development of phylogenetically adapted behavior in a highly specialized mammal. *Viltrevy Swedish Wildlife* 8,3: 115-266.