THE SHIFTING OF THE MOLAR ROW WITH REGARD TO THE ORBIT IN EQUUS AND GIRAFFA

by

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The difference in shape and in function of the postorbital bar in horse and giraffe has been pointed out by Marinelli (1933, pp. 201-222).

In *Giraffa* the molar row extends to below the orbit. The pressure exercised on the molars by the musculus temporalis is diverted principally along the postorbital bar, and to a lesser extent along the zygomatic arch.

In *Equus*, however, the molar row ends in front of the orbit. Therefore, the pressure exercised on the molars cannot be diverted along the postorbital bar. In the horse it is the function of this bar to divert the pressure exercised by the lower jaw in its articulation with the skull. This pressure reaches the postorbital bar by way of the zygomatic arch.

In the Selenodontia (Ruminantia) the development of horns and antlers also has its influence on the postorbital bar (Marinelli, 1933, p. 205). In those animals which use their horns and antlers in fighting, the bar may serve to protect the eye. However this may be, these influences have no bearing on the relation between upper jaw and postorbital bar. Therefore, horse and giraffe may be considered as pronounced types having a postorbital bar which diverts the pressure of articulation and jaw pressure respectively.

Thus in *Giraffa* the position of the molar row with regard to the orbit has an influence on the postorbital bar.

Marinelli (1933, p. 206) states that in *Giraffa* the molar row extends to about half-way below the orbit. In *Okapia* and in fossil giraffes, e.g., *Helladotherium*, the molar row reaches even to below the posterior margin of the orbit, and in connexion therewith a well developed postorbital bar is present.

A clear example of the influence of the position of the maxillary tooth row

on the development of the postorbital bar is given by Marinelli (1929, p. 135): *Sphenodon* ("*Hatteria*"), and the Lizards *Hydrosaurus* ("*Lophura*") and *Iguana*, all with the tooth row extending to below the orbit, have the orbit closed behind; on the other hand, in *Varanus* the tooth row ends in front of the orbit, and the postorbital bar has weakly developed.

The position of the molar row in Mammals apparently is not constant, as is shown by the following examples [1]:

Hippopotamidae. Lydekker (1884, p. 38) considers the position of M^3 with regard to the "posterior border of the anterior zygomatic root" of systematical importance. In *Hippopotamus sivalensis* M^3 is supposed to be totally or partly behind it, while in *H. palaeindicus* it is stated to be in front of it.

In *H. amphibius* this position proved to be very variable. Of 18 skulls (all adult, but teeth in different stages of use) there were three with M^3 totally behind the "anterior zygomatic root"; in fourteen skulls M^3 is placed for the greater part behind it, and in one, the eldest male specimen, for the greater part in front of the "anterior zygomatic root".

Equidae. Lydekker (1882, pp. 90, 95) remarks that the length of the upper tooth row as compared to the distance from M^3 to the foramen magnum is smaller in *Equus sivalensis* than in *E. namadicus*. For the ratio M^3-foramen magnum to length of molar row Lydekker records for *E. sivalensis* 1.13 and 1.16, for *E. namadicus* 1.28. The ratio length of molar row to distance M^3 to foramen magnum according to Lydekker's data for *E. sivalensis* is 0.86 and 0.88, for *E. namadicus* 0.78.

Much greater differences for this latter ratio were found by Hooijer (1945) in skulls of specimens of three different species of *Equus*. As it is possible to determine the age of a horse with some certainty, the following data provide excellent examples: *E. hemionus* 5 years old, 0.90; 21 years old, 0.75; *E. caballus* 4-5 years old, 0.91; 11 years old, 0.72; *E. zebra* 3-3½ years old, 1.00; 24-30 years old, 0.71.

Hystricidae. Jentink (1879, p. 90) states that in *Acanthion brachyurus javanicum* the median posterior margin of the palatum (staphylion, Duerst, 1930, pp. 240-241) is on the same level as the anterior margin of M^3, while in *A. brachyurus longicaudum* (the Sumatran form) the staphylion is situated behind the postdental.

Measurements of the skulls in the Leiden Museum proved that *A. brachyurus javanicum* is totally within the variation range of *A. brachyurus longicaudum*. In the former the postdental varies from 3 to 5 mm behind

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the staphylion, while in the latter the postdental varies from 6½ mm behind to 2 mm in front of the staphylion. This latter case concerns a very old skull in which the tooth row is shorter than in any other skull of this species.

Modern authors do no longer attach any value to characteristics as those mentioned above. To illustrate this, the following quotation from a recent paper by Pocock (1945, p. 443) may be given: "a noticeable variation in the cheek-teeth is the position of the anterior edge of the mesopterygoid fossa as regards the posterior molar teeth. A few instances will serve to illustrate this. In an old skull of [*Rhinoceros*] *sondaicus* from Java... the edge of the fossae is 15 mm behind the anterior edge of M²; in another from the Malay Peninsula ... it is 20 mm behind it, whereas in a third ... it is 15 mm in front of it. The variation is probably due, I think, to the forward shifting of the entire tooth row."

In the present paper the following points are discussed:

1. The shifting of the molar row in *Giraffa* and its influence on the postorbital bar.

2. The shifting of the molar row in horses, its systematical significance, and its usefulness in estimating the age of skulls.

Measurements were taken in the following manner.

The length of the skull is the distance prosthion-basion (Oppenheim, 1930, pp. 542, 543). All the other distances have been measured as projections on a horizontal plane through the basion-prosthion line.

The length of the molar row is a projection of the distance between the anterior margin of the alveolus of P² and the posterior margin of the alveolus of M³ or the last molar in case of an incomplete dentition. The posterior or anterior margin of the orbit, respectively, is the most posterior or anterior point of the aperture. These points are not fixed too well, but depend on individual variation in the shape of the orbit (cf. Petit, 1937, pp. 18-23, figs. 7-10 in horse and ass).

To measure the projections the whole skull was placed on paper, divided into squares of 1 mm², in such a manner that the lower jaw is accurately placed symmetrically with regard to one direction of the pajer. The calvarium, resting in the normal way on the lower jaw, has its basion-prosthion line parallel to this same direction. By means of a support with clamping screw, the anterior end of the calvarium was turned upwards with the mandibular articulation as axis, until the vertical distances from the surface of the paper to the basion and to the prosthion were equal. With the aid of triangles the necessary points could easily be plotted on the paper.

In a few cases the molar rows of left and right side proved not to be at the same level or were of unequal length. In case of small deviations only the right molar row has been measured.

The distance basion to projection of posterior margin of the alveolus of posterior molar on the basion-prosthion line could easily be measured by fixing the point of intersection of basion-prosthion line and the shortest connexion of the mentioned posterior margins.

A small, however negligible error of the method is a slight variability in the angle between the used horizontal plane and the plane into which the alveoli of the upper molars open; the possibility for comparison of the projections thereby is somewhat diminished.

