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Early Pleistocene Cervidae (Mammalia, Artiodactyla) from the Oosterschelde (the Netherlands), with a revision of the cervid genus *Eucladoceros* Falconer, 1868

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The Early Pleistocene cervid genus *Eucladoceros* is revised. It is concluded that there are three species: *E. dicranios* (which includes *E. sedgwickii*), *E. tetraceros*, and *E. ctenoides* (which includes *E. orticeros*, *E. falconeri*, *E. tegulensis*, *E. ertbornii*, *E. senezensis* and *E. darestei*). Within medium sized members of the genus *Cervus*, *C. rhenanus* is considered to include *C. philisi*, *C. perolensis*, *C. ischnoceros*, and *Pseudodama lyra*. *C. pardinensis* is a disinct species, while *C. suttonensis* is considered a *nomen nudum*. The cervid material from the Oosterschelde (province of Zeeland, the Netherlands) is described. Two species are present: *Eucladoceros ctenoides* and *Cervus rhenanus*.

Vroeg Pleistocene Cervidae (Mammalia, Artiodactyla) van de Oosterschelde, met een revisie van het hertengeslacht Eucladoceros *Falconer, 1868*. - Het hertengeslacht *Eucladoceros* uit het Vroeg Pleistoceen wordt in dit artikel gereviseerd. Er wordt geconcludeerd dat drie soorten kunnen worden onderscheiden: *E. dicranios* (waartoe *E. sedgwickii* wordt gerekend), *E. tetraceros*, en *E. ctenoides* (waartoe de taxa *E. orticeros*, *E. falconeri*, *E. tegulensis*, *E. ertbornii*, *E. senezensis* en *E. darestei* worden gerekend). Binnen de middelgrote vertegenwoordigers van het geslacht *Cervus*, wordt *C. rhenanus* gehandhaafd; tot deze soort worden de taxa *C. philisi*, *C. perolensis*, *C. ischnoceros* en *Pseudodama lyra* gerekend. *C. pardinensis* is een afzonderlijke soort, terwijl *C. suttonensis* wordt beschouwd als *nomen nudum*. Het hertenmateriaal uit de Oosterschelde (provincie Zeeland) wordt vervolgens beschreven. Er zitten twee soorten in: *Eucladoceros ctenoides* en *Cervus rhenanus*.

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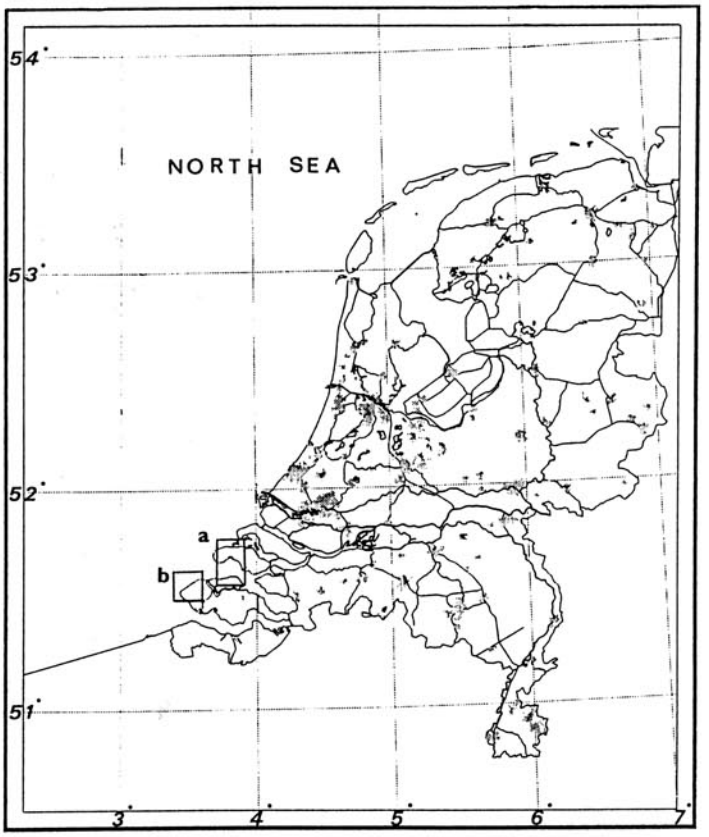
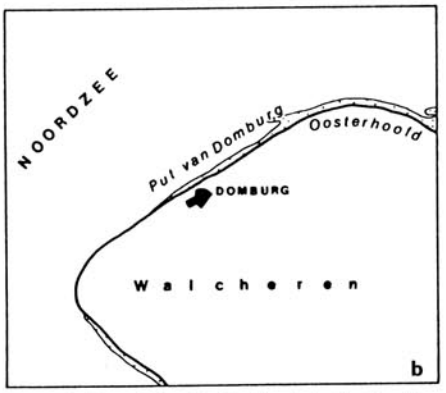
Keywords: Early Pleistocene, Oosterschelde, the Netherlands, Cervidae, *Eucladoceros*, *Cervus rhenanus*.

INTRODUCTION

De Man (1875) was the first to describe dredged fossil mammal remains from the Oosterschelde, Province of Zeeland, the Netherlands. Since then, more material, including cervids, has been described. From 1950 onwards, one day each year fossils are being 'fished' by the mussel vessel ZZ8 'Wilhelmina' from Zierikzee. The problem connected with this way of collecting fossils is that it is unknown from which layers the fossils originate. Probably the heavily mineralized terrestrial mammal fossils originate from a sandy clay layer which was deposited during the Tiglian. Marine mammals are 'fished' in addition to these heavily fossilized bones from terrestrial mammals. There also are less mineralized bones, which are supposedly of Weichselian or Holocene age. In literature, the heavily mineralized fossils, which produce a metallic sound when tapped on, are grouped by some authors (e.g. Schreuder 1950; Hooijer 1953; Van





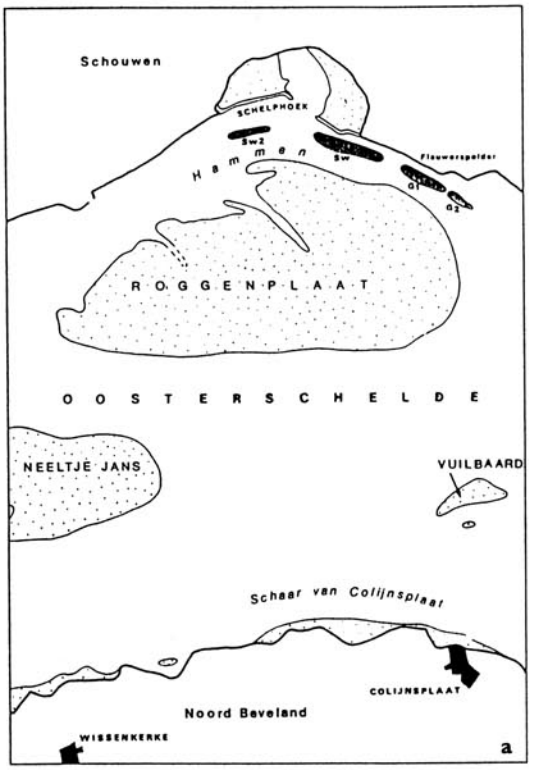


Figure 1 Map of the Netherlands, indicating the localities in the Oosterschelde(**a**) and the coast of Walcheren (**b**) [maps by Rijks Geologische Dienst, Haarlem]

der Vlerk 1953; Kortenbout van der Sluis 1955) as the 'black bones', 'black fauna' or 'black bone fauna'. Drees (1986) showed that these termes are not used in a proper way. Another disadvantage of the fishing method is that only large bones are retrieved, the ones which can not escape through the darns of the net; also, a lot of the material is rather fragmented. Most of the material is stored in the Maritime Museum in Zierik-

zee, in the National Museum of Natural History in Leiden (RMNH, catalogue numbers are preceded with St.) and in the collections of the 'Koninklijk Zeeuwsch Genootschap der Wetenschappen' in Middelburg, the Netherlands. Based on the labels attached to the specimens and on literature sources, the material originates from the following sites in the Oosterschelde (Fig. 1 a,b, although not all mentioned terms can be unambiguously retrieved):

-Oosterhoofd at Domburg, North Sea
-Flauwerspolder Pit 1 Oosterschelde
-Flauwerspolder Pit 2 Oosterschelde
-Wissenkerke, Oosterschelde
-In front of Flauwerspolder
-Oosterschelde, Gastenputje
-Schelpenrug, between Gasten and Olifantenputje
-In front of Flauwerspolder G1
-Fished in front of Flauwers.
-Put van Domburg = Put van Oostkapelle = Urk on official maps.
-Roggendam = Roggenplaat

The following taxa can be recognized among the heavily mineralized material: *Anancus arvernensis*, *Mammuthus meridionalis*, *Stephanorhinus* cf. *etruscus*, a large horse, coprolites of a hyaena (probably *Hyaena [= Pachycrocuta* or *Pliocrocuta] perrieri*), *Sus strozzii* and cervid material. There are at least four species in the cervid material from the Oosterschelde. Based on the morphology, there are clearly two antler fragments of *Cervus elaphus* and one antler fragment of *Megaloceros giganteus*. The material of these species is slightly fossilized only, and will not be discussed in the context of this paper, as it is probably of a Late Pleistocene age.

Based on the morphology and dimensions of the rest of the antler material there are a few fragments of antlers which are comparable to *Eucladoceros tegulensis/senezensis* and clearly one fragment (St. 119565) which is comparable to *Cervus rhenanus/philisi*. The material of these species is heavily fossilized. The presence of two species in the heavily fossilized antler material is also supported by the dimensions of the postcranial material. A few postcranial elements belong to a medium-sized cervid. This medium-sized material will be described and compared with *Cervus rhenanus/philisi/perolensis* and *Cervus pardinensis*. Most of the material belongs to a large cervid comparable with *Eucladoceros tegulensis/senezensis*. As the cervids *Cervus perrieri and Arvernoceros ardei* have the same size (Heintz 1970), the material can belong to these cervids too. However, based on the morphology of a few fragments of antlers comparable to *Eucladoceros tegulensis/senezensis*, which must belong to the large sized cervid, we can exclude *Cervus perrieri and Arvernoceros ardei*. The large sized cervid material will be described and compared with species of the genus *Eucladoceros* Falconer, 1868. However, as at least 12 species are described within this genus, and as there is a lot of confusion concerning delimitations of the species of this genus, a revision of the genus will first be made. In addition, the taxonomy of the medium-sized cervids *C. rhenanus/philisi/perolensis* will be reviewed.

TAXONOMICAL PART

I REVISION OF THE GENUS *EUCLADOCEROS* FALCONER, 1868

At least 12 species have been described within the Early Pleistocene genus *Eucladoceros* Falconer, 1868, all having more or less the same size (comparable with *Cervus elaphus*). All species are associated with a fauna containing *Anancus arvernensis* and/or *Archidiskodon meridionalis* and a large horse (like *Equus stenonis/robustus/bressanus*). However, as the taxonomy of the cervids is based on antlers, and most of the material attributed to the species is fragmented, there is no consensus concerning the validity of the species.

The morphology of the antlers within a species is known to be rather variable. De Vos (1984: 34), based on Heintz (1970), mentioned the following factors contributing to antler variation within a species.

- Intraspecific variation. The intraspecific variation of the antlers is much greater than that of other skeletal elements and of the teeth. This exceptional variability may be caused by the fact that the antlers are peripherally placed structures; their growth would be under hor-

monal control and antlers are thought to be less dependent on the size of other skeletal structures.
- Age (variation as function of ontogeny). The antlers of young individuals are generally simpler than those of older individuals; however, in very old animals the antlers are again simple in structure, and may show malformations; it is said that such antlers are 'set back'.
- The environment. Adequate nutrition is necessary for good antler development. However, development may vary from year to year with varying food supply.
- Seasonal influence. The morphology of the antlers changes during the growth season.
- Pathological aberrations.

To these factors we can add morphological differences caused by different geography (e.g. England or Italy) or by different chronology (e.g. Early or Late Villafranchian). According to Beninde (1937), taxonomic interpretations based on antlers are likely to be valid if based on specimens that are fully grown, reasonably complete and that show a constant morphology in at least four or five specimens coming from one locality. In the case of of *Eucladoceros*, most species are based on fragmentary antlers, a few on one or two fully grown, reasonable complete antlers and at least one species is based on a juvenile antler.

The following species have been described within the genus *Eucladoceros*:

E. ctenoides (Nesti, 1841)
E. orticeros (Nesti, 1841)
E. dicranios (Nesti, 1841)
E. sedgwickii (Falconer, 1868)
E. falconeri (Dawkins, 1868)
E. tetraceros (Dawkins, 1878)
E. ernesti (Fritsch, 1884)
E. tegulensis (Dubois, 1904)
E. ertbornii (Dubois, 1907)
E. senezensis (Depéret, 1910)
E. boulei Teilhard & Piveteau, 1930
E. darestei (Depéret, 1931)

Three morphological types of antlers can be distinguished based on the morphology of the type specimens (antlers) of those species:

Type 1: An antler type consisting of a beam with four tines placed at the anterior side of the beam; the tines are bi- or trifurcated and flattened in lateral direction. This type is found in *E. dicranios* and *E. sedgwickii* (Figs. 2 and 3).

