A revision of the deer from Tegelen (province of Limburg, The Netherlands)

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The larger part of the known material of the deer from Tegelen has served as the base of a reassesment of the taxonomic place of these deer. Comparison with Villafranchian deer from France and Spain makes clear that a great homogeneity exists in the Villafranchian deer.

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Introduction

At the beginning of this century mammal fossils were found in some clay pits east of Tegelen (The Netherlands). In these pits a Lower Pleistocene clay was dug. The fossils are said to come from a gully-fill, situated at the base of the second sedimentation-cycle of this Tegelen Clay (Zagwijn, 1963).

According to Dubois (1904 a-c), who was the first to report on it, the fauna contained four species of cervids: *Cervus sedgwickii* Falconer, 1868 (= *C. dicranius* Nesti, 1879), *Cervus tegulensis* sp. nov., *Cervus* (*Axis*) *rhenanus* sp. nov., and *Cervus* (*Axis*) spec. In 1905 he reduced the number of Cervidae to three, synonymizing *Cervus* (*Axis*) spec. with *C. rhenanus*. The cervids form an important part of the Tegelen fauna. The

remains ascribed to *Cervus dicranius* by Dubois (1905) and Bernsen (1933-'34) could not be distinguished according to Kunst (1937) from those ascribed to *Eucladoceros tegulensis* so that the first is a synonym of the second species and can be removed from the faunal list. Kortenbout van der Sluys and Zagwijn (1962) were the last to mention the cervids from Tegelen. They listed just two cervids: *Eucladoceros tegulensis* and *Cervus rhenanus*.

Since Kunst (1937) last studied the remains of the deer from Tegelen new finds of these species have been dug up. The aim of this study is to describe those specimens in relation with earlier descriptions and to make a comparison between the deer from Tegelen and similar deer species from Lower Pleistocene localities in France and Spain.

Acknowledgements

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MATERIAL

The material used for the study of *Eucladoceros tegulensis* comes from the following collections: Nationaal Natuurhistorisch Museum (formerly: Rijksmuseum van Geologie en Mineralogie), Leiden (RGM); Teylers Museum, Haarlem (Ha); Natuurhistorisch Museum, Maastricht; Instituut voor Aardwetenschappen, Utrecht.

The study is based on the following number of elements:

Antlers	74	Astragali	23
Dental elements	54	Calcanei	12
Scapulae	6	Cubo-naviculari	12
Humeri	21	Metatarsi	14
Radii	10	Phalanges I	16
Metacarpi	12	Phalanges II	12
Tibiae	11	Phalanges III	3

The material used for the study of *Cervus rhenanus* comes from the collections mentioned above and also from the collections of the Zoölogisch Museum in Amsterdam; and the private collection of D. Mol in 's Heerenberg. The study is based on the following numbers of specimens:

Antlers	45	Astragali	17
Dental elements	238	Calcanei	14
Scapulae	13	Cubo-naviculari	9
Humeri	15	Metatarsi	24
Radii	18	Phalanges I	22
Metacarpi	12	Phalanges II	11
Femuri	5	Phalanges III	5
Tibiae	14		

THE TEGELEN PITS

The material which is the subject of this study was found in several clay pits, most of which are now abandoned. These pits all lie south of Venlo between Tegelen and the Dutch-German border in the Venlo Graben area. In these pits the Tegelen Clay was dug, which forms part of the Tegelen Formation described by Kortenbout van der Sluijs & Zagwijn (1962).

The clay pits in the Venlo Graben area, in which the Tegelen Clay was dug, all yield pollendiagrams which can be correlated with the upper part of the Tiglian (pollenzones TC2-6) and with the lower part of the Eburonian (pollenzones EB I-III: Kortenbout van der Sluys & Zagwijn, 1962; Zagwijn, 1963).

Only in two pits this whole section of pollenzones TC2 to EBIII is met with, viz. the pits Canoy-Herfkens and Russel-Tiglia-Egypte. In the pit Russel-Tiglia the first sedimentary cycle of the Tegelen Clay (pollenzones TC2-4b) is missing. This part is also missing in the pits Russel-Tiglia-Wambach, Kurstjens and Teeuwen. In these three pits also the Eburonian part of the Tegelen Formation (pollenzones EBI-III) is missing. In the pit Laumans only pollenzones TC3 and TC4 are found, which belong to the first sedimentary cycle of the Tegelen Clay. Finally pit Maalbeek shows a pollendiagram pointing to a cold, subarctic phase which must belong to a glacial period, which Zagwijn (1963) assumed to be the Eburonian (pollenzone EB III). The reasons for this assumption were that thus far the only glacial period that is known to occur in the Venlo Graben area is the Eburonian and that the pollendiagram from the pit Maalbeek in its lower part is identical to the uppermost spectra from the pit Russel-Tiglia-Egypte. The finds of *Anancus* and *Tapirus* in the pit Maalbeek and the presence of Tertiary floral elements in the pollen assemblage from this pit, however, point to a very Early Villafranchian, possibly Praetiglian age. This means that *Anancus arvernensis* and *Tapirus arvernensis* are not part of the Tegelen fauna since they were exclusively found in the pit Maalbeek near Belfeld.

For most of the fossil mammal remains from Tegelen it is not known from which pit they have come. Most of the remains of which it is known come from the pits Canoy-Herfkens, Russel-Tiglia and Russel-Tiglia-Egypte while all other pits have yielded some remains also (van Regteren Altena, 1951). Summarizing, it can be said that most of the large mammal fossils are dating from the upper part of the Tiglian (pollenzones TC2-6) and possibly from the lower part of the Eburonian (pollenzones EBI-III).

There has been some discussion on the question whether the small mammal assemblage described by Freudenthal et al. (1976) and the large mammal fauna from Tegelen are of the same age or not (Hooyer, 1947; Loose, 1960, 1975; Guérin, 1980). The small mammal assemblage from Tegelen was for the greater part collected by Freudenthal et al. (1976) and they were 'concentrating their efforts on the central part of the gully' in the pit Russel-Tiglia-Egypte. This is the gully which is situated at the base of the sediments belonging to the second sedimentary cycle. These sediments belong to pollenzones TC5-6 (Zagwijn, 1963). As was stated before, the large mammal remains were for the greater part found in sediments belonging to pollenzones TC2 to EBIII. Both parts of the Tegelen fauna are therefore probably of the same age.

Another indication for this time-correspondence is given by the find of a

mandibula of *Eucladoceros tegulensis* together with the small mammal assemblage collected by Freudenthal and coworkers. This mandibula is incomplete. The whole part posterior of the third molar has broken off and the canines and incisives are missing. The molars and premolars are very much worn down. Most of the teeth which are present are a little damaged; part of the hypoconid of the M_1 is missing. Parts of the jaw bone itself are missing, revealing the roots of the teeth. The dimensions of the teeth and dental segments are given in Table 1. The teeth in this jaw do not differ morphologically, nor biometrically, from other teeth found in the Tegelen area.

ABBREVIATIONS

The abbreviations used in this paper are:

APD	= antero-posterior diameter	Min	= minimum
TD	= transverse diameter	Max	= maximum
p	= proximal	M	= mean value
d	= distal	SD	= standard deviation
l	= length	df	= degrees of freedom
h	= height	P	= probability
w	= width	95%	= significance at 95% probability
N	= number of measurements		

METHODS

For the method of measuring the reader is referred to Heintz (1970). This method was used to be able to compare the results of this study with the work of Heintz (1970). In January 1991 the author had the opportunity to study the material of *E. senezensis* in the Musée national d'Histoire naturelle at Paris and thus the measurements taken according to this method could be calibrated.

Most of the data are presented in scatter diagrams. Of all measurements the minimum, maximum and mean values are determined as well as the standard deviation. The data from the Tegelen fauna are put in tables together with those gathered by Heintz (1970) on the cervid populations from Peyrolles, Senèze, La Puebla de Valverde, and St Vallier.

The Student's t-test is used to compare the data from Tegelen with those from the localities mentioned above. This t-test is a statistical test by which the mean values of two populations can be compared. The t-value is in all cases obtained with the use of the formula:

$$t = \frac{(M_1-M_2)*\sqrt{(N_1*N_2)/(N_1+N_2)}}{\sqrt{((N_1-1)*SD_1^2+(N_2-1)*SD_2^2/(N_1+N_2-2)}}$$

Two means differ significantly when t exceeds the 95% significance level. The results of these tests are presented in tables.

Morphological descriptions of the antlers and dental elements are given, and are compared with morphological descriptions of the antlers and dental elements of the deer from the localities mentioned above as given by Heintz (1970).

Systematical part

Genus *Eucladoceros* Falconer, 1868

Eucladoceros tegulensis (Dubois, 1904)
Figs. 1-7.

1904a *Cervus tegulensis* sp. nov. – Dubois, p. 247, fig. 1.
1904b *Cervus teguliensis* sp. nov. – Dubois, p. 218, fig. 1.
1937 *Cervus (Eucladoceros) teguliensis* Dubois – Kunst, p. 30.
1945 *Eucladoceros tegulensis* Dubois – Schreuder, p. 155.
1962 *Euctenoceros tegelensis* Dubois – Kortenbout van der Sluys & Zagwijn, p. 36.
1970 *Eucladoceros teguliensis* Dubois – Heintz, p. 186.
For complete listing of synonymy see bibliographic analysis.

Holotype — Left antler figured by Dubois (1904a, p. 247, fig. 1) and Dubois (1904b, p. 218, fig. 1); same antler figured by Dubois (1905, pl. 1, fig. 1).

Type locality — Tegelen, The Netherlands (Tegelen Clay).

Other localities — La Campine, Belgium (Germonpré, 1983).

Bibliographic analysis — Dubois (1904a) was the first to use the term *Cervus tegulensis* to indicate a large species of deer closely resembling *Eucladoceros tetraceros* Dawk., 1878. This introduction was accompanied by a picture of the (wrongly) restored type antler. No description was given. Some of the antlers of the large deer from Tegelen were ascribed to *C. sedgwickii* Falc., 1868 which was considered to be identical to *C. dicranius* Nesti, 1879.

Dubois (1904b,c) also introduced an alternative spelling for *C. tegulensis* and changed it to *C. teguliensis*

In 1905 Dubois gave a description of the type antler and accompanied it with a picture of the antler. He ascribed two antlers to *C. dicranius*, which he now stated to be differing from *C. sedgwickii.*

In 1906 Dubois stated that *C. teguliensis* is a primitive form of the subgenus *Elaphus* and still ascribed certain antlers to *C. dicranius.*

Stehlin (1923) stated that, in spite of the great resemblance, *C. teguliensis* and *C. senezensis* Dep., 1910 do not belong to one and the same species, but are very closely akin of each other. He also underlines the great affinity of both species to *C. tetraceros* and *C. ctenoides* Nesti, 1879.

In 1930-'34 Bernsen distinguished three species of large deer in the Tegelen fauna: *C. teguliensis*, *C. dicranius* and *C. ctenoides.*

Kunst (1937) denied the differences between the antlers ascribed to *C. (Eucladoceros) teguliensis* and those ascribed to *C. dicranius* and *C. ctenoides* and argued that all the remains of the large deer from Tegelen should be ascribed to just one species: *C. (Eucladoceros) teguliensis.* This species was considered to be identical to *C. tetraceros.*

Schreuder (1945) mentioned two species of large deer for the Tegelen fauna: *Eucladoceros tegulensis* and *C. dicranius.*

Azzaroli (in Bout & Azzaroli, 1953) stated that *C. teguliensis* was larger than *Euctenoceros tetraceros* but gave no comment on the synonymy established by Kunst (1937). He also stated: 'The distinction between *E. ctenoides* and *E. teguliensis* doesn't seem to be valid.' (Azzaroli, 1953).

Viret (1954) underlined the great resemblance between *C.* (*Euctenoceros*) *teguliensis* and *C. senezensis* and stated to prefer to maintain 'le nom de *senezensis* parce que ce dernier s'applique à des documents d'une exceptionelle beauté'.

Kortenbout van der Sluys & Zagwijn (1962) mentioned just one species of large deer in the Tegelen fauna: *Eucladoceros teguliensis*.

Germonpré (1983) considered *E. senezensis* to be a junior synonym for *E. tegulensis*. Azzaroli et al. (1988) agreed with this.

DESCRIPTION

The antlers

Morphology — In order to illustrate the morphology of the antlers of *E. tegulensis* first a summary of the description by Dubois (1905) of the type antler will be given, followed by some descriptions of newly found antlers. More descriptions of antlers of this deer species were given by Dubois (1906), Bernsen (1934) and Kunst (1937). The biometrical data on the antlers of *E. tegulensis* from Tegelen are presented in Table 2.

Ha 15 776 (Holotype; Fig. 1) — Summary of the description by Dubois (1905): Left shed antler with four tines belonging to an adult specimen. The browtine is implanted close to the burr on the antero-lateral side of the beam with an obtuse angle to the beam above the browtine. The browtine has a slightly sigmoid form. On the anterior side of the second segment of the beam there is a ridge which makes the second segment oval in section. There is no accessory tine. At the place where the browtine is implanted the beam bends strongly backwards. Beyond this bend the beam is rather straight except for two inflexions to the anterior at the places where the second and third tine are implanted. The beam is round or slightly oval in section. The second and third tine are implanted on the anterior side of the beam with a right angle to the beam. Of these two tines the second tine is the longer one. The distance between the

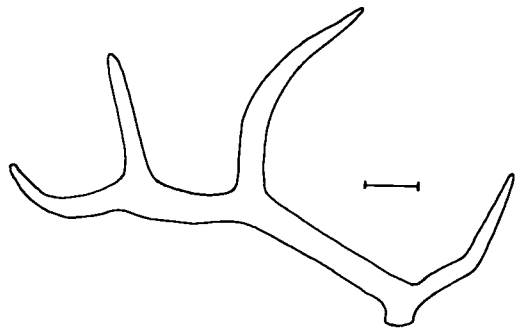

Fig. 1. Left antler of *Eucladoceros tegulensis* (holotype), Ha 15 776; lateral view. Length of the scale bar in all figures is 10 cm.

first and second tine is larger than the distance between the second and third tine. The end of the beam is formed by the fourth tine which is implanted on the posterior side of the base of the third tine. The fourth tine bends a little to the anterior.

RGM 20 685 (Fig. 2) — Nearly complete left and right shed antlers with five tines each, belonging to an adult individual.

The right antler is complete, except for the burr which is damaged. The beam below the browtine is slightly oval in section. The browtine is implanted close to the burr at the antero-lateral side of the beam with a very obtuse angle (130°) to the beam above the browtine. The form of the browtine is slightly sigmoid with the tip pointing upwards. The length of the browtine is c. 33.5 cm. The beam bends strongly backwards at the point where the browtine is implanted.

Between the browtine and the second tine on the antero-median side of the beam, an accessory tine is implanted at c. 7 cm distance from the base of the browtine. Its length is c. 8 cm. At its base it passes into a ridge which stretches over the antero-median side of the beam towards the browtine and towards the second tine. This ridge makes the section of the second segment of the beam strongly oval between the browtine and the accessory tine and a little less oval between the accessory tine and the second tine.

The second tine is implanted at the anterior side of the beam at a distance of 25 cm from the browtine with an angle of 80° to the beam above the second tine. A little above its base it bends slightly backwards and at about two-thirds of its length it bends back forwards again causing its tip to point in a forward and upward direction. The length of the second tine is c. 38 cm.

The third segment of the beam has about half the length of the second segment.

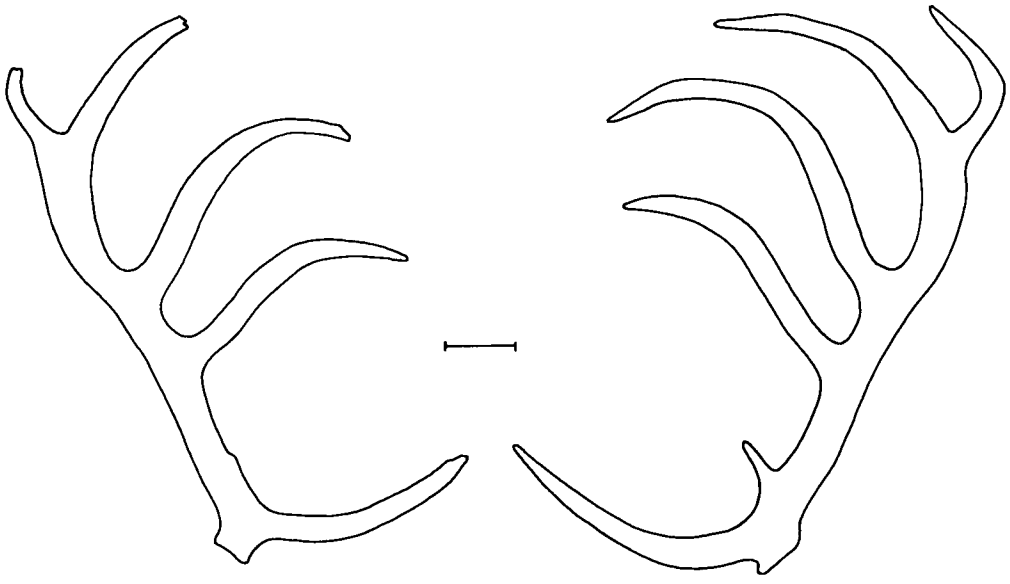

Fig. 2. Left and right antler of *Eucladoceros tegulensis*, RGM 20 685; lateral view.

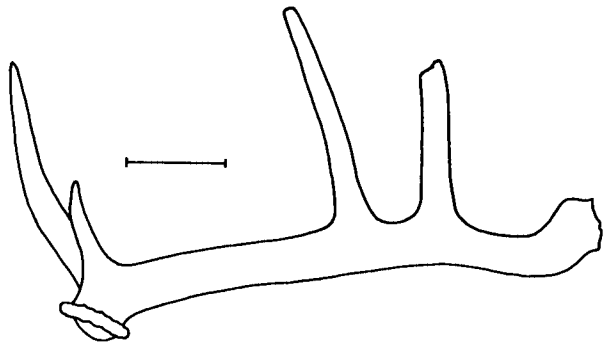

Fig. 3. Right antler of *Eucladoceros tegulensis*, RGM 86 834; lateral view.

The third tine is implanted at the anterior side of the beam with an angle of 60° to the fourth segment which, at its anterior part, bends a little backward with regard to the second and third segment. The third tine has about the same form as the second tine but its bends are somewhat stronger. The length of the third tine (c. 55 cm) exceeds the length of the second tine.

After its slight backward bend near the base of the third tine, the fourth segment of the beam bends forward again. The length of the fourth segment is c. 22 cm. The fourth tine can be regarded as the continuation of the fourth segment of the beam and is implanted at the anterior side of that beam. In its lower part it points in the same direction as the fourth segment but over the whole of its length it bends forward so that its tip points in an upward and forward direction. The length of the fourth tine is c. 43 cm.

The end of the beam is formed by the fifth tine which is implanted at the back of the base of the fourth tine. The base of the fifth tine points backwards but at one-third of its length it shows an upward bend. Its length is c. 28 cm.

The beam and all tines are more or less oval in section. The length of the beam is 85 cm measured in a straight line from burr to tip and 91 cm measured along the posterior side of the beam. The whole antler has an ornamentation of small ridges and grooves stretching out over the length of the beam and tines.

The left antler under the same number belongs to the same individual and has a similar morphology. Some little differences are: The accessory tine in the left antler is very small. The forward bend of the second and third tine is stronger than they are in the right antler. The browtine and the second and third tine are implanted with less sharp angles to the beam above them. In the left antler the tips of the browtine and of the third, fourth and fifth tine have broken off.

RGM 86 834 (Fig. 3) — The greater part of a right shed antler. The antler has four tines of which the browtine is implanted on the antero-lateral side of the beam. The other three tines are implanted on the anterior side of the beam and all lie in one plane.

The browtine bends at its base a little to the lateral side, but at one-third of its

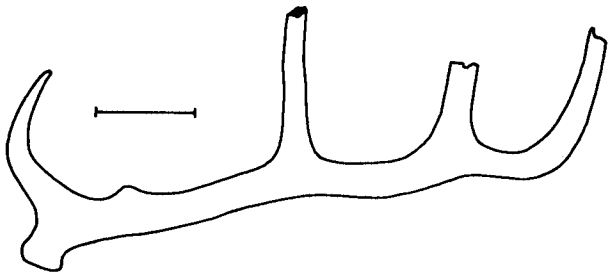

Fig. 4. Right antler of *Eucladoceros tegulensis*, RGM 122 955; lateral view.

length it bends back to the median side. Its length is 33.5 cm. A little above the base of the browtine, at the median side of the browtine there is an accessory tine with a length of 5 cm. This accessory tine passes into a ridge which stretches over the anterior side of the second segment of the beam to the base of the second tine. This ridge makes the angle between the browtine and the second segment of the beam very obtuse.

The second and third tine are implanted with a right angle to the beam and are both very straight but at their tops bend a little to the anterior side. The tops of both the second and third tine have broken off.

At the base of the third tine the beam bends a little to the posterior side but after a short distance it makes a stronger bend back to the anterior side, giving rise to the fourth tine which has broken off a little above its base. The end of the beam is implanted at the posterior side of the base of the fourth tine. It has broken off just above its base. It is probable that the end of the beam has been just a little projection.

RGM 122 955 (Fig. 4) — Incomplete right shed antler of an adult individual. The burr is slightly damaged. The browtine is implanted at the antero-lateral side of the beam. Its form is slightly sigmoid. There is a little accessory tine on the medio-anterior side of the second segment of the beam a few centimetres above the bifurcation of the browtine. The second and third tine have broken off at 17 and 9 cm above their bases, respectively. The fourth tine forms the end of the beam.

The beam is slightly oval in section and rather straight but at the places where the second and third tine are implanted it bends a bit to the anterior side. The second, third and fourth tine all lie in one plane and are all implanted at the anterior side of the beam.

RGM 79 235 (Fig. 5) — A very robust left antler, shed by a fully grown adult individual. This specimen seems to be the most robust specimen collected in the Tegelen area.

The burr is badly damaged, The browtine is not preserved. Halfway the second segment, a short accessory tine is implanted at the medio-anterior side of the beam. The second and third tine are implanted with a nearly right angle on the anterior side of the beam. The fourth and fifth tine are implanted with sharper angles to the beam. All tines have broken off at a little distance above their bases. At the posterior side of the base of the fifth tine their seems to have been a projection, probably forming the end of the beam. The beam is oval in section and tends to become more ovoid going from base to top.

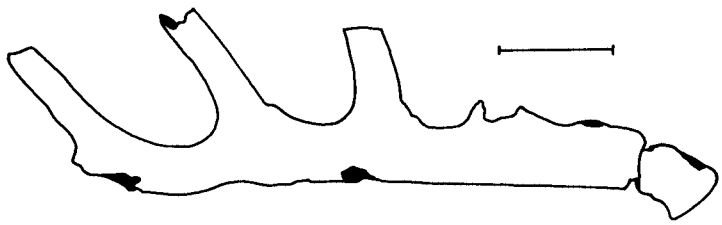

Fig. 5. Left antler of *Eucladoceros tegulensis*, RGM 79 235; lateral view.

RGM 87 407 (Fig. 6) — Part of a right shed antler belonging to a young individual, consisting of a beam with a browtine. It has broken into two pieces. The burr is badly damaged and stands oblique to the first segment of the beam. The browtine is implanted very near to the burr with an obtuse angle to the beam and it has broken off at a little distance above its base.

The beam bends just a little backwards at the place where the browtine is implanted, but proximally it bends back to the anterior. The top of the beam has broken off. The beam is ornamented with small ridges and grooves.

RGM 75 124 (Fig. 7) — The greater part of a left shed antler belonging to a young individual, consisting of a beam with a browtine. It is broken into several pieces.

The browtine is implanted very near to the burr with an angle to the beam

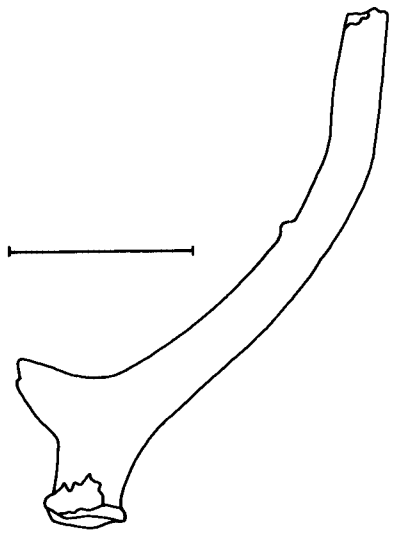

Fig. 6. Right antler of *Eucladoceros tegulensis*, RGM 87 407; lateral view.

