

ON DREDGED SPECIMENS OF ANANCUS,
ARCHIDISKODON, AND EQUUS FROM THE SCHELDE
ESTUARY, NETHERLANDS

BY

D. A. HOOIJER

(Rijksmuseum van Natuurlijke Historie, Leiden)

Last year Prof. Dr. I. M. VAN DER VLERK brought to my attention a collection of fossil remains of mammals dredged up in the East Schelde, province of Zeeland, Netherlands. The fossils were obtained by the SCHOT brothers of the ZZ 8 from the bottom of a through ca. 1500 m long, 200 m wide, and 35 to 45 m deep along the South coast of Schouwen island North of the Roggenplaat, and belong to the municipal museum of Zieriksee. The keeper, Mr. P. VAN BEVEREN, suggested that they be identified. Prof. VAN DER VLERK kindly arranged a short visit to Zieriksee to enable me to select the specimens described in the present contribution, and Prof. Dr. B. G. ESCHER, director of the Geological Museum at Leiden, had the photographs taken at his institution by Mr. W. F. TEGELAAR. This cooperation is here gratefully acknowledged.

The fossils dredged from the East Schelde, as might be expected, are of various ages. Besides remains of mammoth, woolly rhinoceros, bison, and red deer, there are teeth of bunomastodontids and of primitive elephantines. Very similar teeth from the East Schelde have already been described by the late Miss Dr. A. SCHREUDER (1944, 1945a, 1949), who identified them as *Anancus arvernensis* (CROIZET et JOBERT) and *Archidiskodon planifrons* (FALCONER et CAUTLEY) respectively. The fossils thus identified are stained jet black, and for this reason have been referred to as "black fossils" in the Dutch literature (VAN DER VLERK, 1938, p. 10; VAN DER VLERK and FLOR-SCHÜTZ, 1950, p. 63; VAN DER VLERK, 1951, p. 119/120; 1952, pp. 156, 157). They are taken to represent a fauna somewhat older than that of Tegelen in Limburg province (= Upper Villafranchian: SCHREUDER, 1945b), and have been correlated with the Red Crags of England, Upper Pliocene or Lower Pleistocene according to one's own favoured definition of the Plio-Pleistocene boundary.

The most interesting specimens in the collection of the Zieriksee Museum are three molars, two of which unworn, belonging to a brevirostrine bunomastodontid widely spread in Europe but thus far only scantily represented in collections from the Dutch soil:

Anancus arvernensis (CROIZET et JOBERT).

The specimen represented on pl. I figs. 1, 3, 4 (Zieriksee Museum no. 2.0) is a right upper third molar, broken off anteriorly through the fourth ridge