Type 2: An antler type consisting of a beam with four or five tines, which are placed more or less perpendicular to the anterior side of the beam. The tines are first rather straight, but bend backwards at the ends. The distance between the first and second tine is more or less the same as between the second and third, and the third and the fourth. The beam and tines become flattened distally. This type of antler is found in *E. tetraceros* (Fig. 4).

Type 3: An antler type consisting of a beam with four or five tines, which are placed more or less perpendicular to the anterior side of the beam. First, the tines bend a little backwards and after one third of the length of the tine the points bend forwards again. The distance between the first and second tine is relatively large compared to the distance between the second and third, and third and fourth tines. An accessory tine is sometimes present between the first and second tine. The beam and tines become flattened distally. This type of antler is found in *E. ctenoides*, *E. orticeros*, *E. falconeri*, *E. tegulensis*, *E. ertbornii*, *E. senezensis*, and *E. darestei* (see Figs. 5-10).

Antler type I contains:

***Eucladoceros dicranios* (Nesti, 1841)**

Holotype: Nesti (1841) based the species on specimens from the Upper Valdarno, Tuscany; it was called *Cervus dicranios*. According to Azzaroli & Mazza (1992: 47, pl. 1 and 2) the holotype is specimen IGF 270, a skull with antlers. The left antler was already figured by Rütimeyer (1883, pl. I) and this figure is partly reproduced by Heintz (1970: 93, fig. 198). Here it is reproduced in mirror image, for comparison with the holotype of *E. sedgwickii* as Fig. 2.

Description: The description Nesti (1841) gave was repeated by Azzaroli & Mazza (1992: 47). They add the following description to the holotype of *Eucladoceros dicranios*:
'Its anterior (outer) tines, as well as the second (crown 1) tines are actually divided into three

Figure 2 Holotype, left antler IGF 270 of *Eucladoceros dicranios* (Nesti, 1841) from Upper Valdarno, mirror image (from Heintz, 1970, fig. 198).

prongs, and the following tines are bifurcated, so that the report by the secretaries (meant are Savi & Sismonda; JdV/DM/JWFR) is not very accurate. The skull bears 26 points in all, 14 on the right and 12 on the left; in spite of this difference the assymmetry is not very pronounced. The outer tines are implanted a few cm above the burr; they diverge laterally and turn upwards, with a characteristic ridge dorsally at the axil, and divided into three prongs in a frontal plane. There is a small inner tine on both sides, implanted mesially on the beam at the basal axil and directed upwards. The crown tines are more or less strongly flattened, implanted dorsally on the beam, and expand in a vertical plane diverging at 45^0 from the sagittal plane. They show a marked backward bend beginning near their bases and are all bifurcated, except crown tine 1 which divides into three prongs, the anterior of which is directed upwards. Crown tine 2 divides into two very long prongs, one of which, on the right side, bears a small accessory point directly mesially. Crown tines 3 are broadly flattened and bifurcated; the beams continue into two short, flattened posterior tines, the right side one bifurcated. The total antler span is 190 cm'.

***Eucladoceros sedgwickii* (Falconer, 1868)**

Holotype: The species *Cervus (Eucladoceros) sedgwickii* was based on only one fine, though damaged, right antler from Bacton, Norfolk and on two basal parts of antlers. The two basal parts and the holotype are figured by Falconer (1868, Vol II, Plate 37), the holotype by Azzaroli (1953: 42, fig. 18), Heintz (1970: 92, fig. 195) and Azzaroli & Mazza (1992: 54, fig 8 no. 2, modified from Falconer). It is reproduced here as Fig. 3.

Description: Falconer (1868: 471- 475) himself gave a very long description, which we will not repeat here. Azzaroli & Mazza (1992: 57) gave the following description for the holotype of *E. sedgwickii*:

'The outer tine is large, broadly flattened and divides into two broad tines, dividing in their turn into four prongs, partly broken in the specimen. The antler was broken and the position in the outertine relative to the others is not very clear. The beam is also flattened and gives off a crown tine 1 at a short distance from the outer tine; this crown tine 1 divides into three prongs, one of which is broken. Crown tine 2 is also broad and bifurcated. Behind its base the beam is broken, but a separate fragment, very long,

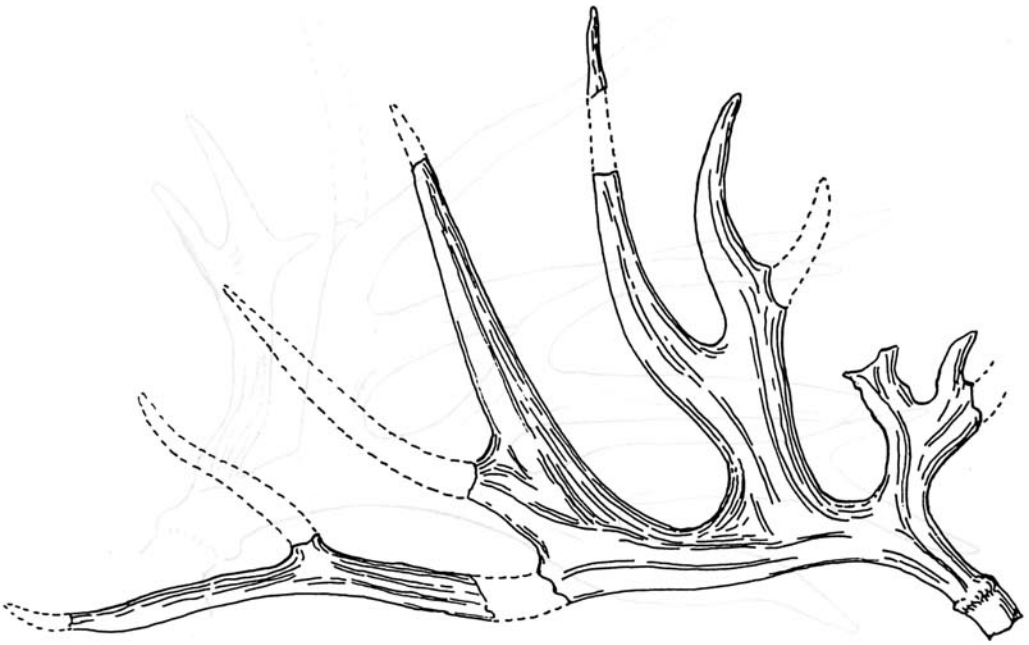


Figure 3 Holotype, the right antler of *Eucladoceros sedgwickii* (Falconer, 1868) from Bacton, Norfolk, Norwich Castle Museum (taken from Azzaroli & Mazza, 1992, fig. 8).

slender and bifurcated, may perhaps represent part of its backwards extension, with a very long posterior tine'

Discussion and conclusions on this morphotype

Falconer (1868) missed the paper of Nesti (1841), which is not surprising, because it was a verbal description, given by Nesti at a scientific meeting in Florence in September 1841. It was summarized by the secretaries prof. Paolo Savi and prof. Angelo Sismonda (Azzaroli & Mazza, 1992: 50). Falconer (1868: 472) made a new species, which he called *Cervus (Eucladoceros) sedgwickii*. Dawkins (1878: 420 and 1883: 579), Lydekker (1885: 93), Dubois (1904c: 214-222), and Teilhard de Chardin & Piveteau (1930:52) considered *E. dicranios* and *E. sedgwickii* as being the same species. Dubois (1905: 605-615), describing material from Tegelen, the Netherlands, changed his opinion and considered the two species to be different. This is based on the opinion of Dawkins (1887) and Newton (1882), that the basilar tine originates rather high at the beam in *Cervus sedgwickii* while it originates lower in *C. dicranios* (wrongly spelled *dicranius* by Dubois); furthermore, that the first tine is in the same plane and that the antler is more flattened in *C. sedgwickii*. Also Azzaroli (1953: 52) and Azzaroli & Mazza (1992: 48) considered the two species to be different. In 1953 (p. 45) Azzaroli wrote: 'The relationships of *E. sedgwicki* (sic) with *E. dicranios* from the Upper Valdarno (...) seems to be less close. The range of variation of this species is little known; but it is always distinguished by the low position of the brow tine, by a peculiar backward bending of the upper tines and by their low grade of flattening. The tines of the lectotype of *E. dicranios* are more numerous than in the type of *E. sedgwicki*'. However, in *Eucladoceros* the first tine can vary from basilar to sub-basilar, and the low grade of flattening is no argument for discriminating the species. The statement 'The tines of the lectotype of *E. dicranios* are more numerous than in the type of *E. sedgwicki*', does not hold when comparing the type specimens (Figures 2 and 3). Azzaroli & Mazza (1992: 48) wrote: 'In western Europe only *Eucladoceros sedgwickii* shows some resemblance with our species [*Eucladoceros dicranios*]; however, if the restoration of the only known antler is correct, it lacks the typical backward bend of the crown tines and the outer tine is flattened and branched into four prongs'. These characteristics are not enough to

distinguish two different species. We may thus conclude that there is only one species. As *Eucladoceros dicranios* (Nesti, 1841) has priority over *Eucladoceros sedgwickii* (Falconer, 1868), this species must be called: *Eucladoceros dicranios* (Nesti, 1841). The differences can be explained as geographical or chronological variations.

Antler type 2 contains:

***Eucladoceros tetraceros* (Dawkins, 1878)**

Type-specimen: This species was based on a set of seven shed antlers from Pliocene strata of Peyrolles in the Puy-de-Dôme, France, (Dawkins 1878: 416-419). Lydekker (1885: 113-115) catalogued all the material which he attributed to

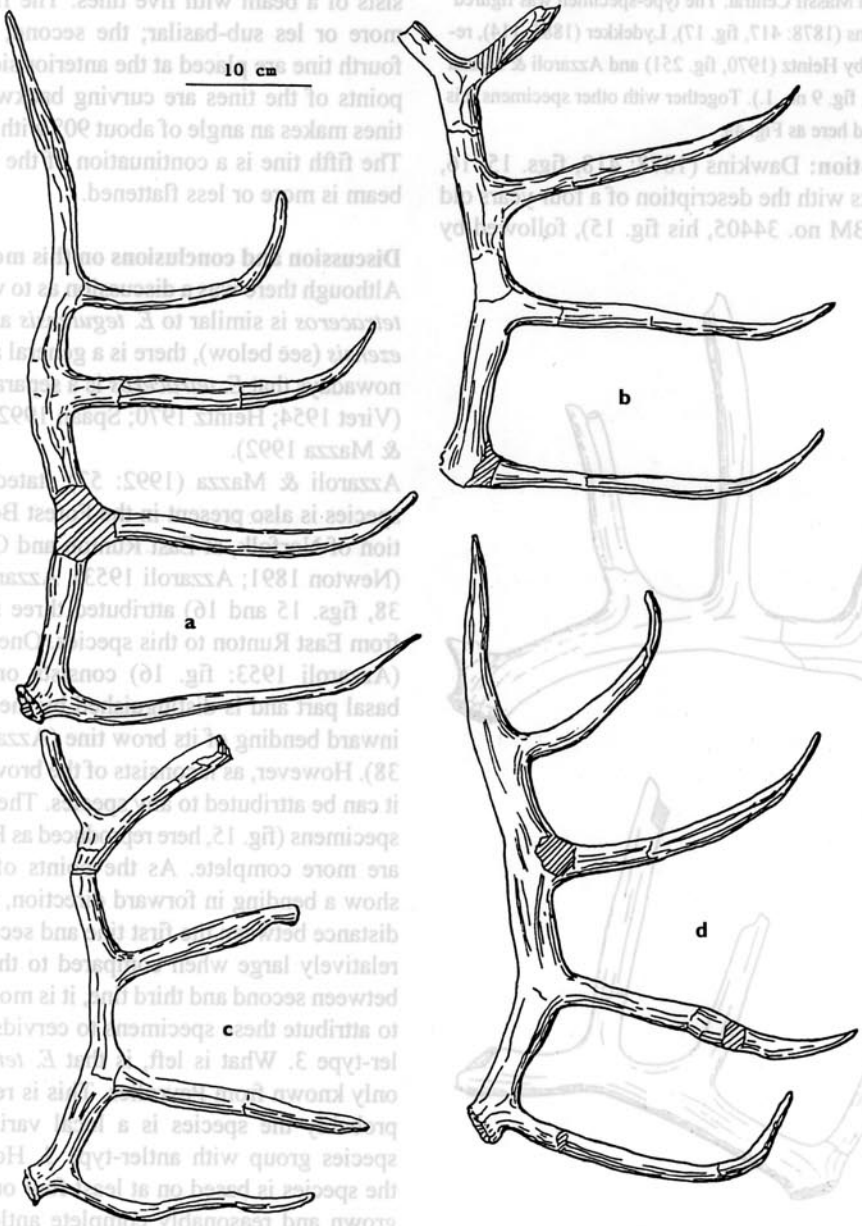


Figure 4 **a:** Holotype, left antler BM 34409 of *Eucladoceros tetraceros* (Dawkins, 1878) from Peyrolles (Coll. The Natural History Museum, London). **b:** Left antler BM 34408b. **c:** Left antler BM 34408a; **d:** Right antler BM 34408 (from Azzaroli & Mazza, 1992, fig. 9).

this species; the material was from the Bravard collection, purchased in 1852 by the British Museum (Natural History) [Now: The Natural History Museum , London].
Azzaroli (1952: 49) indicated the left antler BM 34409 as lectotype, which was followed by Heintz (1970, p. 211). However, Azzaroli & Mazza (1992: 55, fig. 9 no. 1) indicated this specimen now as being the holotype, without giving arguments. They stated (p. 57) that the antlers were coming from the Creux de Peyrolles, a gully near Perrier in the French Massif Central. The type-specimen was figured by Dawkins (1878: 417, fig. 17), Lydekker (1885: 114), reproduced by Heintz (1970, fig. 251) and Azzaroli & Mazza (1992: 55, fig. 9 no. 1.). Together with other specimens it is reproduced here as Fig. 4a.

