'Practice with Science': Molar Tooth Eruption Ages in Domestic, Feral and Wild Pigs (Sus scrofa)

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'Up to three years of age the boar is very small, from the size of a rat to a young lamb, very hairy, with dark longitudinal stripes on its back and sides.'

(Baden-Powell 1889, 28)

Introduction

Baden-Powell's criteria for ageing pigs are best ignored though the process is fraught with uncertainties. In the 19th century the Royal Agricultural Society of England encouraged new agricultural methods, their motto provides the title of this paper. Among their aims was the development of more accurate dental ageing methods for domestic mammals, though the use of tooth eruption data has been profoundly unscientific since then.

The growing urban population in 19th century Britain demanded more intensive food production, with accurate means for the ageing of breeding animals. Substantial money prizes were offered at agricultural shows, but open to widespread fraud if the animals were inaccurately aged. Professor J. B. Simonds was appointed as the official 'Veterinary Inspector' for the Royal Agricultural Society, based on his publications of new data for tooth eruption in cattle, sheep and pigs (Simonds, 1854, 1855). Simonds was later the President of the Royal Veterinary College and, in 1855, the 'referee for the age of pigs' for the Royal Agricultural Society (*The Times*, 12th December 1855, 10A, Pattison, 1990).

'...long-continued and repeated observations had convinced him [Simonds] that the opinions advanced by veterinary writers, both of this country and of France, were often incorrect...Several years since I became satisfied that nothing which had been written on the dentition of the ox or sheep in this country could be relied upon...' (Simonds, 1854, preface, name inserted in square brackets for clarity).

Simonds had in mind the very long tooth eruption ages given by Youatt (1831, 1834, 1837, 1847) for the domestic species describing these as '...rather the result of imagination than of practical investigation...fanciful in the extreme...' (Simonds op. cit., 58). However, in spite of Simonds' caution, these early works have been rediscovered (for example, Silver, 1969) and the data have been used to advance two hypotheses: (a) That the long eruption ages given in historic sources are appropriate for ageing dental specimens from historic and prehistoric periods and (b) that dental development has been much accelerated by modern intensive husbandry and breed selection.

For cattle, these propositions gain no support from the available evidence (Legge, 1992; Payne, 1984). It is shown below that these are equally doubtful for the pig.

Physical influences on dental development in domestic mammals

Tooth development studies on domestic mammals have seldom been conducted in a scientifically controlled

Simonds expressed his doubts about the accuracy of the ageing methods previously in use (1854, preface):

[†] Deceased.

 $^{^1}$ Relatively less so now, the maximum prize for Young Pig of the Year' is £200.

Table 1. Cranial dimensions (mm) of 2 modern pigs, raised and 10 °C and 35 °C

'	1a* length	13* parietal length	14 * frontal length	15* nasal length	43* zygomatic breadth	tooth row dp ² -dp ⁴	cranium weight (g)
35°C	173.5	35.0	61.5	71.3	98.0	36.2	146.7
10°C	153.0	31.0	56.7	56.8	98.0	35.2	133.0

^{*}measurements after von den Driesch, 1976, fig. 12a, 39.

manner, so that the environmental and breed influences on cranial and dental development are poorly understood. Most work has dealt with the eruption of the incisor teeth as these are more easily accessible; for example, Brookes & Hodges (1979) found that young cattle showed a small variation in incisor tooth eruption according to plane of nutrition, this being slightly faster with a higher plane, but with little difference shown between breeds. Weiner & Forster (1982) reported that incisor tooth eruption in Friesian cattle was slightly faster than in Jersey cattle, though the variation was small. Data is equally uncertain for the smaller domestic species. Noddle (1974) reported that feral goats in Britain have slower tooth eruption than those living under full human control; the lower third molar being in full wear only by 4 years of age, while in those under close human control, this is found at 3 years of age. However, with a small sample and assumed ages for the feral goats based on a 'probable' birth season, the data is uncertain. Moran & O'Connor (1994) surveyed the published data on tooth eruption ages in sheep:

'Overall, it is concluded that much of the received wisdom on skeletal maturation in sheep is poorly founded and unreliable, and that tightly controlled test populations are needed if better data are to be obtained...the published evidence is contradictory and ambiguous.' (op. cit., 280)

The evidence for tooth eruption ages in the pig is no more certain. The environmental impact on morphology in growing pigs can be pronounced, perhaps more so than in other familiar domestic mammals. McMeekan (1940a, 1940b, 1940c, 1941) published comprehensive accounts of body development in growing pigs under different planes of nutrition. He found that skeletal growth continued to '...a remarkable degree...' even with a low plane of nutrition. While his study presents an important data set relating to growth, tooth eruption ages were not observed. More recently, Heath & Ingram (1980, 1983) divided litters of Large White (Yorkshire breed) piglets into two groups, raising each at ambient temperatures of either 10 °C or 35 °C. Even at eight weeks the morphology of each group was very different.

Those raised at 10 °C had shorter limbs, less subcutaneous fat, a lesser vascular supply to the skin and smaller heads, than those raised at 35 °C (Heath & Ingram, 1983, fig. 2). Dental development was not examined as part of this experiment, but two skulls (one from each temperature group) were retained by the author here. The skulls each have a very different form, with those from the warm environment appearing longer and more slender than the skull of its litter mate from the colder environment:

The difference between the specimens is marked in the length measurements, while the zygomatic widths are the same, and the length of the deciduous tooth row is nearly so. It is noteworthy that the state of tooth eruption is identical in each skull; the deciduous premolars (dp2-dp4, upper and lower) are fully erupted, while the crowns of M1 are visible within the alveolus, but the tooth is unerupted. These and other data are in marked contrast to Nehring's findings (1888; see below).

The uses of dental ageing in archaeology

The study of animal remains in archaeology gained momentum in the 1960s, when new interpretations about past animal husbandry systems were based upon dental ageing (Higgs & White, 1963; Ewbank et al., 1964; Higham, 1967a, 1967b). Archaeology was then in process of absorbing methods from a range of sciences, shown by the publication of the influential volume Science in Archaeology (Brothwell & Higgs, 1963, 1969). This work included a synopsis of data concerning the ageing of mammals by tooth eruption and bone fusion (Silver, 1963, 1969) in a paper that has been widely cited.

The use of Silver's synopsis continues even now, in spite of its limitations (Bull & Payne, 1982), Payne (1984) and Legge (1992). Bull & Payne (1982, 65) questioned the long tooth eruption ages given for 18th century pigs, and Payne (1984) challenged the long tooth eruption ages given for 19th century cattle.

 $^{^2\,\}mbox{The}$ author was once a member of this research group. The skulls were given to him by the late D L Ingram.

These data had been earlier questioned by Simonds (1854, and see below). Payne (1982) showed that German veterinary sources of pre-1850 gave very long tooth eruption ages for cattle, while those published after 1850 gave much shorter times – the same as seen in cattle now (Payne, 1984, fig. 10, 78). Further, the earlier publications gave the wrong order for the eruption of P₄ and M₃ (fig. 11, 79). Payne argued that an abrupt change in the timing or order of cattle tooth eruption in the mid-19th century was improbable. This was further discussed by Legge (1992, 18-22), who concluded that unacknowledged borrowing from early 19th century publications gave the 'long' eruption ages, while the 'short' eruption ages could be followed back to Simonds (1854).