The obtained values were used to determine the following ratios:

1.
$$\frac{\text{length of molar row}}{\text{length of skull}} \times 100$$

2.
$$\frac{\text{posterior margin of posterior alveolus} - \text{posterior margin of orbit}}{\text{length of skull}} \times 100$$

3.
$$\frac{\text{posterior margin of posterior alveolus} - \text{basion}}{\text{length of molar row}} \times 100$$

4.
$$\frac{\text{posterior margin of posterior alveolus} - \text{basion}}{\text{length of skull}} \times 100$$

5.
$$\frac{\text{anterior margin of anterior alveolus} - \text{prosthion}}{\text{length of skull}} \times 100$$

6.
$$\frac{\text{posterior margin of posterior alveolus} - \text{anterior margin of orbit}}{\text{length of orbit}} \times 100$$

I. The shifting of the molar row in *Giraffa*.

Seventeen skulls were examined [1]).

Giraffa camelopardalis (L.) Subspecies not mentioned.

1. Skeleton of ♂, Zoological Laboratory, Amsterdam, born 26.10.1926 in the Amsterdam Zoo, died 3.11.1926. Number 11 is its mother. Complete lactal dentition. M^1 within the jaw.

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1) I am indebted to Mr. P. J. van der Feen for his help in providing the specimens from the Zoological Museum of Amsterdam.

2. Skull, Leiden Museum, probably Jentink, 1887, p. 156, specimen c, 1866, van Lidth de Jeude. A part of the skull base lacking.

3. Skull of ♂, Leiden Museum, reg. no. 4216. Adult when captured, lived for about one year in captivity in the Zool. Garden of Rotterdam until 3.7.1940. M² in function, M³ not yet erupted.

4. Skull of ♂, Zool. Museum Amsterdam, no. 962, arrived in the Amsterdam Zoo 20.8.1927 from Rhodesia, estimated to be 1½ years at arrival, died 9.12.1928. M² in function, M³ not yet erupted.

5. Skull, Zool. Lab. Amsterdam, no. 262.

6. Skeleton of ♂, Leiden Museum, Jentink 1887, p. 156, specimen a, adult, Senegal, from the Paris Museum, 1820.

7. Skeleton, Zool. Mus. Amsterdam, no. 968.

10. Skull of ♀, Leiden Museum, reg. no. 6741. Imported from E. Africa in May 1939, estimated 2 years old at arrival, lived in the Zool. Garden of Rotterdam until 30.5.1944.

11. Skull, Zool. Mus. Amsterdam, no. 534, Africa, premaxillaries lacking.

12. Skull of ♂, Zool. Mus. Amsterdam, no. 964. Born in the Zoological Garden of Cologne 10.7.1914, died in the Amsterdam Zoo, 25.5.1927.

13. Skeleton of ♀, Zool. Mus. Amsterdam, no. 967. Arrived in the Amsterdam Zoo 17.7.1912 from Rhodesia, 1½ years old, died 17.11.1926 of pulmonar tuberculosis.

14. Skull of ♀, Zool. Mus. Amsterdam, no. 966. Arrived in the Amsterdam Zoo 20.8.1927 from Rhodesia, estimated 2 years old at arrival, died 16.11.1944.

15. Skull, Zool. Mus. Amsterdam, no. 533. Africa. A part of the occipital, M¹ dext., P⁴ sin., the incisors and canines lacking.

16. Skull, Leiden Museum, Jentink, 1887, p. 156, specimen b. This skull is of a very old individual. Incisors and canines lacking.

17. Skull, Zool. Mus. Amsterdam, no. 532. Africa.

Giraffa camelopardalis tippelskirchi Matschie.

8. Skull of ♂, Zool. Mus. Amsterdam, no. 963. Arrived 25.7.1930 from Kilimandjaro, purchased from Chr. Schulz, who mentioned its age as less than 2 years, Dr. A. F. J. Portielje estimated it at one year, died 5.6.1935.

Giraffa reticulata reticulata de Winton.

9. Skull of ♂, Zool. Mus. Amsterdam, no. 965. Northern Frontier Province, Kenya, Brit. E. Africa, leg. B. Carp, April 1938.

So the approximate age is known of seven specimens. The remaining skulls were compared to those of which the age was known. The following points were taken into consideration: the disappearance of the sutures between temporal and occipital, that of the mandibular symphysis and that of the suture between the frontals, the wear of the teeth. As a result from this comparison the probable ages were estimated for these remaining specimens, these ages are recorded in Table I.

A comparison of the ratios in Table I gives the following results:

1. There is a distinct shortening of the molar row; with advancing age the ratio 1 diminishes.

2. The question whether there is an increase of the distance between the

caudal end of the molar row and the posterior margin of the orbit may be answered by the results obtained with ratio 2.

For the older specimens ratio 2 shows a definite increase. In the younger skulls the values are irregular; this is most probably due to the non correlation of the length of the orbit to the length of the skull. The older specimens make it obvious that the posterior margin of the molar row shifts forward.

3. Ratio 3 decreases with advancing age. This is caused both by the shortening of the molar row and the forward shifting of the posterior border of the molar row.

4. A comparison of the ratios 6 can help us in answering the following question. Is the shifting of the molar row sufficient to influence the parts diverting the pressure of mastication, viz., the postorbital bar?

Marinelli (1933, p. 206) mentions the tooth row as extending to half-way below the orbit. In Table I there is no regular decrease of ratio 6 with increasing age, although the elder specimens show the lower values. The extreme values are 76% (no. 11) and 35 % (no. 16) of length of orbit, occupied by the last part of the molar row.

In *Giraffa* the pressure of mastication is not diverted along the anterior border of the orbit. This is obvious (Marinelli, 1933, p. 206) from the large surface of the lacrimals, from the direction of the sutures, and from the fact that the surface of the skull is perforated just in front of the orbit.

This holds true in the skull of the lowest value (35 %, no. 16). The pressure of mastication apparently is completely diverted along the postorbital bar, which can easily be performed considering the shape ofmaxillary and jugal. It is possible as there is a very slight, indeed doubtful, difference in the situation of the postorbital bar compared to that of the skull of high value (76 %, no. 11), as a consequence of the difference in the direction of the pressure.

The ratios 4 and 5 will be discussed later.

Nos. 8 and 9 are rather deviating in their values. As the subspecies to which the number 1 to 7 and 10 to 17 belong are not determined, it is impossible to say whether specific or subspecific differences may be of influence when computing these ratios.

The lactal and incomplete dentitions.

The values obtained depend on the presence or absence of molars within the jaw behind the last tooth in function. This is mentioned in the list of specimens.

An interesting case is specimen number 1, where M^1, situated within

the jaw, extends up to 10 mm behind the posterior margin of the orbit. In fossil giraffes and in *Okapia* the tooth row extends backwards for about the same distance, viz., to behind the posterior margin of the orbit (Marinelli, 1933, p. 206).

II. The shifting of the molar row in *Equus*.

The skulls examined belong to *Equus quagga* Gmelin, *E. zebra* L., *E. hemionus* Pallas, *E. grevyi* Oust., *E. asinus* L. and *E. caballus* L.