Description: Dawkins (1878: 418, figs. 15, 16, 17) starts with the description of a four years old antler (BM no. 34405, his fig. 15), followed by the five and six years old antler (BM nos. 34406 and 34409; his figs. 16 and 17). The description by Dawkins (1878: 418) of specimen BM no. 34409 runs as follows: 'In the antler of six years old (...) all the tines spring at right angles to the beam, and the second (D), third (E), and fourth (F) are gently reflected, the curvature being the greatest in the fourth tine'.
To this we can add that the type-specimen consists of a beam with five tines. The first tine is more or les sub-basilar; the second, third and fourth tine are placed at the anterior side and the points of the tines are curving backwards. The tines makes an angle of about 90° with the beam. The fifth tine is a continuation of the beam; the beam is more or less flattened.

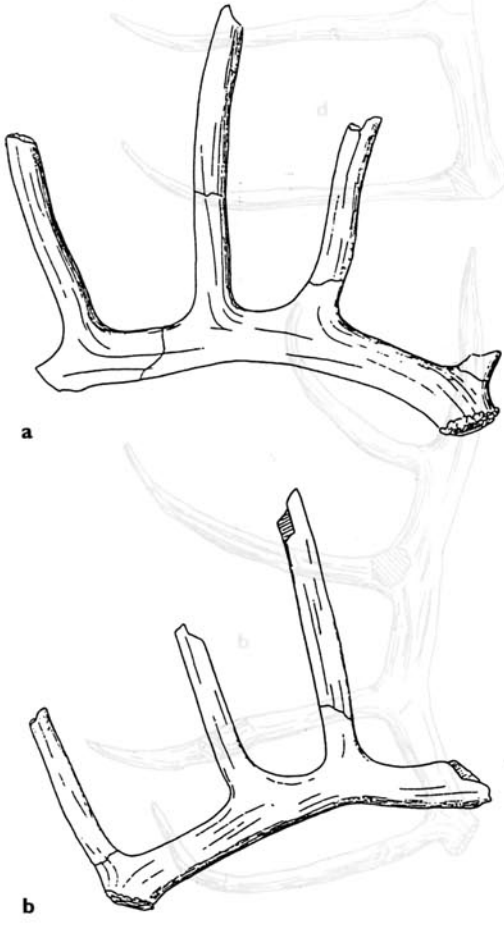


Figure 5 The two specimens from East Runton (see text). **a:** Left antler B.M.(G.D.), M. 6369. **b**: Right antler, B.M.(G.D.), M. 6370 (from Azzaroli, 1953, fig. 15).

Discussion and conclusions on this morphotype
Although there was a discussion as to whether *E. tetraceros* is similar to *E. tegulensis* and *E. senezensis* (see below), there is a general agreement nowadays that *E. tetraceros* is a separate species (Viret 1954; Heintz 1970; Spaan 1992; Azzaroli & Mazza 1992).
Azzaroli & Mazza (1992: 57) stated that this species is also present in the Forest Bed Formation of Norfolk, at East Runton and Overstrand (Newton 1891; Azzaroli 1953). Azzaroli (1953: 38, figs. 15 and 16) attributed three specimens from East Runton to this species. One specimen (Azzaroli 1953: fig. 16) consists only of the basal part and is distinguished by the abnormal inward bending of its brow tine (Azzaroli 1953: 38). However, as it consists of the brow tine only it can be attributed to any species. The other two specimens (fig. 15, here reproduced as Figs. 5 a, b) are more complete. As the points of the tines show a bending in forward direction, and as the distance between the first tine and second tine is relatively large when compared to the distance between second and third tine, it is more realistic to attribute these specimens to cervids with antler-type 3. What is left, is that *E. tetraceros* is only known from Peyrolles. This is remarkable, probably the species is a local variant of the species group with antler-type 3. However, as the species is based on at least four or five fully grown and reasonably complete antlers, showing a constant morphology, we consider (at least for the time being) this species as a separate one.

Antler type 3 contains:

Eucladoceros ctenoides (Nesti, 1841)

Holotype: The type specimen is IGF 377, a right fragmented antler from Upper Valdarno in the Museum of Geology and Paleontology of Florence. IGF 377 is figured by Azzaroli (1947: 63, fig. 6, 1ab) and by Azzaroli & Mazza (1992: 49, fig. 5 no. 1); it is reproduced here as Fig. 6.

Description: Based on Azzaroli & Mazza (1992: 50), the following description can be given for the holotype of *Eucladoceros ctenoides*. The holotype, IGF 377, is damaged: the outer tine is broken at the base. Crown tines 1 and 2 are very long and show a characteristic undulation in frontal view. The point of tine 1 points in forward direction. Crown tine 3 is large and flattened and it is broken a few cm above the diversification point. Crown tine 4 is a continuation of the beam, which is flattened.

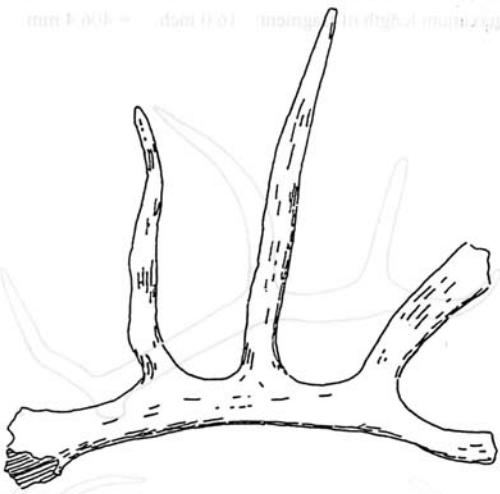


Figure 6 Holotype, right antler IGF 377 of *Eucladoceros ctenoides* (Nesti, 1841) from Upper Valdarno, Museum of Geology and Paleontology of Florence (from Azzaroli & Mazza, 1992, fig. 5, no. 1a).

***Eucladoceros orticeros* (Nesti, 1841)**

Holotype: The type specimen is IGF 369 (incorrectly defined as the lectotype of *E. ctenoides* by Azzaroli 1947), a frontal with two fragmented antlers. The right antler, in the Florence collection (Azzaroli & Mazza (1992: 50) is figured by Azzaroli (1947: 63, fig. 6, 2ab, wrongly indicated as Fi. 169) and by Azzaroli & Mazza (1992: 49, fig. 5, no. 2). It is reproduced here as Fig. 7.

Description: Azzaroli & Mazza (1992: 50) gave the following description for the holotype of *E. orticeros*. The left antler is broken at the bifurcation of crown tine 2, the right one behind tine 3. All tines except the outer tines and the right side crown tine 2 are broken at their bases, the three tines preserved are also broken, as are two strong inner tines. The outer tines arise close to the burr and diverge at a very open angle, pointing downwards. The beams are cylindrical and very strong, deeply furrowed and gently curved between the bifurcations.

***Eucladoceros falconeri* (Dawkins, 1868)**

Holotype: A left shed antler figured by Dawkins (1868: 516-518, Pl. VIII, figs. 9-11).

The species is based on only one fragmented juvenile antler, the type specimen, and four fragments of the basal portion of the antler, which, according to Dawkins (1868), may be referred to this species: one in the British Museum (no. 35857), two in the magnificent collection of fossil mammals made by Mr. Jarvis, of Cromer, and one from the Crag

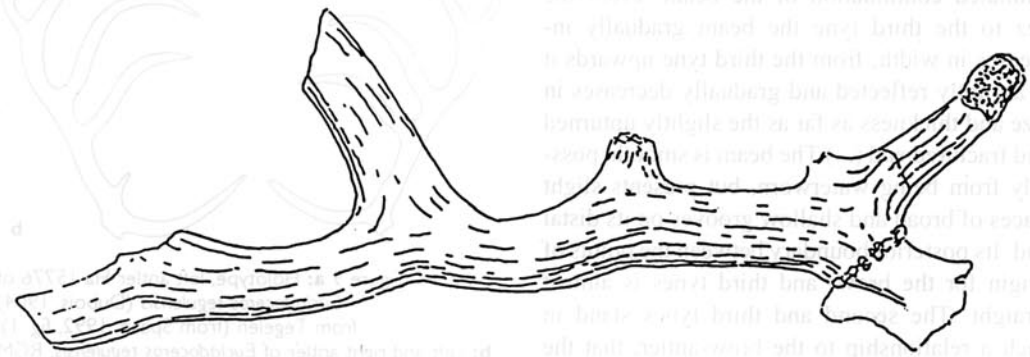


Figure 7 Holotype, right antler IGF 369 of *Eucladoceros orticeros* (Nesti, 1841) from Upper Valdarno, Museum of Geology and Paleontology of Florence (from Azzaroli & Mazza, 1992, fig. 5, no. 2).

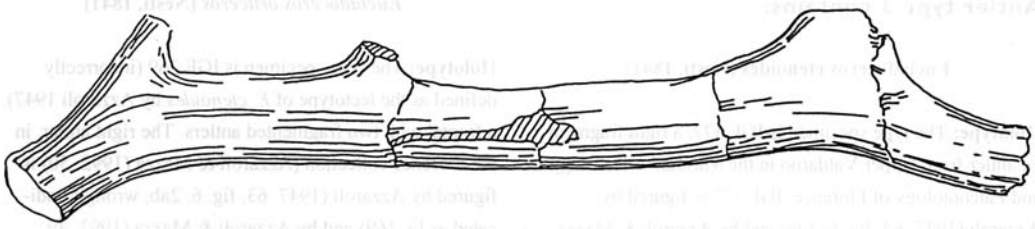


Figure 8 Holotype, right antler BM 33509 of *Eucladoceros falconeri* (Dawkins, 1868) (from Azzaroli & Mazza, 1992, fig. 1 no. 3).

of Lowestoft. Kunst (1937) stated that the holotype has number Cat. Br. Mus. 33507. Azzaroli & Mazza (1992) stated that the holotype is a right antler, no. BM 33509, and depicted it in their fig. 1 no. 3. It is reproduced here as Fig. 8.

Description: The morphological description given for the holotype by Dawkins (1868: 517) will here be repeated: 'The antler is a shed one of the left side, with its base slightly waterworn, and presenting a rounded section. There is no trace of a burr; but it may possibly have been worn away. The brow-tyne is given off at a distance of 1.9 inch [= 48.3 mm] above the base, on the outerside, at a very obtuse angle to the basal part, and at right angles to the main body of the beam. At its point of junction with the beam it is oval in section; (...) Its direction is obliquely downwards. The basal portion of the beam is put on at a very obtuse angle to the main body, and is hollowed and flattened at the point where the brow-tyne is given off. Immediately above it the beam becomes flattened both above and below, and especially at the points of origin of the bez-antler and the third tyne. The former is small and of slightly oval section (...) The latter is flattened, and presents an oval section; its basal measurements is about half as wide again as the palmated continuation of the beam. From the bez to the third tyne the beam gradually increases in width; from the third tyne upwards it is abruptly reflected and gradually decreases in size and thickness as far as the slightly upturned and fractured end (...) The beam is smooth, possibly from being waterworn, but presents slight traces of broad and shallow grooves on its distal end. Its posterior boundary between the points of origin for the brow- and third tynes is almost straight. The second and third tynes stand in such a relationship to the brow-antler, that the angle made by the plane passing through them with that of a plane passing through the latter and the basal part of the beam is almost a right angle, giving the appearance of the basal portion of the antler having been twisted a quarter of a turn downwards (...).' The basal parts of the other specimens 'repeat the characters that have been given in the description of the basal portion of the type specimen.'

Measurements given:

length of first segment:	1.9 inch	= 48.3 mm;
length of second segment:	3.0 inch	= 76.2 mm;
length of third segment:	5.5 inch	= 139.7 mm;
maximum length of fragment:	16.0 inch	= 406.4 mm.

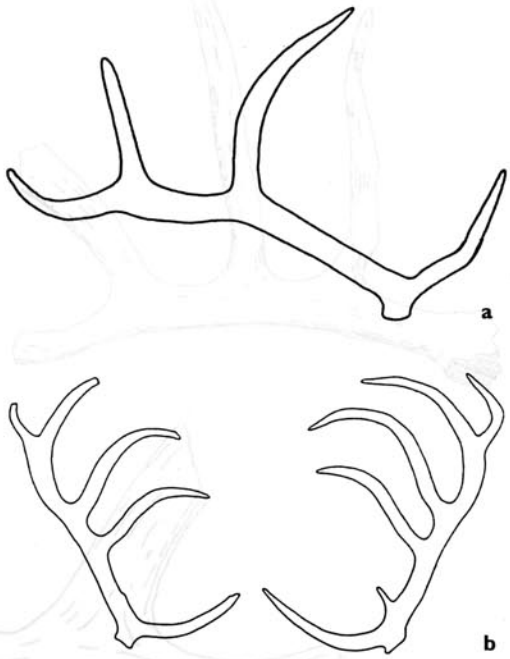


Figure 9 **a:** Holotype, left antler Ha 15776 of *Eucladoceros tegulensis* (Dubois, 1904) from Tegelen (from Spaan, 1992, fig. 1). **b:** Left and right antler of *Eucladoceros tegulensis*, RGM 20685 from Tegelen (from Spaan, 1992, fig. 2).