from behind and thus consisting of three ridges, a broken ridge in front, and a low talon. Roots are missing. The crown is unworn as far as preserved. In crown view each ridge is seen to consist of an outer and an inner cone; the inner cone (pretrite in upper molars) is the larger, and has a conule attached to it projecting anteriorly and outward toward the median line of the crown; these central conules are seen to block the transverse valleys of the crown. The pretrite cones are single, as far as the crown cement permits judgment, with the exception of the hindmost that appears to have two transversely placed cones at its apex. Each pretrite cone and central conule are separated from the buccal (posttrite) part of their ridge by a very deep cleft; these median clefts in the transverse ridges and the talon are arranged in a straight anteroposterior line that runs parallel to the inner border of the crown so that the pretrite halves of the ridges are of the same width at their bases throughout. The outer, posttrite, parts of the ridges diminish in width when passing along the crown from front to back; the posttrite part of the hindmost ridge is a single cone only about three-fourths as wide as the pretrite part, while in the third and fourth ridges from behind the posttrite part is fully as wide as the pretrite. This is because of the convexity of the outer margin of the crown, which curves inward posteriorly, especially behind the penultimate ridge. Several structural gradations can be observed when passing along the preserved ridges of the tooth from behind forward, thus: The pretrite as well as the posttrite halves of the ridges, while increasing in height, become more inclined forward anteriorly; the hindmost cones are the most erect. This divergence of the axes of the cones from root to crown is typical of upper molars. The central conules increase in size anteriorly with the pretrite cones to which they belong, and become more firmly attached to them. The posttrite cone, in keeping with its increasing transverse width, is single behind, buds off an inner cone in the penultimate ridge, and is duplicated, forming two equally large cones placed in a transverse line, in the third and fourth ridges from behind. The groove separating the two posttrite cones, however, is only very shallow compared with the main anteroposterior cleft of the crown which latter extends down to the base almost as far as do the transverse valleys. There is hardly any alternation between the pretrite and the posttrite portion of the ridges; although the anterior central conules of the pretrite cones are somewhat pushed obliquely outward toward the median anteroposterior line they do not interlock to any marked degree with the posttrite cones. In the penultimate ridge the pretrite cone is placed somewhat more forward than the posttrite cone; this is less marked in the third and fourth ridges from behind, while in the hindmost ridge no dislocation of the two main cones can be observed. The posterior talon is very low, smoothly rounded off from side to side posteriorly, and consists of one rounded cusp behind the last pretrite cone just internal to the median anteroposterior cleft, and a pair of still less elevated cusps on the posttrite side of the crown. The valleys of the crown seem to be wider on the posttrite side than on the pretrite side; this is due to the greater massiveness of the pretrite cones as compared to the posttrite cones which latter are more straight, conical, and less swollen. The cingulum is only slightly developed; on the outer side it forms a low bulging out with tubercles at the entrances to the valleys between the posttrite cones. This seems to be so along the base of the pretrite cones, too, but this is masked by cement. Cement appears to have been plentiful but is preserved

otherwise in clots in the valleys and on the surfaces of the cones of the second and third ridges from behind only. It is brown in colour, sharply contrasting to the enamel which is black almost all over, being bluish grey in places mostly on the marginal surfaces of the cones of the third ridge from behind, and on the posterior slope of the partially preserved fourth ridge from behind. It appears that this peculiar black staining of the fossil has not penetrated to any great extent into the thick enamel of the cones; wherever the enamel can be seen in cross section it is definitely greyish, not black. The black coloration consequently is only superficial. The roots are missing, but all of the "roof" of the pulp cavity of the molar is exposed. In this unworn specimen it shows the cavities extending into the pretrite and into the posttrite cones, the former are decidedly deeper than the latter. As might be expected from the relative position of the cones on the crown as described above, the pulp cavities become more inclined forward anteriorly, and those of the pretrite cones are also placed more anteriorly than their neighbour posttrite pulp cavities, especially so in the second ridge from behind. Even the small central conules that extend forward and also somewhat outward from the base of the big pretrite cones of the crown do show up as small pointed holes, forming antero-external expansions of the pretrite pulp cavities. It can be seen, again, that due to their presence the main longitudinal cleft of the crown runs somewhat in zigzag fashion. The sharp ridge that represents this anteroposterior cleft is, however, much less dislocated than are the transverse ridges formed by the bottoms of the transverse valleys of the crown. These ridges, which are higher and more blunted than the anteroposterior ridge, make sharp angles as they pass anteriorly around the central conules in each valley, most markedly so in front. Thus, the alternation of the pretrite and posttrite parts of the ridges, however slight, can be studied on the root surface as well as on the crown surface of the present molar.