The age of the specimens.

As far as these are known the ages are mentioned in the list of specimens. For the other specimens the ages have been computed from veterinary data based on *Equus caballus* (Ellenberger and Baum, 1921; Kroon, 1915; Anonymus, 1899). No data are available on the changes due to age in the other species. In the present paper the data based on *E. caballus* have been applied also to the other species. This may partly explain the differences between known and estimated ages as mentioned below.

Considering the eruption of I^2 and the starting eruption of M^3 the age of *E. caballus* no. 13 is estimated at 3-3½ years instead of 2½. In no. 29, 11 years old, the incisors are worn as if 9-10 years old; in no. 37, 22 years old, as if 8 years old, the sutures grown together as if 15-40 years.

E. quagga chapmanni × *burchellii*, no. 15, age 5 months, is 7 months considering the eruption of the teeth. *E. asinus* no. 2 is labelled as adult, after the eruption of the teeth only 1½ years old.

Estimation of the age after the vanishing of the sutures of the skull (Ellenberger and Baum, 1921, pp. 72-73) proved to give higher values than those estimated from the wear of the teeth in a few cases. *E. quagga quagga* no. 1, age considering the teeth 6 years, considering the sutures 15-40 years (bone substance somewhat abnormal); *E. quagga burchellii* no. 4, age after the teeth 13 years, after the sutures 15-40 years; no. 3, 6 and 15-40 years respectively; *E. zebra* no. 3, 8 and 15-40 years; no. 5, 13-14 and about 15 years; *E. greyi* no. 4, about 14 and about 15 years; *E. asinus* no. 7, 13-14 and 15-40 years; *E. caballus* no. 26, 8-9 and about 10 years.

In *E. quagga burchellii* Gray no. 5 the teeth have worn rather vertically, which probably causes them to seem older than in reality. Hooijer (1945, p. 102) estimates the age at 10 (?) years. The teeth have worn as if 16 years old; judging by the sutures the age is fully 15 years.

These differences may lose some of their importance on account of the following remarks by Martin (1914, pp. 147, 148): all the sutures of the skull have vanished at the age of ten years, except the suture between the

nasals. This is, however, no fixed rule; there is an influence of food and race, and some sutures of the facial part of the skull often for a long time only partly grow together.

List of specimens:

Equus quagga quagga Gmelin.

1. Skeleton of ♂, Leiden Museum, Jentink, 1887, p. 159, specimen a, Cape, from van Horstock, 15.6.1827.
2. Skull of ♀, Zool. Mus. Amsterdam, no. 522, from an animal living in the Amsterdam Zoo from 9.5.1867 to 12.8.1883.

Equus quagga burchellii (Gray).

3. Skull of ♂, Zool. Mus. Amsterdam, no. 529.
4. Skeleton of ♀, Leiden Museum, reg. no. 1513. From the Zoological Garden of Rotterdam 4.8.1926.
5. Skull of ♀, Zool. Mus. Amsterdam.

Equus quagga chapmanni Layard.

6. Skull of ♀, Zool. Mus. Amsterdam. From the Amsterdam Zoo 3.2.1940. Purchased from L. Ruhe, Alfeld, Germany, 26.6.1930. Between the upper central incisors there is a malformed extra incisor.
7. Skeleton of ♀, Leiden Museum, cat. ost. a. From the Zoological Garden of Rotterdam 20.8.1907. I^3 sin. and its alveolus absent, M_1 sin. displaced lingually.
8. Skeleton of ♂, Leiden Museum, reg. no. 2284. From the Zoological Garden of Rotterdam 16.11.1934. Born in the Amsterdam Zoo in 1914. The upper C sin. absent.

Equus quagga granti de Winton.

9. Skull of ♀, Leiden Museum, reg. no. 1729. From Tanganyika in the surroundings of Mt. Abern 6.6.1927. Imported 25.1.1929. M^2 erupted, M^3 within the jaw, Pd^1 shedding, I^1 present in the upper jaw.
10. Skull of ♂, Zool. Mus. Amsterdam, coll. Carp. From an animal shot at Margereni in March 1939.
11. Skeleton of ♂, Leiden Museum, reg. no. 2204. From the Zoological Garden of Rotterdam 7.12.1933.

Equus quagga chapmanni Layard ♂ × *E. q. burchellii* (Gray) ♀.

12. Skull of ♀, Leiden Museum, reg. no. 512. From the Zoological Garden of Rotterdam 16.7.1915. Id 1, 2 and all lactal premolars present. M^1 within the jaw, just starting its eruption.
13. Skull of ♀, Leiden Museum, reg. no. 1103. From the Zoological Garden of Rotterdam 4.10.1921. Dentition as in no. 12, M^1 totally within the jaw.
14. Skull of ♂, Leiden Museum, reg. no. 1228. From the Zoological Garden of Rotterdam 1.6.1923. Dentition as in no. 12. M^1 within the jaw.
15. Skull of ♂, Leiden Museum, reg. no. 719. Died in captivity 13.1.1917. Born 15.8.1916. Dentition as in no. 12. M^1 and M^2 within the jaw.

Equus zebra L.

1. Skull of ♀, Leiden Museum, reg. no. 3458. From the Zoological Garden of Rotterdam 14.5.1938. Lactal incisors and premolars present. M^1 within the jaw (reaching to 20 mm behind the anterior margin of the orbit).

2. Skeleton of ♀, Leiden Museum, Jentink, 1887, p. 159, specimen a. Cape, adult. M³ only for a small part erupted.

3. *E. zebra* ? skull of ♂, Zool. Mus. Amsterdam, no. 528, Africa.

4. Skull of ♂, Zool. Mus. Amsterdam, died in the Amsterdam Zoo 16.8.1903.

5. Skeleton of ♂, Leiden Museum, Cape (in Jentink, 1887, p. 159, as *E. montanus* specimen a), don. van Aken.

Equus hemionus Pallas.

1. Skull of ♂, Zool. Mus. Amsterdam, no. 524. All the teeth lacking.

2. Skull of ♂, Leiden Museum, Jentink, 1887, p. 159, specimen a. From Tibet, Hodgson, 1853. A part of the occiput lacking.

3. Skull of ♀, Leiden Museum, Jentink, 1887, p. 159, specimen b. From the Museum of St. Petersburg, Frank, 1862. Transbaikalia. Calvarium and lower jaw do not belong together. Age of lower jaw estimated as 10 years.

4. Skeleton of ♂, Zool. Mus. Amsterdam, no. 509.

5. Skull of ♀, Zool. Mus. Amsterdam. Born 1916, died 26.8.1939.

6. Skeleton of ♂, Zool. Mus. Amsterdam. Born 1916, died 22.9.1937.

Equus grevyi Oust.

1. Skull of ♀, Zool. Mus. Amsterdam, died in the Amsterdam Zoo 21.12.1927. M³ not yet erupted.

2. Skull of ♂, Zool. Mus. Amsterdam, died in the Amsterdam Zoo, pathological. Eruption of M³ nearly finished, a small part already worn.