***Eucladoceros tegulensis* (Dubois, 1904)**

Holotype: This species is based on the left antler (Ha 15 776) figured by Dubois (1904a, p. 247, fig. 1; 1904c, p. 218, fig. 1; 1905a, pl. 1, fig. 1). The specimen originates from Tegelen. It was reproduced by Heintz (1970, fig. 199) and Spaan (1992, fig. 1) and it is reproduced here as Fig. 9a. As the material from Tegelen is considered by Kunst (1937) and Spaan (1992) to belong to one species, *E. tegulensis*, a second pair of antlers (left and right antler, RGM 20 685; fig. 2 of Spaan 1992: 7) is also figured here as Fig. 9b.

Description: Summary of the description by Dubois (1905) in Spaan (1992: 6): '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 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.

***Eucladoceros ertbornii* (Dubois, 1907)**

Type specimen: Dubois (1907) described a new species *Cervus ertbornii* from the Clay of the Kempen (= Campina, Belgium). A holotype was not designated. Three syntypes, viz. two basal parts and one mandible, are figured by Dubois (1907, figs. 1-3). They are reproduced here as Fig. 10. Fully grown or reasonably complete antlers, showing a constant morphology are not present.

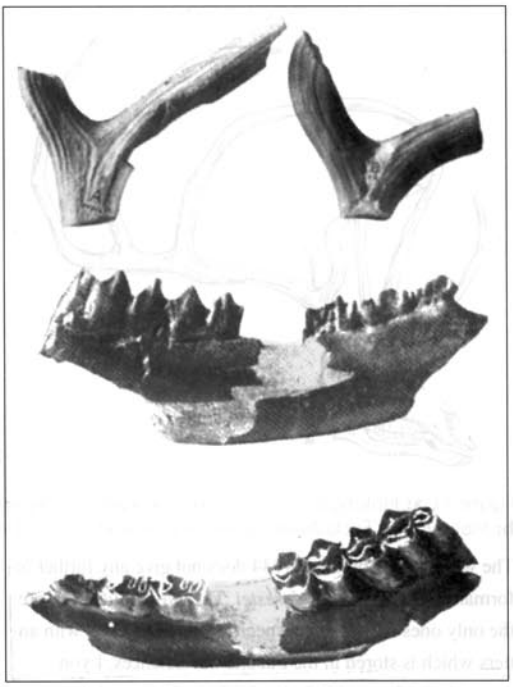


Figure 10 Types of *Eucladoceros ertbornii* (Dubois, 1907) (from Dubois, 1907, figs. 1-3).

Description: Dubois (1907: 4-5) described five portions of antlers and concluded that they were different from *Eucladoceros tetraceros*.

***Eucladoceros senezensis* (Depéret & Mayet, 1910)**

Holotype: a complete mounted skeleton, in the Faculté des Sciences, Lyon, France. The right antler was figured by Roman (1934: 251, fig. 17), Viret (1954: 177, fig 18a), and Heintz (1970, fig. 202). Azzaroli & Mazza (1992, fig. 2 no. 1) figured the antlered skull. It is reproduced here as Fig. 11a. Nomenclature after Heintz (1970: 189).

Description: See Heintz (1970: 191-192), who gave an extensive description that will not be repeated here.

***Eucladoceros darestei* (Depéret, 1931)**

Holotype: This species is mentioned for the first time in a bibliography of 1931, the year in which F. Roman and J. Dareste de la Chavanne marked the presence of an *Alces latifrons* John. at Senèze. In the faunal list which is given in this publication (Roman & Dareste 1931), *Cervus senezensis* and *Cervus darestei* are mentioned at the same time. Neither a figure, nor a description were given for this new species.

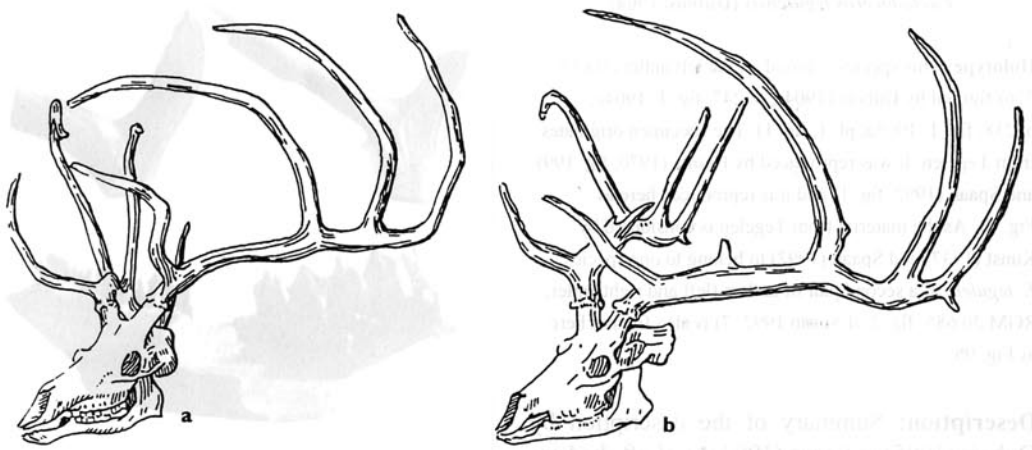


Figure 11 **a:** Holotype of *Eucladoceros senezensis* (Depéret, 1910), Univerity of Lyon.
b: Holotype of *Eucladoceros darestei* (Depéret, 1931), Lyon. (from Azzaroli & Mazza, 1992, fig. 2, nos. 1 and 2).

The work of F. Roman of 1934 does not give any further information concerning *E. darestei*. The two publications are the only ones which give a specific value to a skull with antlers which is stored in the Faculté des Sciences, Lyon. Azzaroli & Mazza (1992: 46, fig. 2 no. 2) figured this specimen which is considered to be the holotype of *'Eucladoceros darestei'* (wrongly spelled *derestei* by Azzaroli & Mazza, 1992); it is reproduced here as Fig. 11b.

Discussion and conclusion on this morphotype

We will first consider *E. tegulensis* and *E. senezensis*. The following is mostly based on Spaan (1992). Dubois (1904a) made a new species which he called *Cervus tegulensis* to indicate a large species of deer closely resembling *Cervus tetraceros* Dawkins, 1878. The publication was accompanied by a picture of the (wrongly) restored type antler from Tegelen. No description was given. Some of the antlers of the large deer from Tegelen were ascribed to *C. sedgwickii*, which was considered to be identical to *C. dicranios*. Dubois (1904b, c) also introduced an alternative spelling for *C. tegulensis* and changed it into *C. teguliensis*. Dubois (1905) described and figured the type antler. He ascribed two antlers to *C. dicranios*, which he considered to be different from *C. sedgwickii*. Dubois (1906) then stated that *C. teguliensis* is a primitive form of the subgenus *Elaphus* and still ascribed certain antlers to *C. dicranios*. Depéret & Mayet (1910) made a new species: *Cervus senezensis*. Stehlin (1923) stated that, in spite of the great resemblance, *C. tegulensis* and *C. senezensis* do not belong to one and the same species, but are very closely related to each other. Bernsen (1930-1934) distinguished three species of larger deer in the Tegelen fauna: *C. teguliensis, C. dicranios* and *C. ctenoides*. Kunst (1937) denied the differences between the antlers ascribed to *(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 *Cervus dicranios*. Azzaroli (in Bout & Azzaroli 1952) stated that *C. teguliensis* was larger than *Euctenoceros tetraceros*, but gave no comment on the synonymy established by Kunst (1937). Viret (1954) underlined the great resemblance between *C. (Euctenoceros) teguliensis* and *C. senezensis* and preferred 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*. This opinion is followed by Azzaroli et al. (1988), Spaan (1992) and Azzaroli & Mazza (1992).

There is thus a general agreement nowadays that Eucladoceros tegulensis and *E. senezensis* are one and the same species (Figs. 9 and 11a).

Concerning *Eucladoceros darestei*: Heintz (1970: 191) considered *Cervus darestei* Depéret, 1931 as a synonym of *C. senezensis*. Azzaroli & Mazza (1992: 44) considered *C. darestei* as a synonym of *Eucladoceros tegulensis*, which again is a senior synonym of *Cervus senezensis*. Azzaroli & Mazza (1992: 46 fig. 2 no. 2) figured the holotype of '*Eucladoceros derestei*', which is similar to the holotype of *Eucladoceros senezensis*, also figured by Azzaroli & Mazza (1992: 46, fig. 1). Based on the morphology of the holotypes, we agree with these authors; compare Figs. 11a and 11b. This means that *E. tegulensis*, *E. senezensis* and *E. darestei* all belong to the same species.

Concerning *Eucladoceros falconeri*: this species is based on a left shed antler and, according to Dawkins, four other fragments of the basal portion of the antler may be referred to this species. As the brow tine is removed from the base, it differs according to Dawkins (1868) from *Cervus dama* and *Cervus Brownii*. It is in this respect closely related to the French Pliocene *Cervus tetraceros* in the British Museum (Dawkins 1868). However, again according to Dawkins (1868), the smoothness, the absence of deep wrinkles, and the size differentiate it from *C. tetraceros*.

The basal fragments do not discriminate the species level. As far as size is concerned we have to realize that the holotype is a juvenile shed antler, with its base slightly waterworn. As the tines 1, 2 and 3 are broken off and missing (Fig. 8), it is difficult to judge whether we are dealing with *C. tetraceros* or with *C. tegulensis*. According to Dawkins (1868: 517) the bez (second) tine is small; it might be called an accessory tine. In this case the distance between the first and second tine is relatively large, which hints at the diagnosis for *E. senezensis* as given by Heintz (1970). According to Azzaroli (1953: 37-38) *E. falconeri* is not similar to *E. teguliensis*. He wrote: 'Kunst (1937) pointed out its ('*C. falconeri*') affinities to *E. tegulensis* (= *E. ctenoides*; see below), but as a matter of fact these two species differ in many characters. On the contrary its affinities with *E. sedgwicki* are very close'. Azzaroli (1953: 45) stated: 'The relationship of *E. falconeri* and *E. sedgwicki* are very close. They are both distinguished by the high position of the first bifurcation and by the well marked flattening of the upper portion of the antlers'.

From the above it may be concluded that there are no arguments to separate *C. falconeri* from *E. tegulensis* and from *E. senezensis*. This means that *E. tegulensis*, *E. senezensis*, *E. darestei* and *E. falconeri* all belong to the same species.

Concerning *Eucladoceros ertbornii* (Dubois, 1907): this species is based on a basal fragment of the antlers. Kunst (1937: 101) considered *Cervus ertbornii* Dubois 1907 to be a synonym of *Cervus falconeri* and this is followed by Azzaroli & Mazza (1992: 44). We agree with them. This means that *E. ertbornii* belongs to the same species as the taxa mentioned above (*E. tegulensis*, *E. senezensis*, *E. darestei*, and *E. falconeri*).

Concerning *Eucladoceros ctenoides* (Nesti, 1841): Stehlin (1923) underlines the great affinity of *Cervus teguliensis* and *C. senezensis* to *C. tetraceros* and *C. ctenoides*. Azzaroli (1953) held the view that *ctenoides* and *tegulensis* (incorrectly spelled *teguliensis* by Azzaroli 1953) are the same species. He wrote: 'The distinction between *E. ctenoides* and *E. teguliensis* does not seem valid. The ranges of variation of these two species widely overlap. The antlers from Tegelen do not attain the size of the larger specimens from the Upper Valdarno, but this may be due merely to the incompleteness of the record. The dentition and limb bones are of the same size'. According to Azzaroli & Mazza (1992: 50) 'the holotype is damaged: the outer tine is broken at the base and there is no trace of an inner tine. Crown tines 1 and 2 are very long and show a characteristic undulation in frontal view. Crown tine 3 is large and flattened (...) Not much can be said of crown tine 4, which is equally broken'. In contradiction to this opinion (Azzaroli 1953) that *E. tegulensis* and *E. ctenoides* are the same species, but without giving any comments, Azzaroli & Mazza (1992: 50) consider *E. tegulensis* and *E. ctenoides* to be two distinct species again.

As the distance between the first and second tine is rather long, and the second point is bending forwards, we consider *E. ctenoides* to be the same species as *E. falconeri, E. tegulensis, E. senezensis* and *E. darestei*. Based on the mor-

phology of the holotype we agree with Azzaroli (1953) that *E. ctenoides* and *E. tegulensis* are the same species. This means that *E. tegulensis*, *E. senezensis*, *E. darestei*, *E. falconeri*, *E. ertbornii* and *E. ctenoides* all belong to the same species.