For example, Silver (1969) gave the eruption age for the lower third permanent molar (M₃) as 24 months of age in 'commercial cross-bred stock of 1950' and compared this with the 4-5 years of eruption age given by Chauveau for this tooth (1888 cited, but probably the English language edition of 1891; Silver, op. cit., table D. 296). At face value, this offers clear evidence for the acceleration of dental development in cattle, yet both sources are questionable. Firstly, Silver took the 1950 data for cattle tooth eruption from Miller and Robertson's Practical Animal Husbandry (1947, 5th edition). This is a very general textbook in which the source of the tooth eruption data is not cited. The 1st edition of this work was published in 1934 with the same tooth eruption data. Furthermore, these data are practically identical to those given by Simonds (1854), which is the probable source for Miller and Robertson. A further twist comes from the data cited by Silver (1969) as 'from Chaveau.' This tabulation is not found in the original French edition (Chauveau, 1857), but was inserted into the English translation of 1873 as a generalised table 'for ruminants.' This tabulation gives the eruption of the 'seventh' molar (upper or lower M3) as 4-5 years, the source being 'from Leyh' (F. A. Leyh, 1850), where the same table is found (see also Legge, 1992, pp 18-22).

The variations in these data led Silver to conclude that '...tooth eruption dates...differ very significantly between individual breeds within a single species...' and that tooth eruption had been accelerated both by '...intensive selective breeding...' as well as improved nutrition (Silver, 1969, 283). Accordingly, he suggested that the 'long' tooth eruption ages of the early 19th century should be used for the ageing of archaeological specimens, assuming that these were of a more 'primitive' nature.

This belief continues in both archaeological and veterinary sources. Hillson (2005, 210-11) states that the plane of nutrition is 'known' to accelerate tooth development in selectively bred domestic animals and the same view is found in scientific investigations; for

example, in Bradley (1930) and Sweeney & Sweeney (1982). In the latter, tooth eruption in domestic pigs is said to be 'often' earlier than in wild pigs, quoting Sisson & Grossman (1938) among others, these too having tooth eruption data of uncertain origin. The same sources are given by Miles & Grigson (2003, table 16.9, 342-3, also citing Reiland, 1978, see below) to support the view that 'The timing of eruption does seems to be affected by breed and particularly by whether the members of the breed mature early or late.' More recently, Zeder (2006, 95) wrote of "...feral, rough or 'semi-wild' animals with delayed eruption rates when compared to carefully tended 'improved' breeds." Additionally, Rolett & Chiu (1994, table 2, 378) suggested that domestic pigs have fast or slow maturing dentition, according to breed, but do not give supporting evidence for this.

The problems of recording tooth eruption in the pig

In the 19th century pigs were usually raised at the cottage level of husbandry so that there was little interest in accurate methods of dental ageing. As Girard (1834, author's translation) wrote:

'Knowing the age of the pig by inspection of the teeth has little usefulness, we know. In trade, the teeth are rarely used to determine if the animal is young or old. Dental examination in the pig also presents a special difficulty because of their physical strength.' Cornevin & Lesbre (1894) were more expressive:

'Of all animals, the pig is the most difficult for dental examination. It is very uncooperative and shrieks as soon as it is held, it clenches its jaws when you try to open its mouth, it has considerable strength in its head and neck. All circumstances that create difficulties or at least problems.' (Cornevin & Lesbre, 1894, 14).

The strength of the pig jaw muscles is such that in certain studies, routine anaesthesia has been used to allow the examination of the posterior molars (Matschke, 1967; Boitani & Mattei, 2002). While such procedures may not be ideal under experimental conditions, the procedure seems unavoidable if observations are to be repeated in mature pigs. Though even this is attended by problems, as described by Mount & Ingram (1971):

The chief problems of anaesthesia in the pig arise from the size of the animal and the difficulties associated with restraint and handling.'

Pigs thus present a special difficulty for dental examination, as this needs considerable force and causes both pronounced distress to the animal and damage to the hearing of the handler.

A further variable arises from the manner in which 'eruption' was considered by different authors. A few describe their criteria, while most do not. The following details are commonly uncertain:

- 1. Were the jaws examined when fleshed, or defleshed?
- 2. Was x-ray examination employed?
- 3. Was tooth 'eruption' taken to be the emergence of the anterior cusps, or when the full occlusal surface was visible, whether though gum or bone?

The examination of fleshed or defleshed specimens may give rise to quite different views of the early eruption stages. For example, Simonds (1854) worked largely with living animals, but the illustrated specimens were shown as defleshed. In Brown (1882), some of the illustrations are of defleshed specimens, taken from Simonds' earlier work without acknowledgement of source, while others are of mandibles in a fleshed state.

The sources of information

The discussion below is mainly concerned with the eruption of the permanent dentition, and in particular on the cheek tooth row $P_4 - M_3$ (4th permanent lower premolar to 3rd permanent lower molar). These teeth are of the greatest utility in archaeological studies, as this part of the mandibular tooth row is robust, and

most often found intact. The eruption of these teeth also extends from the early months to full adulthood. For the purposes of uniformity, all eruption events given below are based on months of 30 days.

The pigs in the various investigations below lived under a variety of conditions:

- 1. Domestic pigs, living under normal farm husbandry
- 2. Domestic pigs living in the wild, more usually described as 'feral'
- 3. Cross bred pigs (wild X domestic) living confined under a form of husbandry
- Wild pigs living confined, under conditions of husbandry
- 5. Wild pigs living in a natural, free-ranging condition

The data relating to each group is reviewed below, concentrating on those investigations with original data, though certain secondary sources are noted as these are commonly cited.

(i) Studies on the dentition of domestic pigs

Girard 1834

This work gives data on tooth eruption in horse, cattle, pig and dog, derived from a variety of sources. For the pig, Girard gave M_1 eruption ages at $5\frac{1}{2}$ -6 months and the M_2 at 10 months, ages that seem precocious when compared to more recent studies of both wild and domestic pigs (see Figure 1). On the other hand, the eruption of M_3 is given as 36 months, an age more likely to correspond to the emergence of the posterior cusps of this slow-erupting tooth. Girard was the

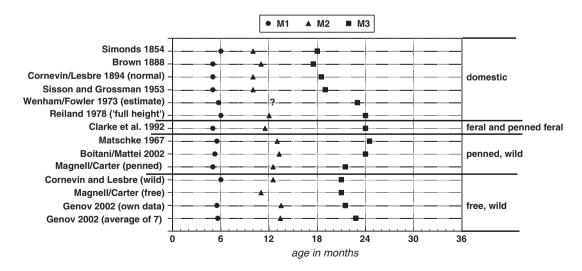


Figure 1. Tooth eruption ages from a variety of sources, from pigs living under different conditions. Where an age range is given in the original, the mean age is plotted.

source of the 'long' tooth eruption ages cited in Youatt (1847), while other French veterinarians doubted Girard's data (for example, Bouley & Reynal, 1856).

Simonds (1854) and Brown (1882)

Simonds' (1854) comprehensive work gives tooth eruption data for cattle, sheep and pig. He stated that his observations were based on over 500 pigs '...of attested ages...' though the manner of attestation is not described. Brown (1854) published in the same year, but only on the incisor teeth in cattle, regarding ageing by means of the molar teeth as scarcely possible:

'...they [i.e. the molar teeth] are not likely to be of the smallest use in defining the age – the difficulty of examination in the living animal...rendering it unlikely that they will ever be consulted with advantage.' (Brown, 1854, 11, comment in square brackets inserted for clarity).

Brown also commented on '...the very few observations that I have made' with regard to the molar teeth (Brown, 1854, 12), though in a later work (Brown, 1882) much more data is given, which clearly owes much to Simonds (1854). Brown borrowed both diagrams and tooth eruption ages from Simonds with little acknowledgement of the source. However, both Simonds (1854) and Brown (1882) assert that selective breeding and intensive feeding had *little or no* influence on tooth eruption ages. The lack of acknowledgement of Simonds' earlier work by Brown is surprising, as the two men knew each other well, and had a long association in their veterinary careers (Pattison, 1990).