A fragment belonging to a left upper molar (pl. II fig. 2) is Zieriksee Museum no. 3.0. It is worn and shows the anterior two ridges; it is broken off through the middle of the third ridge from the front. Much of the anterior talon is worn off. The pretrite (inner) cones are much worn down, and are confluent with the central conules antero-buccally. As is the case in the right M³ above described, these central conules block up the transverse valleys and are somewhat squeezed in between the posttrite cones in the median line of the crown, thereby making the longitudinal cleft slightly zigzag in its course. The posttrite (outer) cones are narrower antero-posteriorly at their bases than the pretrite cones, and consequently have wider transverse valleys between them. They are more inclined forward than the pretrite cones; this difference in degree of forward inclination between the inner and the outer cones is most marked in the anterior ridge. The enamel of the posttrite cones of the first and second ridge is produced backward lingually, forming a loop to the transversely elongated enamel figure that is about one-half as large as the enamel figure of the anterior pretrite central conule of the second and the third ridge, and that makes a broad contact with the latter obliquely across the transverse valleys. It appears that the posterior posttrite buttress, like the anterior pretrite central conule, is biggest in the anteriorly placed plates. The pretrite cones do seem to have had a small posterior projection, too, as shown by a slight but distinct incurvation of the enamel in the outer half of the posterior border of the enamel figures, marking off a small lobe that is pressed

against the central conule of the ridge behind. These details could not be brought out in the description of the foregoing right M^3 , but it is probable that this is simply due to the fact that the posterior posttrite and pretrite lobes are most developed in the anterior ridges (missing in the unworn specimen), and that in the ridges of the M^3 dext. preserved these structures are masked by cement. Cement is found in the present worn molar fragment down in the wide outer valleys, and along the outer and inner surfaces, covering parts of the cingulum, which seems most developed lingually.

Parts of the root system are preserved in the present specimen, namely the backwardly curved stump of the anterior outer root, and the bases of the pair of roots supporting the second ridge from the front. Because of damage no further details can be given but that the pretrite root seems to be heavier developed than that on the posttrite side.

Anteriorly, most of the talon is gone as a result of wear; it seems to have had a rather big pretrite cusp. The crown bulges out over the roots to a greater extent anteriorly than on the buccal and lingual sides; the anterior contact facet is extensive.

The enamel of the present molar is black and polished except along the base where it was probably covered with cement. The enamel colour is bluish grey on most of the cingulum, higher up also on the outer slopes of the posttrite cones, and on fractured surfaces, as shown on the posterior surface of the fragment. The dentine exposed on the worn surfaces of the cones is blackish, and so is the crown cement, while the remains of the roots are brown in colour.

The third and last molar of a bunomastodontid in the collection of the Zieriksee Museum is of the lower jaw, M_3 dext. (pl. II figs. 1, 3). Unfortunately it is less well preserved than the M^3 dext., but likewise unworn. It has four ridges, the foremost preserved internally down to its base, at which level the crown is broken off. The cingulum is only partially preserved; on the lingual (convex) surface of the crown it remains only below the anterior two ridges, while on the flattened buccal surface it is left along the base of the second ridge from the front, and below the valleys on either side of this ridge. The talonid of the molar is for the greater part gone, too, but enough is preserved to show that it consisted of a large outer and a small inner cone, with a narrow and deep cleft in between, and thus that it was built on the same general plan as are the full-sized ridges. As in the upper molar, each ridge consists of outer and inner cones, but in the lower molar the outer cones are the higher and are referred to as pretrite cones (in contradistinction to upper molars in which the pretrite cones are placed internally). As in upper molars, the posttrite cones in the present lower molar are narrower anteroposteriorly than the pretrite cones, and consequently have valleys between them that are wider than those opening on the outer surface. Furthermore, the posttrite cones are duplicated, most markedly so in the front ridges. The pretrite cones also have central conules associated with them, but instead of being placed in front (as in upper molars) they are attached to the pretrite cones postero-internally. Moreover, these central pretrite conules do not block the transverse valleys of the crown, this "function" being taken over in the lower molar by the outer cone of the posttrite portion of the ridge, as will be fully described below. The crown ridges are not divergent, but converge toward their apices; the foremost ridge cones are the most erect, and the cones become pro-

gressively more inclined forward when passing backward along the crown.