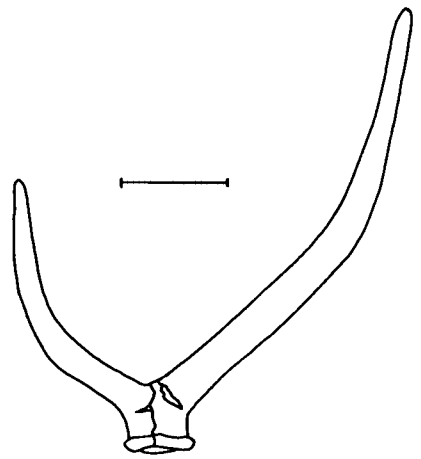

Fig. 7. Left antler of *Eucladoceros tegulensis*, RGM 75 124; lateral view.

above the tine which is just a little obtuse. Halfway from base to top the browtine shows an upward bend. The beam shows the same features as the beam of antler RGM 87 407, except that the bend to the anterior seems to be a little weaker.

Summary of the morphology — The antlers of *E. tegulensis* consist of a beam with three to six tines of which the browtine is implanted near to the burr at the antero-lateral side of the beam with an oblique angle to the beam or, in younger specimens, with a somewhat sharper angle. The other tines are all implanted on the anterior side of the beam and all lie in one plane (like the teeth of a comb).

The burr is nearly round to slightly oval in section and has greater dimensions in elder specimens. The antero-posterior diameter varies from 4 to 8 cm as well as the transverse diameter (see Table 2).

The beam shows a sudden backward bend at the place where the browtine is implanted. Below this bend the beam is round to nearly round in section. Above the bend the beam becomes more oval in section. In elder specimens a ridge, which stretches over the anterior side of the second segment of the beam and of the browtine, is observed. This ridge can amplify the ovalness of the section of the second segment of the beam. On the whole the beam is rather straight, but at the places where the tines are implanted a little kink towards the anterior side can be observed. The end of the beam is formed either by the last tine or by a little projection at the posterior side of the base of the last tine.

In general the browtine is implanted very near to the burr so that the first segment of the beam is very short. The second segment of the beam is in general the longest. The second, third, fourth, and possibly fifth tine are all placed rather near to each other so that the third, fourth and possibly fifth segment are relatively short.

The browtine is implanted on the antero-lateral side of the beam. The basal part of the browtine is set in an antero-lateral direction but at about half of its length it bends inwards so that a sigmoid form of the browtine is the result.

In some specimens, especially those of elder individuals, a small accessory tine is found on the anterior or medio-anterior side of the second segment of the beam or near the base of the browtine.

The second and third tine are both implanted with a right angle to the beam, while the fourth tine is implanted with a somewhat sharper angle to the beam. The tines are rather straight but the tops of the tines usually bend forward and inward. The second tine is a little smaller than the third and fourth tine. In the case that the end of the beam is formed by the last tine this last tine can be much smaller than the other tines.

The total length of the beam varies from 59 to 91 cm in adult specimens. A very young specimen from Tegelen (RGM 28 093) measured a little over 30 cm.

The whole antler has an ornamentation of little ridges and grooves.

Comparisons

The pedicles — In Table 2 the length and the antero-posterior diameter of the pedicle are listed. The pedicles from Tegelen are, like those from St Vallier and Pardines relatively wider than the pedicles from Senèze and Peyrolles.

Tegelen-Senèze — Descriptions of the antlers from Senèze are given by Heintz (1970). The resemblances between the antlers from Tegelen (Te) and those from Senèze (Se) are numerous: total length of the beam; antero-posterior diameter of the burr; length of the segments 1-4; length of the fourth tine; implantation of the first tine on the anterio-lateral side of the beam; implantation of the tines, other than the first tine, on the anterior side of the beam; sudden backward bend at the place where the browtine is implanted; angle of implantation of the browtine; implantation of the second and third tine with a right angle to the beam and of the fourth tine with a somewhat sharper angle to the beam; form of the browtine: the sigmoid form of the browtine of the antlers from Tegelen seems to be a little tempered in comparison with the specimens from Senèze, but still there is a great resemblance; presence of an accessory tine in some specimens on the (medio)anterior side of the second segment of the beam; the end of the beam is in both populations formed either by the last tine or by a little projection at the posterior side of the base of the last tine.

The differences between the antlers from the two populations are: length of the first tine (177-337 mm in Te; 233-480 mm in Se); length of the second tine (181-426 mm in Te; 500-790 mm in Se); length of the third tine (250-547 mm in Te; 500-790 mm in Se); form of the second, third and fourth tine: the antlers from Te have tines which are less curved forwardly and inwardly and less flattened than the tines in the antlers from Se; in the antlers from Tegelen the tines do not show any ramification whereas the tines in the antlers from Senèze sometimes do; number of tines: in Se the number of tines per antler does not exceed four, whilst in Te at least one antler with five tines and another with five or possibly six tines has been found.

Tegelen-Peyrolles — The differences between the antlers from Tegelen and those from Peyrolles are: length of the first (40-120 mm in Te; 25-60 mm in Peyrolles) and second segment (114-412 mm in Te; 132-205 mm in Pe); length of the fourth tine (412-433 mm in Te; 280-310 mm in Pe); form of the end of the beam: the end of the beam in the antlers from Te is formed either by the last tine or by a projection at the posterior side of the base of the last tine while all antlers from Pe end in a very long point (240-330 mm) in which the beam continues beyond the last tine; form of the tines, other than the first tine. The antlers from Tegelen have tines which bend forward while in the antlers from Peyrolles the tines, and especially the fourth tine, bend backward; an accessory tine on the second segment of the beam is absent in all specimens from Peyrolles but present in some specimens from Tegelen.

In other than the characteristics mentioned the antlers from Tegelen and those from Peyrolles are about equal for as far as this can rightly be said on the basis of such small numbers of specimens in especially the population from Peyrolles.

The antlers from St Vallier (SV) — Only five antler fragments have been found in SV. Even though the material is very scanty Viret (1954) stated that the antlers from St Vallier have all essential characteristics of the antlers from Senèze. The only exact information on the antlers from St Vallier comes from two pedicles which seem to differ from the pedicles from Senèze in their length and antero-posterior diameter (Heintz, 1970). The pedicles from Tegelen are comparable with the pedicles from St Vallier.

The antlers from La Puebla de Valverde (PV) — From La Puebla de Valverde

four antler fragments were obtained which seem to belong to one individual. One of these fragments was found to be identical to a part of a fourth tine of an antler found in Senèze (Heintz, 1970).

Discussion and conclusions — Variation in antlers is always very large and caused by a number of factors such as quality of the nutrition, environment, climate, and age of the specimen. As a result, it is hard to distinguish intraspecific variation from interspecific variation. Especially the biometrical features of the antlers tend to vary enormously. So the significance of the biometrical data should not be overestimated.

The morphology of the antlers of the *Eucladoceros* species seem to be variations on one basic form. This makes it hard to decide which morphological features do have a specific significance and which do not. At this point a few remarks will be made on some morphological features described above.

The difference observed between the form of the tines of the antlers from Tegelen and those from Senèze might be of (specific) significance but that is not at all certain. The measure of bendings and flattenings and ramification of the tines are known to vary considerably. Even within the population of Senèze there is considerable variation in these features (Heintz, 1970).

The difference in the form of the end of the beam between the antlers from Tegelen and those from Peyrolles could very well be a real morphological difference separating two species. As the antlers from Senèze show the same morphology of the end of the beam as the antlers from Tegelen this would indicate that the deer from these two localities are conspecific.

In the antlers from Peyrolles the tines are observed to point to the posterior. This is in contrast to the situation known in the specimens from Tegelen and Senèze. This is also a rather striking morphological difference which, together with the difference in the end of the beam, seems to give the antler from Peyrolles a differing appearance from the antlers from Tegelen and Senèze.

This seems to give enough reason to justify a division on the species level between the deer from Tegelen and those from Peyrolles. The differences between the antlers of the deer from Senèze and those from Tegelen seem to be of less significance and not sufficient to justify a division on the species level between the deer from these two populations.

The dentition

Morphology

The upper molars — In *E. tegulensis* the upper molars have a uniform morphology. The protoconus has practically never a protoconal fold. Such a structure is observed in only one specimen of M^2 in which it is very small. In the M^2 sometimes a projection is found on the anterior wing of the protoconus. Very often the posterior wing of the hypoconus shows a projection on its inner side. This projection varies in length and can be absent also. Between the protoconus and the hypoconus an entostyl is found, which varies in length and at its base passes into a cingulum. This cingulum is moderately developed and stretches out over the lingual side of the hypoconus and the lingual and posterior side of the protoconus. The parastyl is well developed (width

= c. 3 mm) but relatively less than in *C. rhenanus*. At its base it bends to the posterior while widening at the same time. The central column of the paraconus is clearly visible. The mesostyl is in general well developed. At its base it widens and backs down to the buccal side. The central column of the metaconus is comparable with the central column of the paraconus. The metastyl is, like the parastyl, well developed and at its base bends to the anterior side.

Of the three upper molars the M^2 is in general the longer one and the M^1 the shorter one. The M^1 is on average wider than long while the M^2 and M^3 are longer than wide. The lingual side of the M^1 is relatively narrower in comparison with the M^2 and M^3.

The upper premolars — The P^4 has on its lingual side only one lobe, which is formed by the protoconus which can be very narrow. The buccal side is formed by the para- and metaconus. The central column of the paraconus lies halfway between the para- and metastyl. The central column of the metaconus lies between the central column of the paraconus and the metastyl. The parastyl is clearly visible as well as the metastyl. The first of these two bends at its base to the posterior while the second bends to the anterior. The central column of the paraconus is very well developed, while the central column of the metaconus is hardly visible. From the internal side of the protoconus a projection emerges which points to the posterior. In at least one specimen of P^4 two projections are visible, the second of which points to the anterior. An unarticulated cingulum is present in most specimens.

In the P^3 the lingual side is formed by the protoconus and hypoconus of which the first is the slightly larger one. On the buccal side the central column of the paraconus lies very near the parastyl. The central column of the metaconus lies about halfway between the central column of the paraconus and the metastyl. The central column of the paraconus and the parastyl meet at their bases. The cingulum is not articulated.

The P^2 is not as wide as the P^3 and P^4. On the lingual side the separation of the protoconus and the hypoconus is complete. An enamel lamel has formed between the two coni. On the buccal side the central column of the paraconus lies very near the parastyl and the bases of these structures meet. The cingulum is, as it is in the P^3, not articulated.

The upper milkmolars — The morphology of the D^4 is very much like the morphology of the M^1 but there are some little differences: the parastyl and metastyl seem to be a little less pronounced in the D^4; the cingulum and entostyl are better developed in the D^4.

The lower molars — The M_3 consists of three lobes. The first of these is formed by the proto- and metaconid. The second is formed by the hypo- and entoconid. The third consists of only one conid. Between the first and second lobe, at the buccal side of the molar, an ectostylid is situated. A cingulum can be present but is in most cases very unarticulated. Para- and metastylid are at the base of the molar less pronounced than they are in the upper part of the molar. The entostylid is at the top of the molar less pronounced than the para- and metastylid. The central columns of the meta- and entoconid are clearly visible at the top of the molar but are less visible near the base of the molar. The third lobe is smaller than the first and second lobe, which

are about equal in size. The lingual side of the third lobe makes an angle with the lingual sides of the first and second lobe.

Between the M_2 and M_1 there seems to be no appreciable difference except that the M_2 is slightly larger than the M_1. Both molars consist of two lobes, both consisting of two conids. Between the two lobes, at the buccal side of the molars, there is an ectostylid which seems to be larger in the M_1 and M_2 than it is in the M_3. The cingulum is variable but in general better developed than it is in the M_3.

The lower premolars — The P_4 is very variable, in particular the metaconid. The metaconid can be developed very strongly in the direction of the entoconid as a result of which the third valley can be shut off. It can also be strongly developed in the direction of the paraconid but the second valley is never shut off entirely. The entoconid is sometimes separated from protoconid whereas in general it is connected with it.

In the P_3 the metaconid is much more uniform than it is in the P_4 and it is not so well developed. The second valley between the para- and metaconid is opened much wider than in the P_4. Parastylid and -conid are grown together in some specimens.

The P_2 is the smaller one of the lower premolars. The metaconid is very small as a result of which the second valley is opened wide. The paraconid is absent in most specimens. The cingulum is absent in all three lower premolars.

The lower milkmolars — The D_4 consists of three lobes of which the first is smaller than the other two. The three lobes are very much like the lobes of the lower molars. On the buccal side of the D_4 between the first and second lobe and between the second and third lobe a little column is found (the protostylid and ectostylid respectively). A cingulum is absent. On the lingual side no accessory tubercles were found.

The morphology of the D_3 is almost identical to the morphology of the P_3. The paraconid seems to be a little better developed. The metaconid can be grown together with the entoconid, so that the first valley is closed. The D_3 is smaller than the P_3.

The D_2 is identical to the P_2: here also the paraconid is absent. The difference between the two lies in their size. The D_2 is the smaller one.

Comparisons — A morphological description of the dentition of *E. senezensis* and of *E. tetraceros* is given by Heintz (1970). These descriptions make clear that these deer have a very uniform dentition. The morphology of the dentition of *E. tegulensis* only confirms this. All morphological forms which appear in the dentition of the large deer from Tegelen were also found in the dentition of *E. senezensis* and *E. tetraceros*.

Biometry — The dimensions of the dentition of *Eucladoceros* from the diverse localities are presented in Diagrams 1-4 and Tables 3-7 and 12-13.

Comparison between Tegelen and St Vallier — The upper molars are on the average longer in Tegelen than they are in St Vallier, only the M^3 is not significantly longer; all three upper molars are significantly wider in Tegelen; the P^4 and P^3 are longer in Tegelen, but the difference is not significant; the P^2 is significantly longer in St Vallier; all three upper premolars are wider in Tegelen, though not significantly so; the M_3 is longer in St Vallier, though not significantly so; the M_2 and M_1 are longer in Tegelen, but the difference is not significant either; the M_3 and M_2 are wider in

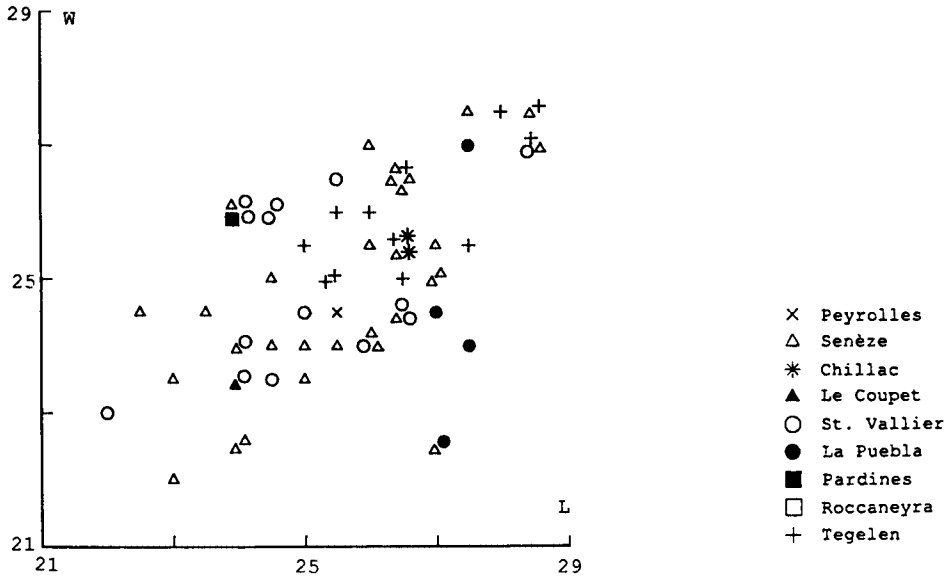

Diagram 1 - Length and width of the second upper molar of *Eucladoceros* from the diverse localities.

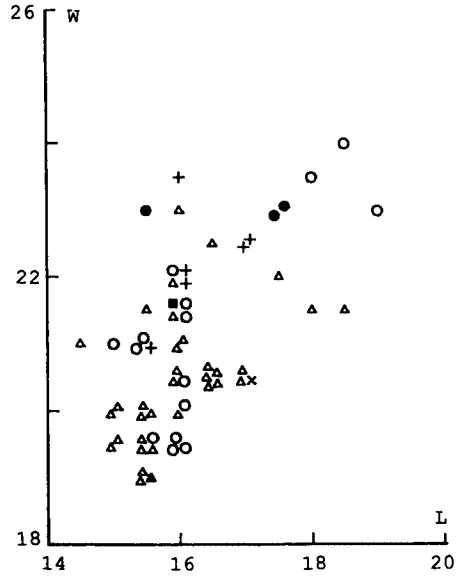

Diagram 2 - Length and width of the fourth upper premolar of *Eucladoceros* from the diverse localities.

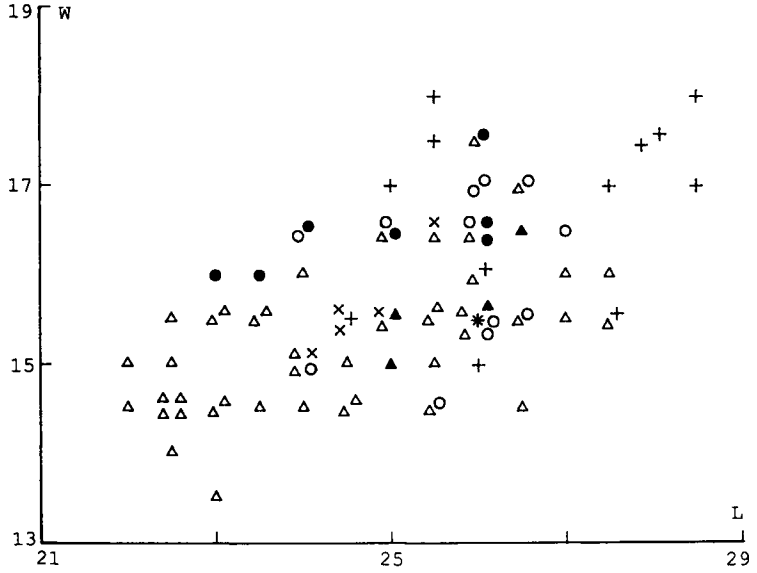

Diagram 3 - Length and width of the second lower molar of *Eucladoceros* from the diverse localities.

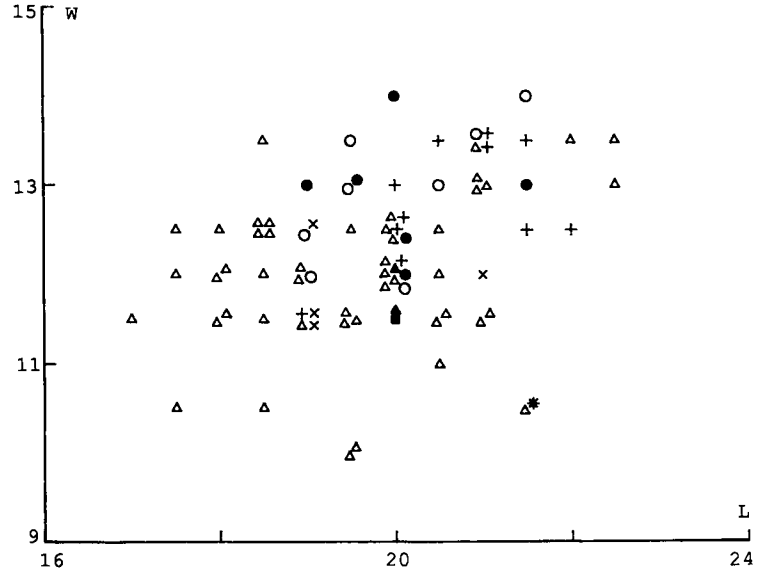

Diagram 4 - Length and width of the fourth lower premolar of *Eucladoceros* from the diverse localities.

Tegelen and the M_1 is wider in St Vallier, but the differences are not significant; the P_4 is longer in Tegelen but the P_3 and P_2 are longer in St Vallier, the differences are not significant; the P_4 is on the average as wide in Tegelen as it is in St Vallier; the P_3 and P_2 are wider in Tegelen, though not significantly so; the M^3, M^1, P^4, P^3, P^2, M_3, M_2, P_3, and P_2 are relatively longer in St Vallier whereas the M^2, M_1 and P_4 are relatively longer in Tegelen.

The minimum in the variation is in nearly two-thirds of the measurements higher in Tegelen (14-24), and in a little less than one-third it is higher in St Vallier (7-24). In about half of the measurements the maximum of the variation is higher in Tegelen (10-24) and in the other half it is higher in St Vallier (11-24). The mean values, however, are in general higher in Tegelen (18-24), but only in four measurements, all concerning the upper molars, the differences are significant (see also Table 8).

Comparison between Tegelen and La Puebla — The M^3 and M^2 are longer in La Puebla, the M^1 is longer in Tegelen, the differences are not significant; the upper molars are wider in Tegelen, the difference is only significant in the case of the M^1; the P^4 and P^3 are longer in Tegelen, the P^2 is longer in La Puebla, the differences are not significant; the P^4 is wider in La Puebla, the P^3 and P^2 are wider in Tegelen, the differences are not significant; the M_3 is longer in La Puebla, though not significantly so; the M_2 and M_1 are longer in Tegelen, in the case of the M_2 the difference is significant; the M_3 and M_2 are wider in Tegelen, the differences are not significant; the M_1 is significantly wider in La Puebla; the P_4 is longer in Tegelen, the P_3 and P_2 are longer in La Puebla, the differences are not significant; the P_4 is equally wide in both populations, the P_3 is wider in La Puebla, the P_2 is wider in Tegelen, the differences are not significant.

The population from La Puebla has in about an equal number of measurements as the population from Tegelen the highest minimum (15-22), the highest maximum (13-22) and the highest mean value (8-22) in the variation of the measurements. In two cases the mean is significantly higher in Tegelen: the width of the M^1 and the length of the M_2, and in one case the mean is significanly higher in La Puebla: the width of the M_1 (see also Table 9).

Comparison between Tegelen and Senèze — All upper molars are on the average longer and wider in Tegelen, the differences are significant in the cases of the length of the M^1 and the width of all upper molars; the P^4 and P^3 are significantly longer in Tegelen, the P^2 is longer in Senèze, but not significantly so; all upper premolars are significantly wider in Tegelen; all lower molars are longer and wider in Tegelen, in the cases of the length of the M_2 and M_1 and the width of the M_3 and M_2 the differences are significant; all lower premolars are longer in Tegelen, but the differences are not significant; all lower premolars are significantly wider in Tegelen; all lower and upper molars and premolars except for the M_1 are relatively longer in Senèze; the M_1 is relatively longer in Tegelen.

The minimum in the variation is in nearly all measurements higher in Tegelen (22-24). The maximum is in one-third of the number of measures higher in Tegelen (8-24), as well as in Senèze (9-24), while in the remaining third it is equal in both populations. The mean values are in general higher in Tegelen (23-24). In seventeen measures, concerning all dental elements, the mean is significantly higher in Tegelen (see also Table 10).

Comparison between Tegelen and Peyrolles — All upper molars are longer and wider in Tegelen, but the difference is only significant in the case of the width of the M^3; the P^4 is longer in Peyrolles, but wider in Tegelen, the differences are not significant; all lower molars and premolars are longer and wider in Tegelen, but the differences are only significant in the cases of the length and width of the M_2 and of the width of the P_4 and P_3; all upper molars, the P^4, the M_3 and all lower premolars are relatively longer in Peyrolles; the M_2 and M_1 are relatively longer in Tegelen.

The minimum is in an equal number of measures higher in both populations (5-14). The maximum and mean values are always higher in Tegelen, but only in a few cases the differences in the mean values between the two populations are significant: the width of the M^3, M_2, P_4 and P_3, and the length of the M_2 (see also Table 11).

Conclusions — As a result of the morphological study it can be stated that *E. tegulensis*, *E. senezensis* and *E. tetraceros* can not be distinguished on the basis of their dental morphology alone.