3. Skull of ♂, Zool. Mus. Amsterdam, died in the Amsterdam Zoo.

4. Skeleton of ♀, Leiden Museum, reg. no. 885. Imported from E. Africa 1910. F. E. Blaauw, 's Graveland, 23.10.1918.

Equus asinus L.

1. Skull, Leiden Museum, Jentink, 1887, p. 158, specimen d, Europe. Young individual. Lactal dentition present, M¹ rather far erupted, a small part of its surface worn. M² within the jaw.

2. Skull, Leiden Museum, Jentink, 1887, p. 158, specimen a, Holland, adult (inexact, see p. 10). A part of the occiput lacking. Dentition as in no. 1.

3. Skull of ♀, Leiden Museum, Jentink, 1887, p. 158, specimen f, age 3 years. M² in function, M³ starting its eruption, Pd³ shedding, I¹ and I₁ present.

4. Skull of ♀, Leiden Museum, Jentink, 1887, p. 158, specimen c. From the museum of van Lidth de Jeude, 1866.

5. *E. asinus africanus* Fitzinger. Skull of ♀, Leiden Museum, reg. no. 756.

6. Skull of ♂, Leiden Museum, Jentink, 1887, p. 158, specimen g, Jiddah, don. J. A. Kruyt, 1880. Calvarium and lower jaw do not belong together. Age of lower jaw estimated 14 years old.

7. *E. asinus* ?

8. Skull of ♀, Leiden Museum, Jentink, 1887, p. 158, specimen e. Jiddah, don. J. A. Kruyt.

9. Skull of ♂, Leiden Museum, Jentink, 1887, p. 158, specimen b, adult, Europe. All the incisors as well as P² dext. and sin., P³ dext., M² and M³ dext., P₂ sin. lacking.

10. Skull of ♂, Leiden Museum, Jentink, 1887, p. 158, specimen f. Jiddah, don. J. A. Kruyt, 1880. P² dext., M³ dext. and M² sin. lacking.

11. *E. asinus taeniopus* Heuglin. Skeleton of ♂, Leiden Museum, reg. no. 1441. From the Zoological Garden of Rotterdam 10.12.1925. The left molar row longer than the right. Teeth worn in abnormal way.

Equus caballus L.

1. *E. caballus* ? Skull, Leiden Museum, Cabinet d'Anatomie, 1860, very young. Not a single tooth erupted.

2. Skull, Veterinary Anatomical Institute of Utrecht [1]), no. 274, fetus. Pd 2, 3 and 4 partly erupted.

3. Skull, V. A. I. U., no. 275, fetus. Pd 2, 3 and 4 partly erupted, Id_1 starting its eruption.

4. Skull, V. A. I. U., no. 2320, fetus. Pd 2, 3 and 4 partly erupted, Id_1^1 starting their eruption.

5. Skull, V. A. I. U., no. 276, seven days old. Pd 2, 3, 4 partly erupted, Id_1^1 starting their eruption.

6. Skull. V. A. I. U., no. 277, ten days old. Pd 2, 3, 4 partly erupted, Id_1^1 starting their eruption.

7. Skull, V. A. I. U., no. 278, fifteen days old. Pd 2, 3, 4 partly erupted, Id^1 starting its eruption, M^1 within the jaw. (Lower jaw lacking?).

8. Skull, Leiden Museum, foal. Id 1 and 2, Pd 2, 3 and 4 erupted in lower and upper jaw.

9. Skull, V. A. I. U., no. 279, age 5-6 months. M^1 within the jaw.

10. Skull, V. A. I. U., no. 280, age 8-10 months. M^1 and M^2 within the jaw.

11. Skull, V. A. I. U., no. 281, age 1 year. M^1 starting its eruption, M^2 within the jaw.

12. Skull, V. A. I. U., no. 282, age 2 years. M^2 erupted, M^3 within the jaw.

13. Skull, V. A. I. U., no. 283, age 2½ years. I^2 starting its eruption, P^4 erupting, M^3 rather far erupted.

14. Skull, V. A. I. U., no. 284, age 2½ years. M^2 rather far erupted.

15. Skull, V. A. I. U., no. 286, age 4 years and 3 months. P^4 and M^3 nearly at the level of the other molars.

16. Skull of ♂, Leiden Museum, Jentink, 1887, p. 158, specimen e. Age 4½ years. M^3 in function, Id 3 shedding, C 1 in lower and upper jaw partly erupted.

17. Skull, V. A. I. U., no. 288. Age 5 years.

18. Skull of ♀, V. A. I. U., no. 289. Age 5 years.

19. Skull of ♂, Leiden Museum, Jentink, 1887, p. 158, specimen d. Europe, don. Prof. Ekema.

20. Skeleton of ♂, Leiden Museum, Jentink, 1887, p. 158, specimen b.

21. Skeleton of ♀, Leiden Museum, Jentink, 1887, p. 158, specimen a. Europe.

22. Skull of ♀, Leiden Museum, Jentink, 1887, p. 158, specimen l.

23. Skull of ♂, V. A. I. U., no. 290. Age 6 years. M^2 sin., M^3 sin. and dext. lacking.

24. Skull of ♀, Leiden Museum, reg. no. 4943. Of the lower incisors only I_3 sin. present. This skull is extremely small.

25. Skull of ♂, V. A. I. U., no. 291. Age 8 years.

26. Skull of ♂, Leiden Museum, Jentink, 1887, p. 158, specimen c, Europe. Gift of Prof. Ekema. I_1 dext. and sin. lacking.

27. Skull of ♂, V. A. I. U., no. 292. Age 10-11 years, nasals very concave.

28. Skull of ♀, Leiden Museum, cat. ost. m. Cabinet d'Anatomie 1860 (as *E. hemionus*, Jentink, 1887, p. 159, specimen c).

29. Skull of ♂, Leiden Museum, Jentink, 1887, p. 158, specimen h. Europe, age 11 years. "Phénix" of B. Loiset.

30. Skull of ♂, Leiden Museum, reg. no. 2603. Presented by D. J. Kienjet, 8.1.1937.

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1) Dr. E. J. Slijper was so kind as to place the material of the Veterinary Anatomical Institute of Utrecht at my disposal.

31. Skull of ♂, V. A. I. U., no. 293. Age 11½-12 years, Brabant horse.

32. Skull of ♀, Leiden Museum, reg. no. 3199. Presented by D. J. Kienjet, 27.9.1937.

33. Skull of ♂, Leiden Museum, Jentink, 1887, p. 158, specimen k.

34. Skull of ♂, Leiden Museum, Jentink, 1887, p. 158, specimen j. Cabinet d'Anatomie, 1860.

35. Skull of ♀, V. A. I. U., no. 294, Age 19 years.

36. Skull of ♀, V. A. I. U., no. 295. Age 20 years. M³ sin. lacking.

37. Skull of ♀, V. A. I. U., no. 296. Age 22 years. Teeth very long, hardly worn just as the molars.

38. Skull of ♀, V. A. I. U., no. 297. Age 32 years. Suture between premaxillaries closed, the teeth of the lower jaw heavily protruding forward. All bones very thin. The projection of the occipital very well developed. P¹ sin. lacking.