The posttrite cone and the cone attached to it buccally are placed distinctly in front of the pretrite cone in the foremost preserved ridge; this alternation becomes less distinct in the more posteriorly placed ridges in which the posttrite cone, although still in front of the pretrite at its apex, is better lined up with the latter at the base. In the posterior ridge of the crown pretrite and posttrite cone are placed in a transverse line.

In the present lower molar, as well as in the above described upper molar, there are definite median clefts in each crown ridge (and in the talonid); when seen from the crown these clefts are placed in a straight line parallel to the outer border of the crown which is approximately straight. Thus the pretrite ridge portions are of equal width throughout. (This, of course, is what we found in the upper molar too, the difference being that the straight crown border which parallels the longitudinal median cleft forms the inner border of the upper, and the outer border of the lower molar). The posttrite cones (internal to the longitudinal cleft) become narrower transversely at the base from front to back as the molar narrows behind. The posterior tapering of the crown is more gradual in the present lower molar than in the upper molar above described.

As is the case in the upper molar, the pretrite central conules keep well to the pretrite side of the longitudinal median cleft in the present lower molar. They are placed postero-internally to the pretrite cone, and diminish in size from front to back; in the posterior two ridges they can hardly be seen. On the other hand, the outer cones of the posttrite ridge portions are seen to transgress this longitudinal median line when passing along the crown; they are posttrite behind and pretrite in front, as follows: In the posterior ridge the posttrite cone has a cone that is only slightly smaller attached to it anteriorly and outwardly. This outer cone is pressed against the pretrite cone of the ridge in front of it and thus blocks up the transverse valley, although it remains on the posttrite side of the crown. The penultimate posttrite cone has its twin cone placed more outward than forward, with the result that the latter is wedged in with its outer half between the second and third pretrite cones (counted from behind forwards), and thus is halfway on the pretrite side of the crown, the demarcation line being the longitudinal cleft that borders the big pretrite cones internally. In the third and fourth ridges from behind the now outer cones of the posttrite side are fully pretrite; they are placed in a transverse line with the posttrite cones but are fully wedged in between the pretrite cones. The median longitudinal cleft (fully exposed in the front surface of the foremost preserved ridge) is just internal to them. These outer cones of the posttrite ridge portions, though placed between the pretrite cones, remain distinct from the pretrite cone in front as well as from that behind down to the base of the crown. Their association is definitely with the posttrite cone, as is also evident from the inspection of the partially preserved roof of the pulp cavity. Below the posterior two ridges, the pits representing the anterior and outer of the twin posttrite cones are separated from those representing the main posttrite cone only by a slight elevation, while they are marked off from the pits representing the big pretrite cones by ridges that are decidedly higher, indicating that the cones in question are most firmly attached at their bases to the posttrite main cones. The postero-internal projections of the big pretrite cones, as said above, can be observed only in the anterior ridges; the most posteriorly placed pretrite cone is single.

The cingulum is very distinct buccally, it is not less than 16 mm high and forms a rounded ledge, 5 mm in thickness. As shown in the buccal view (pl. II fig. 3) its surface is finely crimped horizontally. It forms little knobs at the entrances to the transverse valleys between the pretrite cones. Most of the cingulum is broken off, but what is preserved on the lingual side shows that it was less developed lingually than buccally.

Cement, as far as preserved (mainly in the least exposed grooves of the anterior ridges) is, again, brown in colour. The enamel is black only on the outer surfaces of the cones and on their tips; on most of the surface of the posttrite cones, however, the black enamel colour is gone. As the anterior and posterior slopes of the valleys are bluish grey (the colour also displayed on broken edges of the enamel of the cones, talonid, and cingulum) it would seem that this black staining did not affect the enamel once covered with cement. What is preserved of the roots, namely a narrow wall at most 2 cm high along the posterior and buccal margin, is brown.