Finally, concerning *Eucladoceros orticeros* (Nesti, 1841): Azzaroli & Mazza (1992: 80) wrote: 'The specimens referred to by Nesti are easily traced in the Florence collection. The type (holotype) of *Cervus ctenoides* is the antler IGF 377, while IGF 369 is the holotype of *Cervus orticeros*, a name which was not mentioned later, and does not appear in the labels of the collection. In the catalogue of 1845 referred to above there is a mention of "Corno del *Cervus ctenoides*" and of three more antlers of "un grosso Cervo", but the name *orticeros* is never mentioned'. Azzaroli & Mazza (1992: 50) consider *E. orticeros* to be a synonym of *E. ctenoides*; it is according to them a *'nomen oblitum'*. We agree with them.

It means that also *Eucladoceros orticeros* belongs to the same species as *E. tegulensis*, *E. senezensis*, *E. darestei*, *E. falconeri*, *E. ertbornii*, and *E. ctenoides*. This is our main conclusion. As the name *Eucladoceros ctenoides* (Nesti, 1841) has priority over the other species names, the taxon should be called *Eucladoceros ctenoides* (Nesti, 1841). The small differences can be explained as either geographical or chronological variations.

Species that can not be placed in one of the antler types mentioned above

***Cervus ernesti* Fritsch, 1884**

Synonyms:

1953 - *Euctenoceros ernesti* Fritsch; Dietrich, p. 419.

1970 - *Eucladoceros ernesti* Fritsch 1884; Heintz, p. 185

Type specimen. The species is based on fragments of antlers from the lignite formations of Rippersroda. No holotype has been designated for this species. The material figured by K. von Fritsch (and reproduced here as Fig. 12) is insufficient for defining the affinities of the genus, according to Heintz (1970: 185). We can agree with that statement. The name *Cervus ernesti* Fritsch, 1884 should be dropped.

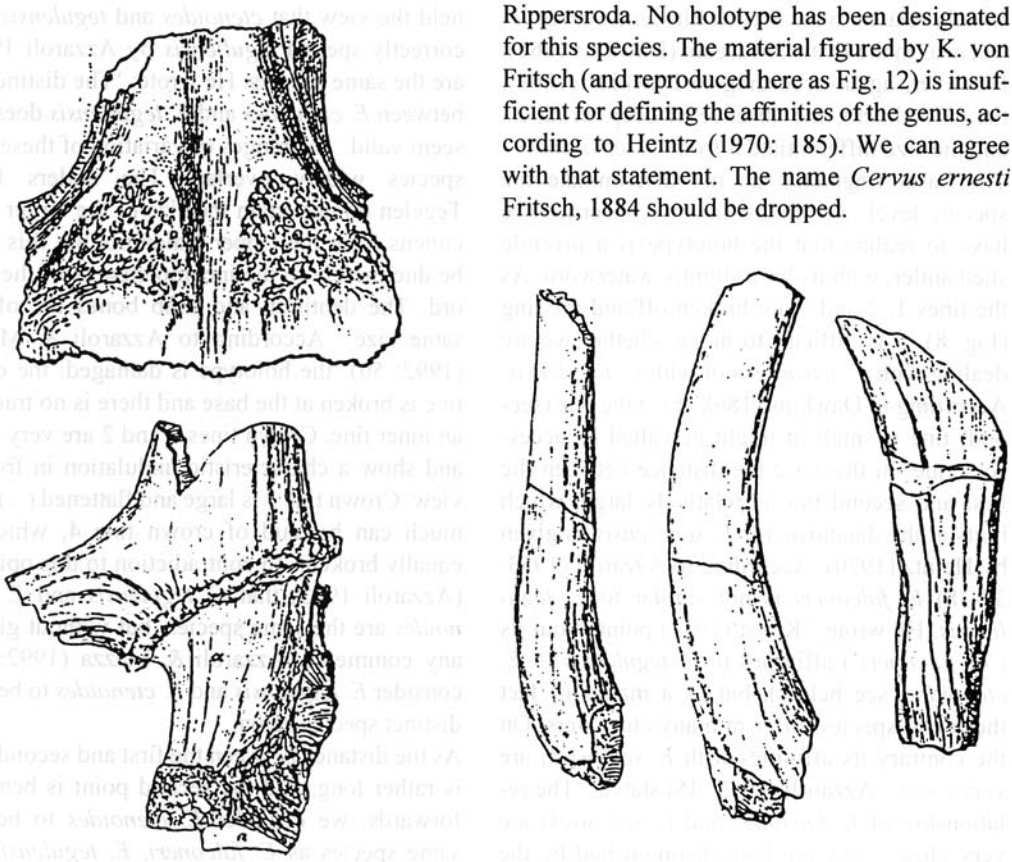


Figure 12 Types of *Eucladoceros ernesti* (Fritsch, 1884) (from Fritsch, 1884, Tafel XXV, figs. 5-9).

***Eucladoceros boulei* Teilhard and Piveteau, 1930**

Type specimen. No type specimen has been designated for this species. Heintz (1970: 187) proposed to designate a left antler figured by Teilhard de Chardin & Piveteau (1930, pl. IX, fig. 2).

The species is only known from Nihovan, China, although Steensma (1988: 164) described antler material from Kapetanios (Greece) as *Eucladoceros* aff. *boulei* Teilhard & Piveteau, 1930. We leave this species out of consideration.

General conclusion

Three out of the 12 species mentioned in the literature seem to be valid. These are: *Eucladoceros dicranios* (Nesti, 1841), *Eucladoceros tetraceros* (Dawkins, 1878) and *Eucladoceros ctenoides* (Nesti, 1841):

Genus *Eucladoceros* Falconer, 1868

Synonym:

Euctenoceros Trouessart, 1898-1899

***Eucladoceros dicranios* (Nesti, 1841)**

Synonyms:

1841 - *Cervus dicranios* Nesti, 1841

1868 - *Cervus (Eucladoceros) sedgwickii* Falconer (ex. Gunn Mss.), vol. II, p. 471-480, pl. 37, fig. 1-3.

1882 - *Cervus sedgwicki* Falc.; Newton, p. 60.

1891 - *Cervus sedgwicki* Falc.; Gunn, pl.3, fig. 99 and 100.

1891 - *Cervus* sp., Gunn, pl. 3, fig. 105 and 106.

1891 - *Cervus sedgwicki* Falc.; Newton, p. 31.

1970 - *Eucladoceros dicranios* Nesti 1879; Heintz, p. 185.

1970 - *Eucladoceros sedgwicki* Falconer 1868; Heintz, p. 183.

1992 - *Eucladoceros dicranios* (Nesti) 1841; Azzaroli & Mazza, pp. 47-50, figs. 6, no. 4, 5; Pl. 1-2.

1992 - *Eucladoceros sedgwickii* (Falconer) 1868 (ex Gunn MSS); Azzaroli & Mazza, p. 57, fig. 8.

Holotype: see holotype of *Cervus dicranios* Nesti, 1841 above.

Type locality: Figline, Upper Valdarno, Tuscany

Type horizon: Upper Villafranchian

Other localities: Italy, Olivola; England, Bacton at Norfolk

Original diagnosis: Nesti, 1841

Proposed diagnosis: Large sized cervid with the size of *Cervus elaphus*. Antler consisting of a beam with four tines placed at the anterior side of the beam; the tines are bifurcated or trifurcated and flattened in lateral direction.

(For bibliographic analysis and for description of the holotype see above.)

***Eucladoceros tetraceros* (Dawkins, 1878)**

For the description see Heintz (1970: chapter 9)

Heintz (1970) gave the following diagnosis for the antlers: The antlers are characterized by

- -the relatively small distance between tines 1 and 2;
- -the relatively small length of tines 2, 3, and 4;
- -the similiraty in circumference of tines 1 and 2;
- -the posterior bend of the tines 2, 3 and 4.

(For bibliographic analysis see above and in Heintz (1970: 211-220).)

***Eucladoceros ctenoides* (Nesti, 1841)**

Synonyms:

1841 - *Cervus ctenoides* Nesti 1841; Savi & Sismonda, p. 159

1841 - *Cervus orticeros* Nesti 1841; Savi & Sismonda, p. 159

1858 - 1871 *Cervus ctenoides* Nesti 1841; Cornalia, p. 61.

1868 - *Cervus falconeri*, Dawkins 1868, p. 516-518, pl. XVIII, fig. 9-12.

1884 - *Cervus ernesti*, K. von Fritsch, p. 412-421, pl. XXV, fig. 5-9.

1887 - *Cervus savini* Dawkins (pars); Dawkins, pl.3, fig.4.

1904 - *Cervus tegulensis*, Dubois 1904a, p. 247, fig. 1.

1904 - *Cervus teguliensis*, Dubois 1904c, p. 218, fig. 1.

1907 - *Cervus ertbornii*, Dubois 1907, p. 3-7.

1910 - *Cervus senezensis*, Depéret & Mayet, p. 261.

1923 - *Cervus senezensis* Depéret; Stehlin, p. 276-277.

1931 - *Cervus senezensis* Depéret; Roman & Dareste de la Chavanne, p. 1256.

1931 - *Cervus darestei* Depéret; Roman & Dareste de la Chavanne, p. 1256.

1934 - *Cervus senezensis* Depéret; Roman, p. 251, fig. 17.

1934 - *Cervus darestei* Depéret; Roman, p. 251.

1937 - *Cervus ertbornii* Dubois 1907; Kunst, p. 106-107.

1937 - *Cervus (Eucladoceros) teguliensis* Dubois 1904; Kunst, p. 30.

1943 - *Cervus senezensis* Depéret =*Cervus darestei* Depéret, Schaub, p. 284.

1945 - *Cervus (Eucladoceros) tegulensis* Dubois 1904; Schreuder, p. 155.
1947 - *Cervus (Euctenoceros) ctenoides* Nesti; Azzaroli (pars), p. 62-65, fig. 6, 7 and 9.
1953 - *Euctenoceros falconeri* Dawkins 1868; Azzaroli, p. 37-38, fig. 20B and 20 C, p. 43.
1953 - *Euctenoceros ctenoides* Nesti; Azzaroli, p. 38-40.
1953 - *Euctenoceros ernesti* Fritsch; Dietrich, p. 419.
1954 - *Cervus (Euctenoceros) senezensis* Depéret; Viret, p. 116-122, fig. 18, p. 117.
1961 - *Cervus (Euctenoceros) senezensis* Depéret; Viret in Piveteau, fig. 115, p. 1014.
1962 - *Cervus (Euctenoceros) tegulensis* Dubois 1904; Kortenbout van der Sluys & Zagwijn, p. 36.
1970 - *Eucladoceros teguliensis* Dubois 1904; Heintz, p. 186.
1970 - *Eucladoceros falconeri* Dawkins 1868; Heintz, p. 183.
1970 - *Eucladoceros ctenoides* Nesti 1879; Heintz, p. 184.
1970 - ? *Eucladoceros ernesti* Fritsch 1885; Heintz, p. 185.
1992 - *Cervus ertbornii* Dubois 1905; Azzaroli & Mazza, p. 44
1992 - *Eucladoceros tegulensis* (Dubois, 1904); Spaan, p. 7, fig. 1-7.

Holotype: see above.
Type locality: Upper Valdarno.
Other known localities: France: Senèze, Saint-Vallier, La Roche-Lambert, Chillac, Coupet, Pardines, Roccaneyra, La Roche-Lambert, Chilhac; Spain: La Puebla de Valverde; Germany: Erpfinger Cave; England: Red Crag, Norwich Crag; Netherlands: Tegelen, the Oosterschelde; Belgium: Kempen.
Original diagnosis: a description is given by Nesti (1841), but no specific diagnosis.
Proposed diagnosis: As there is no diagnosis for *E. ctenoides*, and *E. ctenoides* is a senior synonym for *E. tegulensis* and for *E. senezensis*, it is proposed here to take the diagnosis given by Heintz (1970: 190) for *E. senezensis* as a basis and to add a few amendations. The diagnosis then runs as follows:
Cervid of large size (comparable to *Cervus elaphus*). Antlers very large; the beam can have a length up to 800 mm. The beam varies in cross section, strongly curving to the back at the level of the first tine. In old specimens an accessory tubercle between the first and second tine is frequently present. Generally four tines, sometimes five, all implanted perpendicular to the anterior border of the beam; decreasing inward curvature, starting with the first tine.
The first tine is basilar or somewhat subbasilar, of a simple structure, forming a S-shape, at about 3/5 of the length; its cross section is subcircular. The distance between the first and second tine is rather long, the second tine is curving to the anterior side, simple or bifurcate; its cross section is flattened in lateral direction. The distance between the second tine and the third tine is smaller than that between the first and second tine. The third tine is curving to the anterior and of a simple structure; length about the same as, or a little shorter than the second tine. The distance between the second tine and the fourth tine is in general shorter than that between the first tine and the second tine. The fourth tine is simple in structure; its cross section is flattened to subcircular in lateral direction; the tine is curved in an S-shape.
Dental elements are of the cervoid type, characterized by its dimensions; in the upper molars the protoconal fault is regressed; the premolars are in general bilobed at the lingual side; the lower fourth premolar (p4) is very variable and in general a little molarized.
Plesiometacarpal cervid; the postcranial elements are characterized by their dimensions, comparable to *Cervus elaphus*.
For a bibliographic analysis see above. For more information concerning *E. senezensis* see Heintz (1970: 189-210), and for *E. tegulensis* see Spaan (1992: 5-23).