39. Skull of ♀, V. A. I. U., no. 298. Age 33 years.

40. Skull of ♂, V. A. I. U., no. 299. Pony, age 44 years. Posterior margin of M³ at the left side 6 mm before, at the right side on the same level as the anterior margin of the orbit

The ratios are given in Tables II and III.

Equus quagga (Table II). As far as concerns the subspecies separately, with increasing age there is a decrease of ratio 1, an increase of ratio 2, a decrease of ratio 3. An exception is ratio 2 in nos. 4 and 11, where the molar row extends to 2 mm in front of the anterior margin of the orbit. Number 8 is aberrant as there is an interspace of several millimeters between P² and P³ and between M² and M³, the other molars join close together at their occlusial faces.

E. zebra and *E. grevyi* (Table II) show corresponding increases and decreases of the ratios as *E. quagga*.

E. hemionus (Table II) shows very irregular values. It was impossible to obtain exact values of nos. 2 and 3. Nos. 4, 5 and 6, of about the same age, have greatly varying values.

Of *E. asinus* (Table II) nos. 5 and 11 have been referred to separate subspecies, while it is not certain that no. 7 belongs to *E. asinus*. The remaining specimens show increases and decreases of the ratios as *E. quagga*, with the exception of ratio 2 in nos. 6 and 9.

E. caballus (Table III) shows the same tendency as the other species. Number 36 is an exception, as the molar row is relatively very short.

Sex influence on the values is not distinct. In younger specimens ratio 1 is lower in females, in older specimens it is lower in males.

As a whole we may draw the following conclusions from the values in Tables II and III:

1. With progressing age the length of the molar row diminishes.

2. With progressing age the posterior border of the molar row shifts forward with regard to the posterior margin of the orbit.

In consequence of this, ratio 3 decreases (ratio 3 was used by Hooijer,

1945), the molar row becomes shorter and the distance M³-basion increases. The values of Hooijer concern *E. hemionus* nos. 1 and 6, *E. caballus* nos. 17 and 29, *E. zebra* no. 2 (M³ not yet at the level of the other molars) and no. 5. The differences between the values of Hooijer and mine are caused by a different method of taking measurements.

Can ratio 1 be used in estimating the age of *Equus* specimens?
Only *E. caballus* provides sufficient values to compare age and ratio 1.
The correlation coëfficient proves to be 66 % ± 12 %.
Estimation of age after wear of the incisors gives an exact result in more than half of the cases (Kroon, 1915, pp. 39-43). The latter method has the advantage of leading (after some exercise) to quick results.
Whether the correlation of age and ratio 1 is about the same in the other species I am not able to tell. There are several reasons which in *E. caballus* are the cause of a wider range of variation resulting in a less good correlation, viz., *E. caballus* is a domestic animal, so the food is very different, and it is the kind of food which is responsable for the wear of the molars and the shortening of the molar row (see p. 323). The same holds for the specimens of the other species which have been in captivity, compared mutually (e.g., *E. hemionus* nos. 5 and 6) and compared to the wild specimens. *E. caballus* most probably has its origin in several ancestral forms. From the values of *E. quagga* there is a slight indication of small differences in the various subspecies.

More material has to be examined to determine whether the other species have as great a range of variation as *E. caballus*. We find the greatest range of variation in *E. hemionus*, nos. 4, 5, and 6, the two latter specimens, however, are out of captivity.
The inaccuracy of age determination and of the measurements themselves in all species is the cause of a certain range of variation.

Can ratio 1 be used for taxonomic purposes?
The values of ratio 1 of *Equus quagga, E. zebra, E. hemionus* and *E. grevyi* are within the range of variation of *E. caballus*. Only *E. asinus* shows higher values in equal ages, which means a relatively longer molar row with an equal length of skull. However, the data are too scanty to allow of a definite conclusion.
The significance of ratio 1 for taxonomic purposes seems to be rather doubtful.

The position of the molar row with regard to the orbit.

In the lactal and incomplete dentitions this position depends on the number of molars hidden within the jaw behind the last functioning tooth. In these dentitions the last molar in function is always situated behind the anterior margin of the orbit, or, if it is situated in front of the orbit, it is always followed by molars within the jaw or partly erupted, which are situated far behind the anterior margin of the orbit; e. g., in *E. caballus* nos. 10 and 11. M^2 ends here behind the anterior margin of the orbit, 27 and 23 mm respectively. Taking the length of the orbit into consideration (56 and 61 mm respectively) the molar row ends at 48 % and 38 % of the orbital width. In *E. caballus* nos. 13 and 15 and in *E. grevyi* no. 2, M^3 has not yet completely erupted.

The permanent dentition depasses the anterior margin of the orbit in *E. zebra* no. 3 (8 years old), *E. asinus* no. 4 (age 9-10 years) and no. 6 (age 10-15 years), *E. caballus* no. 20 (age 6 years) and no. 24 (age 8 years).

According to Marinelli there is no influence of the molar row on the postorbital bar, and therefore neither of its length.

The cause of the shortening of the molar row.

At the occlusial face the molars always join close together, lower down they become narrower and diverge within the jaw, the rate of divergence decreases with progressing use (Ellenberger and Baum, 1921, p. 207).

The decrease in length of the molar row in the extreme case for all the examined specimens is 38.8 (*E. asinus* no. 4) minus 29.0 (*E. grevyi* no. 4) mm, divided by two, which makes 49 mm, for a skull of 500 mm length. Within the species these values for *E. caballus* are 32 mm (compare no. 24, age 8 years, and no. 39, age 33 years), for *E. asinus* 33 mm (compare the values of ratio 1 of no. 4, age 9-10 years, and no. 10, age 19 years), for *E. grevyi* 26 mm (compare no. 3, age 3-5 years, and no. 4, age 14 years) for a skull of 500 mm length, so on an average of about 30 mm in at least ten years for a skull of 500 mm length. The molar row consists of three premolars and three molars of nearly the same size. Thus approximately the free surface of each molar decreases half a mm in length pro year.

The wear of the teeth with as a consequence a decrease of the length of the teeth is a sufficient explication for the shortening of the molar row. A condition is that during the process of wearing the occlusial faces of the molars and premolars remain joined together.

The shifting of the anterior and the posterior border of the molar row in *Equus* and *Giraffa*.

Considering ratios 4 and 5 for *Giraffa* (Table I) and *Equus* (Tables II and III), the values appear not to give a clear image. In general in *Equus* and *Giraffa* there is a shifting of the posterior margin forward as well as of the anterior margin backward. There are several exceptions, in *E. zebra* this shifting is not obvious, in *E. hemionus* and *E. quagga chapmanni* the anterior margin of the molar row seems to shift in a forward direction (cf. p. 313, the quotation from Pocock, mentioning a probable shifting forward of the entire tooth row in *Rhinoceros*).