The state of preservation of the three bunomastodontid teeth from the Zieriksee Museum above described differs somewhat from that of the earlier found proboscidean molars, dredged from the East Schelde off the coast of Zuid Beveland near Ierseke (SCHREUDER, 1944, 1945a, 1949) in being less thoroughly black. Although Miss SCHREUDER in her description carefully stated that the black enamel is stained with many colourless spots best to be seen at fractured surfaces, the Ierseke molars have definitely black crown cement and roots, thus making the teeth as a whole more black than are the three molars above described in which cement and dentine are brown.

The M^3 dext. dredged from the East Schelde near Ierseke preserved in the Geological Museum at Leiden (no. 56478) described and figured by SCHREUDER (1944) is more complete than the M^3 dext. here described in so far as the front ridge and anterior talon are (partially) preserved, but all of the cingulum of the Ierseke molar is gone, and the anterior three ridges are worn. As far as the preserved and comparable parts go, the Zieriksee M^3 differs from that of Ierseke (SCHREUDER, l. c., pl. III figs. 1—2, textfig. 1), in the less development of the central conules anterior to the pretrite cone, and especially in the simpler build of the posttrite ridge portions and their greater relative height. In the Ierseke molar the central conules (anterior pretrite buttresses) are as high as the pretrite cones to which they belong (this, of course, can be seen in the unworn posterior ridges only), while in the present unworn M^3 the central conules are all lower than the pretrite cones. Furthermore, the posttrite ridge portions in the M^3 described by Miss SCHREUDER (l. c.) consist of at least three cones, one outer, one inner, and one or two little cones wedged in between them, while, as we have seen above, the present M^3 has only two cones on the posttrite side in the fourth, third, and second ridge from behind (the inner posttrite cone smaller than the outer in the last mentioned ridge), and one isolated posttrite cone in the ultimate ridge. Consequently, the posttrite ridge portions are more extended transversely in the Ierseke M^3 previously described by Miss SCHREUDER than they are in the present specimen. The innermost cones of the posttrite ridge portions are pressed against the big pretrite cones, or rather against the outer (central) division of the pretrite cones, in the Ierseke molar, thus making the anteroposterior median cleft less distinct than it is in the specimen now at hand. Moreover, there is hardly any

difference in height between posttrite and pretrite cone in each of the two unworn posterior ridges in the Ierseke molar; in our specimens the pretrite cones are distinctly the higher (table 1).

TABLE 1. *Anancus arvernensis* (CROIZET et JOBERT).

No. of ridge from behind:	M ³			M ₃		
	Width	Height		Width	Height	
		pretrite	posttrite		pretrite	posttrite
fourth	—	—	—	—	64	61
third	79	67	62	77	63	58
second	77	68	63	72	58	56
first	67	64	56	—	52	48

The differences observed between the M³ from the East Schelde described by SCHREUDER (1944) and that above described, however, do not amount to very much with a view to the great overall resemblance; both last upper molars show a slight alternation of pretrite and posttrite ridge portions, mainly in the anterior part of the molar where the pretrite central conule is somewhat pushed outward between the innermost posttrite cones, thereby blocking up the transverse valleys. Further resemblances to be stressed are that these central conules are most developed in the anteriorly placed ridges, and that posterior pretrite buttresses cannot be observed except in the foremost ridge of the Ierseke molar (missing in the above described M³), and not in the remaining ridges. I found posterior pretrite buttresses only in the worn upper molar of the present collection (above, p. 187). There is a weak posterior enamel projection on the posttrite cone, too, in the fourth ridge from behind in the Ierseke molar; this was also observed in the worn upper molar, and such a small lobe may well be hidden below the cement in the unworn M³.