2 REVISION OF THE MEDIUM-SIZED DEER OF THE GENUS *CERVUS*

A number of medium sized species with six-tined antlers is described or mentioned in the literature from the Early Pleistocene of Europe. The most important ones are *Cervus pardinensis* Croizet & Jobert, 1828; *Cervus suttonensis* Dawkins, 1878; *Cervus rhenanus* Dubois, 1904; *Cervus philisi* Schaub, 1941; and *Cervus perolensis* Bout & Azzaroli, 1952. Azzaroli (1992) attributed the species *C. pardinensis*, *C. rhenanus* (= *C. philisi*), and *C. perolensis* to a new genus, *Pseudodama*, to which he also joined *Dama nestii* Azzaroli, 1947 and two new species *P. lyra* Azzaroli, 1992 and *P. farnetensis* Azza-

roli, 1992. The two latter species have 8 tines. Furthermore, Boeuf et al. (1992) described a new species as *Cervus ischnoceros*. These named taxa will now be shortly dealt with.

***Cervus pardinensis* Croizet & Jobert, 1828**

This species was described in detail by Heintz (1970: 133-148). It is a medium sized cervid, nearly identical to *Cervus philisi* and *Cervus perolensis*, from which species it can be distinguished by having large cingula in the upper molars. Synonyms provided by Heintz are: *Cervus pardinalis* Bravard Mss., catalogue et collections du Muséum de Paris; and *Cervus cros-rolandi* Bravard Mss., catalogue et collections du Muséum de Paris.

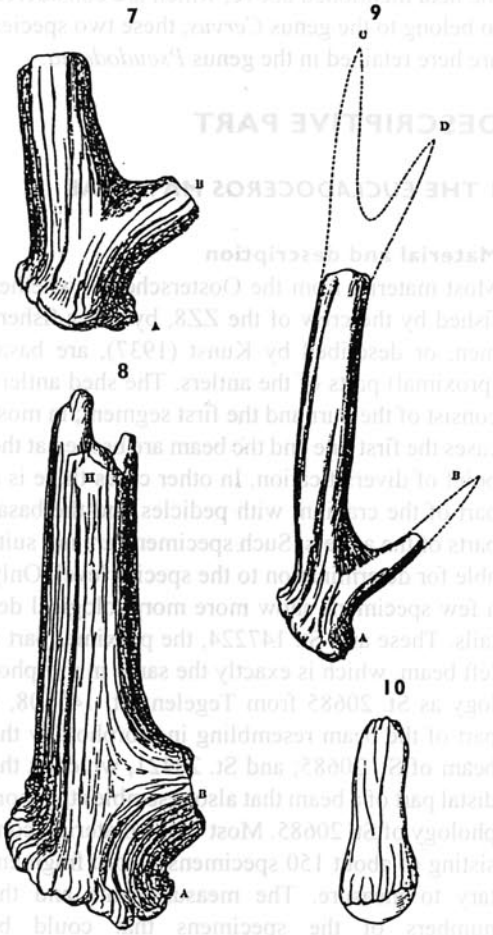


Figure 13 Types of *Cervus suttonensis* Dawkins, 1878. **No. 7** is BM 27858; **no. 8** is BM 27515; **no. 9** is BM 27516. (from Dawkins, 1878 figs. 7-10).

***Cervus suttonensis* Dawkins, 1878**

The species is based on a series of fragmentary antlers from the Crags in Norfolk and Suffolk. The species was named after the Crag of Sutton, from which the best two specimens originate. The material is in The Natural History Museum, London. Four specimens have been figured (Dawkins 1878: 412, figs. 7 [BM 27858], 8 [BM 27515], 9 [BM 27516], and 10; the BM numbers are from Lydekker 1885). They are reproduced here as Fig. 13. No holotype has been designated. Dawkins (1878 414) wrote: 'The *Cervus suttonensis* is, in its general form, closely allied to *C. pardinensis*, of which it may be a small breed or variety; but, considering the fragmentary nature of the specimens referable to it, we think it safe to keep the two series distinct and under different names'. The specimens attributed to this species were listed by Lydekker (1885: 109-111). Azzaroli & Mazza (1992: 44) wrote: '*Cervus suttonensis* Dawkins mentioned in this context by Kunst (1937: 113), is practically indeterminable'. We can agree with their statement. The name *Cervus suttonensis* Dawkins, 1878 should be dropped, being a *nomen nudum*.

***Cervus rhenanus* Dubois, 1904**

Spaan (1992), after a detailed study, concluded that the species *Cervus rhenanus* Dubois, 1904, *C. philisi* Schaub, 1941 and *C. perolensis* Bout & Azzaroli, 1952 must be considered as one species. The taxon *C. rhenanus* Dubois, 1904 has priority over the other ones. Here we follow Spaan's (1992) opinion. Apart from Spaan's description of *C. rhenanus*, Heintz (1970: 149-175) gave a detailed description of *C. philisi* and *C. perolensis*. These authors also provided lists of synomyms, and emended diagnoses. The holotype is a left antler figured by Dubois (1904: 219, fig. 2, and 1905: fig. 6). The type locality is Tegelen (the Netherlands); *C. rhenanus* is also known from France (Senèze, Saint-Vallier, Chillac, Coupet, Pardines, Chilhac, Blassac-la-Gironde), Spain (La Puebla), the Netherlands (Oosterschelde), and Belgium (La Campina = Kempen).

***Pseudodama lyra* Azzaroli, 1992**

Only one pair of antlers with pedicles and parts of the frontals are known. This is also the holotype. Furthermore, Azzaroli (1992: 6) considered a part of a left metacarpal, presumably of the same animal. The description given by Azzaroli (1992: 6) gives, runs as follows:
'*Pseudodama lyra* recalls *P. pardinensis* and *P. rhenanus* but is more derived than both in the incipient third bifurcation of the left antler and in the flattening of the upper end of the right antler, which preludes to a bifurcation. In total length the antlers, taking into account their curvature, exceed those of *P. pardinensis* and equal those of *P. rhenanus*; the inward curvature of the beam above the trez is a unique feature that distinguishes *P. lyra* from the other species of its genus'.
Based on this description and the figure (Azzaroli 1992: fig. 2) we consider *P. lyra* to be a synonym of *Cervus rhenanus*.

***Cervus ischnoceros* Boeuf, Geraads & Guth, 1992**

Synonyms: *Cervus perolensis* Bout & Azzaroli, 1952 in: Beden & Guth 1970; Guth 1975a, b; Heintz et al. 1974.

Boeuf et al. (1992: 166) wrote: '*C. ischnoceros* évoque surtout *C. perolensis* de Peyrolles'. The taxon *C. perolensis* is insufficiently known. The dentition is only known from a few specimens. The length of the second segment of the antlers, which is an important characteristic for cervids, is also unknown. For those reasons, Boeuf *et al.* (1992) argued that the name should be reserved only for the material from Peyrolles. Between Peyrolles and Blassac not only the *Eucladoceros* differs, but the two localities are not contemporaneous, according to Boeuf et al. (1992). They thus propose a new specific name (*C. ischnoceros*) for the material from Blassac. However, this is no argument for making a new species. The measurements show a similarity with *Cervus perolensis* for the length of the pedicle; they show similarities in the length of the first segment/Dap burr with *C. perolensis* and *C. philisi*. As *C. ischnoceros* is similar to *C. perolensis* and as *C. perolensis* is the same as *C. rhenanus*, it seems realistic to consider *C. ischnoceros* to be a junior synonym of *C. rhenanus*.

Conclusion: The name *Cervus rhenanus* Dubois, 1904 is to be preserved and used; *Cervus philisi* Schaub, 1941, *Cervus perolensis* Bout & Azzaroli, 1952, *Cervus ischnoceros* Boeuf et al., 1992, and *Pseudodama lyra* Azzaroli, 1992, all are junior synonyms. *Cervus pardinensis* Croizet & Jobert, 1828 is a distinct species, it differs from *C. rhenanus* by having cingula on the upper molars. Finally, the species *Cervus suttonensis* Dawkins, 1878 must be dropped for being a *nomen nudum*.

***Pseudodama nestii* (Azzaroli, 1947) and *Pseudodama farnetensis* Azzaroli, 1992**

These two species are characterized by the fact that the antlers each have four tines (the complete set of antlers has eight tines). In contrast to the taxa mentioned above, which are considered to belong to the genus *Cervus*, these two species are here retained in the genus *Pseudodama*.

DESCRIPTIVE PART

I THE *EUCLADOCEROS* MATERIAL

Material and description

Most material from the Oosterschelde, whether fished by the crew of the ZZ8, by other fishermen, or described by Kunst (1937), are basal (proximal) parts of the antlers. The shed antlers consist of the burr and the first segment; in most cases the first tine and the beam are broken at the point of diversification. In other cases there is a part of the cranium with pedicles and the basal parts of the antlers. Such specimens are not suitable for determination to the species level. Only a few specimens show more morphological details. These are: St. 147224, the proximal part a left beam, which is exactly the same in morphology as St. 20685 from Tegelen; St. 145508, a part of the beam resembling in morphology the beam of St. 20685; and St. 28421, which is the distal part of a beam that also resembles the morphology of St. 20685. Most of the material (consisting of about 150 specimens) is too fragmentary to measure. The measurements and the numbers of the specimens that could be measured, are given in Table 1.

Table 1 Dimensions of the *Eucladoceros* antlers from the Oosterschelde. [after De Vos, 1984]

Specimen no.	sym	DAP	DT	1st segment	angle
St 118774	d	41.1	50.4	-	-
St 118673	s	83.4	72.8	-	-
St 118440	s	72.8	66.1	-	-
St 118988	d	62.5	63.3	-	-
St 118201	s	64.8	67.6	103.7	-
St 146202	s	58.7	57.6	-	-
St 118360	-	59.5	51.2	91.0	-
St 118848	-	-	-	100.8	-
St 118826	-	-	-	95.7	-
St 118875	s	60.0	54.4	115.9	-
St 118729	s	55.1	50.9	95.5	-
St 118382	-	-	-	138.1	-
St 118854	-	-	-	78.5	-
St 118905	-	62.7	60.4	144.7	-
St 119474	-	62.1	55.4	93.8	130
St 119505	s	64.0	62.7	103.7	95
St 119008	-	-	-	69.9	90
St 119971	s	75.6	64.4	102.6	125
St 119563	d	50.5	41.7	72.8	110
St 119499	-	-	-	74.0	85
St 119479	s	-	-	88.1	80
St 145364	-	68.7	65.4	-	95
St 145834	-	65.5	62.0	113.5	-
St 145307	s	70.8	60.5	112.1	-
St 145368	-	60.4	52.5	-	-
St 145571	d	-	-	114.1	-
St 145352	-	73.7	71.9	-	-
St 145386	d	60.0	61.6	127.2	120
St 146032	s	76.6	67.3	-	-
St 147126	s	40.9	42.5	81.5	130
St 147079	s	51.4	40.8	95.2	105
St 146102	-	39.1	23.7	57.2	85
St 147181	d	50.7	42.8	89.6	-
St 147192	-	49.9	44.7	-	-
St 147395	-	56.8	49.8	-	-
St 152528	s	39.2	39.9	73.1	-
St 147190	-	68.4	68.2	-	-
St 147159	s	59.4	54.0	122.7	-
St 147389	d	59.8	55.4	91.6	-
St 152535	d	64.6	56.4	112.2	-
St 152529	s	50.6	48.4	85.8	-
St 152534	d	46.4	45.2	108.1	-
St 118657	-	71.9	60.5	-	-
St 118650	-	61.6	57.4	-	-
St 118980	-	56.4	51.7	89.1	-
St 118915	-	65.3	59.5	-	-
St 145294	-	72.4	67.2	-	-
St 118407	-	61.0	55.6	-	-
St 145292	-	58.5	48.4	80.3	120

Table 1 (continued)

Specimen no.	sym	DAP	DT	1st segment	angle
St 147046	-	-	-	68.2	-
St 147187	-	61.7	58.0	74.3	-
St 145359	-	58.3	54.0	116.2	-
St 145569	-	73.0	69.1	113.3	-
St 147184	-	69.0	62.7	-	-
St 146592	-	68.1	62.0	122.6	-
St 119056	-	57.1	48.5	75.6	130
St 146091	-	50.5	46.4	77.6	-
St 147210	-	-	-	119.0	-
St 145303	-	58.8	56.6	91.5	95
St 146034	-	56.5	48.0	62.1	125
St 145348	-	67.3	74.5	114.4	105
St 145306	-	66.7	48.6	66.7	-
St 146070	-	70.7	70.2	98.4	-
St 147155	-	57.0	56.6	100.1	-
St 147055	-	52.5	49.6	88.3	125
St 147057	-	55.5	50.5	85.2	-
St 147042	-	50.5	50.4	103.4	-
St 147054	-	-	-	106.6	-

The postcranial material is of the cervoid type as described by Heintz (1970). Most of this material is too fragmentary to be measured. The measurements and the numbers of the specimens that could be measured are given in Table 2.