From the biometrical study on the dentition it appears that *E. tegulensis* from Tegelen and *E. senezensis* from St Vallier and La Puebla are very much alike (see Tables 8 and 9). The differences between the deer from Tegelen and *E. senezensis* from Senèze can easily be recognized (Table 10), but those between the deer from Tegelen and *E. tetraceros* from Peyrolles are much less clear (Table 11). Looking at the differences in the variation of the two populations it can be seen that the deer from Tegelen are in general larger than the deer from Peyrolles (see comparison between Tegelen and Peyrolles).

The post-cranial skeletal elements

Morphology — In comparing descriptions of the post-cranial elements of *E. tegulensis* as given by Kunst (1937) with descriptions of the post-cranial elements of *E. senezensis* and *E. tetraceros* as given by Heintz (1970) no differences were found between these species.

Biometry — The dimensions of the post-cranial elements are presented in the Diagrams 5-8 and Tables 14-25.

Comparison between Tegelen and St Vallier — The minimum in the variation of the measures from Tegelen is in about half of the number of measures (15-34) higher than the minimum in the variation of the measures from St Vallier and in the other half of the number of measures (18-34) the opposite is observed. The maximum is in most measures higher in St Vallier (22-34). Also the mean values are in general higher in St Vallier (26-34) but in only four cases the differences are significant: APD-p of the metacarpus, TD-d of the tibia, TD-d of the astragalus, and APD-d of the metatarsus (see also Table 26).

Comparison between Tegelen and La Puebla — In the material from Tegelen the minimum (16-35), maximum (19-35) and mean values (22-35) are higher than the minimum, maximum and mean values in the material from La Puebla in about half of the number of measurements taken. The mean differs in not one case significantly

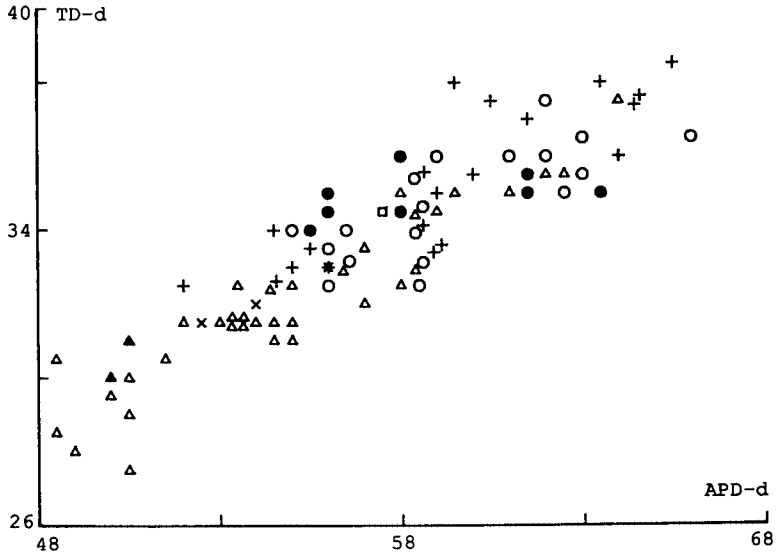

Diagram 5 - APD-d and TD-d of the humerus of *Eucladoceros* from the diverse localities.

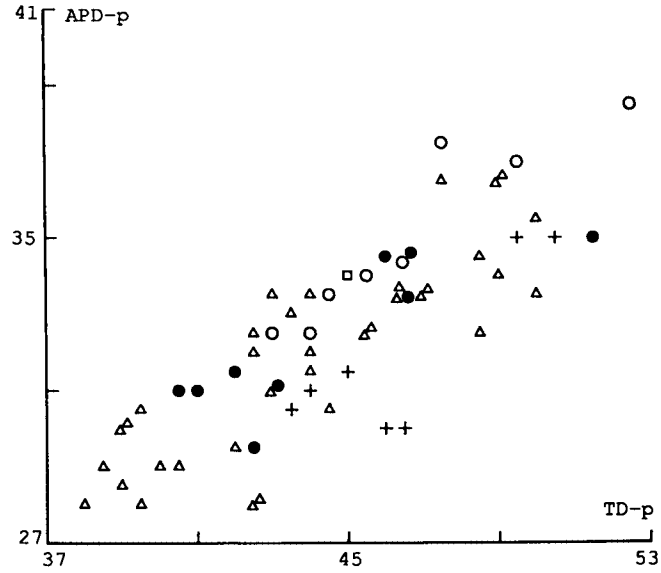

Diagram 6 - TD-p and APD-p of the metacarpus of *Eucladoceros* from the diverse localities.

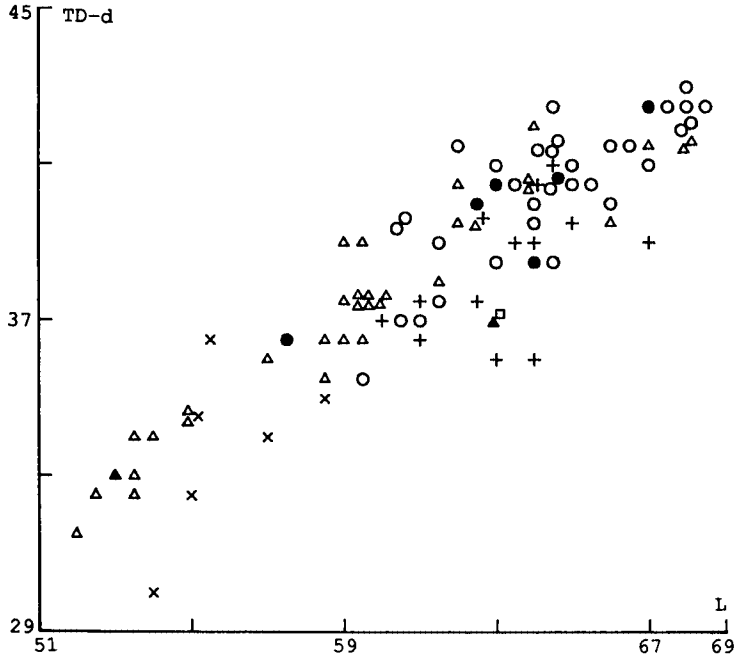

Diagram 7 - Length and TD-d of the astragalus of *Eucladoceros* from the diverse localities.

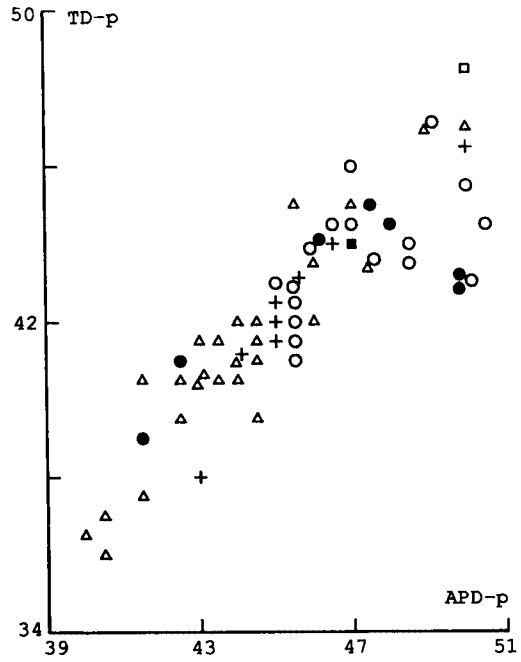

Diagram 8 - APD-p and TD-p of the metatarsus of *Eucladoceros* from the diverse localities.

between the two populations (see Table 27).

Comparison between Tegelen and Senèze — In most of the measurements taken the minimum (36-38) and mean values (34-38) are higher in Tegelen than they are in Senèze. The maximum is in most cases higher in Senèze (22-38) but in some cases it is higher in Tegelen (14-38). The mean is significantly higher in Tegelen in about one-third of the measurements taken (see Table 28).

Comparison between Tegelen and Peyrolles — The material from Peyrolles is very scanty but it can still be observed that the minimum, maximum and mean values are in general lower in Peyrolles than they are in Tegelen. The differences in the mean values between the two populations are nearly all significant (see Table 29).

Conclusions — *E. tegulensis*, *E. senezensis* and *E. tetraceros* do not show any morphological difference in their post-cranial elements.

The measurements taken on the large deer from Tegelen correspond mostly to those taken on *E. senezensis* from St Vallier and La Puebla (Tables 26 and 27). The deer from these three localities differ very little or not at all in size. The deer from Tegelen is slightly larger than *E. senezensis* from Senèze (Table 28) and it is also larger than *E. tetraceros* from Peyrolles (Table 29), which is even a little smaller than the deer from Senèze (Heintz, 1970).

DISCUSSION

The large deer from Tegelen is compared in this study with the deer from St Vallier, La Puebla de Valverde, Senèze, and Peyrolles. The deer from these localities were studied by Heintz (1970) and represent two different species, *Eucladoceros tetraceros* and *E. senezensis*, which both resemble very much *E. tegulensis* from Tegelen. Peyrolles (Dawkins, 1878; Bout & Azzaroli, 1953) is the only locality of *E. tetraceros* in France and Spain. *E. senezensis* was found at Mt Coupet (Heintz, 1970), Chillac (Schaub, 1943; Guth, 1982), Senèze (Deperet & Mayet, 1910-1911; Stehlin, 1923; Schaub, 1943), St Vallier (Viret, 1954), and La Puebla de Valverde (Crusafont Pairo et al., 1964). According to Heintz (1970), this species can be divided into two subspecies: *E. s. senezensis* from Senèze, Mt Coupet and Chillac and *E. s. vireti* from St Vallier and La Puebla. Of the localities mentioned Senèze is the most important one because here numerous remains were found in a very good state of preservation. St Vallier is the most important locality of *E. senezensis vireti*. The deer from La Puebla was identified as *E. senezensis vireti* but in fact it is intermediate between the deer from Senèze and those from St Vallier, being closer related to the latter (Heintz, 1970). The material from Mt Coupet and Chillac gives no, or very little, extra information and is therefore left out of the comparisons. The large deer from Tegelen is not compared with species from localities outside France and Spain, because of the lack of easily accessible data on these species and the lack of time neccesary to gather those data.

Some important differences between *E. tetraceros* from Peyrolles and *E. tegulensis* from Tegelen were brought to light in the study on the antlers. The most important of these differences are found in the morphology of the terminal end of the beam and in the direction of the bendings of the tines. The basic form of the antlers from both populations is similar so that the attribution of both species to the same genus is

justified. The only differences between the teeth and bones of both species are found in the biometrical analysis: *E. tegulensis* is in general larger than *E. tetraceros*.

The antlers from Senèze and those from Tegelen do not show important morphological differences. The attribution of these two groups of deer to the same genus is fully justified and the attribution to the same species, even on the basis of the data on the antlers alone, seems reasonable. However, between the populations from Tegelen and Senèze some differences have been found in the biometrical analysis of the dentition and the post-cranial skeleton. The deer from Tegelen is a little larger than the deer from Senèze. The biometrical differences between the deer from Tegelen and the deer from St Vallier and La Puebla are negligible.

On the basis of this information it can be concluded that *Eucladoceros tegulensis* and *E. senezensis* are one and the same species. *E. senezensis* (Depéret, 1910) thus appears to be a junior synonym of *E. tegulensis* (Dubois, 1904). The differences in size between the deer from St Vallier and La Puebla on the one side and that from Senèze on the other were reason for Heintz (1970) to divide the species *E. senezensis* into two chronosubspecies. According to Heintz size differences between two populations can only occur when these two populations are separated in time or space. As the French localities in this study are relatively close to each other in space a difference in size would suggest a seperation in time (see Heintz, 1970, p. 18). The locality of Tegelen is separated in space from all the French localities. This makes it impossible to decide whether a difference in size is the result of a separation in space or a separation in time. Therefore it does not seem reasonable to identify the deer from Tegelen with one of these two chronosubspecies and, indeed, to make any subdivision of the species *E. tegulensis*.

The deer from Peyrolles belongs to a separate species: *E. tetraceros* Dawkins (1878).

Genus *Cervus* Linnaeus, 1758

Cervus rhenanus Dubois, 1904
Figs. 8-14.

1904a *Cervus (Axis) rhenanus* sp. nov. – Dubois, p. 248, fig. 2.
1904b *Cervus (Axis) rhenanus* sp. nov. – Dubois, p. 219, fig. 2.
1905 *Cervus rhenanus* Dubois – Dubois, p. 613, pl., figs. 6-8.
1938 *Cervus (Rusa) rhenanus* Dubois – van der Vlerk, table.
For complete listing of synonymy see bibliographic analysis

Holotype — Left antler figured by Dubois in 1904, p. 219, fig. 2, same antler figured by Dubois (1905, pl., fig. 6).

Type locality — Tegelen, The Netherlands (Tegelen Clay).

Other localities — La Campine, Belgium (Germonpré, 1983).

Bibliographic analysis — Dubois (1904) introduced the term *Cervus (Axis) rhenanus*

indicating a species of deer of the *Axis* type. This introduction is accompanied by a picture of the type antler but not by any description. Some fossils from the Tegelen area were ascribed by Dubois to *Cervus* (*Axis*) spec.

Dubois (1905) regarded the antler, formerly ascribed to *Cervus* (*Axis*) spec., to be a semi-adult specimen of *C. rhenanus*.

Dubois (1906) assigned *C. rhenanus* to the subgenus *Axis*. Bernsen (1934) reported that *C. rhenanus* was identical to the small deer from Senèze (= *C. philisi* Schaub, 1941) and also to *C. cylindroceros* Dawk., 1878 from Ardé. Bernsen distinguished also a second species of small deer in Tegelen.

Kunst (1937) confirmed the first statement of Bernsen but rejected the second. This *C. cylindroceros* should be assigned to the subgenus *Pseudaxis*, whereas *C. rhenanus* belonged to the subgenus *Rusa*. Kunst denied the presence of a second species of small deer in the Tegelen area.

Schreuder (1945) mentioned one species of small deer for the Tegelen fauna: *C. rhenanus* but did not give any comment on the subject of its relationships to other species of similar deer.

Azzaroli (1953) stated that *C. perolensis* Azzaroli, 1952, *C. rhenanus* and *C. philisi* could not be assigned to any genus known at the time, but that these species do show a great similarity with *Dama nestii nestii* F. M., 1885.

Viret (1954) pointed out the difficulties in separating *C. rhenanus* from *C. philisi*.

Germonpré (1983) considered *C. rhenanus* to be close to *Croitzetoceros ramosus* Croizet & Jobert, 1828 after comparing descriptions of both species.

Azzaroli et al. (1988) stated that *C. philisi* was a junior synonym for *C. rhenanus*.

DESCRIPTION

The antlers

Morphology — In order to illustrate the morphology of the antlers of *Cervus rhenanus* first a description of the holotype will be given, followed by descriptions of some recently found antlers. More descriptions of antlers of *C. rhenanus* are given by Dubois (1906), Bernsen (1930-1934) and Kunst (1937). The biometrical data on the antlers of *C. rhenanus* from Tegelen are presented in Table 30.

Ha 15 777 (Holotype) (Fig. 8) — This antler was first described by Dubois (1905). Description after van den Berg (1986): Unshed left antler. Viewed from the anterior the beam diverges from the sagital plane. The divergence is weak in the lower part of the beam but becomes stronger at the level of the first tine. The divergence stops at the level of the second tine. The third segment of the beam lies approximately parallel with the sagital plane. Viewed from the lateral side the beam shows various bendings. At the level of the first tine the beam bends strongly backwards. The second segment of the beam bends back to the anterior so that the end of the second segment points in approximately the same direction as the first segment of the beam. At the level of the second tine the beam bends backwards again but not as strongly as it does at the level of the first tine. The third segment of the beam is almost straight. The

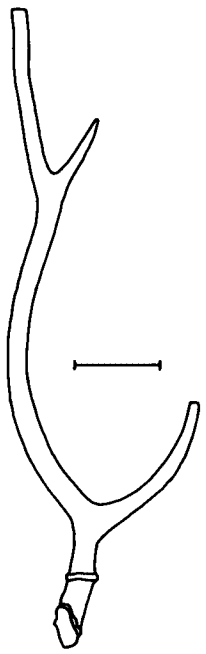

Fig. 8. Left antler of *Cervus rhenanus* (holotype), Ha 15 777; lateral view.

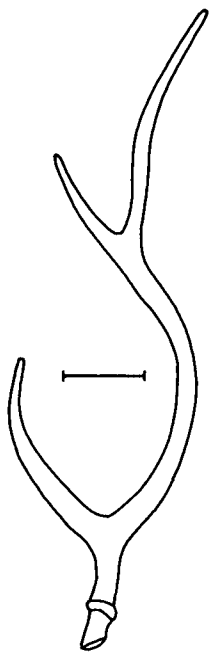

Fig. 9. Right antler of *Cervus rhenanus*, Ha 15 921; lateral view.

beam is round or nearly round in section.

At the anterior side the beam carries two tines. The first tine is implanted at a considerable distance from the burr and has a length of 19 cm. The tine is bended upwards and round in section. The angle between the first tine and the second segment of the beam measures 105°. The second tine has a length of 8.5 cm, is slightly bended upwards and is round in section. The angle between the second tine and the third segment measures 55°.

The first segment of the beam has a length of 8.5 cm, the second has a length of 39 cm, the incomplete third segment has a length of 21 cm and points straight upwards. The total length of the antler measures 68 cm.

Ha 15 921 (Fig. 9) — Description after van den Berg (1986): Unshed right antler, possibly belonging to the same individual to which belongs the holotype also. The morphology of this antler is similar to the morphology of the holotype. Some minor differences will be discussed here.

The bending of the second segment in this antler is more gradual than it is in the holotype. The angle between the first tine and the second segment of the beam measures 100° and the length of this second segment is 33 cm. The length of the second tine is 12.5 cm but the tip has broken off. The second tine lies in approximately the same plane as the first tine. The length of the third segment is 34 cm.

RGM 93 199 (Fig. 10) — Part of a skull bearing two incomplete two-tined antlers. The right antler has a damaged burr and first tine. Most of its second tine is also missing.

The pedicle is c. 4 cm long and 23 mm wide. It diverges slightly from the sagital plane. The burr lies horizontally with a slight angle to the pedicle and to the first segment of the beam which point in the same direction as the pedicle. The first segment of the beam is 44 mm long. The second segment of the beam has a length of 23 cm. At its base it bends slightly to the posterior and halfway its total length it bends back forwards again. At the same time it bends to the lateral side so that the upper part of the second segment points slightly forwards and strongly outwards making an angle of c. 40° with the sagital plane. At the bifurcation of the second tine the beam bends inwards and backwards so that the third segment of the beam points upwards and backwards. The beam is round in cross section.

The first tine is implanted at a little distance above the burr and points in an antero-lateral and upward direction. The angle between the first tine and the beam above the first tine measures 70°. The tip of the first tine is broken off. The second tine is implanted with an angle of c. 80° to the third segment of the beam. It is broken off just above its base. Both tines are about round in cross section.

The left antler looks a lot like the right antler, but differs in the following respects: the second segment of the beam is longer (its length measures 24 cm) than it

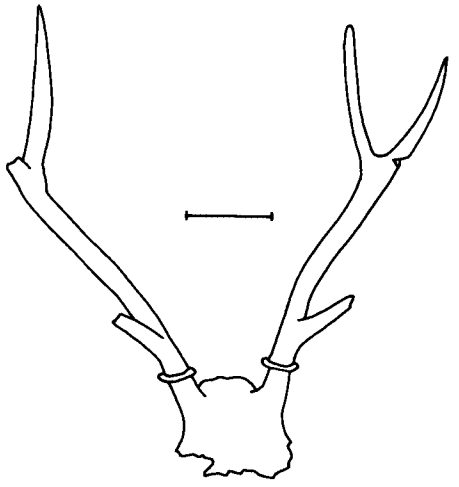

Fig. 10. Skullcap with left and right antler of *Cervus rhenanus*, RGM 93 199; frontal view.

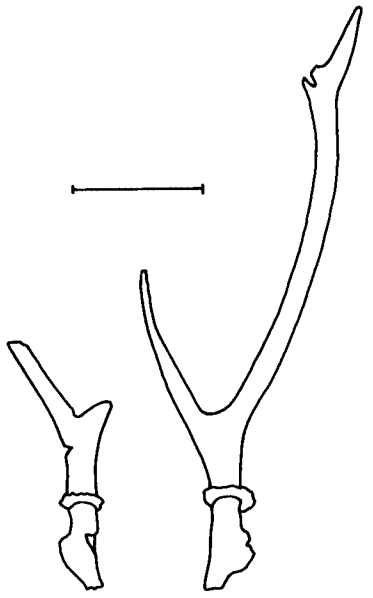

Fig. 11. Left and right antler of *Cervus rhenanus*, RGM 86 968; lateral view.

is in the right antler and it bends at its top a little more to the anterior, the third segment bends more backwards than it does in the right antler; both the first tine and second tine are implanted with an angle of 75° to the beam above the respective tines, the second tine is complete and has a length of 13.5 cm, making a slight upward bend.

RGM 86 968 (Fig. 11) — Description after van den Berg (1986): Right and left unshed antlers. The right antler is complete except for the second tine. The pedicle is 2 cm long and 23 mm wide. The burr is strongly marked and, viewed from the anterior side, makes an oblique angle with the pedicle. The first segment of the beam is set in the same direction as the pedicle. Its length is 5.5 cm. At the bifurcation of the first tine the beam makes a slight backward and outward bend. The second segment of the beam itself bends back forward again at the same time bending back a bit to the median. The third segment of the beam is rather short and points upwards and slightly backwards.

The first tine is implanted with a sharp angle (65°) to the second segment. It is 13 cm long and rather straight but at the tip bends slightly upwards. The second tine is implanted with a sharp angle (65°) to the third segment of the beam and has broken off directly above its base.

Of the left antler only the lower part has been preserved. The pedicle is damaged. Its length measures 2.5 cm. The first segment of the beam is nearly 6.5 cm long. The first tine is implanted with an angle of about 60° to the second segment of the beam which has broken off at a little distance above the bifurcation of the first tine. The first tine has broken off at a distance of 8 cm above its base.

RGM 86 837 (Fig. 12) — Description after van den Berg (1986): Left and right incomplete shed antlers. The burr of the right antler is round in section and 44 mm wide. The first tine is implanted at nearly 6 cm above the burr with an angle of 85° to

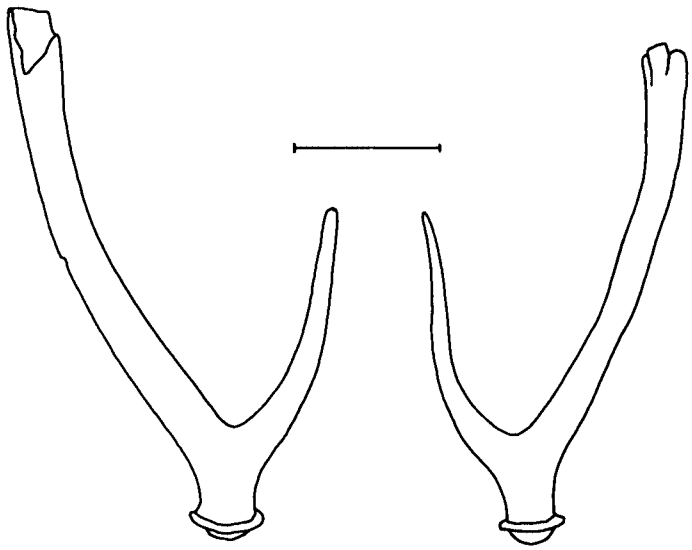

Fig. 12. Left and right antler of *Cervus rhenanus*, RGM 86 837; lateral view.

the second segment of the beam. The first tine is over 16 cm long and has a slightly sigmoid form. Of the second segment of the beam the lower 29 cm have been preserved. At its top the beam widens a little; possibly the beam has broken off just below the bifurcation of the second tine. The beam is round in section, except for the upper part of the second segment which is slightly oval in section.

The left antler has the same morphology as the right antler. A minor difference can be found in the angle between the first tine and the second segment of the beam, which measures 80° in the left antler.

RGM 53 089 (Fig. 13) — Incomplete unshed left antler belonging to a young individual. The pedicle is relatively long and narrow. The burr is slightly damaged, 3.5 cm wide and round in section. The first segment of the beam is damaged and very long (over 9 cm). The first tine is short (5 cm) and is implanted with a very sharp angle (40°) to the beam above the tine. The beam above the first tine is 17 cm long, the top having broken off. Its lower part is straight but at a distance of 11 cm above the bifurcation of the first tine it bends slightly forwards. Just above this bend it has broken off.