The tooth eruption ages given by each are as follows:

Significantly, both give the eruption age for M_3 as 18 months. However, here Simonds' data (fig. 55, 144) may be questioned. He illustrated the M_3 in full eruption in a defleshed mandible, giving this as at 18 months '...when the dentition is perfected.' However, in the light of studies since, it is improbable that this degree of eruption would be seen by this time. The early stages of eruption would be the most likely condition, and it is probable that Simonds was at fault here.

Certain later studies also give an 18 month age for early M_3 eruption, though it is probable that these derive from Simonds' work. A general agreement places M_3 eruption at about 20-24 months, recognised by the first occlusion of the anterior cusps. Simonds' work was well known in the later 19^{th} century, though seldom acknowledged by citation. An exception is the veterinary dictionary of Bouley & Reynal (1856) which gives fulsome

Table 2. Pig tooth eruption ages from Simonds (1854) and Brown (1882)

Tooth	Simonds 1854	Brown 1882
P ₄ M ₁ M ₂ M ₃	12 months 6 months ?12 months** 18 months	12 months 5 months* 12 months 18 months

*earliest eruption stage described; given as 'signs' of eruption. **fig. 51, 109, shows M_2 in early eruption through the bone, the age given as 10 months. The age of oral eruption is not made explicit in the text

credit to Simonds' work, those authors stating that he had corrected the errors of Girard and others. However, it is very probable that Simonds propagated the very young age, at 18 months, for the full eruption of M₃.

Nebring 1888

Nehring's work was significant in promoting the belief that tooth eruption ages differed between domestic and wild pigs, and that certain breeds were precocious in this respect. Curiously, while Nehring cited Brown (1882) as a principle source of his data, Simonds work (1854) was little noticed (Nehring op. cit., pp 37, 46). Yet this scant reference to Simonds' work belies its importance, as most of Nehring's illustrations were taken from Simonds without acknowledgement (see figs. 2, 4, 6, 8, 10, 11, and 12 in Nehring, 1888, comparing these with Simonds, 1854). Simonds' illustration of the mandible of an 18 month old pig (figure 55, 114) became Nehring's figure 12 (48), but with the age adjusted to 18-20 months. Apparently Nehring had some concerns about the early age attributed to this specimen by Simonds, having increased this slightly.

Nehring's own sample was of 84 skulls from domestic pigs, 24 skulls from wild pigs, and a few cross bred (wild X domestic) and almost all were infantile or juvenile. His sample was mainly of English breeds (given as Berkshire, 'English race', Essex, Yorkshire, Suffolk) with a few other European breeds. Only seventeen piglets were older than one year, and only *four* were over 2 years of age. Many would have presented a significant biohazard, the cause of death being recorded as tuberculosis, scrophula or 'wasting.' Nehring (figs. 14 and 15, 67) illustrates the impact of such disease on the cranial development in a young pig, a condition hardly conducive to 'normal' tooth eruption. Nehring described his recognition of the early stages of tooth

³ There was much interest worldwide in British pig breeds at this time; the Yorkshire pig (Large White) remains a popular breed.

⁴ In humans, tuberculosis in the lymph gland of the neck.

eruption in defleshed mandibles (74) and tabulated the eruption state for each specimen (75-82). He listed:

- 1. Five Yorkshire breed pigs and 1 Essex breed with the M₁ visible at the 'possible' age of 5 weeks (given as: '5 weeks?' The footnote on p. 41 says 'possibly 9 weeks of age' which seems the more probable from the state of development.)
- Nine pigs (6 of them with chronic disease) at 2.0 -2.5 months of age. None show early eruption of M₁. The state of development agrees with the author's 2 'Babraham' specimens at 2 months of age, noted above.
- 3. Six Yorkshire pigs at 9 weeks of age in which early eruption of the M_1 was claimed.
- 4. Twelve pigs of different breeds (5 diseased, 3 'died') aged between 2.5 and 3.0 months of age showing no eruption of the M_1 .

Nehring's data thus claims early eruption of the M₁ in 6 pigs of 5 (or 'possibly' 9) weeks of age, and also in a further 6 pigs at a little over 2 months of age. These data are implausible, as the eruption of M_1 at 5 weeks of age would be very precocious indeed, and even at 2 months development would be very advanced. Yorkshire pigs (usually named 'Large White' in the UK now) do not show such precocious development. In the recent publications discussed below, this breed shows the earliest eruption of M_1 at no more than 3 or even 4 months (Teonge & McCance, 1973; Wenham & Fowler, 1973; Reiland, 1978). These data contradict the reported findings of Nehring. His sample was rather few, of uncertain age, and the animals were often diseased. It is not possible to argue that these data show precocious deciduous tooth eruption in the Yorkshire breed. Further, Nehring's sample of adult dentition was negligible, with the development of M₃ based on only 3 specimens. The two younger of these had the M₃ cutting the gum at 15 and 19 months, and one specimen showed early eruption at 22 months age. The dentition of four pigs aged 24-28 months of age was described as 'finished' in defleshed specimens. Based on his very limited sample, Nehring gave the following generalised eruption ages (p.73, table) which, for domestic pigs, are strikingly like those given earlier by Simonds (1854):

Nehring's work was promoted in North America by Schwartzkopff (1889), who was also active in supporting the conclusions that 'modern feeding' had resulted in accelerated dental maturity (Schwartzkopff, 1889, p 72-73). Yet once again the influence of Simonds' work is evident. Schwartzkopff's figure 1 (piglet skull, p 87) was taken from Nehring, (fig. 2, p 38, though one tooth, the I₃, has been lost in translation). This diagram in turn

was taken from Simonds (1854, fig. 47, p 102), as were others. In his conclusions Schwartzkopff asserted the proposition that the timing of tooth eruption is dependant upon '...race, feeding and health.' It is very doubtful that this proposition can be sustained from the data as given, which was not original.

Huidekoper 1891

This author did not claim originality, but rather summarised a range of French, German and Italian publications in a compendium of dental ageing, though mainly relating to the horse. The accuracy of that data is not considered here, though caution may be advised in the light of Huidekoper's information for other species. He preferred the 'long' tooth eruption ages for cattle, derived from Girard (1834), dismissing Simonds' data on the grounds that '...he evidently studied on very precocious cattle' (op. cit., 162). Huidekoper's data for pig tooth eruption relied largely upon Schwartzkopff (1889), who in turn relied on Nehring (1888), who in turn derived the data, at least for older pigs, from Simonds (1854).

Cornevin and Lesbre 1894

The *Traité d'Age des Animaux Domestiques* is a comprehensive work, in which Simonds (1854), Girard (1st edition, 1818-20) and Huidekoper (1891) are cited as sources. The last is essentially a repetition of Girard (1818, 1834). Cornevin and Lesbre disbelieved Girard's 'long' tooth eruption ages for cattle, describing these as '...tres discordant...' with other information. For pig tooth eruption, they simplified Nehring's observations, giving tooth eruption data only for 'precocious' and 'ordinary' domestic pigs, and for wild pigs (table, 374), regarding these data as 'concordant.' This is unsurprising, as a good deal of Nehring's data (1888) was derived from Simonds (1854).

The synopsis given by Cornevin and Lesbre (374) is:

Again, the 18-19 months eruption age for M_3 is early, although they emphasise that the eruption of M_3 is 'very slow', attaining full eruption only by 2.5 years (op. cit., 375). This is broadly in accordance

Table 3. Synopsis of tooth eruption ages, Nehring (1888)

		domestic pigs			
	early	normal	late	wild pigs	
P ₄ M ₁ M ₂ M ₃	12 2 7-8 17	14-15 5 9-10 18-19	16 6 12-14 21-22	15-16 5-6 12-13 20-24	

with their figure 164 (op. cit., p 363) which shows the mandible of a 'two year' boar, in which three paired cusps of M_3 are erupted, but not the final single cusp.