Whether the shifting is more intensive at the anterior or at the posterior margin cannot be ascertained. In *Giraffa* in the greater number of cases the shifting is most strongly pronounced at the anterior margin. It is possible that in *Giraffa* there is a tendency to keep the posterior border of the molar row in place with regard to its situation below the orbit, as the pressure of mastication is diverted along the postorbital bar.

In *Equus* the rate of shifting at the anterior and the posterior border of the molar row is very variable.

The position of the postorbital bar.

Marinelli (1933, p. 213) maintains that the difference in direction of the post-orbital bar in horse and giraffe agrees totally with the difference in direction of diverting the pressure of mastication.

Concerning the direction of the postorbital bar in horses, there is a difference in the skulls of young and adult individuals. In *E. caballus* no. 4 (fetus) the bar is situated parallel to the frontal plane and it is very thin. The processus postorbitalis of the frontal and the projection of the squamosum touch each other, without having grown together. In no. 5 (age 7 days) the postorbital bar is placed somewhat obliquely in regard to the frontal plane and this increases with progressing age. At ages of over 5 or 6 years the direction seems to be fairly constant.

The same obtains in *Equus zebra*, *E. quagga* and *E. asinus*, and even in *E. grevyi*, of which the youngest skull in the present material is that of a 2½ years old specimen. Of *E. hemionus* only skulls of adult specimens were available.

The data given above furnish another indication that the postorbital bar in horses has the function of diverting the pressure exercised by the mandibular articulation.

With regard to the state of affairs in young individuals, Marinelli (1933, p. 216) remarks that *Protohippus* has the orbit closed behind, without, however, the shape of the postorbital bar being noticeably influenced by the region of articulation via the zygomatic arch.

In young specimens of *Equus* we have the same peculiarity as long as the teeth are not functioning.

Among mammals a postorbital bar appears in Hippopotamidae, all ruminants and primates. Concerning the latter Bluntschli (1936, p. XLIV) regards the outer (post)orbital bar in *Homo* as one of the pillars transmitting the pressure of the basal maxillary arch to the roof of the skull. The situation of the orbit and the direction of the pressure of the postorbital bar in a more or less frontal plane (slightly bent backwards in adults; Bluntschli, 1936, figs. 4 and 5, pp. XLII and XLIII) makes it hardly possible that there is an influence of the length of the tooth row on the postorbital bar. The tooth row extends to just behind the postorbital bar.

Conclusions.

In *Giraffa* and *Equus* with progressing age there is a shortening of the molar row. The shifting of the molar row in forward direction in *Giraffa* apparently has no influence on the diverting of the pressure of mastication.

The dental index in *Equus* cannot be used for taxonomic purposes, nor does it offer advantages in estimating the age of the specimens.

The shortening of the molar row depends only on the decrease in length of the occlusial face with progressing use.

The shortening of the molar row in *Equus* and *Giraffa* in most cases proves to cause a shifting of the anterior margin backward as well as of the posterior margin forward.

Leiden, April 1946.

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TABLE I

	Giraffa camelopardalis (L.)							Giraffa camelopardalis tippelskirchi Matschie	Giraffa reticulata reticulata de Winton	Giraffa camelopardalis (L.)							
Number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Sex			♂	♂		♂		♂	♂	♀		♂	♀	♀			
Age	8 days			3 yrs	3—7 yrs	3—7 yrs	3—7 yrs	6—7 yrs	±7 yrs	7 yrs	7—13 yrs	13 yrs	15—16 yrs	19 yrs	old	old	old
Out of captivity (c) or wild (w)	c		w,c	w,c				w,c	w	w,c	w	c	w,c	w,c	w	w	w
Last tooth in function	Pd^4	M^1	M^2	M^2	M^3	M^3	M^3	M^3	M^3	M^3	M^3	M^3	M^3	M^3	M^3	M^3	M^3
Ratio 1	24.8	± 20.8	24.5	23.5	27.6	± 26.9	26.3	22.8	23.0	25.4	± 25.0	23.4	23.3	23.1	± 24.0	23.0	22.4
Ratio 2	4.59	± 7.8	12.4	9.75	4.56	± 4.43	3.71	6.99	5.79	4.33	± 3.00	3.05	4.62	3.94	± 6.12	7.95	4.91
Ratio 3	68.6	± 51	74	64.7	87	± 78	81	65.3	66	74	± 73	71	70	69	± 72.5	65	68
Ratio 4					31.6	± 34.5	32.3	34.9	34.6	34.3	± 34.4	32.8	33.2	33.5	± 33.0	35.4	33.1
Ratio 5					40.7	± 38.7	41.1	42.4	42.3	40.0	± 40.6	43.8	43.4	43.2	± 42.9	41.4	44.3
Ratio 6	72.8	± 43.5	41.5	27.3	56.9	66.1	67.2	43.9	51.5	63.5	75.9	72.5	62.4	63.0	44.8	35.6	50.0
Length of skull	26.2	± 38.5	44.5	50.2	48.3	± 52	51.2	58.8	57.1	53.1	± 50	52.7	58.4	58.3	± 60.5	59.1	63.2
Length of molar row	6.5	± 8.0	10.9	11.8	13.3	14.0	13.5	13.4	13.1	13.5	12.5	12.3	13.6	13.5	14.5	13.6	14.2
Posterior margin of M^3 — basion	9.5	± 15.7	14.7	18.3	15.3	17.9	16.6	20.5	19.8	18.3	17.2	17.3	19.4	19.6	± 20	21.0	20.9
Posterior margin of M^3 — posterior margin of orbit	1.2 (M^1 1.0)	± 3.0	5.5	4.8 (M^3 2.2)	2.2	2.3	1.9	4.1	3.3	2.3	1.5	1.6	2.7	2.3	3.7	4.7	3.1
Posterior margin of M^3 — anterior margin of orbit	3.2	± 2.3	3.9	1.8	2.9	4.5	3.9	3.2	3.5	4.0	4.7	4.2	4.5	3.9	3.0	2.6	3.1
Width of orbit	4.4	± 5.3	9.4	6.6	5.1	6.8	5.8	7.3	6.8	6.3	6.2	5.8	7.2	6.2	6.7	7.3	6.2
Anterior margin of P^2 — prosthion					19.7	20.1	21.1	24.9	24.2	21.3	± 20.3	23.1	25.4	25.2	26.0	24.5	28.1

Nos. 1—4, measurements taken starting from last functioning tooth. In no. 1, M^1 not yet erupted; in no 4, M^3 not yet erupted.