The alternation of the pretrite and the posttrite ridge portions of the molars, more pronounced in the lower last molar than in the upper last molar, as I have just described, is highly characteristic of the earliest as well as of the latest members of the species *Anancus arvernensis*. This species has a wide range both geographically and temporally. It ranges all over Europe, including Russia (SCHLESINGER, 1917, p. 142), and we find it from the post-Pontian of Austria and Hungary, where temporally it succeeds *Tetralophodon longirostris*, up to Red Crag of England, the hauts-niveaux de Perrier, and Chilhac near Senèze in France, where it is associated with *Archidiskodon (meridionalis)* (SCHAUUB, 1944, p. 275), and thus *Anancus arvernensis* is as characteristic of the Pliocene as it is of the Villafranchian. There is a great deal of variation in the molars from the Levantin (Middle Pliocene) of Austria and Hungary described by SCHLESINGER (1917, 1922) as typically *Anancus arvernensis*, and all the characters of the Zeeland molars can be matched in their homologues figured in these monographs (e. g., M³ dext.: SCHLESINGER, 1922, pl. X figs. 4—6; worn M¹: *ibid.*, pl. XI fig. 4; M₃ dext.: *ibid.*, pl. XI fig. 2 (not sin. as stated in legend to this fig.), pl. XII fig. 3b). The variation in these Pliocene molars is so wide as to include

specimens that are as small as the Zeeland molars, although most of the Eastern European specimens are larger than the latter.

Various names have been given to the European *Anancus* (see OSBORN, 1936, pp. 632—640); the Astian form from Montpellier in France is known as *Anancus arvernensis brevisrostris* (GERVAIS et DE SERRES) and is stated to be more brachyodont and simply built than the form from the English Craggs, which latter was separated by OSBORN (l. c., p. 636) as *A. falconeri*. This species, based on an almost unworn M_3 sin. described and figured by FALCONER (1868 II, p. 31, pl. 4 figs. 3—4) is stated by OSBORN to be more strikingly hypsodont and to have the summit of the crown more closely compressed than typical *Anancus arvernensis* from Auvergne (Perrier). The comparison, however, is somewhat difficult to make since height measurements of the crowns are necessarily omitted in most descriptions, and, if given, are not exactly comparable. It seems doubtful whether there is an evolutionary advance in hypsodonty in *Anancus arvernensis* in the course of its stratigraphic range from the post-Pontian up to the Lower Pleistocene, a point to be decided upon a first-hand study of all the material on hand. The variation in molar size within one and the same species of mastodonts is considerable: LEHMANN (1950, p. 199) observes that the M^3 of *Trilophodon angustidens* varies from 114 to 187 mm in length, and from 58 to 97 mm in width, and in *Anancus arvernensis* a similarly wide variation, notably in the development of the cingulum and in the crown width of the molars, has been observed (SCHLESINGER, 1922, p. 261). Consequently, the molars dredged from the East Schelde cannot be accorded a certain evolutionary stage within the species *Anancus arvernensis*, and they do not furnish a clue as to their exact stratigraphic position. In Upper Villafranchian faunas such as that of Senèze (SCHAUB, 1944) and Tegelen (SCHREUDER, 1945b) *Anancus arvernensis* does not occur any more, and thus the Lower Villafranchian seems to be the upper limit of the range of this bunomastodontid.

Archidiskodon meridionalis (NESTI) or *A. planifrons* (FALCONER et CAUTLEY).

The Zieriksee Museum collection contains further a number of molars, one of which complete, that belong to an archidiskodont elephant:

The specimen marked 1.0 comprises five plates of a right upper molar and an additional half-plate on the lingual side behind, all unworn and broken off at the base. The fragment is almost perfect otherwise (pl. II figs. 4, 5). The preserved plates are very similar in size and build, broad transversely at their bases with the buccal and lingual edges somewhat convex from above downward in the basal third, then straight and converging to their apices which carry from four to six conelets in a transverse space which is just a little less than half the width of the plates at the crown base. The (unworn) apical parts of the plates are convex transversely but the conelets are of equal size throughout. There are four of them in the foremost plate, five in the second plate from the front, six both in the third and in the fourth plate from the front, and five again in the fifth plate from the front (two of which broken). On all of these plates there is plentiful cement covering the anterior and posterior surfaces, but the buccal and lingual edges of the plates are exposed, and so are most of the conelets. On the broken half-plate behind, which is placed lingually, there were two, or possibly three, conelets only.