Ha 15 828 (Fig. 14) — Description after van den Berg (1986): Skullcap of a young individual carrying two spikes, of which the right one has broken off at some distance above its base.

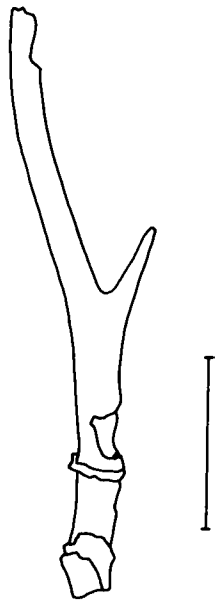

Fig. 13. Left antler of *Cervus rhenanus*, RGM 53 089; lateral view.

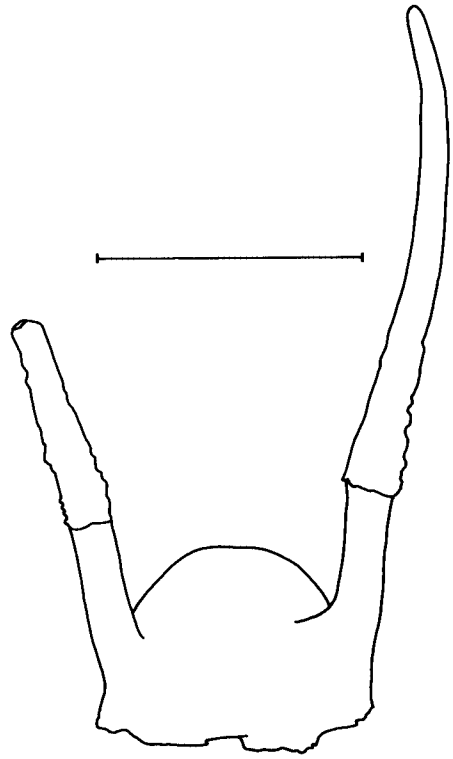

Fig. 14. Skullcap with left and right antler of *Cervus rhenanus*, Ha 15 828; frontal view.

The left spike bends slightly inwards and is round in section. At a distance of 1.5 cm above the spot where it breaks when it is shed the surface shows grooves and blotches. At this spot the diameter of the spike is largest: 20 mm. Going to the top of the spike the diameter becomes less and the surface becomes smoother. The length of the spike is 18 cm. The pedicle is relatively long and narrow. The right spike has the same morphology as the left spike for what its lower part is concerned.

Comparisons

Tegelen-Senèze — Comparing the descriptions of the antlers of *C. rhenanus* with those of *C. philisi* from Senèze as given by Heintz (1970) there seems to be no real morphological difference between the antlers of both species, but for the length of the first tine which seems to be longer in Senèze.

Tegelen-St Vallier — There seems to be no real difference in morphology between the antlers from Tegelen and those from St Vallier. There might be, however, a difference between the two populations in the length of the second segment of the beam which seems to be longer in Tegelen.

Tegelen-Peyrolles — Because the morphology of the antlers belonging to *C. perolensis* is only poorly known (Heintz, 1970) no definite morphological distinction between these and the antlers belonging to *C. rhenanus* can be made as yet. There seem to be some biometrical differences between the antlers from both populations: the angle between the first tine and the second segment of the beam seems to be sharper in the antlers from Tegelen, and the length of the pedicle in relation with its width seems to be larger in Tegelen.

Tegelen-Vialette and Etouaires — Heintz (1970) described the differences between the antlers of *C. pardinensis* from Vialette and Etouaires and the antlers of *C. philisi*. These differences are the relatively straight beam (in lateral and front view) and the relatively short and straight first tine in the antlers from Vialette and Etouaires. These differences resemble the differences between the antlers of *C. pardinensis* and the antlers of *C. rhenanus* with due observance of the restriction as noted by Heintz (1970) that there are very few antlers known which belong to *C. pardinensis*.

Conclusions — After comparison with descriptions given by Heintz (1970) it becomes clear that the antlers of *C. rhenanus* from Tegelen are identical to those of *C. philisi* from Senèze and St Vallier and possibly to those of *C. perolensis* from Peyrolles. Between the antlers from Tegelen and those of *C. pardinensis* there seem to be small morphological differences.

From this it follows that no specific distinction between the small deer from Tegelen and those from Senèze and St Vallier can be made on the basis of the data on the antlers alone. The relationships between the deer from Tegelen and those from Peyrolles and those from Vialette and Etouaires remain not altogether clear.

The dentition

Morphology

The upper molars— In most unworn upper molars a protoconal fold is found but as the wearing down proceeds this protoconal fold tends to disappear. A projection

on the inner side of the anterior wing of the protoconus is found in few specimens and is in general very small. The projection on the inner side of the posterior wing of the hypoconus is uniform and larger than the just mentioned projection on the inner side of the protoconus. The endostyl is allways well developed. The lingual side of the upper molars shows a faint cingulum, which is highly variable. The parastyl is strongly developed and at its base meets with the central column of the paraconus, which is less prominent and a little wider than the parastyl. The central column of the paraconus widens towards its base and leans over to the posterior side. The mesostyl is the most protruding element at the buccal side of the molars. It widens a little towards its base. The central column of the metaconus is relatively faint and narrow. The metastyl is variable, it can be prominent or largely reduced.

Of all three upper molars the M^2 is the wider one. Its two lobes are very similar. In the M^3 the anterior lobe is smaller than the posterior one.

The upper premolars — The crown of the P^4 is nearly symmetrical. The parastyl is very prominent whereas the metastyl is less developed. The central column of the paraconus lies halfway between the para- and metastyl. Paraconus and parastyl converge towards the base of the crown but do not meet. The lingual side of the P^4 consists of just one lobe which is formed by the protoconus. In most specimens an unarticulated cingulum can be seen.

In the P^3 the parastyl is rather weak and converges in the direction of the central column of the paraconus towards the base of the crown. The distance between the metastyl and the central column of the paraconus is always larger than the distance between the parastyl and the central column. The lingual side of the P^3 has two lobes.

The P^2 is similar to the P^3 but is more asymmetrical; the posterior side is much wider than the anterior side. At the lingual side the two lobes stand wider apart than they do in the P^3.

The upper milkmolars — In the D^4 the para- and mesostyl are rather prominent. A protoconal fold has not been found. Apart from these characteristics the D^4 does not differ morphologically from the M^1. However the D^4 is a little smaller than the M^1.

The lower molars — In the M_3 the parastylid is unarticulated. The central column of the metaconid is well developed and widens towards its base. The metastylid is very articulated and partly covers the entoconid. The central column of the entoconid is less well developed than the central column of the metaconid. The entostylid is variable; sometimes it clearly separates the second lobe from the third lobe, sometimes it is hardly visible resulting in a gradual transition from the second to the third lobe at the lingual side of the molar. At the buccal side of the M_3 between the proto- and hypoconid an ectostylid can be found, which is well developed. Between the hypoconid and the third lobe a tubercle can be found also, but this tubercle is always smaller than the ectostylid. The cingulum is faint at the buccal side of the molar but can form a strong anterior fold at the anterior side of the protoconid.

The M_2 and M_1 both consist of only two lobes. These two lobes fit the description of the first two lobes of the M_3. The M_1 is in general smaller than the M_2. The anterior lobe of the M_1 is relatively narrow in comparison with the anterior lobe of the M_2 and M_3. In all three lower molars sometimes a rudiment of the palaeomeryx fold can be observed.

The lower premolars — The P_4 has a very complex morphology. The entostylid is small. The entoconid is rather wide. The metaconid is variable. It is extended towards the entoconid as well as towards the paraconid. The paraconid can be grown together with the parastylid shutting off the first valley. The protoconid consists of a central column, an anterior wing which is connected with the bucco-anterior conid, a posterior wing which is connected with the metaconid, and a palaeomeryx fold which is connected with the hypoconid.

The P_3 looks a lot like the P_4 but it is smaller in size and shows a reduction of the paraconid. The metaconid is reduced also: it shows no extension in the direction of the paraconid.

The paraconid lacks in the P_2 which, as a result of this, shows only three valleys. The first of these is very shallow. The entoconid and entostylid are very small. The P_2 is the smaller one of the lower premolars.

The lower milkmolars — The D_4 consists of three molariform lobes, all three consisting of two conids. Of these three lobes the anterior one is the smaller one and the posterior one the larger. An ectostylid is always present in the D_4, as well as a protostylid, which is smaller than the ectostylid.

The D_3 is almost identical to the P_3. The paraconid and parastylid may be fused thus forming a ridge. The D_3 is smaller than the P_3.

In the D_2 the paraconid is always absent. The D_2 can be distinguished from the P_2 by its smaller size.

Comparisons — Comparing these descriptions with descriptions of the dentition of *C. philisi* and *C. perolensis*, as given by Heintz (1970), it becomes clear that there are no morphological differences between the dentitions of *C. rhenanus*, *C. philisi* and *C. perolensis*.

Between the dentitions of *C. rhenanus* from Tegelen an *C. pardinensis* from Vialette and Etouaires a morphological difference has been found. The last mentioned species has upper molars characterised by a very pronounced, gutter shaped, cingulum. The P^4 also has such a cingulum though less pronounced (Heintz, 1970). Such a cingulum has never been found in the upper molars and P^4 of *C. rhenanus*, nor in those of *C. philisi* and *C. perolensis*.

Biometry — The biometrical data on the dentition of *Cervus* from the various localities are presented in Diagrams 9-12 and Tables 31-36 and 40 and 41.

Comparison between Tegelen and St Vallier — The upper dental segments P^2-M^3, M^1-M^3 and P^2-P^4 are on the average longer in Tegelen than they are in St Vallier, but the differences are never significant; the ratio between the total upper premolar length (P^2-P^4) and the total upper molar length (M^1-M^3) is higher in Tegelen, but again the difference is not significant; the upper molars are on average longer in Tegelen, but the differences are not significant; the M^1 and M^3 are wider in Tegelen, the differences are not significant; the M^2 is wider in St Vallier, but not significantly so; the P^4 is significantly longer in Tegelen; the P^3 and P^2 are longer in St Vallier, but only in the case of the P^2 the difference is significant; all upper premolars are wider in Tegelen, only in the case of the P^3 the difference is significant; the total lower dental length (P_2-

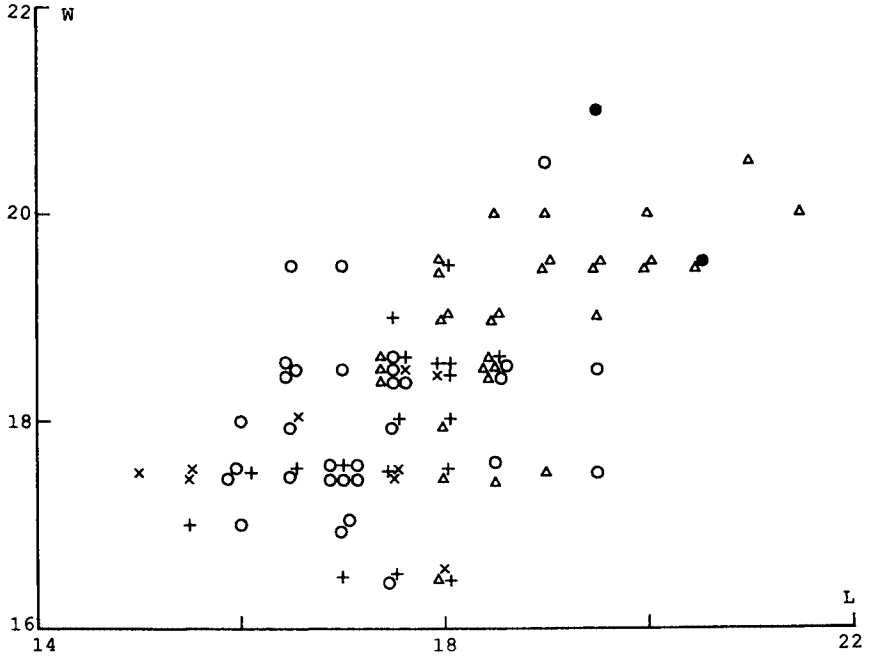

Diagram 9 - Length and width of the second upper molar of *Cervus* from the diverse localities.

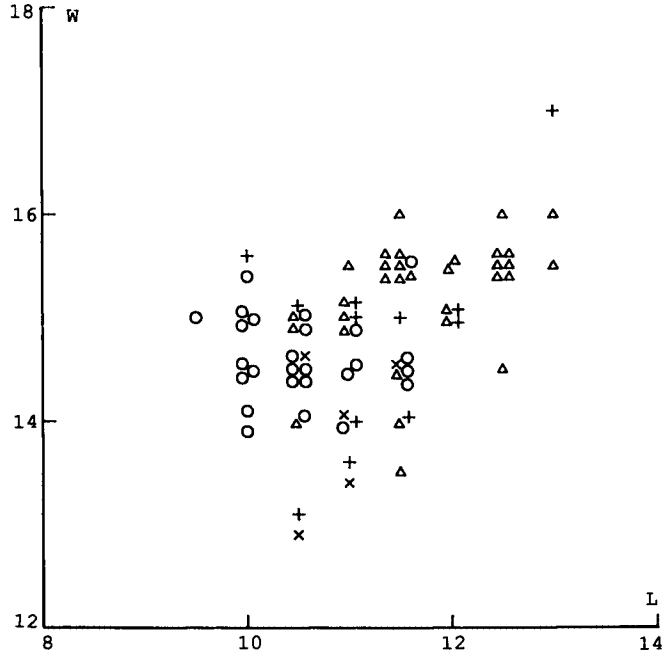

Diagram 10 - Length and width of the fourth upper premolar of *Cervus* from the diverse localities.

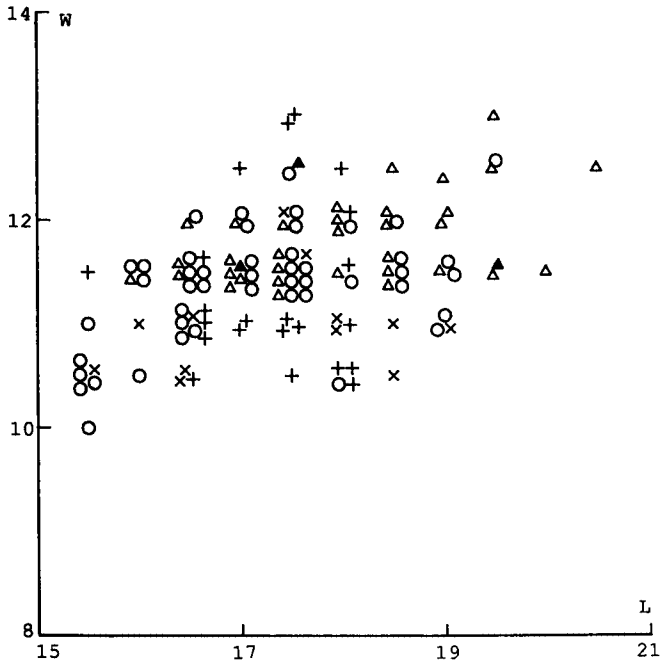

Diagram 11 - Length and width of the second lower molar of *Cervus* from the diverse localities.

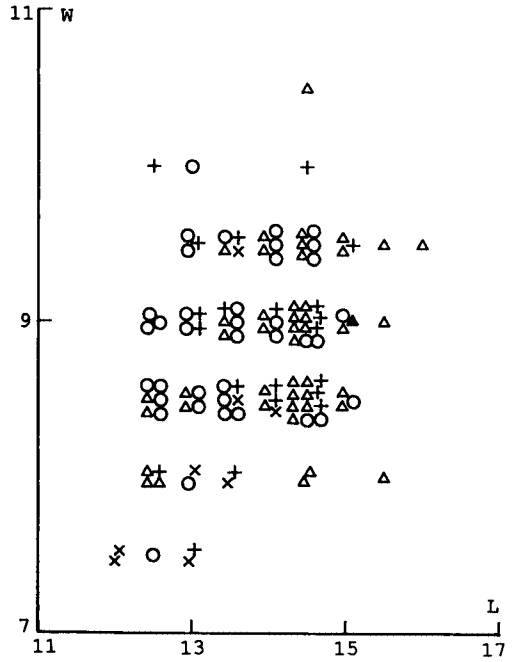

Diagram 12 - Length and width of the fourth lower premolar of *Cervus* from the diverse localities.

M_3) and the total lower molar length (M_1-M_3) are slightly, but not significantly, larger in St Vallier; the total lower premolar length (P_2-P_4) and the ratio between P_2-P_4 and M_1-M_3 are larger in Tegelen, but the differences are not significant; the M_3 is longer, though not significantly, in St Vallier; the M_2 and M_1 are longer in Tegelen, the differences are not significant; the M_3 and M_2 are wider in Tegelen and the M_1 is wider in St Vallier, but the differences are never significant; the P_4 is significantly longer in Tegelen; the P_3 is equally long in both populations; the P_2 is significantly longer in St Vallier; the P_4 is equally wide in both populations; the P_3 and P_2 are significantly wider in St Vallier; the M^3, P^3, P^2, M_3, and P_2 are relatively longer in St Vallier, whereas the M^2, M^1, P^4, M_2, M_1, P_4, and P_3 are relatively longer in Tegelen.

In nearly two-thirds of the measurements taken the minimum is higher in Tegelen (18-30) and in one-third it is higher in St Vallier (11-30). In two-thirds of the measurements the maximum in the variation is higher in St Vallier (22-30). In the population from Tegelen the mean values are highest in two-thirds of the measurements (18-30). In only three cases the difference is significant: length of the P^4 and P_4 and width of the P^3. In one-third of the measures the mean is higher in St Vallier (10-30). Here in four cases is the difference significant: length of P^2 and P_2 and width of P_3 and P_2 (see Table 37).

Comparison between Tegelen and Senèze — The upper dental segments are on the average longer in Senèze, only in the case of the M^1-M^3 the difference is significant; the ratio between P^2-P^4 and M^1-M^3 is higher in Tegelen, though not significantly so; the upper molars are significantly longer in Senèze; the M^3 is wider in Senèze, but the difference is not significant; the M^2 and M^1 are significantly wider in Senèze; the upper premolars are significantly longer in Senèze; the P^4 and P^2 are wider in Senèze, but only the P^4 is significantly wider; the P^3 is significantly wider in Tegelen; the lower dental segments are longer in Senèze, in the cases of the P_2-M_3 and the M_1-M_3 the difference is significant; the ratio between P_2-P_4 and M_1-M_3 is significantly longer in Tegelen; all three lower molars are significantly longer and wider in Senèze; all three lower premolars are significantly longer in Senèze; all three lower premolars are wider in Senèze but only the P_2 is significantly wider; all teeth, except for the M_1, are relatively longer in Senèze.

The minimum (24-30), maximum (26-30) and mean values (29-30) are in most cases higher in Senèze than they are in Tegelen, most of the differences in the mean values between the two populations are significant (see Table 38).

Comparison between Tegelen and Peyrolles — The P^2-M^3 and P^2-P^4 are on average longer in Tegelen, in the case of the P^2-P^4 the difference is significant; the M^1-M^3 is longer in Peyrolles, the difference is not significant; the ratio between P^2-P^4 and M^1-M^3 is higher in Tegelen, the difference is not significant; the M^3 is equally long in both populations; the M^2 is longer in Tegelen, but not significantly so; the M^1 is longer in Peyrolles, but the difference is not significant; the M^3 and M^2 are wider in Tegelen, the difference is not significant; the M^1 is equally wide in both populations; all upper premolars are longer in Tegelen, the difference is never significant; all upper premolars are wider in Tegelen, the difference is only significant for the P^3; the lower dental segments are longer in Tegelen, the difference is just significant in the P_2-P_4; the ratio between P_2-P_4 and M_1-M_3 is significantly larger in Tegelen; the M_3 and M_2 are longer

in Peyrolles, but only the M_3 significantly so: the M_1 is longer in Tegelen, the difference is not significant; all lower molars are wider in Tegelen, but the difference is never significant; all lower premolars are longer in Tegelen, but only in the case of the P_4 the difference is significant; both the P_4 and P_3 are significantly wider in Tegelen; the P_2 is wider in Peyrolles, but the difference is not significant; except for the M^2, M_1 and P_2 all teeth are relatively longer in Peyrolles.

In one-third (10-29) of the measurements the minimum is higher in Tegelen than it is in Peyrolles. The opposite is the case in half the number of measurements (16-29). The maximum is higher in Tegelen in two-thirds of the measurements (20-29). The mean values are in three-fourths of the measurements (22-29) higher in Tegelen. In six cases the mean values are significantly higher in Tegelen: total length of the upper and of the lower premolars, length of the P_4 and breadth of the P^3, P_4 and P_3. Only the length of the M_3 is significantly larger in Peyrolles (see Table 39).

Conclusions — From the morphological description of the teeth of *C. rhenanus* it becomes apparent that there are neither any morphological differences between the teeth of *C. rhenanus* from Tegelen and those of *C. philisi* from Senèze and St Vallier, nor any between *C. rhenanus* and *C. perolensis* from Peyrolles. But there is an important difference between the teeth of *C. rhenanus* and those of *C. pardinensis*.

On the basis of the biometrical data it can be concluded that there is no important difference between *C. rhenanus* and *C. philisi valliensis* from St Vallier. The significant differences which have been signaled in the comparison between the two populations only concern the length and width of the premolars (see Table 37).

C. rhenanus from Tegelen, like *C. philisi valliensis* from St Vallier (Heintz, 1970), has shorter dental segments than *C. philisi philisi* from Senèze and also has shorter and narrower teeth (Table 38).

C. rhenanus from Tegelen has longer dental segments (difference is significant in three out of six cases) than *C. perolensis* from Peyrolles. No other important differences are signaled (see Table 39).

C. rhenanus seems to have, like *C. philisi valliensis* (Heintz, 1970), relatively shorter teeth than both *C. philisi philisi* and *C. perolensis* (see Tables 40 and 41).

The post-cranial skeletal elements

Morphology — Morphological descriptions of several post-cranial elements of *C. rhenanus* from Tegelen are given by Kunst (1937). After comparison with descriptions of post-cranial elements of *C. philisi*, as given by Heintz (1970), it appeared that the post-cranial elements of these two species could not be distinguished from each other. Neither was any difference found between these two species and *C. perolensis* and *C. pardinensis*.

Biometry — The dimensions of the post-cranial elements of *Cervus* from the diverse localities are presented in Diagrams 13-16 and Tables 42-54.

Comparison between Tegelen and St Vallier — In the material from St Vallier the minimum of the variation of the measures taken is in three-quarters of the number of measures (31-43) higher than it is in Tegelen. The maximum and mean values are

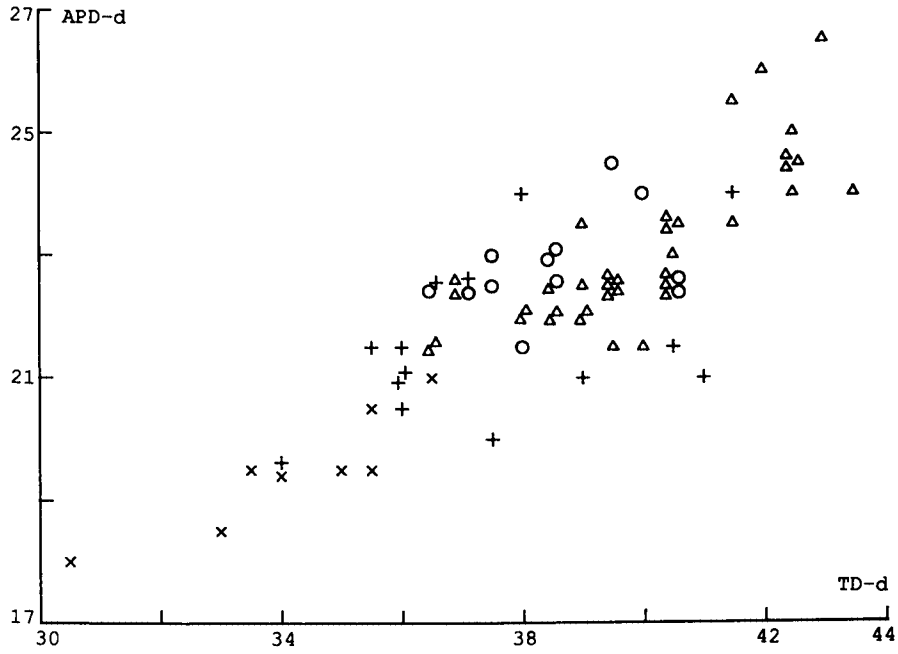

Diagram 13 - TD-d and APD-d of the humerus of *Cervus* from the diverse localities.