Engelberg 1917

This paper reviews earlier German and other works on pig tooth eruption, with some original data, though again mostly from the juvenile dentition. Engelberg also observed that pre-1850 sources for tooth eruption gave longer eruption ages than those published after that date (table 1, 12), though he too assumed that this was evidence for breed improvement rather than faulty observation. Simonds' work was among those cited, though Engelberg's data are mainly concerned with the eruption of the milk teeth, with some data for M₁ and M₂ (table VI, 64). M₁ was said to begin eruption at about 4 months, while in a single specimen M₂ began erupting at 11 months. Two specimens aged 16 and 18 months had the M2 fully erupted. A footnote states that the eruption of M₃ could not be followed in the sample available.

Sisson and Grossman (1938, 1953, 1975)

This veterinary text is commonly cited in archaeological publications, though the earlier editions offer no indication of the source for the eruption data. The tabulated ages of tooth eruption are unchanged in the 1st to 4th editions of the book. That for pigs is given as:

 P_4 12-15 months M_1 4 to 6 months M_2 8 to 12 months M_3 18 to 20 months

The fifth edition (1975) included a new section on tooth eruption in the pig (St Clair, 1975), where the eruption data is attributed to Bradley (1930), who in turn cited Sisson (1914) as a source of this data. Bradley's own sample was of pigs aged 9 months only. The edition of 1975 even gives an earlier edition of itself as a source of data. From the eruption ages given, it is probable that Simonds (1854) was the source of the data.

Bradley (1930)

In his study, Bradley cited Sisson and Grossman (1914) and Brown (1882), saying that these '...were not entirely in agreement...' although both can be traced to the same original study (Simonds, 1854). Bradley summarised his own observations, but advised caution, setting out the necessary conditions for proper investigations into the timings of tooth eruption (Bradley, 1930, 960):

Table 4. pig tooth eruption ages from Cornevin & Lesbre (1894)

	early (domestic)	normal (domestic)	wild pigs
P ₄	12	13-14	15
M ₁	3	5	6
M ₂	8	10	12-13
M ₃	17	18-19	20-22

'...the ideal method of studying dentition is to examine a large collection of living animals at definite intervals from the time of birth to the time when the last permanent tooth is cut...such a method is not practicable unless unlimited time and facilities are available.'

Following Brown (1882) Bradley goes on to caution that breeders:

'...may or may not have a definite and precise record of the day of birth, and who may or may not be concerned more with a desire to convince than to disclose cold facts.'

Bradley collected a sample of pig heads around 9 months of age from commercial butchery practices, although he regarded his sample of 176 specimens as too few for definite conclusions. In reality, they were from a very narrow age range and his notes were offered as 'introductory.' The paper gives no details of birth dates, or the number at each eruption stage, or on the observed variation in eruption ages at each stage. Tooth development was followed only to the eruption of M_1 , which was said to vary from 15 - 26 weeks (about 4 months to $6\frac{1}{2}$ months), but without any information on the distribution of the data.

McCance, Ford and Brown, 1961

This work involved the investigation of severe under nourishment in growing pigs, to about one year of age. These animals had a diet so restricted that while life was maintained, there was little or no weight gain. Yet these data have been recently cited as showing that poor nutrition delayed tooth eruption (for example in Sweeney *et al.*, 1982, p 488; Carter & Magnell, 2007, table 10.5 and p 210). These citations overlook the extreme severity of the starvation inflicted, a state of prolonged malnourishment that would not be met in nature. Coincidentally, the author here measured the

⁵ Staff at the Royal Veterinary College, University of Edinburgh, have kindly examined their records and find that Bradley's collection is not there now.

Table 5. Pig tooth eruption after McCance et al. (1961) and Teonge & McCance (1973)

Tooth	eruption time, McCance et al. 1961	eruption time, Teonge and McCance 1973	occlusion time, Teonge and McCance 1973	root closure, Teonge and McCance 1973
P ₄	12-13	8-12	8-12	12-16
M ₁	3-4	4 (erup.)	4 (occl.)	8
M_2 M_3	8-9	16 (erup.)	24 (occl.)	30
	13-14	16 (erup.)	24 (occl.)	30

The notations 'erup.' and 'occl.' above refer to the authors' designations of 'eruption beginning' and 'occlusal level attained.' The erroneous eruption ages are in bold.

oxygen consumption of the starved pigs (McCance & Mount, 1960; Mount *et al.*, 1967). Tooth eruption and skeletal development were monitored in normal 'control' pigs, sixteen of which were sequentially slaughtered. Tooth eruption ages were given for the normal and starved pigs; Tables 5 and 6 (McCance *et al.*, 1961, pp 219-20) show that gross malnourishment affected the development and eruption of the deciduous teeth and M₁, those teeth where crown formation began *in utero*. The result of this experiment is considered in conjunction with the paper below:

Teonge and McCance 1973

Seventy large white pigs were fed a normal diet and their development was followed from early life to the 5th year. Forty further pigs were subject to severe malnourishment to one year of age, as noted above. During that first year of life, growth in the malnourished group was restricted so that weekly body weight gain was less than 50 gm. By one year of age the normal pigs weighed an average 180 kg each while the 'undernourished' pigs averaged only 5.5 kilograms, a scarcely credible 3% or so of the 'normal' pigs (Teonge and McCance op. cit., 2; McCance & Mount, 1960, table 1, 511). Of the malnourished pigs, 22 were then put on an excellent diet, fed ad lib, to follow the progress of post-starvation rehabilitation. McCance et al. (1961) showed that the 'calorie-deficient diet' resulted in severely malformed jaws with extreme tooth crowding and malocclusion. It is important to note that these data can only be taken to show the influence of diet on tooth eruption under extreme starvation, and cannot possibly reflect any condition to be found in nature or in normal husbandry. Tooth eruption in the control group of 37 normal pigs (Table 3, 5) was examined by X-ray in defleshed mandibles. However, the tabulated ages for tooth eruption events are seriously flawed:

The erroneous data are shown in bold above. Firstly, the M₁ (column 2) cannot possibly erupt and enter occlusion at the simultaneous age of 4 months. Secondly, while the age of 24 months for early occlusion of M₃ is unexceptional (column 3), the same age for this event in M₂ is again clearly mistaken as these cannot be simultaneous events. The identical age given for root closure of both M_2 and M_3 is also questionable (column 4). Furthermore, in the earlier study cited above, McCance et al. (1961, table 6, p 220; column 1 in Table 5 above) gave the M₃ as erupting at 13-14 months for 'normal' pigs, which is precocious indeed, though it should be noted that this was judged from an x-ray study, and thus unrelated to visual inspection of the mandible. Their x-ray of this specimen (their plate 1, p 224) shows the M₃ with its most anterior cusps about level with the bone, but this would not be seen as 'erupted' in the living specimen. Even in a defleshed specimen the tooth would not be seen barely beyond the formation of the alveolus.