Comparison, discussion and conclusion

Kunst (1937) described for the first time material from the Oosterschelde (Roompot) and attributed the material to *Cervus falconeri*. This opinion was followed by Van der Vlerk (1938, 1939, 1953) and by Schreuder (1945: *Eucladoceros falconeri*). The morphology of the holotype of *Cervus falconeri* agrees with the material from the Oosterschelde. However, the measurements of the holotype give smaller sizes than in the Oosterschelde material. This is caused by the fact that the holotype can be considered a juvenile antler (Kunst 1937). Kunst (1937) reported on several occasions that the Oosterschelde material resembles *Eucladoceros tegulensis* and *Eucladoceros senezensis*. Kunst (1937: 103) wrote: 'Neben obigen finden sich in Mi. mehrere Fragmente der Stange höher hinauf, welche alle mehr oder weniger seitlich abgeplattet sind; überhaupt analoge Fragmente von *C. teguliensis* oder etwa *C. senezensis* gleich kom-

Table 2 Dimensions of the dental and postcranial *Eucladoceros* material from the Oosterschelde

M3 dex.	DAP	DT		
St 119501	35.3	15.7		
St 118987	30.1	13.8		
M2 dex.	DAP	DT		
	21.5	13.9		
Scapula glenoid cavity	DAP	DT		
St 145846	59.6	45.5		
St 118371	58.7	51.9		
St 119497	46.1	40.0		
St 148545	51.3	31.1		
St 145391	57.7	43.4		
Humerus dist.	DAP	DT		
St 145853	-	68.5		
St 145389	43.6	45.4		
St 119801	-	68.0		
St 146107	-	47.1		
St 118918	-	55.2		
St 119618	-	64.1		
St 146365	-	71.1		
St 118706	-	57.9		
St 118221	49.6	45.6		
Radius prox.	DAP	DT		
St 146071	33.7	62.2		
St 146069	23.6	47.1		
St 118455	32.7	61.4		
Radius dist.				
St 145849	34.2	52.3		
St 118904	33.5	53.3		
St 146439	36.1	58.3		
Ulna prox.	DAP	DT		
St 118696	53.9	16.1		
Cuneiform	DAP	DT		
St 118312	31.3	28.2		
Metacarpal prox.	DAP	DT		
St 146082	35.4	45.8		
Patella			Length	Width
St 118417			62.4	59.6
Tibia dist.	DAP	DT		
St 146064	41.3	53.3		
St 119490	47.1	51.2		
St 118378	43.5	57.5		
St 146033	41.2	48.3		
Calcaneum	DAP	DT	Length	
St 118385	47.6	35.1	129.3	
St 145831 juv	42.1	35.8	122.7	
Metatarsal prox.	DAP	DT		
St 145881	43.4	38.8		
St 152532	39.4	38.1		
St 119470	44.4	37.9		

Table 2 (continued)

Astragali	Length	DAPp	DTp	DAPd	DTd
St 118857	57.1	28.0	32.0	27.7	34.4
St 118391	59.2	25.0	35.5	24.4	34.8
St 118651	67.6	29.6	39.3	29.5	40.6
St 119023	69.4	35.3	40.1	33.4	41.8

men. Z.B. gebogene Stangenstrecken zwischen dritten und vierten Sprosse der genannten Vergleichsobjekte. Ein Stück (Mi. 1622, Stangenfragment mit der Basis eines Seitensprosses) war sogar ausgeprägt oval im Durchschnitt.'

The difference with the *Eucladoceros* cervids (*E. ctenoides, E. sezensis and E. tegulensis*) is according to Kunst (1937 :112): '(...) zu finden in dem Fehlen beim erstgenannten, von der beim letztgenannten normalen, Knickung der Stange hinter dem Augenspross. Wo diese Knickung an den Kempen- oder Roompot-Stangen auftritt, ist ihr Auftreten augenscheinlich bedingt worden von der extremen Schwere der Stange oder des Augensprosses.' This means that the angle between the first tine and the beam is very obtuse. In *Eucladoceros tegulensis* there is not always a backwards curving: the angle between the first tine and the second tine varies from 85°-130°, the type specimen Ha 15776 has an angle of 115° (data taken from Spaan 1992: table 2); the measurements Heintz (1970: table 76) gave for *Eucladoceros senezensis* vary from 65° - 135°; while the type specimen of Lyon has an angle of 90°. However, we concluded above that *Eucladoceros falconeri* is a junior synonym for *Eucladoceros ctenoides* (= *E. tegulensis, E. senezensis).*

The measurements of the material described by Kunst (1937) are given in Table 3 (own measurements). Fig. 14 shows that these dimensions agree with those of the Oosterschelde material. Comparison of the Oosterschelde material with that from Tegelen and Senèze shows that the morphology of specimens St 147224, St 145508 and St 28421 is similar to that of Tegelen specimen St 20685. Fig. 14 shows that the dimensions of the Oosterschelde material agree with those of the *Eucladoceros* material from Tegelen and Senèze, although in Tegelen the first segment is somewhat shorter.

Table 3 Dimensions of the antlers described by Kunst (1937)

Specimen no.	DAP	DT	1st segment	2nd segment
St 28418	80.5	76.8	-	-
St 28420	62.4	65.4	130	-
St 28421	55.9	57.2	94.7	180.0
St 28424	65.1	68.4	-	-
St 28425	52.2	46.8	94.4	-
St 28426	46.4	39.4	70.5	-
St 28428	-	-	96.0	-
St 28430	-	-	-	-
St 28432/27/41	49.3	43.2	83.7	-

The morphological description of the antlers from the Oosterschelde agrees with the morphological description given by Spaan (1992) for the antlers from Tegelen and Heintz (1970) for the antlers from Senèze. As also the dimensions of the Oosterschelde antlers agree with those from Tegelen and Senèze, it it clear that we have to attribute the Oosterschelde antlers to *Eucladoceros ctenoides*.

The dimensions of the postcranial elements of the material from the Oosterschelde are compared with *Eucladoceros* material from various localities and are presented in Figs. 15 - 22. Figs. 15 (second lower molar), 16 (third lower molar), 17 (radius), 18 (metacarpus), 19 (calcaneum), 20 (astragalus), 21 (tibia), and 22 (metatarsus) all show that the Oosterschelde material is well comparable in size with material from Senèze, Tegelen, and other localities. We can thus safely attribute the Oosterschelde postcranial material to *Eucladoceros ctenoides*.

In conclusion, we may say that the material from the large-sized cervid from the Oosterschelde has to be attributed to *Eucladoceros ctenoides* (Nesti, 1841). In dimensions it seems closer to the Senèze material than to the Tegelen material.

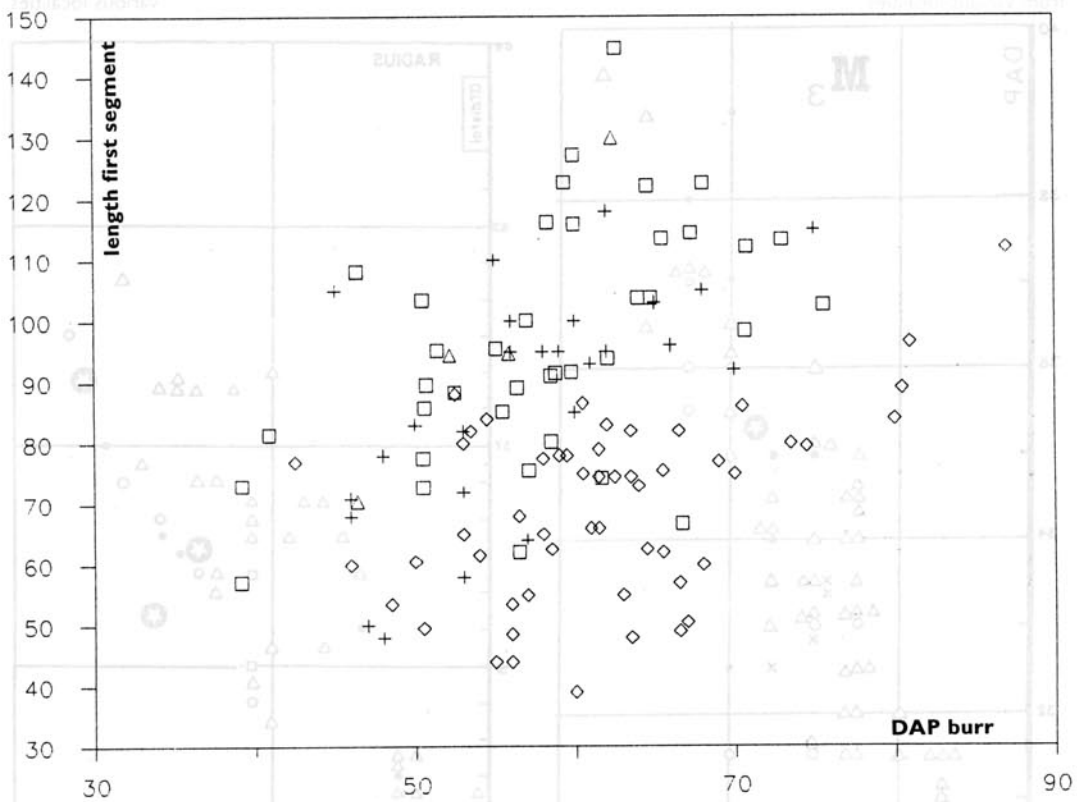
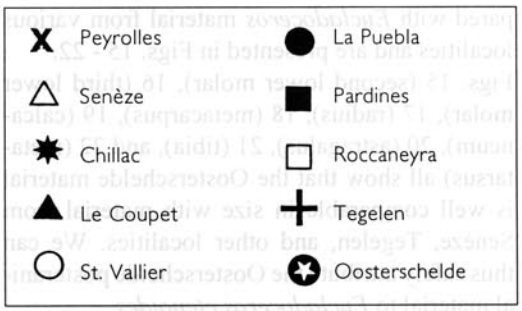


Figure 14 Scatterdiagram of DAP of the burr and the length of the first segment of the antlers of *Eucladoceros* from the Oosterschelde (squares), Tegelen (diamonds), Senèze (crosses)and material measured by Kunst (1937) (triangles).



Legend of symbols used in Figs 15-25

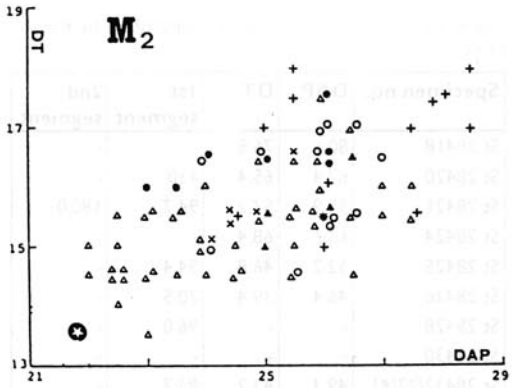


Figure 15 Scatterdiagram of DAP and DT of M_2 from *Eucladoceros* from the Oosterschelde plotted in diagram 3 of Spaan (1992) of the DAP and DT of the second lower molar of *Eucladoceros* from various localities.

Figure 16 Scatterdiagram of DAP and DT of M_3 from *Eucladoceros* from the Oosterschelde plotted in fig. 227 of Heintz (1970) of DAP and DT of M_3 of *Eucladoceros* from various localities.

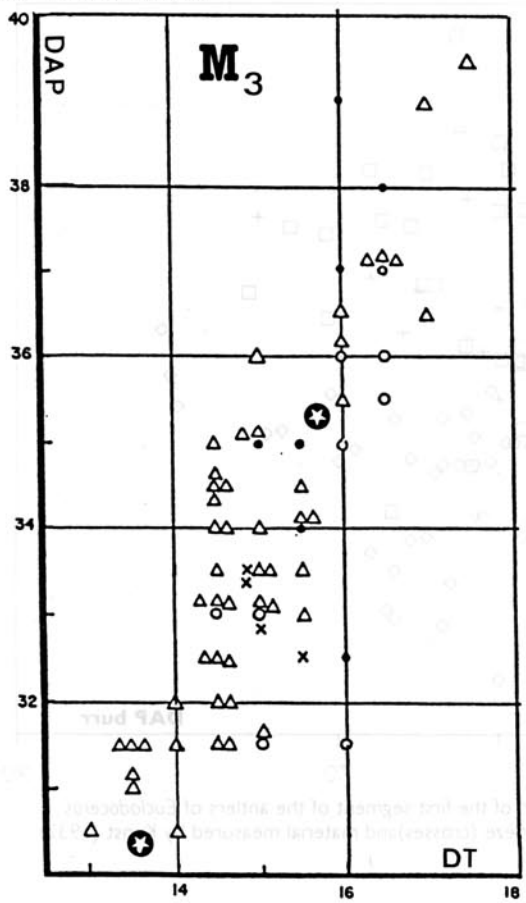
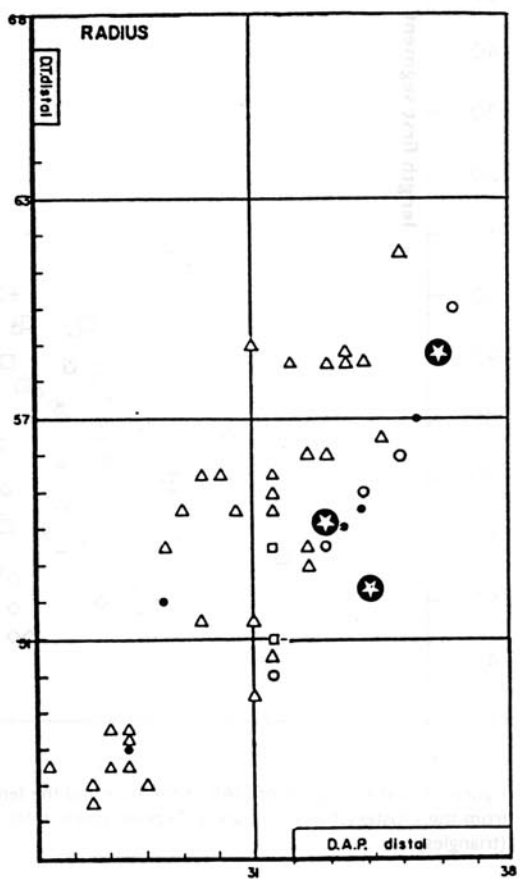


Figure 17 Scatterdiagram of DAP and DT of the distal part of the radius of *Eucladoceros* from the Oosterschelde plotted in fig. 236 of Heintz (1970) of radius DAP and DT of *Eucladoceros* from various localities.