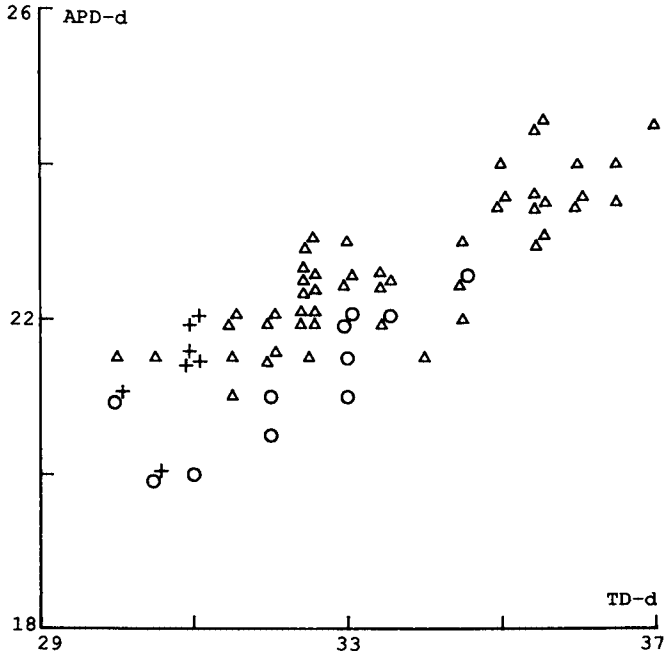

Diagram 14 - TD-d and APD-d of the metacarpus of *Cervus* from the diverse localities

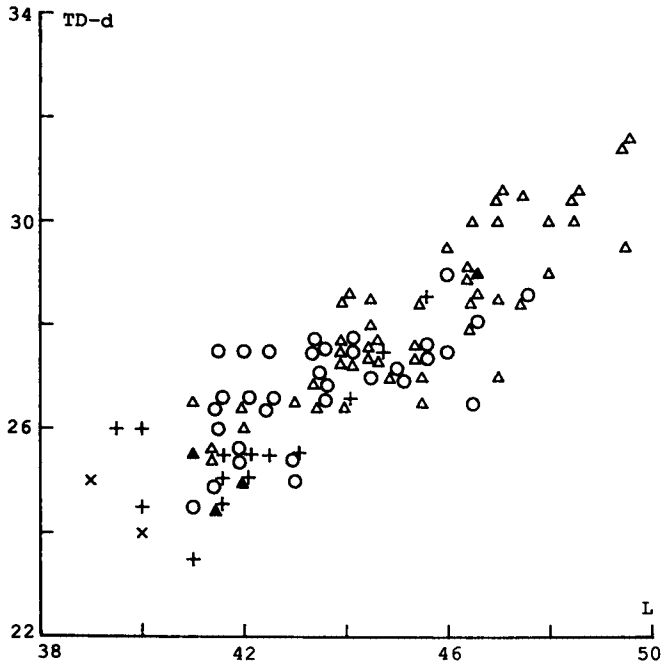

Diagram 15 - Length and TD-d of the astragalus of *Cervus* from the diverse localities.

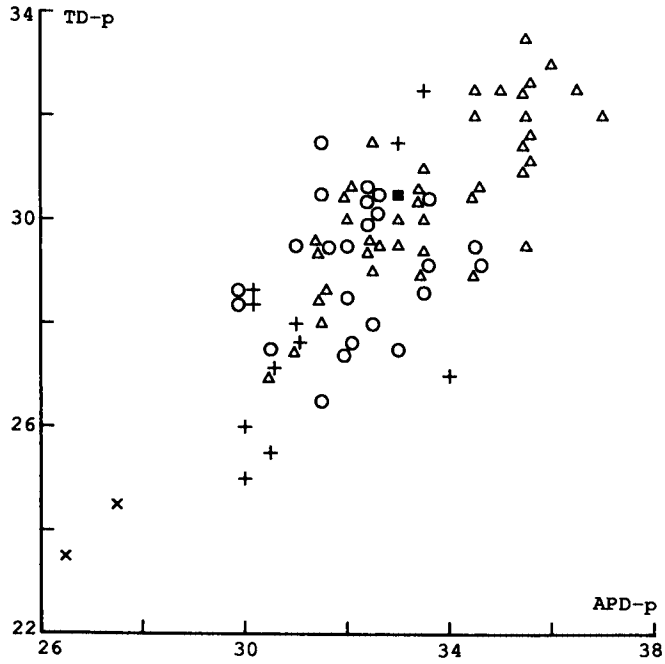

Diagram 16 - APD-p and TD-p of the metatarsus of *Cervus* from the diverse localities.

in most cases (35-43) higher in St Vallier than they are in Tegelen. In 20 measures the mean is significantly higher in St Vallier. The opposite is just once the case. The significance has in most cases a low level of probability (see Table 55).

Comparison between Tegelen and Senèze — The minimum (37-46), maximum (45-46) and mean values (45-46) are in most cases higher in Senèze. In all but eight of the measures the difference in the mean values between the two populations is significant. Here the significance has in most cases a high level of probability (see Table 56).

Comparison between Tegelen and Peyrolles — In most cases the minimum is higher in Tegelen (9-14). The same goes for the maximum (14-14) and mean (13-14) values. The mean differs between the two populations significantly in 11 of the measures (see Table 57).

Conclusions — From the biometrical study on the post-cranial elements of *C. rhenanus* it appears that this species is slightly smaller than *C. philisi valliensis* from St Vallier. Both the deer from Tegelen and St Vallier are smaller than *C. philisi philisi* from Senèze and larger than *C. perolensis* from Peyrolles.

DISCUSSION

In this study the small deer from Tegelen, *Cervus rhenanus*, is compared to three similar species from Early Pleistocene localities in France. Similar deer from other localities are omitted from this study for the same reasons as given in the discussion and conclusion on *E. tegulensis*. The first species in these comparisons is *C. pardinensis* from Vialette (Mayet & Roman, 1923) and Etouaires (Croizet & Jobert, 1928). This deer is regarded by Heintz (1970) to be of an Early Villafranchian age. The second species is *C. philisi*. This species was divided into two subspecies. The elder of these two, *C. p. valliensis*, is found at St Vallier (Viret, 1954) and is supposed to be restricted to the Middle Villafranchian. The second subspecies is *C. p. philisi* which is found abundantly at Senèze (Schaub, 1941) and is supposed to be restricted to the lower part of the Upper Villafranchian. This subspecies is larger than the first mentioned subspecies (Heintz, 1970). There are some important differences between *C. pardinensis* and *C. philisi* of which the most important is the cingulum in the upper molars and $P^4$of the first species. The third species in the comparisons is *C. perolensis* from Peyrolles (Bout & Azzaroli, 1953) and dates from the upper part of the Upper Villafranchian. This deer seems to be morphologically identical to *C. philisi* but is slightly smaller in size (Heintz, 1970).

Comparing *C. pardinensis* with *C. rhenanus* we find enough differences in the morphology of the antlers and the dentition between these deer to justify the assignation of these deer to two different species.

Between *C rhenanus* and *C. philisi* no morphological differences have been found and the biometrical differences appear to be very small. Therefore it seems reasonable to assign these deer to one and the same species. The size differences between the deer from Tegelen and the deer from Senèze are statistically significant but don't in themselves justify a division on the subspecies level as was proposed by Heintz (1970) for *Cervus philisi* from Senèze and St Vallier (see Discussion on *E. tegulensis*).

Between *C. rhenanus* from Tegelen and *C. perolensis* from Peyrolles there seems to be no, or very little, morphological difference. The biometrical differences between the two species seem to be small. Because the material from Peyrolles is very scanty, it is not entirely clear how the data are to be properly interpreted but it seems reasonable to appoint these deer to one and the same species.

It can now be concluded that both names *Cervus philisi* Schaub (1941) and *C. perolensis* Bout & Azzaroli (1953) are junior synonyms of *C. rhenanus* Dubois (1904) and should accordingly be renamed *Cervus rhenanus*.

Conclusions

In earlier years a considerable number of Villafranchian Cervidae has been described. One of the most striking characteristics of these Villafranchian cervids is their restricted dispersion through space (and time). Most of these cervids are restricted to one or two countries and a small period of time. This can be considered to be very strange because all Recent deer are much wider dispersed and there is no reason to assume that the Villafranchian deer would not be equally widely dispersed.

Heintz (1967) was one of the first to question this extraordinary character by showing the homogeneity of the Villafranchian deer for the whole of Europe.

From the present study it has been concluded that the Villafranchian deer from Tegelen are the same as certain Villafranchian deer from France and Spain. This shows that the homogeneity of the Villafranchian deer as pointed out by Heintz follows in this particular case from the conspecificness of these deer. Further taxonomic studies of other Villafranchian deer from European localities are neccessary to unravel the relationships between the Villafranchian cervids.

References

Azzaroli, A., 1953. The deer of the Weybourn Crag and Forest Bed of Norfolk. — Bull. Brit. Mus. (Nat. Hist.) Geol., 2, 1: 4-96.

Azzaroli, A., C. De Guilli, G. Ficcarelli & D. Torre, 1988. Late Pliocene to early mid-Pleistocene mammals in Eurasia: faunal succession and dispersal events. — Palaeogeogr., Palaeoecol., Palaeoclimatol., 66: 77-100.

Berg, R.A. van den, 1986. *Cervus rhenanus* Dubois, 1904 (Mammalia, Cervidae) uit de klei van Tegelen: een onderzoek naar het voorkomen van synoniemen buiten Nederland. — Inst. Aardwet. Utrecht Univ., unpubl. report.

Bernsen, J.J.A., 1930-1934. Eine Revision der fossilen Saugetierfauna aus den Tonen von Tegelen. — Natuurhist. Maandbl., 19: 146-153; 20: 25-31, 67-71, 104-108, 153-158; 21: 20-26, 78-81, 96; 22: 136-138; 23: 38-46, 71-77, 83-86.

Bout, R., & A. Azzaroli, 1953. Stratigraphie et faune du Creux de Peyrolles. — Ann. Paléont., 38: 34-56.

Croizet, J.B., & A. Jobert, 1928. Recherches sur les ossements fossilles du département du Puy-de-Dôme. — Paris, 1-226.

Crusafont Pairo, M., J.L. Hartenberger & E. Heintz, 1964. Un nouveau gisement de mammifères fossiles d'âge Villafranchien à La Puebla de Valverde (Province de Teruel, Espagne). — C.R. Séanc. Acad. Sci., 9, 258, 10: 2869-2871.

Dawkins, W.B., 1878. Contribution to the history of the deer of the European Miocene and Pliocene

strata. — Quart. Jour. Geol. Soc. London, 34, 134: 402-420.
Depéret, Ch. & L. Mayet, 1911. Le gisement de Senèze et sa faune paléomammalogique. — Assoc. Fr. Avanc. Sci. C.R., 39e sess., Toulouse, 1910, Notes Mém., 2: 261-263.
Dubois, E., 1904a. Over een equivalent van het Cromer Forest-Bed in Nederland. — Versl. Gew. Verg. Wis- en Natuurk. Afd. Kon. Akad. Wetensch., 13: 243-251.
Dubois, E., 1904b. On an equivalent of the Cromer Forest Bed in The Netherlands. — Proceed. Kon. Ned. Akad. Wetensch., Sect. Sci., 7, 3: 214-222.
Dubois, E., 1904c. Corrigenda en addenda bij de mededeeling van den Heer Eugène Dubois: "Over een equivalent van het Cromer Forest-Bed in Nederland". — Versl. Gew. Verg. Wis- Natuurk. Afd. Kon. Akad. Wetensch., 13: 453-454.
Dubois, E., 1905. L'âge de l'argile de Tegelen et les espèces de Cervides qu'elle contient. — Arch. Mus. Teyler, 2, 9: 605-615.
Dubois, E., 1906. La pluralité des périodes glaciaires dans les dépôts Pleistocènes et Pliocènes des Pays-Bas. — Arch. Mus. Teyler, 2, 10, 2: 163-179.
Freudenthal, M., T. Meijer & A.J. van der Meulen, 1976. Preliminary report on a field campaign in the continental Pleistocene of Tegelen (The Netherlands). — Scripta Geol., 34: 1-27.
Germonpré, M., 1983. Les mammifères de la Formation de la Campine. — Bull. Belg. Ver. Geol., 92, 2: 111-123.
Guérin, C., 1980. Les rhinoceros (Mammalia, Perissodactyla) du Miocène terminal au Pleistocène supérieur en Europe occidentale. Comparaison avec les espèces actuelles. — Docum. Lab. Géol. Lyon, 79, 3: 1-1185.
Guth, C., 1982. Chilhac in der Auvergne - eine Wirbeltierfundstätte des Villafranchiums in Mittelfrankreich. — Z. Geol. Wiss., 10, 7: 913-921.
Heintz, E., 1967. Données préliminaires sur les cervidés Villafranchiens de France et d'Espagne. — Coll. Intern. C.N.R.S., 163: 539-552.
Heintz, E., 1970. Les cervidés Villafranchiens de France et d'Espagne. — Mém. Mus. Nat. Hist. Nat., N.S., C, 22, 1: 1-303, 40 pls; 2: 1-206.
Hooyer, D.A., 1947. Notes on some fossil mammals of The Netherlands. — Arch. Mus. Teyler, 3, 10: 33-51.
Kortenbout van der Sluijs, G. & W.H. Zagwijn, 1962. An introduction to the stratigraphy and geology of the Tegelen claypits. — Meded. Geol. Stichting, N.S., 15: 31-37.
Kunst, C.E., 1937. Die Niederländischen Pleistozänen Hirsche. — Doctor's Thesis Rijksuniv. Leiden: i-iv, 1-126, pls 1-6.
Loose, H., 1960. *Dicerorhinus kirchbergensis* in the Tiglian? — Proceed. Kon. Ned. Acad. Wetensch., B, Phys. Sci., 63: 380-382.
Loose, H., 1975. Pleistocene Rhinoceratidae of W. Europe with reference to the recent two-horned species of Africa and S.E. Asia. — Scripta Geol., 33: 1-59, 13 pls.
Mayet, L., & F. Roman, 1923. Les éléphants pliocènes, 1. *Elephas planifrons* Falconer des sables de Chagny et faunes de mammifères d'âge villafranchien Saint-Prestien. — Ann. Univ. Lyon, N. S., 1: Sci. Médec., 42: 1-87, pl. 1.
Regteren Altena, C.O. van, 1951. Systematic catalogue of the palaeontological collection, suppl. 7. — Arch. Mus. Teyler, 3, 10: 182-208.
Schaub, S., 1941. Die kleine Hirschart aus dem Oberpliocaen von Senèze (Haute-Loire). — Eclog. Geol. Helv., 34, 2: 264-271, pl. 17.
Schaub, S., 1943. Die oberpliocaene Säugetierfauna von Senèze (Haute Loire) und ihre verbreitungsgeschichtliche Stellung. — Eclog. Geol. Helv., 36, 2: 270-289.
Schreuder, A., 1945. The Tegelen fauna, with a description of new remains of its rare components (*Leptobos, Archidiskodon meridionalis, Macaca, Sus strozzii*). — Arch. Neerl. Zool., 7: 153-204.
Stehlin, H.G., 1923. Die Oberpliocaene Fauna von Senèze (Haute Loire). — Eclog. Geol. Helv., 18, 2: 268-281.

Viret, J., 1954. Le loess à bancs durcis de Saint Vallier (Drôme) et sa faune de Mammifères Villafranchiens. — Nouv. Arch. Mus. Hist. Nat. Lyon, 4: 1-200, 33 pls.

Vlerk, I.M. van der, 1938. Nederland in het ijstijdvak. — IJdo, Leiden: 1-24.

Vlerk, I.M. van der, & F. Florschutz, 1950. Nederland in het ijstijdvak (De geschiedenis van flora, fauna en klimaat, toen aap en mamoet ons land bewoonden). — W. de Haan N.V., Utrecht: 1-287.

Zagwijn, W.H., 1963. Pollen-analytic investigations in the Tiglian of the Netherlands. — Meded. Geol. Stichting, N.S., 16: 49-71, pls 2-3, enclosures 4-6.

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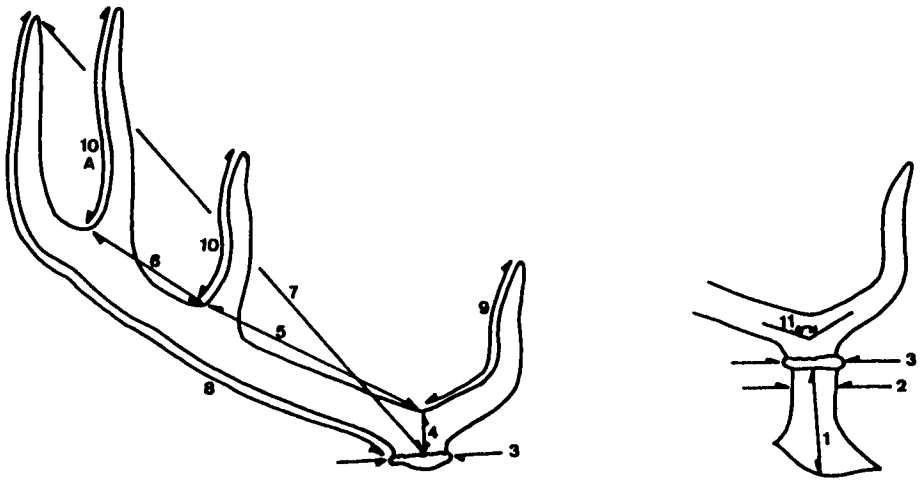

Fig. 15. Summary of the method of measuring of the antlers

Table 1. Length in mm of the dentary segments and molars and premolars of a mandibula belonging to *Eucladoceros tegulensis*.

P_2-M_3	131.3	M_3	35.0	P_4	18.7
M_1-M_3	85.3	M_2	24.7	P_3	18.7
P_2-P_4	48.9	M_1	20.9	P_2	13.8

Table 2. Dimensions of the antlers of *Eucladoceros tegulensis* from Tegelen (see Fig. 15).

C	Cn	sym	1	2	3	4	5	6	6a	7	8	9	10	10a	10b	11
RGM-			—	—	60.5	86.5	—	—	—	—	—	—	—	—	—	125
RGM 20685		s	—	—	61.5	79.0	250	110	225	+740	+730	+290	400	+425	+290	120
		d	—	—	63.5	82.0	250	130	220	850	910	335	380	545	435	130
RGM 28093			—	—	39.5	—	—	—	—	+320	—	—	—	—	—	—
RGM 30705			—	—	59.5	—	—	—	—	—	—	—	—	—	—	—
RGM 36978			—	—	56.5	+68	—	—	—	—	—	+240	—	—	—	105
RGM 51674			—	—	—	—	—	175	—	—	—	—	—	+225	—	—
RGM 53074			—	—	57.0	55.0	—	—	—	—	—	—	—	—	—	120
RGM 53078			—	—	46.0	60.0	—	—	—	—	—	—	—	—	—	110
RGM 53091			—	—	—	—	—	140	—	—	—	—	180	—	—	—
RGM 53093			—	—	56.0	53.5	—	—	—	—	—	—	—	—	—	105
RGM 53096			—	—	62.0	83.0	—	—	—	—	—	—	—	—	—	110
RGM 53162			31.5	+48	—	—	—	—	—	—	—	—	—	—	—	—
RGM 53423			—	—	60.0	—	—	177	—	—	—	—	—	—	—	—
RGM 54675			—	—	50.0	60.5	+180	—	—	+500	+585	—	—	—	—	105
RGM 62876			+70	33.5	63.5	48.0	+90	—	—	—	—	—	—	—	—	110
RGM 64001			+43	50.5	—	+73	+215	—	—	—	—	—	—	—	—	115
RGM 65964			—	—	58.0	65.0	305	120	—	575	655	230	+165	250	—	125
RGM 72167		s	77.5	38.5	54.0	61.5	+205	—	—	—	—	—	—	—	—	110
		d	64.0	34.5	58.5	62.5	+190	—	—	—	—	—	—	—	—	120
RGM 75123			—	—	68.0	—	—	—	—	—	—	—	—	—	—	—
RGM 75124			—	—	63.0	+55	—	—	—	—	—	245	—	—	—	105
RGM 79235			—	—	—	—	+180	115	130	+560	+570	—	—	—	—	—
RGM 85781.a			—	—	66.5	+82	—	—	—	—	—	—	—	—	—	—
RGM 85781.b			—	—	53.5	—	—	—	—	—	—	—	—	—	—	—
RGM 85783			—	—	50.5	49.5	—	—	—	—	—	+90	—	—	—	85
RGM 85792			—	—	56.0	+44	—	—	—	—	—	—	—	—	—	—
RGM 86311			—	—	52.5	88.0	245	—	—	—	—	+125	+215	—	—	115
RGM 86834			—	—	61.5	66.0	260	95	145	+520	+525	235	+240	+175	—	120
RGM 87166			—	—	—	—	+300	—	—	—	—	—	+375	—	—	—
RGM 87407			—	—	42.5	77.0	—	—	—	320	+320	—	—	—	—	95
RGM 93069			—	—	53.5	82.0	—	—	—	—	—	—	—	—	—	105
RGM 93672			—	—	48.5	53.5	—	—	—	—	—	—	—	—	—	120
RGM 94960			—	—	60.5	75.0	—	—	—	—	—	—	—	—	—	110
RGM 96553			—	—	69.0	77.0	+165	—	—	—	—	—	—	—	—	105
RGM 96660		s	—	—	53.0	65.0	+250	+150	220	—	—	+210	—	265	—	120
		d	—	—	—	—	+280	145	160	—	+615	+205	—	—	—	—
RGM 96964			—	—	56.0	48.5	—	—	—	—	—	—	—	—	—	120
RGM 102817			—	—	—	—	—	+155	—	—	—	—	270	435	—	—
RGM 122955			—	—	54.5	84.0	290	185	—	620	+785	177	+175	—	—	125

Table 2. Continued.

C	Cn	sym	1	2	3	4	5	6	6a	7	8	9	10	10a	10b	11
Ha	15603		—	—	66.5	+57	285	155	—	615	590	—	+125	—	—	120
Ha	15611		—	—	58.0	77.5	—	—	—	—	—	—	—	—	—	120
Ha	15776		—	—	—	73.0	405	195	—	800	+835	305	425	255	—	115
Ha	15778		—	—	59.0	78.0	412	—	—	+560	+555	+145	—	—	—	120
Ha	15779		—	—	—	—	—	150	—	—	—	—	—	—	—	—
Ha	15780		—	—	62.5	74.5	—	—	—	—	—	155	—	—	—	115
Ha	15781		—	—	64.5	62.5	—	—	—	+290	+275	—	—	—	—	105
Ha	15784		41.0	50.5	61.5	74.5	+80	—	—	—	—	—	—	—	—	110
Ha	15785		38.0	49.5	65.5	62.0	115	—	—	—	—	—	—	—	—	115
Ha	15788		—	—	66.5	49.0	255	155	—	686	750	257	185	270	—	120
Ha	15799		—	—	81.0	96.5	—	—	—	—	—	—	—	—	—	115
Ha	15807		—	—	—	94.5	—	—	—	—	—	—	—	—	—	?130
Ha	15896		—	—	68.0	60.0	—	—	—	—	—	—	—	—	—	120
Ha	15897		—	—	70.5	86.0	+215	—	—	—	—	—	—	—	—	100
Ha	15917		—	—	—	—	—	130	—	—	—	—	—	—	—	130
Ha	15976	s	—	—	80.5	89.0	—	—	—	—	—	220	—	—	—	115
		d	—	—	74.5	79.5	—	—	—	—	—	—	—	—	—	115
Ma	-		—	—	70.0	75.0	—	+125	—	—	—	—	—	—	—	95
Ma	1		51.0	38.0	60.0	39.0	—	—	—	—	—	—	—	—	—	100
Ma	120		—	—	—	75.0	170	155	175	620	780	255	275	425	410	115
Ma	501		30.0	47.0	—	—	—	—	—	—	—	—	—	—	—	—
Ma	524		—	—	73.5	80.0	375	+160	—	—	—	—	—	—	—	120
Ma	527		—	—	+80	84.0	—	—	—	—	—	+190	—	—	—	120
Ma	530		—	—	65.5	75.5	+260	—	—	—	—	—	—	—	—	120
Ma	532		—	—	87.0	112.	—	—	—	—	—	—	—	—	—	—
Ma	533		—	—	64.0	+73	—	—	—	—	—	—	—	—	—	—
Ma	534		—	—	55.0	44.0	—	—	—	—	—	—	—	—	—	115
Ma	537		—	—	61.0	66.0	—	—	—	—	—	—	—	—	—	115
Ma	1275		—	—	+53	80.0	+240	145	+160	+610	+595	+290	—	+385	—	115
Ma	1481		32.5	43.0	—	—	—	—	—	—	—	—	—	—	—	—
Ma	1482		36.0	42.0	—	—	—	—	—	—	—	—	—	—	—	—
Ma	1529		—	—	59.5	78.0	+280	—	—	—	—	—	—	—	—	110
Ma	1914		—	—	—	—	—	+230	180	—	—	—	—	+170	—	—
Ut	Te5021		—	—	63.5	74.5	—	—	—	—	—	—	—	—	—	105
Ut	Te5023		—	—	67.0	50.5	—	—	—	—	—	—	—	—	—	105

C = Collection
Cn = Catalogue number
sym = symmetry; s = sinister, d = dexter
1-11 see methods: antlers
+ = actual value probably slightly larger
± = estimation

Table 3. Length and width of the upper molars of *Eucladoceros* from the various localities.