The x-ray images (Teonge & McCance, 1973, figs. 2-8, p 6-10) enlighten us on certain aspects of their observations. In their figure 2, one mandible shows the anterior cusps of M₁ in early eruption, slightly above the bone at four months of age, but not visible through the gum. Their figure 3 shows the M_1 as fully erupted at 8 months. In their figure 4, the M2 was fully erupted at one year of age, although the age of 24 months was mistakenly given in their tabulation for this event (Table 5 above). Their figure 5 (a 16 month mandible) and figure 6 (a 20 month mandible) each show the M₃ with two pairs of cusps emerged, but with little other difference, despite the different ages given to the specimens. Figure 7 (a 24 month mandible) shows the M₃ with the same degree of crown eruption, but with more root growth. Only by 30 months (Figure 8) is the M₃ nearly fully erupted though the bone, though still unlikely to be fully erupted through the gum. From the x-ray tracings given there appears to be little M₃ crown development between 16 months and 24 months. It is best to view these somewhat confused data with some caution, bearing in mind the modest sample number killed at each stage of tooth development.

⁶ The measurements were done at the former Institute of Animal Physiology, Babraham, Cambridge. The author here was not responsible for experimental design. He is now an archaeologist.

⁷ These experiments, though severe, were directed toward the understanding of starvation and rehabilitation in humans.

Table 6. Tooth eruption ages from Wenham & Fowler (1973), as given and as deduced form x-ray plates

	P4	M1	M2	M3
Given in fig. 4, 454	11 months	3 months	8 months	17 months
Deduced from x-rays	?	5.7 months	?13 months	?23 months

Wenham and Fowler 1973

A small sample of 32 cross-bred pigs (Large White X Landrace) were raised under normal husbandry, and slaughtered in six growth stages at 20 kg increments, up to 120 kg, with roughly equal numbers killed at each stage. The skulls were bisected and examined by X-ray. The authors state (op. cit., 455) that 'The limited number...does not allow a precise estimate of the variation in age of attaining each stage to be calculated.' Tooth eruption was defined, but different criteria were applied to deciduous and permanent teeth. Deciduous teeth were defined as 'subgingival' when the crown had erupted through the bone but was below the gum, and 'erupted' when '...any part of the occlusal surface appeared to be above the level of the gingiva...' (452, 454). The permanent teeth were classified in stages: (i) crypt formed (ii) enamel forming (ii) tooth crown formed and (iv) erupted, presumably again when the gum was cut, though this was not made explicit. No subgingival stage was recognised (fig. 4, 454).

The data (figure 4, 454) show that 'eruption' was judged by an x-ray study, given at 3 months, but this represents a stage that would not be visible. The appendix to the paper shows tracings from the cranial x-rays. Figure 1 (e) shows a 2 month jaw with the M_1 being formed in its crypt, but with the crown well below the bone. At 5.7 months (Figure 1f) the anterior cusps of M_1 have erupted, but not the posterior cusps. The age suggested for the eruption of M_1 to a visible state at 3 months is thus questionable. Similarly, the eruption age for M_2 is given as 8 months (figure 4, 454), which is again very doubtful as it seems very precocious. This tooth is fully erupted at 16 months in Figure 1(g), thus also showing the first cusps of M_3

Table 7. Tooth eruption events as given by Reiland (1978)

	tooth eruption (months)	tooth replacement (months)	tooth to full height
P ₂ P ₃ P ₄ M ₁ M ₂ M ₃	1 0.5 1 4 9 17	12 12 13	13 13 14 6 12 24

in the initial stage of emergence through the bone. The judgement of 17 months for the eruption of M_3 is again from an x-ray study, and this would certainly not be visible in the living specimen. Figure 1(h) shows the M_3 at 23 months, with the first *two* pairs of cusps erupted through the bone and third pair of cusps emerging. In this instance the first cusps would probably be erupted though the gingiva, and possibly the second pair as well, but not the third pair of cusps. However, it is important to note that each is a single individual from a sample slaughtered according to a series of *weight* classes, so that this does not represent particular *age* classes.

The ages given for the eruption events judged by x-rays (appendix to the paper) as tabulated by Wenham and Fowler (fig. 4), are given below. Much later eruption ages may be deduced from the tracings from x-ray plates (Appendix, pp 458-461):

The inferred eruption ages are very close to the ages given for almost all pigs; wild, feral and domestic.

Habermehl 1975

This substantial compendium of dental ageing data is commonly used in archaeozoology; the citations there too numerous to list. Data on the eruption of the deciduous teeth and the incisor teeth is from a variety of sources, but the ages given for the later eruption events (op. cit., pp 146-147) are taken from Sisson & Grossman (1953, p 488), Engelberg (1917) and Ripke (1964). Each of these is unsatisfactory to a varying degree. The data source in Sisson and Grossman is not given, but is probably Simonds (1854). The publications of Engelberg (1917) and Ripke (1964) give little or no data from pigs above 16 months of age. Habermehl's compendium has been used in tabulating tooth eruption ages in Hillson's standard work on

Table 8. tooth eruption events after Matschke (1967)

	mean eruption age	range in eruption age
P ₄	16 months	14.2 - 18.7 months
M ₁	5.7 months	5.3 - 6.0 months
M ₂	12.8 months	12.0 - 13.8 months
M ₃	25.2 months	23.1 - 26.1 months

Table 9. Tooth eruption summary in wild pigs

P ₄ M ₁ M ₂	17¼ months (22)* 5¼ months (31)* 13.25 months (8)*
M ₃ (2 nd pair cusps)	27 months (24)*
M ₃ (3 rd pair cusps)	32 months (14)*
M ₃ (fully erupted)	36 months (8)*

^{*}sample size in brackets

dentition (2005, p 234), though the ages and age ranges suggested there are implausible.

Reiland 1978

The sample of mandibles was derived from '...about 200...' pigs of the Swedish Landrace and Yorkshire breeds. Crown formation, root closure and the degree of tooth eruption were observed by means of x-rays. The recognition of 'eruption' was not defined, nor was the number of mandibles given for each age class. Reiland published the following summary table of eruption events:

The ages of 'eruption' would be the first emergence of the tooth through the jawbone when seen by x-ray. Bearing this in mind, the ages given for tooth eruption accord with other recent studies, as does the attainment of 'full height' for each tooth, though it is not clear if this refers to all cusps of the tooth. While an age of 24 months is plausible for the eruption of the anterior cusps to full height, it is improbable that this would also apply to the posterior cusp.

(ii) Studies on the dentition of feral pigs

Clarke, Dzieciolowski, Batcheler and Frampton 1992

Forty three feral pigs of known age were studied. Some were tagged, released and recaptured for examination, while others were raised in captivity, thus undoing their 'feral' status. These known age data were used to 'calibrate' dental ageing in a sample of 2096 feral pig jaws collected in New Zealand, these of known death date only. Teeth were examined 'in situ', this presumably meaning in the jaw, but it is not clear whether these were defleshed or not. The profiles of the third molar at different degrees of eruption and wear are illustrated (Clarke et al., fig. 1, p 770) although the rather schematic diagram is difficult to interpret. The authors estimated that the third cusp of M₃ did not fully emerge until about 35 months of age. The known age data were compared to that of Matschke (1967), shown in figure 2 here, with good agreement. The slight differences need be no more than the estimation of 'eruption' by each author, as Matschke observed the cutting of the gum in living pigs. while Clarke's mandible sample was probably defleshed, being drawn from a wide area. Clarke et al. give the following ages for eruption events in their known-age feral (19 individuals) and pen-raised, previously feral pigs (13 individuals):

 P_4 14-15 months, erupting 16 months, fully erupted.

3 months, tooth 'visible.' (presumably in process M_1 of alveolus formation.) 4 months, 1st pair of cusps erupting. 5 months, 1st pair of cusps 50% erupted and

'visible.'

6 months, tooth fully erupted.

10 months, 1st pair of cusps 'visible.' M_2 : 11-12 months, in eruption.

13 months, fully erupted.

M3: 22 months, the tooth is 'visible.'

24 months, 1st pair cusps erupted.