TABLE II

	Equus quagga Gmelin															*Equus zebra* L.					*Equus hemionus* Pallas						*Equus grevyi* Oust.				*Equus asinus* L.										
Species																																										
Subspecies	*chapmanni* ♂ × *burchellii* ♀				*granti*			*quagga*		*burchelli*			*chapmanni*																		*africanus*					?		*taeniopus*			
Number	12	13	14	15	9	10	11	1	2	3	4	5	6	7	8	1	2	3	4	5	1	2	3	4	5	6	1	2	3	4	1	2	3	4	5		7	8	9	10	11
Sex	♀	♀	♂	♂	♂	♂	♂	♂	♀	♂	♀	♀	♂	♂	♂	♂	♂	♀	♂	♂	♂	♂	♀	♂	♂	♂	♂	♀	♂	♀	♂	♂	♀	♂	♂		♀	♀	♂	♂	♂
Age	5 mths.	5 mths.	5-6 mths.	!5(7) mths.	!2½-3 yrs	4-5 yrs	10-11 yrs	6 yrs	16 yrs	6 yrs	13 yrs	16 yrs	!10-11 yrs	15 yrs	!20 yrs	5-6 mths	3-3½ yrs	8 yrs	9 yrs	13-14 yrs	5 yrs	9 yrs	15-14 yrs	>20 yrs	!21 yrs	!21 yrs	2½ yrs	4½ yrs	5 yrs	14 yrs	1½ yrs	1½ yrs	!3 yrs	9-10 yrs	10 yrs	10-15 yrs	13-14 yrs	14 yrs	15-40 yrs	19 yrs	15-40 yrs
Out of captivity (c) or wild (w)	c	c	c	c	w,c	w	c	w	c		c		c	c	c	c	w	w	c	w	w	w		c	c	w	c	c			c	c	c								w,c
Last erupted premolar or molar	Pd4[1]	Pd4		Pd4	M2	M3	M3	M3	M3	M3	M3	M3	M3	M3	M3	Pd4	M3	M3	M3	M3	M3	M3	M3	M3	M3	M3	M3	±M2[2]	M3	M3	±M1	±M1	M2	M3	M3	M3	M3	M3	M3	M3	M3
Ratio 1	31.8	28.6	32.1	25.9	±34.8	34.5	34.0	35.0	33.0	33.5	31.6	29.4	31.6	31.6	32.9	±34.6(pd4) / ±43.9(M1)	36.2(M3)	36.4	34.7	30.7	36.3	±35.2	±35.0	36.1	35.4	32.7	31.0	34.2	34.2	29.0	33.1	±31.6	34.6	38.8	36.5	36.9	±34.5	36.2	34.7	32.2	±30.5
Ratio 2	13.9	18.9	13.9	24.7	±11.3	14.0	13.0	13.4	14.8	14.6	13.4	15.0	11.7	15.7	13.1	±16.9(pd4) / ±10.4(M1)	10.6(M3)	10.1	13.8	14.0	13.3	±17.5	±14.2	17.1	17.2	17.7	18.4	14.6	14.9	17.9	15.0	±17.4	12.7	12.4	11.8	10.0	±12.4	14.0	11.0	17.0	12.9
Ratio 3	77	65	82	57	±92	89	87	91	82	87	81	74	81	78	81	±85(pd4) / ±103(M1)	100.2(M3)	100	86	72	93	±96	±92	87	86	76	74	89	84	67	77.4	±69.5	81	98	92	94	±84	93	83	78	72
Ratio 4						38.8	38.9	38.6	40.3	38.7	38.9	40.0	39.2	40.4	40.6			36.4	40.4	30.7	38.7	±36.6	±38.7	41.2	41.0	42.8			40.5	43.5				39.4	38.6	39.3	±40.8	38.9	41.8	41.3	41.7
Ratio 5						26.6	27.2	26.6	26.8	27.8	29.6	30.6	28.9	28.0	26.4			27.3	25.0	26.7	30.2	±33.5	±31.4	22.7	23.6	26.3			25.2	27.6				21.8	25.8	23.8	±24.7	24.9	23.5	26.1	28.0
Length of skull	25.8	24.7	26.5	±34	38.2	44.3	44.5	44.9	45.2	46.0	45.0	46.5	50.2	48.5	46.5	±26	42.6	42.7	44.8	40.8	42.8	±43.5	±46.5	41.0	46.3	46.3	49.1	47.1	54.2	53.0	32.6	±36.2	37.8	34.7	42.5	36.9	±38	35.7	37.5	35.8	38.8
Length of molar row	8.2	8.5	8.5	8.8	13.3	15.3	15.1	15.7	14.9	15.4	14.2	13.7	15.9	15.3	15.3	9(Pd4) / 10(M1)	15.4(M3)	15.5	15.5	12.5	15.5	15.3	16.3	14.8	16.4	15.1	15.2	16.6	18.5	15.4	10.6	11.4	13.1	13.4	15.1	13.6	13.1	12.9	13.0	11.5	L 12.1 / R 11.4
Posterior margin of M3 — basion	10.7	13.1	10.4	15.5	14.5	17.2	17.3	17.3	18.2	17.8	17.5	18.6	19.7	19.6	18.9	10.6(Pd4) / 8.9(M1)	15.0(M3)	15.5	18.1	17.4	16.6	15.9	18.0	16.9	19.0	19.9	20.6	18.7	22.0	23.0	13.7	±15.4	15.2	13.7	16.4	14.5	±15.5	13.9	15.7	14.8	16.2
Posterior margin of M3 — posterior margin of orbit	3.6	5.6	3.7	8.4	4.3	6.2	5.8	6.0	6.7	6.7	6.0	7.1	5.9	7.6	6.1	4.4(Pd4) / 2.7(M1)	4.5(M3)	4.3	6.2	5.7	5.7	7.6	6.6	7.0	7.9	8.4	9.0	6.9	8.1	9.5	4.9	6.3	4.8	4.3	5.0	3.7	4.7	5.0	4.1	6.1	5.0
Posterior margin of M3 — anterior margin of orbit	0.6 p[3]	0.6 a[3]	0.3 p	3.0 a	0.8 p	0.4 a	0.2 a	0.4 a	0.6 a	0.9 a	0.2 a	1.0 a	0.4 a	1.4 a	0.3 a	0.3p(Pd4) / 2.0a(M1)	1.5 p(M3)	0.8 p	1.2 a	1.3 a	0.2 a	1.9 a	0.8 a	1.5 a	1.6 a	2.8 a	2.5 a	1.1 a	1.7 a	3.8 a	0.9 a	1.6 a	0.2 a	0.5 p	±0.5 a	0.3 p	0.5 a	0.5 a	0	±1.7 a	0.3 a
Anterior margin of P2 — prosthion					11.8	12.1	11.9	12.1	12.8	13.3	14.2	14.6	13.6	12.3				11.7	11.2	10.9	11.7	±12.3	±12.2	9.3	10.9	11.3			13.7	14.6				7.6	11.0	8.8	9.4	8.9	8.8	9.3	10.9

[1] In lactal dentitions and in not fully erupted dentitions the measurements were taken starting from the last erupted tooth, except in *Equus zebra* no. 1, in which measurements were taken starting from various teeth.

[2] The indication ± means that the tooth is not yet at the same height as the others in the same row.

[3] a, tooth row ending anteriorly of the anterior margin of the orbit; p, tooth row ending posteriorly of the anterior margin of the orbit. A ! indicates that the age is known.