	Locality	N	Min	M	Max	SD
L M^3	Peyrolles	3	25	25.50	26.5	0.86
	Senèze	32	23	25.39	28.5	1.42
	La Puebla	5	26.5	27.10	27.5	0.41
	St Vallier	12	23	24.95	28.5	1.45
	Tegelen	6	23.5	26.08	28	1.80
W M^3	Peyrolles	3	23.5	23.83	24	0.28
	Senèze	32	21	24.12	26.5	1.32
	La Puebla	5	24	24.70	25.5	0.67
	St Vallier	11	22	24.09	26	1.51
	Tegelen	6	24	25.58	26.5	0.94
L M^2	Peyrolles	1		25.5		—
	Senèze	31	22.5	25.53	28.5	1.59
	La Puebla	4	27	27.25	27.5	0.28
	St Vallier	15	22	25.00	28.5	1.51
	Tegelen	18	24	26.25	28.5	1.25
W M^2	Peyrolles	1		24.5		—
	Senèze	30	22	24.88	27.5	1.51
	La Puebla	4	22.5	24.50	27	1.87
	St Vallier	15	23	24.93	27	1.23
	Tegelen	12	25	26.00	27.5	1.04
L M^1	Peyrolles	2	21.5	23.75	26	3.18
	Senèze	35	20	23.30	26.5	1.67
	La Puebla	4	24	24.62	25	0.47
	St Vallier	20	19	23.47	26.5	1.17
	Tegelen	11	22	24.98	27.5	2.00
W M^1	Peyrolles	2	23	23.50	24	0.70
	Senèze	34	20.5	22.85	25.5	1.30
	La Puebla	3		22.50		—
	St Vallier	17	22.5	23.41	25	0.97
	Tegelen	8	23	24.73	25.5	0.83

Table 4. Length and width of the upper premolars of *Eucladoceros* from the various localities.

	Locality	N	Min	M	Max	SD
L P^4	Peyrolles	1		17		—
	Senèze	38	14.5	16.01	18.5	0.84
	La Puebla	4	15.5	16.50	17.5	1.15
	St Vallier	15	15	16.33	19	1.17
	Tegelen	9	15.5	16.69	17.5	0.84
W P^4	Peyrolles	1		20.5		—
	Senèze	37	19	20.63	23	0.93
	La Puebla	3		23.00		—
	St Vallier	15	19.5	21.13	24	1.48
	Tegelen	7	21	22.27	23.5	0.70
L P^3	Peyrolles	0		—		—
	Senèze	38	16	17.44	19.5	0.76
	La Puebla	6	16.5	17.75	18.5	0.75
	St Vallier	13	16	17.88	19.5	1.02
	Tegelen	7	17	18.21	19.5	1.02
W P^3	Peyrolles	0		—		—
	Senèze	37	16.5	18.18	20	0.82
	La Puebla	4	19	20.25	21.5	1.18
	St Vallier	12	17	19.33	22.5	1.62
	Tegelen	6	19	20.75	21.5	1.00
L P^2	Peyrolles	0		—		—
	Senèze	32	16	18.00	20.00	0.78
	La Puebla	4	17.5	18.87	20	1.31
	St Vallier	8	18	18.93	20.5	0.90
	Tegelen	6	16	17.74	19	1.03
W P^2	Peyrolles	0		—		—
	Senèze	32	14	15.71	17.5	0.83
	La Puebla	4	17	17.87	18.5	0.62
	St.Vallier	8	15.5	17.12	19.5	1.43
	Tegelen	5	16	18.29	19	1.17

Table 5. Length and width of the lower molars of *Eucladoceros* from the various localities.

	Locality	N	Min	M	Max	SD
L M_3	Peyrolles	4	32.5	33.12	33.5	0.47
	Senèze	50	30.5	33.77	39.5	2.10
	La Puebla	7	32.5	35.78	39	2.30
	St Vallier	10	31.5	34.45	37	2.01
	Tegelen	12	37	33.82	37	2.01
W M_3	Peyrolles	4	15	15.12	15.5	0.24
	Senèze	50	13	14.90	17.5	0.97
	La Puebla	7	15	15.78	16.5	0.48
	St Vallier	9	14.5	15.77	16.5	0.75
	Tegelen	12	14	16.25	17	1.04
L M_2	Peyrolles	5	24	24.70	25.5	0.57
	Senèze	43	22	24.53	27.5	1.60
	La Puebla	7	23	24.78	26	1.28
	St Vallier	12	24	25.70	27	0.94
	Tegelen	13	24.5	26.63	28.5	1.28
W M_2	Peyrolles	5	15	15.60	16.5	0.54
	Senèze	41	13.5	15.25	17.5	0.81
	La Puebla	7	16	16.50	17.5	0.50
	St Vallier	12	14.5	16.08	17	0.84
	Tegelen	12	15	16.72	18	1.03
L M_1	Peyrolles	5	22	22.50	23	0.50
	Senèze	40	19	21.65	25	1.57
	La Puebla	10	21.5	23.13	26	1.70
	St Vallier	15	19.5	22.73	25.5	1.57
	Tegelen	10	21	23.54	25	1.78
W M_1	Peyrolles	5	14	14.40	14.5	0.22
	Senèze	40	13	14.36	16.5	0.78
	La Puebla	8	14.5	15.31	16.5	0.59
	St Vallier	13	14	14.84	16	0.71
	Tegelen	10	14	14.78	15.5	0.47

Table 6. Length and width of the lower premolars of *Eucladoceros* from the various localities.

	Locality	N	Min	M	Max	SD
L P_4	Peyrolles	4	19	19.50	21	0.86
	Senèze	48	17	19.67	22.5	1.34
	La Puebla	6	19	20.00	21.5	0.83
	St Vallier	8	19	20.00	21.5	0.92
	Tegelen	11	18.5	20.48	22	0.97
W P_4	Peyrolles	4	11.5	11.87	12.5	0.47
	Senèze	48	10	12.00	13.5	0.84
	La Puebla	6	12	12.91	14	0.66
	St Vallier	8	12	12.93	14	0.72
	Tegelen	13	12	12.93	13.5	0.63
L P_3	Peyrolles	4	17.5	18.12	18.5	0.47
	Senèze	40	16.5	18.37	21	0.96
	La Puebla	9	18	19.00	20	0.74
	St Vallier	7	18.5	19.21	20	0.63
	Tegelen	13	17.5	18.70	19.5	0.78
W P_3	Peyrolles	4	10	10.37	10.5	0.24
	Senèze	40	9	10.28	12	0.90
	La Puebla	9	11.5	12.33	13	0.61
	St Vallier	7	10.5	11.57	12.5	0.78
	Tegelen	14	10.5	11.93	13.5	0.76
L P_2	Peyrolles	1		13.5		—
	Senèze	35	12.5	14.12	16.5	0.79
	La Puebla	7	14	15.07	16.5	0.83
	St Vallier	7	14	14.92	16.5	0.83
	Tegelen	5	13	14.23	15.5	1.18
W P_2	Peyrolles	1		7.5		—
	Senèze	35	6.5	7.82	9	0.60
	La Puebla	7	8.5	9.07	10.5	0.67
	St Vallier	7	8	8.92	10	0.67
	Tegelen	6	7.5	9.56	11	1.38

Table 7. Heigth and height-length index of some teeth of *Eucladoceros* from the various localities.

	Locality	N	H Min	H M	H Max	H/L*100 Min	H/L*100 M	H/L*100 Max
M^2	Peyrolles	0		—			—	
	Senèze	2		25.00			92.59	
	La Puebla	3	20	21.00	22	74.0	76.81	80.0
	St Vallier	6	18.5	20.41	22.5	74.0	79.42	84.9
	Tegelen	4	21.5	22.50	23	89.1	90.98	91.9
P^4	Peyrolles	0		—			—	
	Senèze	1		17.5			106.0	
	La Puebla	2		19.00			108.57	
	St Vallier	4	18	18.25	19	112.5	114.96	118.7
	Tegelen	1		20.3			125.7	
M_2	Peyrolles	0		—			—	
	Senèze	2	23	24.00	25	90.1	94.11	98.0
	La Puebla	2	21	22.00	23	80.7	84.61	88.4
	St Vallier	2	23.5	24.25	25	92.1	93.24	94.3
	Tegelen	1		24.9			87.68	

Table 8. Comparison between *Eucladoceros tegulensis* from Tegelen and *E. senezensis vireti* from St.Vallier.

		t	df	P	95%
L	M^3	1.442	16	—	-
	M^2	2.603	31	0.02	+
	M^1	2.666	29	0.02	+
	P^4	0.804	22	—	-
	P^3	0.690	18	—	-
	P^2	2.304	12	0.05	+
W	M^3	2.179	15	0.05	+
	M^2	2.402	25	0.05	+
	M^1	3.312	23	0.01	+
	P^4	1.921	20	0.1	-
	P^3	1.952	16	0.1	-
	P^2	1.530	11	—	-
L	M_3	0.732	20	—	-
	M_2	2.056	23	0.1	-
	M_1	1.199	23	—	-
	P_4	1.088	17	—	-
	P_3	1.483	18	—	-
	P_2	1.196	10	—	-
W	M_3	1.172	19	—	-
	M_2	1.668	22	—	-
	M_1	0.231	21	—	-
	P_4	0.000	19	—	-
	P_3	1.015	19	—	-
	P_2	1.092	11	—	-

Table 9. Comparison between *Eucladoceros tegulensis* from Tegelen and *E. senezensis vireti* from La Puebla.

		t	df	P	95%
L	M^3	1.230	9	—	-
	M^2	1.563	20	—	-
	M^1	0.349	13	—	-
	P^4	0.338	11	—	-
	P^3	0.911	11	—	-
	P^2	1.532	8	—	-
W	M^3	1.749	9	—	-
	M^2	2.055	14	0.1	-
	M^1	4.500	9	0.002	+
	P^4	1.745	8	—	-
	P^3	1.723	8	—	-
	P^2	0.643	7	—	-
L	M_3	1.947	17	0.1	-
	M_2	3.083	18	0.01	+
	M_1	0.527	18	—	-
	P_4	1.022	15	—	-
	P_3	0.905	20	—	-
	P_2	1.456	10	—	-
W	M_3	1.118	17	—	-
	M_2	0.526	17	—	-
	M_1	2.125	16	0.05	+
	P_4	0.063	17	—	-
	P_3	1.325	21	—	-
	P_2	0.836	11	—	-

Table 10. Comparison between *Eucladoceros tegulensis* from Tegelen and *E. senezensis senezensis* from Senèze.

		t	df	P	95%
L	M^3	1.049	36	—	-
	M^2	1.646	47	—	-
	M^1	2.777	44	0.01	+
	P^4	2.184	45	0.05	+
	P^3	2.336	33	0.05	+
	P^2	0.713	36	0.1	-
W	M^3	2.576	36	0.02	+
	M^2	2.348	40	0.05	+
	M^1	3.887	40	0.001	+
	P^4	4.417	42	0.001	+
	P^3	6.919	41	0.001	+
	P^2	6.128	35	0.001	+
L	M_3	0.075	60	—	-
	M_2	4.323	54	0.001	+
	M_1	3.317	48	0.002	+
	P_4	1.889	57	0.1	-
	P_3	1.123	51	—	-
	P_2	0.274	38	—	-
W	M_3	4.271	60	0.001	+
	M_2	5.195	51	0.001	+
	M_1	1.623	48	—	-
	P_4	3.710	59	0.001	+
	P_3	6.128	52	0.001	+
	P_2	5.272	39	0.001	+

Table 11. Comparison between *Eucladoceros tegulensis* from Tegelen and *E. tetraceros* from Peyrolles.

		t	df	P	95%
L	M^3	0.516	7	—	-
	M^2	0.584	17	—	-
	M^1	0.750	11	—	-
	P^4	0.350	8	—	-
W	M^3	3.061	7	0.02	+
	M^2	1.386	11	—	-
	M^1	1.909	8	0.1	-
	P^4	2.365	6	0.1	-
L	M_3	0.676	14	—	-
	M_2	3.204	16	0.01	+
	M_1	1.261	13	—	-
	P_4	1.775	13	0.1	-
	P_3	1.392	15	—	-
	P_2	0.565	4	—	-
W	M_3	2.108	14	0.1	-
	M_2	2.275	15	0.05	+
	M_1	1.694	13	—	-
	P_4	3.083	15	0.01	+
	P_3	3.971	16	0.001	+
	P_2	1.382	5	—	-

Table 12. Width-length index of the upper molars and premolars of *Eucladoceros* from the various localities.

	Locality	N	Min	M	Max	SD
M^3	Peyrolles	3	88	93.55	96	4.52
	Senèze	29	88	95.64	104	4.29
	La Puebla	0		—		—
	St Vallier	11	89	96.28	106	5.23
	Tegelen	6	93	98.30	106	4.23
M^2	Peyrolles	1		96.07		—
	Senèze	30	83	97.34	108	5.22
	La Puebla	0		—		—
	St Vallier	15	92	99.94	108	5.85
	Tegelen	11	93	98.24	102	2.89
M^1	Peyrolles	2	92	99.63	106	10.37
	Senèze	35	84	98.36	110	6.65
	La Puebla	0		—		—
	St Vallier	17	88	100.97	119	9.52
	Tegelen	8	85	101.02	110	9.43
P^4	Peyrolles	1		120.58		—
	Senèze	37	116	129.08	144	6.79
	La Puebla	0		—		—
	St Vallier	15	121	129.53	140	6.41
	Tegelen	6	130	135.79	136	4.15
P^3	Peyrolles	0		—		—
	Senèze	37	94	104.44	114	4.85
	La Puebla	0		—		—
	St Vallier	12	97	107.62	118	5.95
	Tegelen	6	110	113.78	121	5.89
P^2	Peyrolles	0		—		—
	Senèze	32	75	87.44	97	5.24
	La Puebla	0		—		—
	St Vallier	8	86	90.32	95	3.97
	Tegelen	5	94	102.92	115	7.92

Table 13. Width-length index of the lower molars and premolars of *Eucladoceros* from the various localities.

	Locality	N	Min	M	Max	SD
M_3	Peyrolles	4	44	45.67	47	1.38
	Senèze	50	41	44.14	47	1.41
	La Puebla	0		—		—
	St Vallier	9	43	46.09	50	2.08
	Tegelen	10	42	48.36	53	3.58
M_2	Peyrolles	5	62	63.14	64	1.02
	Senèze	41	54	62.50	68	3.50
	La Puebla	0		—		—
	St Vallier	12	56	62.60	68	3.54
	Tegelen	11	56	63.10	70	4.60
M_1	Peyrolles	5	62	64.02	65	1.74
	Senèze	39	56	66.76	74	4.69
	La Puebla	0		—		—
	St Vallier	13	56	66.15	79	5.63
	Tegelen	9	56	63.59	74	6.70
P_4	Peyrolles	4	57	60.99	65	3.56
	Senèze	48	48	61.57	72	5.17
	La Puebla	0		—		—
	St Vallier	8	60	64.70	69	2.72
	Tegelen	11	57	63.30	70	3.59
P_3	Peyrolles	4	56	57.24	58	0.74
	Senèze	38	46	56.45	64	4.17
	La Puebla	0		—		—
	St Vallier	7	56	60.19	63	3.02
	Tegelen	13	57	63.79	70	4.27
P_2	Peyrolles	1		55.55		—
	Senèze	35	48	55.45	66	3.61
	La Puebla	0		—		—
	St Vallier	7	57	59.78	64	2.65
	Tegelen	5	49	67.33	78	11.85

Table 14. Dimensions of the scapulae of *Eucladoceros* from the various localities.

	Locality	N	Min	M	Max	SD
A.P.D.	Peyrolles	1		50		—
-p	Senèze	25	42	50.78	57	3.55
	La Puebla	2		56.00		—
	St Vallier	0		—		—
	Tegelen	6	45.5	52.95	62	5.61
T.D.-p	Peyrolles	1		45		—
	Senèze	24	37.5	45.31	52	3.50
	La Puebla	2	50	50.25	50.5	0.35
	St Vallier	0		—		—
	Tegelen	6	44.5	48.77	53.5	3.83

Table 15. Dimensions of the humeri of *Eucladoceros* from the various localities.

	Locality	N	Min	M	Max	SD
A.P.D.	Peyrolles	2	31.5	31.75	32	0.35
-d	Senèze	35	27.5	31.78	37.5	2.26
	La Puebla	8	33	34.81	36	0.88
	St Vallier	18	32.5	34.75	37.5	1.30
	Tegelen	21	32.5	35.25	38.5	2.05
T.D.-d	Peyrolles	2	52.5	53.25	54	1.06
	Senèze	35	48.5	54.97	62	3.95
	La Puebla	8	55.5	58.75	63.5	3.03
	St Vallier	18	55	59.50	66	3.05
	Tegelen	23	52	58.90	65.5	3.72

Table 16. Dimensions of the radii of *Eucladoceros* from the various localities.

	Locality	N	Min	M	Max	SD
L	Peyrolles	0		—		—
	Senèze	28	261	297.64	327	18.02
	La Puebla	3	282	300.33	324	21.50
	St Vallier	3	310	322.66	338	14.18
	Tegelen	1		320		—
A.P.D.	Peyrolles	0		—		—
-p	Senèze	33	28	32.77	37	2.78
	La Puebla	9	30.5	33.55	36.5	2.15
	St Vallier	8	32.5	34.12	37.5	1.76
	Tegelen	7	34.5	34.99	37	1.26
T.D.-p	Peyrolles	0		—		—
	Senèze	32	49	55.45	63	3.85
	La Puebla	10	52.5	57.05	60	2.29
	St Vallier	8	53	57.88	61.5	3.18
	Tegelen	6	56.5	58.67	61.5	1.67
A.P.D.	Peyrolles	0		—		—
-d	Senèze	33	25	30.43	35	2.61
	La Puebla	6	27.5	31.75	35.5	3.11
	St Vallier	5	31.5	34.00	36.5	1.90
	Tegelen	2	31	32.55	34	2.05
T.D.-d	Peyrolles	0		—		—
	Senèze	33	46.5	53.25	61.5	4.28
	La Puebla	5	48	53.20	57	3.32
	St Vallier	6	53.5	54.91	60	3.26
	Tegelen	3	53	56.60	60.5	3.70

Table 17. Dimensions of the metacarpi of *Eucladoceros* from the various localities.

	Locality	N	Min	M	Max	SD
L	Peyrolles	0		—		—
	Senèze	32	249	272.21	303	15.56
	La Puebla	1		273		—
	St Vallier	3	266	291.66	308	22.50
	Tegelen	2	281	311.00	341	42.43
A.P.D.	Peyrolles	0		—		—
-p	Senèze	36	28	31.90	36.5	2.50
	La Puebla	9	29.5	32.38	35	1.99
	St Vallier	8	32.5	35.00	38.5	2.34
	Tegelen	7	30	31.83	35	2.29
T.D.-p	Peyrolles	0		—		—
	Senèze	36	38	44.06	50	3.54
	La Puebla	9	40.5	44.38	51.5	3.53
	St Vallier	8	43	46.62	52.5	3.14
	Tegelen	7	43.5	46.43	50.5	2.74
A.P.D.	Peyrolles	0		—		—
-d	Senèze	32	26	29.79	33.5	2.26
	La Puebla	7	27.5	31.42	36	2.72
	St Vallier	4	28.5	33.00	35.5	3.10
	Tegelen	5	31	32.26	35	1.55
T.D.-d	Peyrolles	0		—		—
	Senèze	32	40.5	45.87	51.5	3.24
	La Puebla	5	42.5	47.00	51.5	3.69
	St Vallier	4	44.5	50.12	53.5	4.30
	Tegelen	6	45	47.15	49.5	1.67

Table 18. Dimensions of the tibiae of *Eucladoceros* from the various localities.

	Locality	N	Min	M	Max	SD
A.P.D.	Peyrolles	2	31.5	34.50	37.5	4.24
-d	Senèze	29	35	39.81	45.5	3.16
	La Puebla	6	41	42.33	43.5	0.81
	St Vallier	15	38.5	43.90	47	2.13
	Tegelen	11	39.5	42.87	47	2.51
T.D.-d	Peyrolles	2	43	45.75	48.5	3.88
	Senèze	29	43.5	47.96	56	3.73
	La Puebla	6	48.5	50.50	56	2.75
	St Vallier	15	47	52.63	56	2.31
	Tegelen	7	49	50.25	51.5	1.76

Table 19. Dimensions of the astragali of *Eucladoceros* from the various localities.

	Locality	N	Min	M	Max	SD
L	Peyrolles	6	54	55.75	58	1.47
	Senèze	33	52	59.59	68.5	4.39
	La Puebla	8	57.5	62.81	67	2.91
	St Vallier	33	59.5	64.37	68.5	2.47
	Tegelen	15	60	63.09	67	1.86
T.D.-d	Peyrolles	6	30	33.66	36.5	2.22
	Senèze	37	31.5	37.52	42	2.84
	La Puebla	11	36.5	39.13	42.5	1.71
	St Vallier	35	35.5	40.42	43	1.74
	Tegelen	19	36	38.43	43	2.16

Table 20. Dimensions of the calcanei of *Eucladoceros* from the various localities.

	Locality	N	Min	M	Max	SD
L	Peyrolles	2	115	116.50	118	2.12
	Senèze	26	110	122.53	142.5	10.35
	La Puebla	3	133.5	137.00	139	3.04
	St Vallier	18	122.5	134.19	142.5	6.18
	Tegelen	8	126	132.36	139	4.32
A.P.D. -p	Peyrolles	2	43.5	44.00	44.5	0.70
	Senèze	28	40	45.60	51.5	3.44
	La Puebla	7	46.5	48.28	50	1.67
	St Vallier	21	46.5	49.92	52.5	1.60
	Tegelen	7	45	48.61	52	2.11
T.D.-p	Peyrolles	2	34	34.25	34.5	0.35
	Senèze	33	30.5	35.75	41	3.26
	La Puebla	9	36.5	37.66	39.5	1.19
	St Vallier	24	33.5	37.62	40.5	1.70
	Tegelen	10	35	38.97	42.5	2.21

Table 21. Dimensions of the scapho-cuboides of *Eucladoceros* from the various localities.

	Locality	N	Min	M	Max	SD
A.P.D.	Peyrolles	0		—		—
-p	Senèze	35	32.5	37.34	46	3.49
	La Puebla	5	36.5	38.70	40	1.60
	St Vallier	24	36.5	40.77	47.5	2.33
	Tegelen	9	36	39.56	42.5	2.47
T.D.-p	Peyrolles	0		—		—
	Senèze	33	40.5	46.01	53.5	3.70
	La Puebla	5	46.5	48.70	50.5	1.48
	St Vallier	24	42	50.64	55.5	2.99
	Tegelen	9	45.5	50.26	52.5	2.57

Table 22. Dimensions of the metatarsi of *Eucladoceros* from the various localities.