25 months, M₃ less than 50% erupted. 26 months, 2nd pair of cusps 50-75% erupted. 30-32 months, 3rd pair of cusps erupting. 33-35 months 3rd pair of cusps about 50% erupted.

36-41 months 3rd pair of cusps still erupting.

42 months tooth fully erupted.

It is clear that 'eruption' is a lengthy event, lasting 3 months for M_1 and for M_2 , and 20 months for M_3 ; however, it must be cautioned that the known-age sample was few in number. The authors conclude:

'In New Zealand feral pigs, most tooth eruption and replacement occurred earlier than reported for pigs elsewhere. On average, tooth eruption for permanent teeth preceded by 1-2 months those reported for American-bred European and Malayan pigs." (Clarke et al., op. cit., 775)

Table 10. Summary of tooth eruption events in small samples of cross bred (penned) and wild (free) pigs

	P ₄	M_1	M_2	M ₃ (2 nd cusps)
cross bred, penned wild, free	not given	5 (2)*	12-13 (10)*	18-25 (9)*
	not given	not given	10-12 (3)*	18-24 (3)*

^{*}Numbers in brackets are sample size.

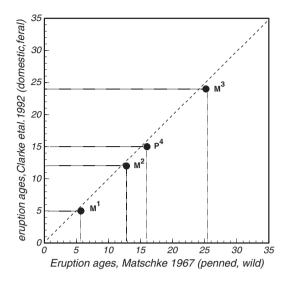


Figure 2. Eruption times for P₄ to M₃, comparing Clarke et al. (1992, table 1, 772)) and Matschke (1967, table 1, 112). Matschke gives slightly later ages for the eruption of the fourth premolar and the 3 molar teeth, as his observation were on living pigs, while those of Clarke et al. (1967) were likely to have been on defleshed specimens.

Data from Matschke (1967) and Diong (1973) are cited in support of this view. However, if the mandibles of the New Zealand pigs observed by Clarke *et al.* were defleshed, as seems likely, Matschke made his observations on the living animal, which would contribute to the difference in eruption time. These data are shown in Figure 2 here, where the ages for tooth eruption events given by each author are compared.

Diong's sample included few known age individuals and, being concerned with SE Asian pigs, is not directly relevant to this enquiry.

(iii) Studies on the dentition of wild pigs

Matschke 1967

Captive wild pigs were used in Matschke's study, and were raised on a '...balanced commercial ration' from weaning at 8 weeks of age, thus being raised under husbandry conditions. Between 24 and 32 animals were observed for each of the later tooth eruption events (Matschke, 1967, table 1, 112). Further to the captive animals, an unstated number of wild piglets were tagged and released, the dentition being recorded when these animals were culled. A tooth was noted as 'erupted' when it broke through the gum. The dentition was observed by using a speculum in younger pigs, but with older pigs the anaesthetic drug Xylocaine was injected into the masseter muscles to facilitate the examination of M2 and M3. Matschke (112, tables 1 and 2) gave mean ages and range for mandibular tooth eruption events:

Matschke further stated (op. cit., p 113) that three free ranging pigs culled in autumn (estimated at 29-30 months of age) had the second pair of cusps of M_3 erupted. The age of eruption of the M_3 penned pigs accords well with other investigations and, though fed on a commercial pig food, the posterior cusp of M_3 was not fully erupted until 4 years of age. Matschke's study stands as one of the more useful data sets for pig tooth eruption, in both the number and detail of the observations.

Barratt (1978) studied feral pigs at Dye Creek Ranch in California, where tooth development in '...a number' of tagged feral pigs compared well with ages from Matschke (p. 288).

Bull and Payne 1982

The authors provide certain original observations, and summarise other data for domestic and wild pigs (table 1, 56). They note that the 18th century data given by Silver (1963) is 'improbable' both in terms of eruption sequence and timing. However, Bull and Payne cite the very early eruption of M_1 at 4 months in both domestic and wild pigs (table 1, 56) and also give eruption ages for 'early' and 'late' maturing pigs (table 2, p 57), following Habermehl (1975) and Reiland (1978). As shown above, these data are of very doubtful utility; Habermehl's sources for 'early' and 'late' eruption in various pig breeds are very limited, and Reiland's study was by means of x-rays, sufficient to account for the early timings given there. Bull and Payne also cite Owen (1868); as is further shown, these data too were probably derived from Simonds (1854).

The original data given by Bull and Payne was from a sample of 18 wild pigs from North-central Turkey, a region where wild pigs were reported as giving birth during March and April. The authors note that this illustrates the problem of estimating the age of tooth eruption in wild pigs, as the uncertain birth date will increase the natural variability in tooth eruption, amounting to \pm several weeks. In addition, some births will take place outside the expected season. Their table 3 (58-59) shows that the pigs were placed into four age groups: 7-11 months, 19-23 months, 31-35 months and 'older'. There were 10 specimens estimated as 19-23 months of age, where the M_3 was recorded as in early eruption in *defleshed* specimens:

Crown well formed, visible in crypt 3 specimens Erupting though bone 4 specimens Erupted to half full height 2 specimens In occlusal plane, but unworn: 1 specimen The early stage of eruption (anterior cusps) of M_3 was estimated to be less than two years of age. Three wild pigs at 31-35 months had varying wear on the M_3 ; two specimens showed wear on 2 pairs of cusps and light wear on the third pair of cusps, while 1 pig had light wear on the first two pairs of cusps. These few observations accord well with other studies of tooth eruption in both domestic pigs and in European wild boars.

Bridault, Vigne, Horard-Herbin, Pellé, Fiquet and Mashkour 2000

Forty-eight wild pigs of known death date were collected in northern France. The sample was aged by Matschke's (1967) criteria, and the development state of each mandible (Bridault et al., op. cit., figure 1, 13) was compared to the ages employed by Rowley-Conwy (1993) for the same tooth eruption events. Here we have an interesting chain of citation. Rowley-Conwy (1993) adapted the system proposed by Higham (1967a, appendix B, 104, 1967b) for dental ageing in domestic pigs, while Higham had based his method on the synopsis given by Silver (1963). In turn, Silver had derived his data in part from Miller & Robertson (1954), which appears to utilise the tooth eruption ages on Brown (1882) and/or Simonds (1854). Thus the methods of Higham and Rowley-Conwy relied through a chain of unacknowledged citation on tooth eruption data from domestic pigs of the 19th century, while Matschke (1967) studied wild pigs that were raised as domestic pigs. In spite of this rather lengthy chain of multiple citations, the agreement in the eruption times is surprisingly good. Higham employed an ingenious interpolation of stages between the eruption ages as given by Silver (1963), in which each tooth was designated as in 'primary' or 'secondary' eruption, assuming times for the sequential eruption of the paired cusps. The M₃ was given a 'tertiary' eruption stage. Higham inferred that the 'primary' eruption stage of M_3 was at 17-19 months, following Silver (1963). However, this is probably wrong, the early timing for this event probably derived from Simonds (1854), as has been noted above.8

The seven citations given by (Bridault *et al.* table 1, 12) for tooth eruption data in domestic pigs thus have a good deal in common. Six of these (Owen, 1868; Sisson & Grossman, 1953; Silver, 1963, 1969; Higham, 1967a; Rowley-Conwy, 1993; Habermehl, 1975) can make no claim to originality, as these are based on other published sources, variously derived from Simonds (1854). The

source of Owen's (1868, 352) tabulation of eruption data for cattle, sheep and pig is unacknowledged, but a comparison of these data with Simonds (1854) provides convincing evidence that this latter was the source.