TABLE III. *Equus caballus* L.

Number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Sex									♂		♂		♂			♂	♂	♀	♂	♂	♀	♀	♂	♀	♂	♂	♂	♀	♂	♂	♂	♂	♀	♂	♂	♀	♀	♀	♀	♂
Age	*fetus?	fetus	fetus	fetus	7 days	10 days	15 days	*1 mth.	5-6 mths.	8-10 mths.	1 yr.	2 yrs.	2¹/₃ yrs.	2¹/₃ yrs.	4¹/₄ yrs.	4¹/₂ yrs.	5 yrs.	5 yrs.	5¹/₈ yrs.	*5¹/₈ yrs.	*5¹/₈-6 yrs.	*±6 yrs.	6¹/₈ yrs.	*±8 yrs.	8 yrs.	*8-9 yrs.	10-11 yrs.	*11 yrs.	*11 yrs.	*11-12 yrs.	11¹/₈-12 yrs.	*12 yrs.	*13-14 yrs.	*14 yrs.	19 yrs.	20 yrs.	22 yrs.	32 yrs.	33 yrs.	44 yrs.
Last erupted premolar or molar	(Pd⁴)	± Pd⁴	± Pd⁴	± Pd⁴	± Pd⁴	± Pd⁴	± Pd⁴	Pd⁴	Pd⁴	Pd⁴	Pd⁴	M²	M³	M³	± M³	M³	M³	M³	M³	M³	M³	M³	M³	M³	M³	M²	M³	M³	M³	M³	M³	M³	M³	M²	M³	M³	M³	M³	M³	M³
Ratio 1	(41.6)	37.7	39.0	43.6	35.0	35.4	34.0	36.7	26.8 (Pd⁴) 34.3 (M¹)	25.6 (Pd⁴) 40.6 (M²)	30.0 (M¹) 38.7 (M²)	33.4	35.8 (M³)	32.0 (M³)	32.7 (± M³)	34.4	35.3	33.0	34.8	34.7	33.2	33.7	35.3	36.0	34.0	31.4	30.8	34.2	30.5	30.8	30.9	31.5	30.0	31.5	31.9	27.3	31.4	30.3	29.6	R 30.0 L 31.3
Ratio 2	(11.1)	10.2	13.6	13.6	15.1	10.7	14.9	11.6	13.8 11.3	21.5 6.9	17.2 8.3	11.4	12.4	11.4	13.2	12.3	13.3	12.8	10.7	11.3	13.8	12.3	12.2	11.4	14.0	12.2	13.8	12.1	15.7	14.2	13.5	14.4	14.8	15.8	13.3	17.2	14.6	14.2	14.9	R 12.8 L 11.4
Ratio 3	(106)	111	103	115	89	88	82	106	58 89	53 116	68 110	87	95	84	83	83	90	82	99	95	85	84	90	92	86	76	73	88	74	74	74	80	71	77	78	65	78	72	71	R 78 L 81
Ratio 4																38.9	39.3	40.3	37.1	36.6	39.1	40.3	39.0	39.2	39.1	41.3	42.3	38.8	41.1	41.5	41.9	40.0	42.2	41.3	40.8	42.0	40.3	41.9	41.6	± 38.5
Ratio 5																26.8	25.4	26.6	27.9	28.4	27.7	25.8	25.7	25.0	26.7	27.1	27.0	26.8	28.2	27.7	27.4	29.4	27.8	27.1	27.1	30.5	28.3	27.7	28.8	± 30.8
Length of skull	20.7	± 25.5	± 28.5	25	29.1	± 28	30.9	26.7	38.8	41.8	45.5	49.2	54.2	52.5	53.2	53.5	51.5	53.0	54.3	48.6	53.7	54.5	51.7	42.0	51.2	56.2	56.7	52.1	53.0	55.6	59.9	57.8	54.7	54.2	53.2	51.2	53.5	49.8	55.8	45.4
Length of molar row	(8.6)	9.6	11.1	10.9	10.2	9.9	10.5	9.8	10.4 (Pd⁴) 13.3 (M¹)	10.7 (M²) 17.0 (M²)	13.6 (M¹) 17.6 (M²)	6.4 (M²)	19.4 (M²)	16.8 (M³)	17.4 (M³)	18.4	18.0	17.5	18.9	16.9	17.8	18.4	18.2	15.1	17.4	17.7	17.4	17.8	16.2	17.1	18.4	18.1	16.4	17.1	17.0	14.0	16.8	15.1	16.5	R 14.2 L 13.6
Posterior margin of M³ — basion	(8.1)	8.7	10.8	9.5	11.5	11.3	12.8	9.2	17.9	20.2	20.0 (M¹) 16.0 (M²)	18.8	20.5	20.0	21.0	20.8	20.1	21.4	20.2	17.8	21.0	22.0	20.2	16.4	20.1	23.2	24.0	20.3	21.8	23.1	25.1	22.7	23.1	22.4	21.8	21.5	21.6	20.9	23.2	17.5
Posterior margin of M³ — posterior margin of orbit	(2.3)	2.6	3.9	3.4	4.4	3.0	4.6	3.1	7.3 4.4	9.2 2.9	7.8 3.0	5.6	6.7	6.0	7.0	6.6	6.8	6.8	5.8	5.5	7.4	6.7	6.3	4.8	7.2	6.9	7.8	6.3	8.3	7.9	8.1	8.3	8.1	8.6	7.1	8.8	7.8	7.1	8.3	R 5.2 L 5.8
Posterior margin of M³ — anterior margin of orbit	(1.7 p)	1.7 p	1.3 p	1.3 p	0	0.6 p	0	1.5 p	1.8 a 1.1 p	3.6 a 2.7 p	1.7 a 2.3 p	0.4 p	0.3 a	0.2 p	0.9 a	0	0.6 a	0.6 a	0	1.0 p	0.9 a	0.5 a	0.3 a	0.2 p	0.5 a	1.0 a	1.4 a	0.3 a	2.5 a	0.9 a	1.9 a	2.1 a	1.7 a	2.4 a	1.3 a	2.6 a	1.3 a	1.3 a	2.4 a	R 0 L 0.6 a
Anterior margin of p² - prosthion												14.3	13.0	14.1	15.2	13.9	14.9	14.1	13.3	10.5	13.7	15.3	15.3	15.3	14.0	15.0	15.4	16.4	17.0	15.2	14.7	14.5	15.7	15.1	13.8	16.1	14.0			

* indicates: age estimated;
± means that the tooth is not yet functioning or not yet at the same height as the others in the same row.
a, tooth row ending anteriorly of the anterior margin of the orbit;
p, tooth row ending posteriorly of the anterior margin of the orbit.

No. 1, measurements starting from the tooth within the jaw.
Nos. 9 and 10, additional measurements starting from not functioning teeth.

No. 11, additional measurements starting from not functioning teeth.
Nos. 13 and 14, measurements exclusively starting from the last not yet functioning tooth.