	Locality	N	Min	M	Max	SD
A.P.D.	Peyrolles	0		—		—
-p	Senèze	26	40	44.07	50	2.51
	La Puebla	7	41.5	46.35	49.5	3.22
	St Vallier	18	44.5	47.08	50.5	1.90
	Tegelen	11	42.5	45.54	50.5	2.63
T.D.-p	Peyrolles	0		—		—
	Senèze	26	36	41.26	47	2.83
	La Puebla	7	39	42.78	45	2.11
	St Vallier	19	40.5	43.63	47	1.71
	Tegelen	8	41	42.44	46.5	2.53
A.P.D.	Peyrolles	1		31.5		—
-d	Senèze	25	27.5	31.06	35.5	2.27
	La Puebla	3	33	33.33	33.5	0.37
	St Vallier	4	33	34.25	35.5	1.04
	Tegelen	3	31	32.10	35.5	0.90
T.D.-d	Peyrolles	1		48.5		—
	Senèze	25	41.5	47.00	55	3.29
	La Puebla	4	47	49.37	51.5	1.88
	St Vallier	4	49.5	51.50	54.5	2.27
	Tegelen	2	46.5	47.55	49	1.77

Table 23. Dimensions of the first phalanges of *Eucladoceros* from the various localities.

	Locality	N	Min	M	Max	SD
L	Peyrolles	0		—		—
	Senèze	77	51.5	59.47	70	4.75
	La Puebla	4	61	63.00	65.5	1.87
	St Vallier	8	63	68.18	70.5	2.69
	Tegelen	9	60.5	65.33	70.5	2.93
A.P.D.	Peyrolles	0		—		—
-p	Senèze	76	23.5	28.21	33.5	2.36
	La Puebla	7	26.5	28.50	32	1.80
	St Vallier	8	27.5	30.25	32.5	2.17
	Tegelen	8	27	28.95	32	1.68
T.D.-p	Peyrolles	0		—		—
	Senèze	77	20	23.22	28	1.87
	La Puebla	5	21	22.40	24	1.19
	St Vallier	8	23.5	25.06	26.5	0.94
	Tegelen	11	20.5	22.75	25.5	1.58
A.P.D.	Peyrolles	0		—		—
-d	Senèze	79	15.5	18.33	21.5	1.66
	La Puebla	7	18.5	19.92	22	1.48
	St Vallier	8	17.5	20.12	22	1.27
	Tegelen	14	17	18.61	20	0.84
T.D.-d	Peyrolles	0		—		—
	Senèze	78	17.5	20.51	24	1.51
	La Puebla	7	20	21.64	22.5	0.85
	St Vallier	8	20	22.12	23.5	1.12
	Tegelen	15	19.5	21.15	23	1.20

Table 24. Dimensions of the second phalanges of *Eucladoceros* from the various localities.

	Locality	N	Min	M	Max	SD
L	Peyrolles	0		—		—
	Senèze	73	37	43.08	50	3.50
	La Puebla	7	43	45.71	48	2.30
	St Vallier	3	45.5	48.00	49.5	2.17
	Tegelen	8	44	47.13	49	2.03
T.D.-p	Peyrolles	0		—		—
	Senèze	73	19	21.84	26	1.80
	La Puebla	8	21	22.87	24	0.95
	St Vallier	3	21.5	23.16	24.5	1.52
	Tegelen	10	15.5	20.51	23	2.27
A.P.D.	Peyrolles	0		—		—
-d	Senèze	71	21.5	25.69	31.5	2.45
	La Puebla	6	26.5	29.16	32.5	2.50
	St Vallier	3	24.5	25.83	27.5	1.52
	Tegelen	10	23	25.33	27.5	1.81
T.D.-d	Peyrolles	0		—		—
	Senèze	72	16	18.60	23	1.63
	La Puebla	6	17.5	19.83	22	1.57
	St Vallier	3	17.5	18.66	20.5	1.60
	Tegelen	9	16	18.73	21	1.66

Table 25. Dimensions of the third phalanges of *Eucladoceros* from the various localities.

	Locality	N	Min	M	Max	SD
L	Peyrolles	0		—		—
	Senèze	65	42.5	49.36	61	4.51
	La Puebla	2	59	60.00	61	1.41
	St Vallier	0		—		—
	Tegelen	2		50.90		0.14
H	Peyrolles	0		—		—
	Senèze	65	27.5	30.46	36.5	2.47
	La Puebla	3	31.5	33.83	35	2.01
	St Vallier	0		—		—
	Tegelen	3	32.5	34.33	37	2.39
T.D.-p	Peyrolles	0		—		—
	Senèze	48	16	18.26	20.5	1.33
	La Puebla	3		22.00		—
	St Vallier	0		—		—
	Tegelen	3	17.5	18.40	19.5	0.92

Table 26. Comparison between *Eucladoceros teguliensis* from Tegelen and *E. senezensis vireti* from St Vallier.

		t	df	P	95%
Humerus	A.P.D.-d	0.892	37	—	-
	T.D.-d	0.554	39	—	-
Radius	L	0.163	2	—	-
	A.P.D.-p	1.085	13	—	-
	T.D.-p	0.551	12	—	-
	A.P.D.-d	0.898	5	—	-
	T.D.-d	0.705	7	—	-
Metacarpus	L	0.622	3	—	-
	A.P.D.-p	2.643	13	0.05	+
	T.D.-p	0.124	13	—	-
	A.P.D.-d	0.471	7	—	-
	T.D.-d	1.562	8	—	-
Tibia	A.P.D.-d	1.130	24	—	-
	T.D.-d	2.407	20	0.05	+
Astragalus	L	1.786	46	0.1	-
	T.D.-d	3.682	52	0.001	+
Calcaneum	L	0.756	24	—	-
	A.P.D.-p	1.734	26	0.1	-
	T.D.-p	1.931	32	0.1	-
Scapho-cuboid	A.P.D.-p	1.308	31	—	-
	T.D.-p	0.337	31	—	-
Metatarsus	A.P.D.-p	1.830	27	0.1	-
	T.D.-p	1.430	25	—	-
	A.P.D.-d	2.854	5	0.05	+
	T.D.-d	2.116	4	—	-
Phalange I	L	2.080	15	0.05	+
	A.P.D.-p	1.340	14	—	-
	T.D.-p	3.673	17	0.001	+
	A.P.D.-d	3.368	20	0.002	+
	T.D.-d	1.887	21	0.05	+
Phalange II	L	0.623	9	—	-
	T.D.-p	1.870	11	0.05	+
	A.P.D.-d	0.431	11	—	-
	T.D.-d	0.064	10	—	-

Table 27. Comparison between *Eucladoceros teguliensis* from Tegelen and *E. senezensis vireti* from La Puebla.

		t	df	P	95%
Scapula	A.P.D.-p	0.729	6	—	-
	T.D.-p	0.518	6	—	-
Humerus	A.P.D.-d	0.582	27	—	-
	T.D.-d	0.103	29	—	-
Radius	L	0.792	2	—	-
	A.P.D.-p	1.588	14	—	-
	T.D.-p	1.501	14	—	-
	A.P.D.-d	0.331	6	—	-
	T.D.-d	1.349	6	—	-
Metacarpus	L	0.731	1	—	-
	A.P.D.-p	0.514	14	—	-
	T.D.-p	1.265	14	—	-
	A.P.D.-d	0.617	10	—	-
	T.D.-d	0.090	9	—	-
Tibia	A.P.D.-d	0.506	15	—	-
	T.D.-d	0.199	11	—	-
Astragalus	L	0.282	21	—	-
	T.D.-d	0.919	28	—	-
Calcaneum	L	1.684	9	—	-
	A.P.D.-p	0.325	12	—	-
	T.D.-p	1.581	17	—	-
Scapho-cuboid	A.P.D.-p	0.695	12	—	-
	T.D.-p	1.234	12	—	-
Metatarsus	A.P.D.-p	0.585	16	—	-
	T.D.-p	0.280	13	—	-
	A.P.D.-d	2.189	4	0.1	-
	T.D.-d	1.134	4	—	-
Phalange I	L	1.445	11	—	-
	A.P.D.-p	0.501	13	—	-
	T.D.-p	0.439	14	—	-
	A.P.D.-d	2.611	19	0.02	+
	T.D.-d	0.967	20	—	-
Phalange II	L	1.271	13	—	-
	T.D.-p	2.742	16	0.02	+
	A.P.D.-d	3.561	14	0.01	+
	T.D.-d	1.284	13	—	-
Phalange III	L	9.083	2	0.02	+
	H	0.277	4	—	-
	T.D.-p	6.778	4	0.01	+

Table 28. Comparison between *Eucladoceros teguliensis* from Tegelen and *E. senezensis senezensis* from Senèze.

		t	df	P	95%
Scapula	A.P.D.-p	1.199	29	—	-
	T.D.-p	2.129	28	0.05	+
Humerus	A.P.D.-d	5.755	54	0.001	+
	T.D.-d	3.792	56	0.001	+
Radius	L	1.219	27	—	-
	A.P.D.-p	2.052	38	0.05	+
	T.D.-p	1.996	36	0.1	-
	A.P.D.-d	1.122	33	—	-
	T.D.-d	1.308	34	—	-
Metacarpus	L	3.121	32	0.01	+
	A.P.D.-p	0.069	41	—	-
	T.D.-p	1.671	41	—	-
	A.P.D.-d	2.345	35	0.05	+
	T.D.-d	0.937	36	—	-
Tibia	A.P.D.-d	2.878	38	0.01	+
	T.D.-d	1.570	34	—	-
Astragalus	L	2.956	46	0.01	+
	T.D.-d	1.225	54	—	-
Calcaneum	L	2.595	32	0.02	+
	A.P.D.-p	2.199	33	0.05	+
	T.D.-p	2.915	41	0.01	+
Scapho-cuboid	A.P.D.-p	1.789	42	0.1	-
	T.D.-p	3.226	40	0.01	+
Metatarsus	A.P.D.-p	1.606	35	—	-
	T.D.-p	1.055	32	—	-
	A.P.D.-d	0.775	26	—	-
	T.D.-d	0.231	25	—	-
Phalange I	L	3.610	84	0.001	+
	A.P.D.-p	0.862	82	—	-
	T.D.-p	0.793	86	—	-
	A.P.D.-d	0.615	91	—	+
	T.D.-d	1.548	91	—	-
Phalange II	L	3.203	13	0.002	+
	T.D.-p	2.123	16	0.05	+
	A.P.D.-d	0.447	14	—	-
	T.D.-d	0.225	13	—	-
Phalange III	L	0.479	65	—	-
	H	2.656	66	0.02	+
	T.D.-p	0.179	49	—	-

Table 29. Comparison between *Eucladoceros teguliensis* from Tegelen and *E. tetraceros* from Peyrolles.

		t	df	P	95%
Scapula	A.P.D.-p	0.487	5	—	-
	T.D.-p	0.911	5	—	-
Humerus	A.P.D.-d	2.362	21	0.05	+
	T.D.-d	2.103	23	0.05	+
Tibia	A.P.D.-d	4.013	11	0.01	+
	T.D.-d	2.560	7	0.05	+
Astragalus	L	8.606	19	0.001	+
	T.D.-d	4.687	23	0.001	+
Calcaneum	L	4.881	8	0.002	+
	A.P.D.-p	2.917	7	0.05	+
	T.D.-p	2.902	10	0.02	+
Metatarsus	A.P.D.-d	0.577	2	—	-
	T.D.-d	0.438	1	—	-

Table 30. Dimensions of the antlers of *Cervus rhenanus* from Tegelen.

C	Cn	sym	1	2	3	4	5	6	7	8	9	10	11
RGM			22.5	24.5	31.5	71.5	—	—	—	—	—	—	90
RGM	28148		—	—	36.5	68.5	380	135	+555	+575	160	130	65
RGM	28290		—	—	—	72.0	530	+145	+620	+625	+95	+85	85
RGM	35256		—	32.0	42.0	73.0	—	—	—	—	—	—	—
RGM	53071		20.0	30.0	44.5	72.0	—	—	—	—	—	—	90
RGM	53088		—	—	44.5	84.5	—	—	—	—	+100	—	75
RGM	53089		25.0	20.0	35.5	94.0	—	—	—	—	50	—	40
RGM	53097	s	26.0	25.0	39.0	88.0	—	—	—	—	—	—	65
		d	25.0	25.0	40.0	—	—	—	—	—	—	—	—
RGM	53155		—	28.5	—	—	—	—	—	—	—	—	—
RGM	53419		—	—	48.5	56.0	—	—	—	—	—	—	—
RGM	53803		±30	31.0	—	—	—	—	—	—	—	—	—
RGM	62904	s	32.0	26.0	+32	—	—	—	—	—	—	—	—
		d	34.5	26.5	40.0	—	—	—	—	—	—	—	—
RGM	65880		—	—	41.5	68.5	—	—	—	—	+125	—	90
RGM	72161		23.0	22.5	39.0	—	—	—	—	—	—	—	—
RGM	74335		20.5	27.5	+34	—	—	—	—	—	—	—	—
RGM	75125		—	—	34.5	71.5	—	—	—	—	65	—	65
RGM	79792		24.5	25.0	+31	—	—	—	—	—	—	—	—
RGM	85938		—	—	+35	53.0	—	—	—	—	—	—	90
RGM	86310		—	—	+37	70.0	—	—	—	—	—	—	80
RGM	86686	s	24.0	27.5	42.0	74.0	305	—	+425	—	175	—	90
		d	24.0	28.5	46.0	84.0	±285	210	±570	—	180	—	85
RGM	86837	s	—	—	45.0	59.5	+290	—	—	—	185	—	80
		d	—	—	44.0	59.5	—	—	+340	+335	165	—	85
RGM	86968	s	24.5	20.5	35.5	63.5	—	—	—	—	—	—	60
		d	20.0	23.0	41.0	55.0	285	55	385	385	135	—	65
RGM	87065		42.0	16.0	—	—	—	—	—	—	—	—	—
RGM	93199	s	50.0	25.0	41.5	42.0	235	185	+450	—	+60	135	75
		d	42.0	23.0	+39	44.0	230	210	470	—	—	—	70
RGM	96356		—	—	+42	50.0	—	—	—	—	—	—	80
RGM	96427		—	—	38.0	69.5	—	—	—	—	—	—	—
RGM	102786		—	—	41.0	60.0	—	—	—	—	—	—	—
RGM	103161		—	—	39.5	—	—	—	—	—	—	—	—
RGM	119904		—	—	34.5	82.5	—	—	—	—	—	—	60
Ha	15613		—	—	—	—	—	—	—	—	210	—	—
Ha	15777		30.5	25.0	33.5	79.0	385	+200	+650	+680	+180	85	105
Ha	15782		—	—	41.0	65.0	200	—	+335	—	—	—	±65
Ha	15828	s	41.0	15.5	—	—	—	—	180	—	—	—	—
		d	40.0	16.5	—	—	—	—	—	—	—	—	—
Ha	15921		35.0	27.0	33.0	76.0	335	335	730	770	210	+125	100
Ha	15923		—	28.0	39.5	75.0	—	—	—	—	—	—	70
Ha	15924		—	—	—	82.0	—	—	—	—	—	—	80
Ha	15925		—	—	+36	82.0	—	—	—	—	—	—	85
Ha	15926		—	—	36.5	±90	—	—	—	—	—	—	—

C = Collection; Cn = Catalogue number; sym = Symmetry; s = sinister, d = dexter; 1-11 see methods: antlers; + = actual value probably slightly larger; ± = estimation

Table 31. Length of the upper dentary segments of *Cervus* of the various localities.

	Locality	N	Min	M	Max	SD
P^2-M^3	Peyrolles	1		78		—
	Senèze	23	81	87.43	92	3.12
	St Vallier	22	78.5	82.92	89.5	3.31
	Tegelen	5	82	84.7	88	2.40
M^1-M^3	Peyrolles	3	46	48.80	51	2.56
	Senèze	43	46	51.56	56	2.33
	St Vallier	46	45	48.00	52	1.56
	Tegelen	8	45.5	48.5	50.5	1.73
	Peyrolles	3	34.5	35.00	35.5	0.50
	Senèze	32	37	39.01	42.5	1.66
P^2-P^4	St Vallier	27	34.5	37.14	40.5	1.62
	Tegelen	6	36	37.8	40.5	1.70
$\frac{P^2\text{-}P^4 * 100}{M^1\text{-}M^3}$	Peyrolles	1		76.0		—
	Senèze	23	69.6	75.50	81.5	3.03
	St Vallier	22	72.6	76.55	81.0	2.11
	Tegelen	5	72.3	77.1	80.0	2.88

Table 32. Length and width of the upper molars of *Cervus* from the various localities.

	Locality	N	Min	M	Max	SD
L M^3	Peyrolles	7	15.5	17.35	18.5	1.10
	Senèze	30	16.5	18.40	20.5	1.12
	St Vallier	26	15.5	16.96	19	0.81
	Tegelen	16	16	17.3	18	0.76
W M^3	Peyrolles	7	17	17.64	18	0.37
	Senèze	28	16.5	18.42	20.5	0.95
	St Vallier	26	16.5	17.46	19.5	0.69
	Tegelen	15	16	17.9	19.5	0.92
L M^2	Peyrolles	9	15	16.77	18	1.17
	Senèze	32	17.5	18.87	21.5	1.00
	St Vallier	31	16	17.27	19.5	0.95
	Tegelen	19	15.5	17.4	18.5	0.76
W M^2	Peyrolles	9	16.5	17.66	18.5	0.61
	Senèze	31	16.5	18.95	20.5	0.88
	St Vallier	31	16.5	18.03	20.5	0.84
	Tegelen	18	16.5	17.8	20	0.91
L M^1	Peyrolles	8	14.5	15.93	17.5	0.90
	Senèze	36	14.5	16.81	19.5	0.92
	St Vallier	30	14	15.20	17	0.87
	Tegelen	18	13.5	15.6	16.5	0.71
W M^1	Peyrolles	9	16	16.72	17.5	0.44
	Senèze	35	16	17.42	19	0.75
	St Vallier	30	14.5	16.56	18.5	0.91
	Tegelen	16	15.5	16.7	17.5	0.51

Table 33. Length and width of the upper premolars of *Cervus* from the various localities.

	Locality	N	Min	M	Max	SD
L P^4	Peyrolles	5	10.5	10.90	11.5	0.41
	Senèze	33	10.5	11.77	13	0.67
	St Vallier	28	9.5	10.50	11.5	0.55
	Tegelen	13	10	11.3	13	0.76
W P^4	Peyrolles	5	13	13.90	14.5	0.98
	Senèze	32	13.5	15.23	16	0.57
	St Vallier	27	14	14.64	15.5	0.40
	Tegelen	12	13	14.7	17	0.99
L P^3	Peyrolles	6	11.5	12.00	13	0.63
	Senèze	33	12	13.07	14	0.61
	St Vallier	24	12	12.75	14	0.50
	Tegelen	9	11	12.3	13.5	0.87
W P^3	Peyrolles	6	11.5	12.08	12.5	0.37
	Senèze	31	12	13.46	14.5	0.64
	St Vallier	24	12	12.93	14	0.48
	Tegelen	9	13	14.5	15.5	0.77
L P^2	Peyrolles	4	11.5	11.75	12	0.28
	Senèze	29	12	13.41	14.5	0.57
	St Vallier	19	12	12.86	14.5	0.55
	Tegelen	8	11	11.9	12.5	0.55
W P^2	Peyrolles	4	10	10.50	11	0.40
	Senèze	29	11	12.05	13	0.64
	St Vallier	19	11	11.52	12.5	0.41
	Tegelen	8	10.5	11.7	13.5	1.08

Table 34. Length of the lower dentary segments of *Cervus* of the various localities.

	Locality	N	Min	M	Max	SD
P_2-M_3	Peyrolles	2	82.5	83.00	83.5	0.70
	Senèze	74	86.5	92.87	102	3.41
	St Vallier	41	80	87.54	97	4.12
	Tegelen	7	81.5	86.9	88.5	2.22
M_1-M_3	Peyrolles	6	50	51.60	53.5	1.15
	Senèze	110	51.5	55.89	61.5	2.05
	St Vallier	70	47.5	52.54	58.5	2.37
	Tegelen	9	49	52.4	54.5	1.63
P_2-P_4	Peyrolles	3	32	33.50	35	1.65
	Senèze	80	34.5	37.54	42	1.72
	St Vallier	53	31.5	35.90	40	1.96
	Tegelen	9	33.5	36.6	39	1.74
$\frac{P_2\text{-}P_4 * 100}{M_1\text{-}M_3}$	Peyrolles	2	62.0	63.50	65.0	2.12
	Senèze	74	62.9	67.12	74.2	2.32
	St Vallier	41	64.1	68.46	74.0	2.37
	Tegelen	6	66.6	69.6	73.1	2.03

Table 35. Length and width of the lower molars of *Cervus* from the various localities.

	Locality	N	Min	M	Max	SD
L M_3	Peyrolles	16	21.5	22.56	23.5	0.65
	Senèze	36	21.5	23.81	26	1.20
	St Vallier	45	19	22.11	24	1.14
	Tegelen	25	20.5	21.6	23	0.83
W M_3	Peyrolles	16	10	10.62	11.5	0.42
	Senèze	35	11	11.55	13.5	0.44
	St Vallier	44	9.5	10.89	12	0.55
	Tegelen	26	10	11.0	13	0.70
L M_2	Peyrolles	12	15.5	17.33	19	1.11
	Senèze	35	16	18.10	20.5	1.14
	St Vallier	49	14.5	17.08	19.5	1.11
	Tegelen	30	15.5	17.2	18	0.58
W M_2	Peyrolles	12	10.5	10.95	12	0.44
	Senèze	33	11	11.81	13.5	0.40
	St Vallier	48	10	11.34	12.5	0.52
	Tegelen	30	10.5	11.3	13	0.70
L M_1	Peyrolles	9	13.5	14.94	16.5	1.04
	Senèze	38	14	16.27	19	1.13
	St Vallier	42	13	14.97	17.5	0.98
	Tegelen	22	14.5	15.4	16	0.51
W M_1	Peyrolles	9	9.5	9.94	11	0.56
	Senèze	36	10	10.81	12.5	0.37
	St Vallier	40	9	10.32	11	0.45
	Tegelen	25	9.5	10.2	11.5	0.55

Table 36. Length and width of the lower premolars of *Cervus* from the various localities.