Boitani and Mattei 2002

This study was based on 31 wild pigs in captivity, held in a partly covered yard and fed a normal commercial pig ration. The difficulty of handling the pigs was overcome by use of the tranquilliser *Azaperone*. The pigs were examined at two week intervals to six months of age, and monthly thereafter. Although there were rather few animals in some of the samples, the authors note a significant variation in eruption age, even within a litter. They expressed their data in 'age intervals' for tooth eruption events rather than precise ages:

The ages for the eruption of M_1 and M_2 are unexceptional for both domestic and wild pigs. M_3 was unerupted in 25 pigs of their age class 14 (22 months), but the second pair of cusps were emerging at 27 months. Obviously the first paired cusps would have emerged rather earlier than this, giving an eruption age perhaps half way between these two age classes, at about 24-25 months. This is in general agreement with other reliable sources for both domestic and wild pigs.

Genov, Massei, Barbalova and Kostova 2002

This study collated data for wild boar tooth eruption ages give in 14 separate investigations. The samples were from Europe (8 publications), the Caucasus region (2), Japan (1), Algeria (1) and the USA (2). These citations overlap with those of Boitani et al. (see above). These studies were highly variable in their nature, not all being original. The known-age material from Poland was probably that also cited by Magnell (2002). Material from the USA relates to captive, European wild pigs (Matschke, 1967). The data cited as Sweeney & Sweeney (1982) is wholly derivative, based in turn on Matschke (1967) and Sisson & Grossman (1938). In their paper, Genov et al. (op. cit.) define 'eruption' as the emergence of the tooth through the gum, though they note the likelihood of variation between observers as a factor in the range of stated ages for tooth eruption events. The data for eruption of M₃ from the different observers (table 1, 400), give a mean eruption age of 19.5 months, but a median nearer to 23 months. Genov et al. comment that the ages given for eruption events vary between different wild pig populations; however, the variation in birth dates (unknown) and between observers in the seven of the sources in Genov et al. render this an untested proposition.

 $^{^{\}rm 8}$ I am grateful to Professor Charles Higham for confirming the nature of his innovative work.

Magnell 2002, Carter and Magnell 2007, Magnell and Carter, 2007

Magnell described tooth eruption in a sample of 16 known-age wild pigs and 53 known-age cross bred pigs (wild X domestic) from Poland. The animals were kept in enclosures and given supplementary feeding, though the quantity is not described. Most of the known-age sample is from pigs under 20 months of age, and few observations relate to the later stages of tooth development (op. cit., figure 2, 191). All specimens were defleshed, and tooth development judged by observation, though the nature of 'eruption' in the sample was not closely defined. The known-age sample was plotted as a scatter diagram, using the known calendar age against the ages as determined from Matschke (1967). The two systems diverged somewhat, with the few specimens over 18 months of age varying by a mean 2.7 months from known age. This is a significantly greater variation than the same test as used here (Figure 2), which compares the known-age feral pigs of Clark et al. (1992) with ages from Matschke's data. The ages for eruption events were given as:

The resulting tooth eruption ages were reported as being similar to those of domestic pigs, which Magnell (2002, 192) regarded as unsurprising on the grounds that the animals were cross bred (wild X domestic) pigs.

Carter and Magnell (2007) give further data on tooth development and mineralisation as observed by x-ray, but do not discuss eruption ages for the tooth crown. They state (op. cit., 197) that 'A problem with age estimation of domestic animals based on tooth eruption is that the ages at eruption are known to vary between different breeds...' citing Habermehl (1961), Silver (1969), Reiland (1978) and Bull & Payne (1982) in support of this. However, not all of these sources are original, or do not have the data to support the contention. Furthermore, in table 10.5 Carter and Magnell (op. cit., p 210) cite the work of McCance et al. (1961) as evidence that a low plane of nutrition will delay tooth eruption in pigs. It has been shown above that these data are best disregarded in relation to tooth eruption ages, as the animals concerned were kept under conditions of the most extreme starvation. Magnell & Carter (2007) further expand on the timings of molar tooth eruption, based upon x-ray studies of a sample of 55 pig mandibles. Of these, 25 were hybrids between wild boar and domestic pig (op. cit, table 2, p 45 and table 3, p 46). M₁ is evidently in early eruption at 5 months of age, and certainly erupted by 6 months of age. M_2 is erupting at 12 months of age, and by 24 months the M_3 has the first two pairs of cusps erupted through the bone. It may be noted that the ages for tooth eruption as inferred here from Magnell and Carter (op. cit., figure 3) are somewhat later than those proposed in Magnell (2002) for the same events. However, these ages accord very well with those given for eruption events in modern domestic and wild pigs.

Anezaki 2009

This gives data on tooth eruption in the skulls of 40 captive, known-age wild pigs of the Japanese subspecies Sus scrofa leucomystax. These animals were raised commercially for the specialist meat trade, and the mandibles seen after slaughter as defleshed specimens. It is worthy of note that the captive Japanese wild boar have a longer breeding season than would be found in the wild, presumably the result of the provision of a more constant and high energy food supply (op. cit., 54). This circumstance has also been reported to the author concerning the husbandry of wild boar in Britain. The tooth eruption ages for 32 captive boars are given in tables 1.1 to 1.3. In addition, data is given from 57 free ranging wild boar of known death date, aged from less than 1 month to 30 months, with two individuals of 96 months. Eruption was defined in several stages (Anezaki op. cit., table 2, 57), though not all stages were used for each tooth as described. The sequence observed begins with (i) alveolus in bone open (ii) 1st cusps erupted (iii) 2nd cusps erupted (iv) tooth almost erupted to full height.

Data for the M₃ is given for the eruption of the three paired cusps and the initial enamel wear, although the number observed was few. The P₄ was erupted in three specimens of 16 months of age. One individual of about 5 months of age had an M₁ in early eruption, and this tooth was fully erupted in a second individual of 6-8 months of age (birth date uncertain). Three specimens of 12 months of age had the 1st cusp of M2 erupted and 3 pigs aged 16 months or older had M₂ fully erupted. M₃ began to erupt through the bone at 18-20 months of age: in 3 pigs this was visible in the open alveolus; in 3 pigs the $1^{s\bar{t}}$ cusps of M_3 were beginning to emerge from the bone; in 6 pigs the first pair of cusps were erupted, and in 1 pig the second cusps were erupted. In one animal (#10) the M₃ was seemingly not in eruption at this age. Given the slow eruption of M_{3} , it is probable that this tooth would have been erupted through the gum and in early occlusion at about 24 months of age. In a single pig of 28-30 months of age the 1^{st} and 2^{nd} cusps of M_3 were erupted. It appears likely that tooth eruption in the Japanese wild boar is little different to that observed generally in wild boar Sus scrofa.

 $^{^9\,\}mathrm{With}$ thanks to Mr Simon Gaskell of The Real Boar Company', Chippenham, England.

Modern veterinary publications

The tooth eruption ages given in modern veterinary publications are largely derived from 19th century sources. Recent examples are (age ranges given in months):

	P4*	M1*	M2*	M3*
Schummer & Nickel 1979 König & Liebich, 2007 Dyce <i>et al.</i> 2010	12-16 12-15 12-16	4-6 4-6 4-8	7-13 8-12 7-13	17-22 18-20 17-22

^{*}Ages given for both upper and lower jaws

These examples have much in common and, where citations of sources are given (as in König & Liebich (2007), the sources are those volumes tabulated above. Again, optimistic views on dental development are freely expressed. Dyce *et al.* (2010, 755) say of the pig: 'The dentition is normally complete by the age of 18 months, long after sexual maturity is reached.' As shown in Figure 1, the eruption of M_1 at 4 months is not reported elsewhere, nor is the M_2 reported to erupt at 7 or 8 months. The appearance of M_3 at 18 months of age is asserted only in those sources derived from Simonds' erroneous judgement of 1854.