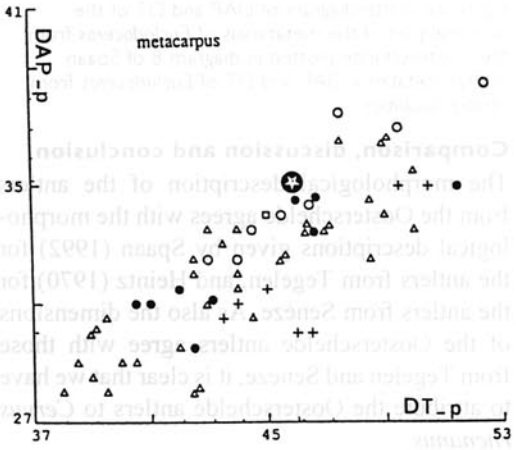


Figure 18 Scatterdiagram of DAP and DT of the proximal part of the metacarpus of *Eucladoceros* from the Oosterschelde plotted in diagram 6 of Spaan (1992) of metacarpal DAP and DT of *Eucladoceros* from various localities

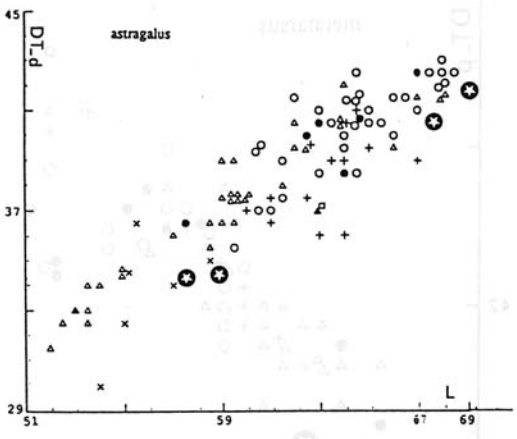


Figure 20 Scatterdiagram of length and DT of the distal part of the astragalus of Eucladoceros from the Oosterschelde, plotted in diagram 7 of Spaan (1992) of these measurements of Eucladoceros from various localities.

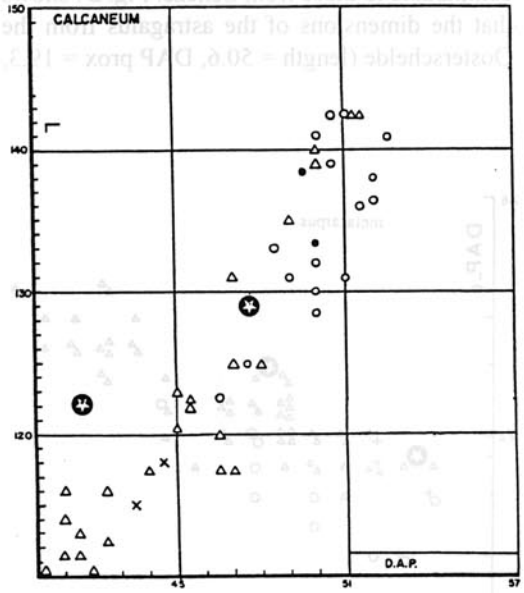


Figure 19 Scatterdiagram of length and DAP of the calcaneum of *Eucladoceros* from the Oosterschelde plotted in fig. 241 of Heintz (1970) of length and DAP of the calcaneum of *Eucladoceros* from various localities.

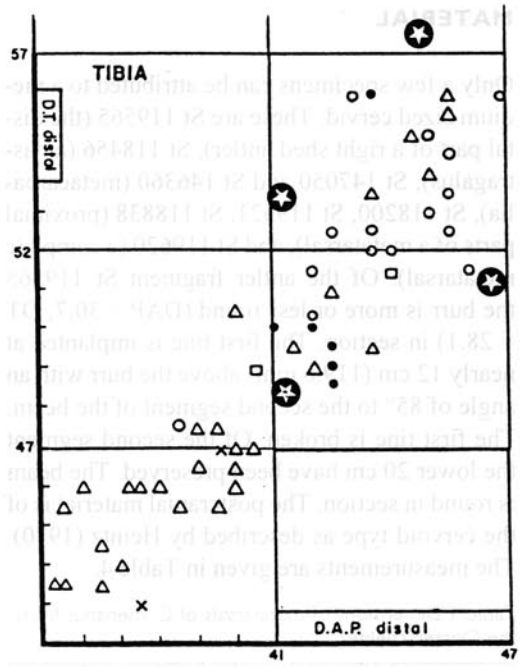


Figure 21 Scatterdiagram of DAP and DT of the distal part of the tibia of *Eucladoceros* from the Oosterschelde plotted in fig. 239 of Heintz (1970) of the same measurements of *Eucladoceros* from various localities.

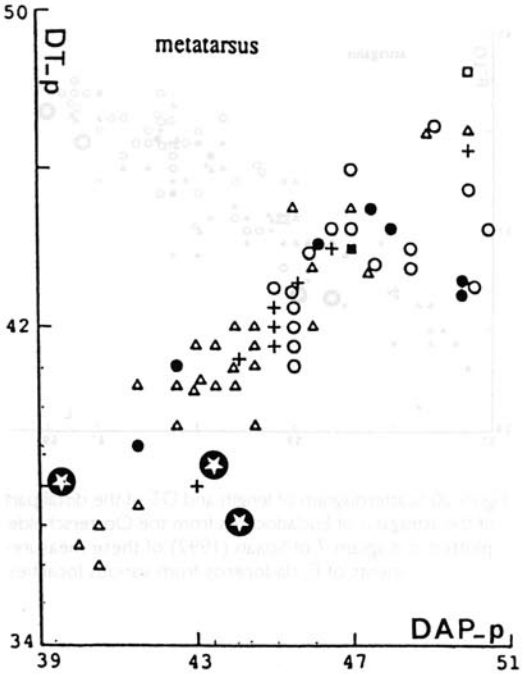


Figure 22 Scatterdiagram of DAP and DT of the proximal part of the metatarsus of *Eucladoceros* from the Oosterschelde plotted in diagram 8 of Spaan (1992) metatarsal DAP and DT of *Eucladoceros* from various localities.

2 THE MEDIUM-SIZED *CERVUS* MATERIAL

Only a few specimens can be attributed to a medium sized cervid. These are St 119565 (the distal part of a right shed antler), St 118456 (an astragalus), St 147050 and St 146360 (metacarpalia), St 118200, St 119621, St 118838 (proximal parts of a metatarsal), and St 119620 (a complete metatarsal). Of the antler fragment St 119565 the burr is more or less round (DAP = 30.7; DT = 28.1) in section. The first tine is implanted at nearly 12 cm (119.6 mm) above the burr with an angle of 85° to the second segment of the beam. The first tine is broken. Of the second segment the lower 20 cm have been preserved. The beam is round in section. The postcranial material is of the cervoid type as described by Heintz (1970). The measurements are given in Table 4.

Table 4 Dimensions of metatarsals of C. rhenanus from the Oosterschelde

Metatarsal	length	DAPp	DTp	DAPd	DTd
St. 118200	-	37.6	32.1	-	-
St. 119621	-	37.1	34.4	-	-
St. 118838	-	37.8	34.8	-	-
St. 119620	265.4	35.7	33.4	25.3	38.1

Comparison, discussion and conclusion

The morphological description of the antlers from the Oosterschelde agrees with the morphological descriptions given by Spaan (1992) for the antlers from Tegelen, and Heintz (1970) for the antlers from Senèze. As also the dimensions of the Oosterschelde antlers agree with those from Tegelen and Senèze, it is clear that we have to attribute the Oosterschelde antlers to *Cervus rhenanus*.

The dimensions of the post-cranial elements of the material from the Oosterschelde are compared with *Cervus* material from various localities and are presented in Figs. 23, 24, and 25. Fig. 23 shows that the dimensions of the two proximal parameters of the metacarpals from the Oosterschelde (St 147050: DAP = 23.2, DT = 32.7 and St 146360: DAP = 21.7, DT = 30.5) are comparable to those from Senèze. Fig. 24 shows that the dimensions of the astragalus from the Oosterschelde (length = 50.6, DAP prox = 19.3,

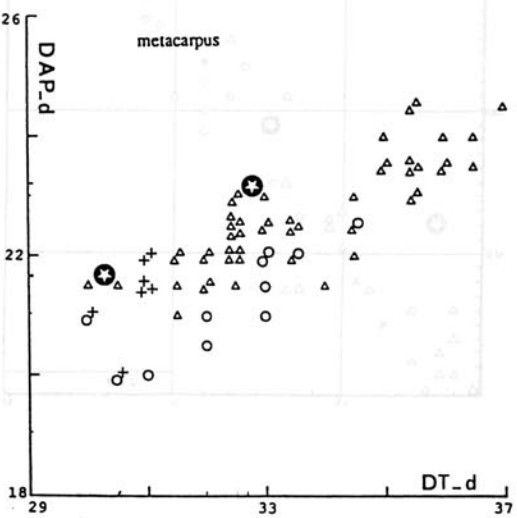


Figure 23 Scatterdiagram of DAP and DT of the proximal part of the metacarpus of *Cervus* from the Oosterschelde plotted in diagram 14 of Spaan (1992) of the same measurements of *Cervus* from various localities.

DT prox = 28.3, DAP dist = 21.4, DT dist = 30.9) are a little larger that the ones from Senèze. Finally, Fig. 25 shows that the dimensions of the metatarsals from the Oosterschelde are also a little larger than those from Senèze.

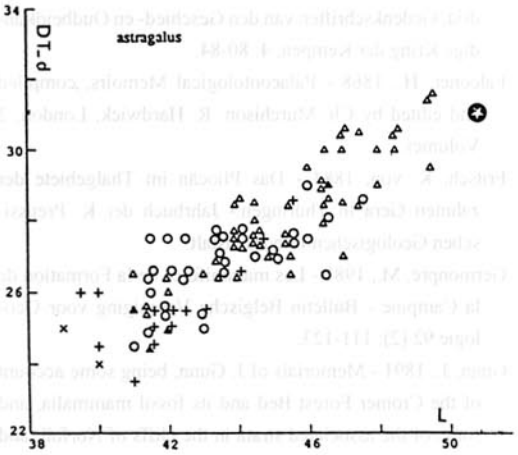


Figure 24 Scatterdiagram of length and DT distal of the astragalus of *Cervus* from the Oosterschelde plotted in diagram 15 of Spaan (1992) of these measurements of *Cervus* from various localities.

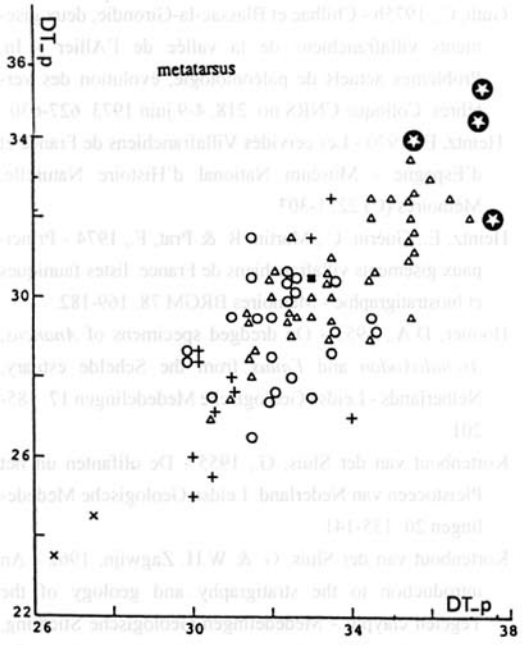


Figure 25 Scatterdiagram of DAP and DT of the proximal part of the metatarsus of *Cervus* from the Oosterschelde plotted in diagram 16 of Spaan (1992) of the same measurements of *Cervus* from various localities.

As the morphology and dimensions of the Oosterschelde postcranial material fit with those of Tegelen and Senèze, the conclusion is confirmed that the medium sized Cervidae from the Oosterschelde belongs to *Cervus rhenanus*.

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