	Locality	N	Min	M	Max	SD
L P_4	Peyrolles	9	11.5	13.00	14.5	0.95
	Senèze	41	12.5	14.35	16	0.74
	St Vallier	43	11.5	13.34	15	0.87
	Tegelen	22	12.5	13.9	15	0.75
W P_4	Peyrolles	9	7.5	8.11	9.5	0.65
	Senèze	41	8	8.91	10.5	0.52
	St Vallier	43	7.5	8.80	10	0.55
	Tegelen	24	7.5	8.8	10	0.69
L P_3	Peyrolles	6	12.5	12.75	13.5	0.41
	Senèze	38	12.5	13.72	15.5	0.62
	St Vallier	38	11.5	12.97	14.5	0.68
	Tegelen	24	12	13.0	14	0.54
W P_3	Peyrolles	6	6.5	7.33	8.5	0.68
	Senèze	38	6	7.90	9	0.48
	St Vallier	38	7	8.03	8.5	0.45
	Tegelen	25	7	7.8	8.5	0.43
L P_2	Peyrolles	3	9	9.66	10.5	0.76
	Senèze	32	9	10.76	12.5	0.69
	St Vallier	30	9	10.56	11.5	0.64
	Tegelen	16	9	10.0	11	0.51
W P_2	Peyrolles	2	5.5	6.00	6.5	0.70
	Senèze	32	5	6.39	7.5	0.56
	St Vallier	29	5.5	6.25	7	0.41
	Tegelen	16	5.5	5.9	6.5	0.26

Table 37. Comparison between *Cervus rhenanus* from Tegelen and *C. philisi valliensis* from St Vallier.

		t	df	P	95%
L	P^2-M^3	1.129	25	0.1	-
	M^1-M^3	0.824	52	—	-
	P^2-P^4	0.895	31	—	-
L	M^3	1.352	40	—	-
	M^2	0.505	48	—	-
	M^1	1.647	46	—	-
	P^4	3.831	39	0.001	+
	P^3	1.866	31	0.1	-
	P^2	4.141	25	—	-
W	M^3	1.739	39	0.1	-
	M^2	0.896	47	—	-
	M^1	0.568	44	—	-
	P^4	0.272	37	—	-
	P^3	7.057	31	0.001	+
	P^2	0.638	25	—	-
L	P_2-M_3	0.399	46	—	-
	M_1-M_3	0.172	77	—	-
	P_2-P_4	1.005	60	—	-
L	M_3	1.964	68	0.1	-
	M_2	0.547	77	—	-
	M_1	1.921	62	0.1	-
	P_4	2.568	63	0.02	+
	P_3	0.183	60	—	-
	P_2	3.021	44	0.01	+
W	M_3	0.730	68	—	-
	M_2	0.289	76	—	-
	M_1	0.960	63	—	-
	P_4	0.000	65	—	-
	P_3	2.020	61	0.05	+
	P_2	3.081	43	0.01	+

Table 38. Comparison between *Cervus rhenanus* from Tegelen and *C. philisi philisi* from Senèze.

		t	df	P	95%
L	P^2-M^3	1.832	26	0.1	-
	M^1-M^3	3.526	49	0.001	+
	P^2-P^4	1.633	36	—	-
L	M^3	3.512	44	0.001	+
	M^2	5.522	49	0.001	+
	M^1	4.891	52	0.001	+
	P^4	2.063	44	0.05	+
	P^3	3.056	40	0.01	+
	P^2	6.680	35	0.001	+
W	M^3	1.729	41	0.1	-
	M^2	4.356	47	0.001	+
	M^1	3.480	49	0.001	+
	P^4	2.222	42	0.05	+
	P^3	4.103	38	0.001	+
	P^2	1.170	35	0.1	-
L	P_2-M_3	4.528	79	0.001	+
	M_1-M_3	4.973	117	0.001	+
	P_2-P_4	2.537	87	—	-
L	M_3	7.970	59	0.001	+
	M_2	3.909	63	0.001	+
	M_1	3.407	58	0.002	+
	P_4	2.290	61	0.05	+
	P_3	4.676	60	0.001	+
	P_2	3.897	46	0.001	+
W	M_3	3.760	59	0.001	+
	M_2	3.591	61	0.001	+
	M_1	5.184	59	0.001	+
	P_4	0.728	63	—	-
	P_3	0.842	61	—	-
	P_2	3.313	46	0.002	+

Table 39. Comparison between *Cervus rhenanus* from Tegelen and *C. perolensis* from Peyrolles.

		t	df	P	95%
L	P^2-M^3	2.548	4	0.1	-
	M^1-M^3	0.228	9	—	-
	P^2-P^4	2.710	7	0.05	+
	M^3	0.127	21	—	-
	M^2	1.718	26	0.1	-
L	M^1	1.008	24	—	-
	P^4	1.103	16	—	-
	P^3	0.724	13	—	-
	P^2	0.505	10	—	-
W	M^3	0.714	20	—	-
	M^2	0.415	25	—	-
	M^1	0.098	23	—	-
	P^4	1.522	15	—	-
	P^3	7.106	13	0.001	+
	P^2	2.108	10	0.1	-
L	P_2-M_3	2.347	7	0.1	-
	M_1-M_3	1.037	13	—	-
	P_2-P_4	2.700	10	0.05	+
L	M_3	3.916	39	0.001	+
	M_2	0.499	40	—	-
	M_1	1.666	29	—	-
	P_4	2.808	29	0.01	+
	P_3	1.055	28	—	-
	P_2	0.991	17	—	-
W	M_3	1.960	40	0.1	-
	M_2	1.603	40	—	-
	M_1	1.211	32	—	-
	P_4	2.596	31	0.02	+
	P_3	2.143	29	0.05	+
	P_2	0.435	16	—	-

Table 40. Width-length index of the upper molars and premolars of *Cervus* from the various localities.

	Locality	N	Min	M	Max	SD
M^3	Peyrolles	7	94	101.92	109	5.29
	Senèze	28	92	100.42	109	3.88
	St Vallier	26	92	103.13	114	5.59
	Tegelen	13	90	103.7	112	6.33
M^2	Peyrolles	8	100	107.50	116	5.90
	Senèze	31	91	100.73	108	4.60
	St Vallier	31	89	104.63	118	6.22
	Tegelen	18	94	102.84	110	4.65
M^1	Peyrolles	8	94	105.03	117	6.92
	Senèze	35	94	103.97	120	5.82
	St Vallier	30	96	109.10	124	6.52
	Tegelen	13	101	108.78	122	5.63
P^4	Peyrolles	5	122	127.59	138	4.80
	Senèze	28	116	129.09	142	5.89
	St Vallier	27	126	139.64	157	6.15
	Tegelen	11	121	130.88	152	10.19
P^3	Peyrolles	6	92	100.97	108	6.97
	Senèze	31	88	102.77	112	6.30
	St Vallier	24	89	106.34	130	9.33
	Tegelen	9	103	117.75	136	11.74
P^2	Peyrolles	4	83	89.39	91	4.51
	Senèze	29	81	89.67	100	5.10
	St Vallier	19	84	89.72	100	5.65
	Tegelen	8	86	98.02	108	7.35

Table 41. Width-length index of the lower molars and premolars of *Cervus* from the various localities.

	Locality	N	Min	M	Max	SD
M_3	Peyrolles	16	44	47.08	51	1.38
	Senèze	35	44	48.70	55	2.48
	St Vallier	44	45	49.26	54	1.95
	Tegelen	25	47	50.6	56	2.47
M_2	Peyrolles	12	56	63.41	68	4.16
	Senèze	33	57	65.60	72	3.44
	St Vallier	48	57	66.61	72	3.64
	Tegelen	30	59	65.9	75	4.57
M_1	Peyrolles	9	57	67.16	72	5.39
	Senèze	36	55	66.81	75	4.78
	St Vallier	40	60	68.97	81	5.12
	Tegelen	22	60	66.6	79	4.64
P_4	Peyrolles	9	57	62.77	70	4.48
	Senèze	41	51	62.24	72	4.55
	St Vallier	43	56	66.18	76	4.31
	Tegelen	22	55	63.8	79	5.71
P_3	Peyrolles	6	52	57.48	65	4.62
	Senèze	38	48	57.70	69	4.52
	St Vallier	38	51	62.05	68	3.67
	Tegelen	24	53	60.1	67	3.57
P_2	Peyrolles	2	57	59.89	61	2.83
	Senèze	32	52	59.36	71	3.82
	St Vallier	29	52	59.38	66	3.37
	Tegelen	16	52	59.6	64	2.83

Table 42. Dimensions of the scapulae of *Cervus* from the various localities.

	Locality	N	Min	M	Max	SD
A.P.D.	Peyrolles	1		32.5		—
-p	Senèze	30	32.5	36.73	39.5	1.93
	St Vallier	0		—		—
	Tegelen	9	31	33.3	36.5	1.93
T.D.-p	Peyrolles	1		28.5		—
	Senèze	30	27.5	32.35	37.5	2.55
	St Vallier	0		—		—
	Tegelen	11	27.5	30.0	34	2.08

Table 43. Dimensions of the humeri of *Cervus* from the various localities.

	Locality	N	Min	M	Max	SD
L	Peyrolles	0		—		—
	Senèze	20	191	201.25	211	6.16
	St.Vallier	0		—		—
	Tegelen	2	187	189.0	191	2.00
A.P.D.	Peyrolles	8	18	19.50	21	0.96
-d	Senèze	38	21.5	23.03	26.5	1.25
	St Vallier	12	21.5	22.83	24.5	0.77
	Tegelen	15	19.5	21.7	24	1.41
T.D.-d	Peyrolles	8	30.5	34.18	36.5	1.88
	Senèze	38	36.5	39.92	43.5	1.81
	St Vallier	12	36.5	38.54	40.5	1.33
	Tegelen	15	34	37.6	41.5	2.29

Table 44. Dimensions of the radii of *Cervus* from the various localities.

	Locality	N	Min	M	Max	SD
L	Peyrolles	1		191		—
	Senèze	30	206	235.30	249	11.28
	St Vallier	6	216	228.58	248	12.00
	Tegelen	4	227	234.8	243	5.67
A.P.D.	Peyrolles	3	18.5	19.16	20	0.76
-p	Senèze	36	21.5	23.19	25	1.14
	St Vallier	18	20.5	22.11	24.5	1.03
	Tegelen	13	18.5	21.0	23.5	1.17
T.D.-p	Peyrolles	3	33	33.83	35	1.01
	Senèze	36	36	40.47	44.5	2.06
	St Vallier	18	34	37.50	41	2.07
	Tegelen	11	31.5	36.3	39.5	2.47
A.P.D.	Peyrolles	2		19.00		—
-d	Senèze	33	20.5	22.66	25	0.98
	St Vallier	9	21.5	22.44	24.5	0.87
	Tegelen	9	19	21.4	23	1.37
T.D.-d	Peyrolles	2	31	31.25	31.5	0.35
	Senèze	33	34.5	36.81	40	1.65
	St Vallier	9	32.5	34.77	37.5	1.81
	Tegelen	9	31	34.2	37	1.84

Table 45. Dimensions of the metacarpi of *Cervus* from the various localities.

	Locality	N	Min	M	Max	SD
L	Peyrolles	1		191		—
	Senèze	30	206	235.30	249	11.28
	St Vallier	6	216	228.58	248	12.00
	Tegelen	4	227	234.8	243	5.67
A.P.D.	Peyrolles	3	18.5	19.16	20	0.76
-p	Senèze	36	21.5	23.19	25	1.14
	St Vallier	18	20.5	22.11	24.5	1.03
	Tegelen	13	18.5	21.0	23.5	1.17
T.D.-p	Peyrolles	3	33	33.83	35	1.01
	Senèze	36	36	40.47	44.5	2.06
	St Vallier	18	34	37.50	41	2.07
	Tegelen	11	31.5	36.3	39.5	2.47
A.P.D.	Peyrolles	2		19.00		—
-d	Senèze	33	20.5	22.66	25	0.98
	St Vallier	9	21.5	22.44	24.5	0.87
	Tegelen	9	19	21.4	23	1.37
T.D.-d	Peyrolles	2	31	31.25	31.5	0.35
	Senèze	33	34.5	36.81	40	1.65
	St Vallier	9	32.5	34.77	37.5	1.81
	Tegelen	9	31	34.2	37	1.84

Table 46. Dimensions of the femuri of *Cervus* from the various localities.

	Locality	N	Min	M	Max	SD
L	Peyrolles	0		—		—
	Senèze	20	241	265.60	280	11.99
	St Vallier	2	237	253.00	269	22.62
	Tegelen	3	233	253.3	266	14.52
T.D.-p	Peyrolles	0		—		—
	Senèze	25	36.5	39.94	45.5	2.40
	St Vallier	2	32.5	35.00	37.5	3.53
	Tegelen	4	36	37.1	39	1.21
A.P.D.	Peyrolles	0		—		—
-d	Senèze	31	68	76.09	83	3.84
	St Vallier	5	66	70.80	77	2.10
	Tegelen	1		76.0		—
T.D.-d	Peyrolles	0		—		—
	Senèze	30	27.5	30.66	35	1.54
	St Vallier	5	27.5	29.60	32.5	1.94
	Tegelen	4	29	30.2	31	0.84

Table 47. Dimensions of the tibiae of *Cervus* from the various localities.

	Locality	N	Min	M	Max	SD
L	Peyrolles	2	267	271.00	275	5.65
	Senèze	26	290	318.57	343	14.40
	St Vallier	4	289	309.50	322	10.96
	Tegelen	3	292	303.0	316	9.90
A.P.D.	Peyrolles	4	23.5	25.37	28	2.24
-d	Senèze	33	27	30.71	33	1.62
	St Vallier	16	27.5	29.28	31.5	1.09
	Tegelen	14	23.5	27.0	29.5	1.39
T.D.-d	Peyrolles	5	28.5	30.30	31.5	1.43
	Senèze	33	33.5	36.43	40	1.78
	St Vallier	15	32	34.53	37.5	1.66
	Tegelen	13	30	33.2	36	1.73

Table 48. Dimensions of the astragali of *Cervus* from the various localities.

	Locality	N	Min	M	Max	SD
L	Peyrolles	2	39	39.50	40	0.70
	Senèze	50	41	45.52	49.5	2.12
	St Vallier	33	41	43.56	47.5	2.53
	Tegelen	16	40	42.1	46	1.58
T.D.-d	Peyrolles	2	24	24.50	25	0.70
	Senèze	55	25.5	28.26	31.5	1.52
	St Vallier	34	24.5	26.77	29	1.07
	Tegelen	17	23.5	25.4	28.5	1.10

Table 49. Dimensions of the calcanei of *Cervus* from the various localities.

	Locality	N	Min	M	Max	SD
L	Peyrolles	1		86.5		—
	Senèze	32	89	97.75	108	5.71
	St Vallier	14	89.5	95.28	100	3.46
	Tegelen	9	90	92.3	96	1.99
A.P.D.	Peyrolles	1		29.5		—
-p	Senèze	35	31.5	34.71	39.5	2.01
	St Vallier	12	31.5	33.00	35.5	1.26
	Tegelen	11	29	31.7	34.5	1.50
T.D.-p	Peyrolles	1		22.5		—
	Senèze	39	24.5	27.06	29.5	1.30
	St Vallier	16	23	25.53	27.5	1.37
	Tegelen	14	21.5	25.2	31.5	2.3

Table 50. Dimensions of the scapho-cuboides of *Cervus* from the various localities.

	Locality	N	Min	M	Max	SD
A.P.D.	Peyrolles	0		—		—
-p	Senèze	40	25.5	28.12	30.5	1.44
	St Vallier	16	24.5	26.59	28.5	1.17
	Tegelen	9	23.5	25.5	27	1.15
T.D.-p	Peyrolles	0		—		—
	Senèze	40	32.5	35.21	38.5	1.78
	St Vallier	16	32	33.62	35.5	1.38
	Tegelen	7	30.5	32.0	35.5	1.49

Table 51. Dimensions of the metatarsi of *Cervus* from the various localities.

	Locality	N	Min	M	Max	SD
L	Peyrolles	0		—		—
	Senèze	29	239	257.17	278	9.73
	St Vallier	10	241	249.70	260	6.41
	Tegelen	4	243	251.8	255	5.07
A.P.D.	Peyrolles	2	26.5	27.00	27.5	0.70
-p	Senèze	41	30.5	33.67	37	1.71
	St Vallier	24	30	32.22	34.5	1.19
	Tegelen	13	30	31.6	34	1.35
T.D.-p	Peyrolles	2	23.5	24.00	24.5	0.70
	Senèze	41	27	30.41	33.5	1.55
	St Vallier	24	26.5	29.10	31.5	1.27
	Tegelen	11	25.5	27.9	32	2.01
A.P.D.	Peyrolles	0		—		—
-d	Senèze	33	22.5	23.75	26.5	0.96
	St Vallier	11	21	22.31	23.5	0.84
	Tegelen	15	20	21.6	23.5	0.96
T.D.-d	Peyrolles	0		—		—
	Senèze	33	31.5	34.54	37.5	1.75
	St Vallier	11	32.5	33.72	35	0.97
	Tegelen	7	30.5	31.6	34	1.15

Table 52. Dimensions of the first phalanges of *Cervus* from the various localities.

	Locality	N	Min	M	Max	SD
L	Peyrolles	1		46.5		—
	Senèze	49	46.5	51.77	59.5	2.44
	St Vallier	32	42	47.90	54.5	3.61
	Tegelen	20	45.5	50.0	55	2.23
A.P.D.	Peyrolles	1		19.5		—
-p	Senèze	49	18.5	21.21	24	1.39
	St Vallier	32	17.5	19.64	22	1.50
	Tegelen	22	15.5	19.5	21	1.15
T.D.-p	Peyrolles	1		15.5		—
	Senèze	49	15	16.71	18.5	1.06
	St Vallier	32	14	15.60	17.5	1.17
	Tegelen	22	13.5	15.8	17.5	0.95
A.P.D.	Peyrolles	1		13.5		—
-d	Senèze	49	13	14.09	15.5	0.77
	St Vallier	32	11	12.82	14.5	1.06
	Tegelen	18	12	13.1	14	0.52
T.D.-d	Peyrolles	1		13		—
	Senèze	49	13.5	14.55	16	0.78
	St Vallier	34	12.5	13.70	15.5	0.95
	Tegelen	19	12.5	13.2	14.5	0.53

Table 53. Dimensions of the second phalanges of *Cervus* from the various localities.

	Locality	N	Min	M	Max	SD
L	Peyrolles	0		—		—
	Senèze	48	32	35.84	41	2.26
	St Vallier	19	32.5	36.71	42.5	2.52
	Tegelen	9	33	35.9	39.5	2.39
A.P.D.	Peyrolles	0		—		—
-p	Senèze	48	19.5	21.95	25	1.43
	St Vallier	18	18.5	21.50	23.5	0.47
	Tegelen	11	18.5	20.1	21.5	0.82
T.D.-p	Peyrolles	0		—		—
	Senèze	48	14.5	15.62	17.5	0.91
	St Vallier	19	14	15.18	16.5	0.80
	Tegelen	11	13.5	14.6	16	0.72
A.P.D.	Peyrolles	0		—		—
-d	Senèze	48	16.5	18.25	21	1.33
	St Vallier	19	14.5	16.92	18.5	1.17
	Tegelen	11	13.5	16.1	18	1.28
T.D.-d	Peyrolles	0		—		—
	Senèze	48	11.5	12.61	14.5	0.73
	St Vallier	19	10.5	12.00	13	0.66
	Tegelen	11	10	11.2	13	0.76

Table 54. Dimensions of the third phalanges of *Cervus* from the various localities.

	Locality	N	Min	M	Max	SD
L	Peyrolles	0		—		—
	Senèze	44	32	36.25	40.5	2.03
	St Vallier	9	33.5	37.27	40	1.98
	Tegelen	4	30	32.2	34.5	1.76
H	Peyrolles	0		—		—
	Senèze	45	20	22.22	25.5	1.16
	St Vallier	9	20	21.22	22.5	0.93
	Tegelen	3	17.5	18.7	20	1.02
T.D.-p	Peyrolles	0		—		—
	Senèze	46	11	12.19	13.5	0.72
	St Vallier	9	11.5	12.22	14	0.74
	Tegelen	5	11.5	12.0	12	0.34

Table 55. Comparison between *Cervus rhenanus* from Tegelen and *C. philisi valliensis* from St Vallier.

		t	df	P	95%
Humerus	A.P.D.-d	2.489	25	0.02	+
	T.D.-d	1.259	25	—	-
Radius	L	0.954	8	—	-
	A.P.D.-p	2.798	29	0.01	+
	T.D.-p	1.408	27	—	-
	A.P.D.-d	1.922	16	0.1	-
	T.D.-d	0.663	16	—	-
Metacarpus	L	0.503	13	—	-
	A.P.D.-p	6.301	21	0.001	+
	T.D.-p	2.952	22	0.01	+
	A.P.D.-d	0.481	17	—	-
	T.D.-d	2.855	16	0.02	+
Femur	L	0.019	3	—	-
	T.D.-p	1.181	4	—	-
	A.P.D.-p	2.260	4	0.1	-
	T.D.-d	0.571	7	—	-
Tibia	L	0.807	5	—	-
	A.P.D.-d	5.031	28	0.001	+
	T.D.-d	2.074	26	0.05	+
Astragalus	L	2.859	47	0.01	+
	T.D.-d	4.271	49	0.001	+
Calcaneum	L	2.335	21	0.05	+
	A.P.D.-p	2.258	21	0.05	+
	T.D.-p	0.482	28	—	-
Scapho-cuboid	A.P.D.-p	2.249	23	0.05	+
	T.D.-p	2.531	21	0.02	+
Metatarsus	L	0.582	12	—	-
	A.P.D.-p	1.444	35	—	-
	T.D.-p	2.151	33	0.05	+
	A.P.D.-d	1.961	24	0.1	-
	T.D.-d	4.211	16	0.001	+
Phalange I	L	2.333	50	0.05	+
	A.P.D.-p	0.369	52	—	-
	T.D.-p	0.665	52	—	-
	A.P.D.-d	1.049	48	—	-
	T.D.-d	2.112	51	0.05	+
Phalange II	L	0.807	26	—	-
	A.P.D.-p	5.872	27	0.001	+
	T.D.-p	1.982	28	0.1	-
	A.P.D.-d	1.788	28	0.1	-
	T.D.-d	3.028	28	0.01	+
Phalange III	L	4.389	11	0.002	+
	H	3.985	10	0.01	+
	T.D.-p	0.621	12	—	-

Table 56. Comparison between *Cervus rhenanus* from Tegelen and *C. philisi philisi* from Senèze.

		t	df	P	95%
Scapula	A.P.D.-p	4.676	37	0.001	+
	T.D.-p	2.734	39	0.01	+
Humerus	L	2.744	20	0.02	+
	A.P.D.-d	3.366	51	0.002	+
	T.D.-d	3.895	51	0.001	+
Radius	L	0.086	32	—	-
	A.P.D.-p	5.897	47	0.001	+
	T.D.-p	5.609	45	0.001	+
	A.P.D.-d	3.133	40	0.01	+
	T.D.-d	4.108	40	0.001	+
Metacarpus	L	3.958	32	0.001	+
	A.P.D.-p	8.945	47	0.001	+
	T.D.-p	5.283	45	0.001	+
	A.P.D.-d	4.976	40	0.001	+
	T.D.-d	4.263	40	0.001	+
Femur	L	1.621	21	—	-
	T.D.-p	2.295	27	0.05	+
	A.P.D.-d	0.023	30	—	-
	T.D.-d	0.581	32	—	-
Tibia	L	1.809	27	0.1	-
	A.P.D.-d	7.470	45	0.001	+
	T.D.-d	5.584	44	0.001	+
Astragalus	L	5.934	64	0.001	+
	T.D.-d	7.183	70	0.001	+
Calcaneum	L	2.794	39	0.01	+
	A.P.D.-p	4.568	44	0.001	+
	T.D.-p	3.680	51	0.001	+
Scapho-cuboid	A.P.D.-p	5.091	47	0.001	+
	T.D.-p	4.492	45	0.001	+
Metatarsus	L	1.073	31	—	-
	A.P.D.-p	3.980	52	0.001	+
	T.D.-p	4.474	50	0.001	+
	A.P.D.-d	7.192	46	0.001	+
	T.D.-d	4.232	38	0.001	+
Phalange I	L	2.800	67	0.01	+
	A.P.D.-p	5.042	69	0.001	+
	T.D.-p	3.450	69	0.002	+
	A.P.D.-d	5.037	65	0.001	+
	T.D.-d	6.933	66	0.001	+
Phalange II	L	0.072	55	—	-
	A.P.D.-p	4.120	57	0.001	+
	T.D.-p	3.469	57	0.002	+
	A.P.D.-d	4.868	57	0.001	+
	T.D.-d	5.736	57	0.001	+
Phalange III	L	3.852	46	0.001	+
	H	5.114	46	0.001	+
	T.D.-p	0.579	49	—	-

Table 57. Comparison between *Cervus rhenanus* from Tegelen and *C. perolensis* from Peyrolles.

		t	df	P	95%
Scapula	A.P.D.-p	0.393	8	—	-
	T.D.-p	0.691	10	—	-
Humerus	A.P.D.-d	3.933	21	0.001	+
	T.D.-d	3.613	21	0.002	+
Radius	L	6.909	3	0.01	+
	A.P.D.-p	2.563	14	0.05	+
	T.D.-p	1.654	12	—	-
	A.P.D.-d	2.377	9	0.05	+
	T.D.-d	2.170	9	0.1	-
Metacarpus	A.P.D.-p	0.850	14	—	-
	T.D.-p	1.972	12	0.1	-
Tibia	L	4.022	3	0.05	+
	A.P.D.-d	1.814	16	0.1	-
	T.D.-d	3.320	16	0.01	+
Astragalus	L	2.251	16	0.05	+
	T.D.-d	1.114	17	—	-
Calcaneum	L	2.765	8	0.05	+
	A.P.D.-p	1.404	10	—	-
	T.D.-p	1.124	13	—	-
Metatarsus	A.P.D.-p	4.618	13	0.001	+
	T.D.-p	2.631	11	0.05	+
Phalange I	L	1.532	19	—	-
	A.P.D.-p	0.000	21	—	-
	T.D.-p	0.309	21	—	-
	A.P.D.-d	0.749	17	—	-
	T.D.-d	0.368	18	—	-