Schummer et al. (1979, 87-88) go further in their assessment:

'Selective breeding, particularly with the object of producing early maturing breeds, has resulted in more or less marked changes in skull conformation. These changes, which must often be considered pathological, have greatly influenced the development, eruption time, shape and placement of the pig's teeth.'

While the authors caution that age determination is an estimate, their general assertion of accelerated development in selectively bred pigs is unproven.

Conclusions

The hypothesis of accelerated dental development in the modern domestic pig remains speculative. This belief has arisen from a lengthy chain of unacknowledged borrowings, often from publications of doubtful accuracy. For example, Genov *et al.* (2002) and Davies (1990) each support their investigations with multiple citations. Davis gives 9 different sources for tooth eruption ages in the pig, though 4 (and probably 5) of these were based upon the uncertain data given in Sisson and Grossman *The Anatomy of the Domestic Mammals* (1953). It has been shown that these data were probably derived from Simonds (1854), attested by the repetition of his mistaken early eruption age for M₃.

The proposition that domestic pigs show accelerated tooth eruption when compared to the wild boar is an attractive proposition to the modern mind. Domestic livestock have been separated from their ancestral species by many millennia of human intervention, although we often overlook the fact that much of the morphological variation seen under domestication was achieved by pre-literate societies, to whom 'science' was unknown. The body form of some domestic mammals has been changed by selection and it is easy to be persuaded that dental development, along with morphology, coat colour and so on, has changed in parallel. Yet physiology and behaviour remain much as in the wild ancestor, witnessed by the ease with which many domestic farm animals will revert to a feral existence when the opportunity presents, excepting the sheep, burdened with its domesticated wool.

Figure 1 here summarises the eruption data for the molar teeth, using sources cited in this review. These investigations are grouped into four conditions under which the pigs lived:

- (a) wholly domestic
- (b) feral, originally domestic
- (c) penned, wild
- (d) free, wild

Figure 1 shows that the M₁ has a remarkable consistency in eruption timing, regardless of the conditions under which the pigs lived, or whether of wild or domestic stock. There are six sources shown for tooth eruption ages in domestic pigs, published between 1854 and 1978. Brown (1882), Cornevin & Lesbre (1894) and Sisson and Grossman (various editions) each give identical eruption ages for the M₁ at 5 months. Simonds (1854), Wenham & Fowler (1973) and Reiland (1978) each cite an eruption age of 6 months for this, while Girard (1834) gave 5½ months. Clarke's (2002) sample of feral pigs, the penned wild pigs of Matschke (1967) and Boitani and Mattei (2002), and the wild pigs (Cornevin & Lesbre, 1894; Magnell & Carter, 2007; Genov, 2002) are all given ages of 5-6 months for the eruption of M₁. The small differences seen need be no more than variation between observers, or the use of different criteria for defining 'eruption'.

The eruption of M₂ presents a slightly different picture. Simonds (1854), and Cornevin & Lesbre (1894) each give ages of 10-11 months for the eruption of this tooth, an age ahead than given in later studies of both domestic and wild pigs. The same age was given in Sisson and Grossman (various editions). Simonds again was the primary source for the data, though Girard (1834) had earlier given 10 months for this event;

possibly Simonds was influenced by this publication. Wenham & Fowler (1973) give an age of 8 months for the eruption of M_2 in their modern domestic pigs, which is very precocious when compared to observations made by others, and the result of using x-ray images. In the other studies, data from both captive and free living wild pigs agree well at 12-14 months for the eruption of M₂. An exception is in Magnell & Carter (2007), who also give a rather precocious age for eruption in free living wild pigs at 11 months. However, the variation is less than it appears from the diagram, as 4 of the 6 examples for domestic pigs are unacknowledged borrowings from Simonds (1854). This leaves only the uncertain estimate from Wenham & Fowler (1973) and that of Reiland (1978), in which ages are given for eruption to full height. Setting these aside, the eruption of M_2 shows ± 1.5 months of variation.

The timings for eruption of M_3 are the most variable, as would be expected, variability increasing with the age of the event. For domestic pigs, 4 of 6 sources give early eruption ages of 17.5-19 months though, as with the data for M_2 , four of these are from Simonds (1854), or derived from his data with slight modifications. Again there are multiple citations of one data set. It is the author's view that Simonds' estimate of 18 months for the eruption of M_3 was mistaken. Yet these same data are widely cited now, with the potential for misguided use in animal science.

Recent studies of domestic pigs (Reiland, 1978; Wenham & Fowler, 1973) give ages of 23-24 months for the eruption of M₃. Clarke *et al.* (1992) gave this event at 24 months for feral pigs in New Zealand, effectively the same as the penned wild pigs of Matschke (1967) and of Boitani & Mattei (1992). One further study of penned wild pigs (Magnell & Carter, 2007) gave an earlier eruption age for M₃ at about 21-22 months (the mean of this range is given in Figure 1) for two samples, these being wild, penned and wild, free living. Notably, the free living wild pigs appear to show earlier in eruption times than do the penned wild pigs.

The four samples of wild pigs have quite consistent eruption ages for $\rm M_3$ of 21 to 23 months, though this must apply to the initial eruption of the tooth. All observers who have followed the development of this tooth agree that eruption continues for a further 12 months, or even more. The very late age of 36 months cited by Girard (1834), is correct only if this was intended for full eruption to the posterior cusp. Full eruption into occlusal wear is given by Boitani and Mattei at 36 months, while Clarke *et al.* suggest that this condition may extend to 42 months of age, and Matschke even to

48 months before the most posterior cusp is involved. Here too the degree of difference between observers arises from the examination of fleshed or defleshed mandibles and perhaps different ways of determining full wear of the tooth.

Most notably, the studies made on all four groups of pigs (domestic, feral, captive wild, free wild) do not show any consistent shift in tooth eruption timings from one to another. When due allowance is made for the variation in the estimation of eruption (cutting the bone, cutting the gum), the variable methods used in examination (fleshed or defleshed and visual or x-ray) and the uncertainties of birth dates in wild pigs (usually estimated), there is little case for arguing that eruption timings are significantly different for any of the four groups; indeed, if the erroneous 19th century sources for M₂ and M₃ are set aside, the pattern of eruption in the three molar teeth is strikingly similar; M₁ erupting at about 5-6 months, followed by M₂ at 11-14 months, and M₃ coming into early eruption at about 24 months. The variation described in different studies is more likely to be that of observer technique rather than the product of genes or husbandry. This review thus provides no support to the hypothesis that the eruption of cheek teeth in domestic pigs is faster than that in the wild, indeed, certain studies of wild pigs can be interpreted to show faster eruption of M₃ than is asserted for modern domestic pigs.

However, little of the available data is of a rigorous and controlled kind; indeed, such data cannot be obtained without very considerable resources and expense. Of the published sources reviewed here, that of Matschke (1967) is in many respects the best controlled and best reported, based upon wild pigs in captivity. The tooth eruption ages given there are applicable to pigs both wild and domestic, and living a wide range of conditions. As Bradley (1930) noted, the proper testing of the many variables that may influence tooth eruption in pigs would require an extensive and costly experiment. A large sample of wild pigs, and of different breeds of domestic pigs, would be needed for adequate testing, including both 'fast maturing' and 'slow maturing' breeds. Each group would be divided and raised under different conditions of husbandry or as free living, with accurate records of birth dates and closely defined observational criteria. Sadly, this type of research is unfashionable now, this being an unlikely experiment at the scale needed. Yet without such investigations the effect of selective breeding and intensive feeding on dental development cannot be understood, and remains the subject of speculation.

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