The plates of the crown become more inclined forward when passing

along the tooth from behind forward; this divergence of the plates from the base to the apex of the crown is typical of an upper molar. Furthermore, the plate edges form a straight anteroposterior line at one side of the crown base, while the other side of the crown base is convex anteroposteriorly; the convex surface is the buccal surface. This determines the molar as belonging to the right side of the upper jaw. There is seen some dislocation in the plates, most pronounced behind; the anterior plates, though most inclined forward, are straight throughout from base to top when seen from the buccal or from the lingual surface, but the fourth plate from the front is somewhat S-shaped seen from the lingual side, convex to the front in its basal half and concave to the front in its apical half; the lingual part of this plate moreover is placed a little forward relative to the buccal part. In the fifth plate from the front this dislocation is more marked, and to its lingual half the extra half-plate is attached behind, which latter, so to say, has been made room for by the forward displacement of the lingual half of the ultimate preserved full plate. When seen from behind, the posterior half-plate passes smoothly into the buccal half of the plate in front of it, but it is free at the apex, and would count as a full plate when seen from the lingual side only. Similar extra half-plates are well-known individual aberrations in the molars of archidiskodonts as well as in more advanced elephants. The dislocation can also be observed on the root surface of the present specimen (pl. II fig. 4), which shows the bases of the transverse valleys of the crown as continuous ridges, highest in the median line anteriorly, but subdivided by a median depression in the posteriorly placed ridges; the ridge on the root surface formed by the valley between the posterior half-plate and the lingual half of the fifth plate from the front terminates abruptly in the median line. The alternation of the half-ridges and valleys in this part of the crown reminds somewhat of the structure observed in *Anancus* molars.

The present molar fragment has five full plates that vary in width at the base only from 111 to 116 mm, and in total (unworn) height from 124 to 126 mm, with only four to six conelets to each plate occupying a transverse space of 50 to 55 mm. It evidently represents the middle portion of a last upper molar of a primitive member of the *Archidiskodon planifrons-meridionalis* line or lines in which the crowns of the ultimate molars are about as high as wide, and in which there are fewer plates per 10 cm of anteroposterior length than in more progressive forms. In the present right M^3 the height-width index is 107 to 113, and the laminar frequency is 5 at the crown base but slightly over 4 ($4\frac{1}{4}$, to be exact) at the apex of the crown, due to the divergence of the plates from base to top. The enamel thickness, as seen in the posterior plates, is 3 mm, and the enamel colour is black as far as exposed; where the cement has been removed artificially it is bluish grey. Cement is brown in colour all over.

A second fragment of an upper last molar (Zieriksee Museum, no. 10.0) is worn and consists of the anterior four ridges plus most of the large anterior talon of an M^3 sin. (pl. I fig. 2). There is very much cement on this specimen, concealing the outer and inner slopes of the plates and filling up the valleys. Roots are preserved for the most part. The enamel figures are very distinctly marked, their jet black colour contrasting with the grey cement. Behind the hindmost preserved full plate are seen the buccal two conelets of a plate just touched by wear; the remainder of this plate is gone. The fourth, third, and second plates from behind all show buccal and

lingual transverse ovals, increasing in size with progressing wear anteriorly, and smaller median enamel figures, three in the hindmost plate, all annular, and two in the third and second plates. Irregularities here observed are a median anterior point in the third plate from behind, and a median posterior projection in the second plate from behind, almost making a contact across the valley separating these two plates, while there is a small intermediate conule that blocks up this valley on the lingual side. The anterior full plate has a single enamel figure, all the conelets being worn out, that is somewhat irregular in shape: convex behind in its lingual half, constricted in the middle, and directed slightly backward buccally. This figure is confluent with the anterior talon in the median line: this talon does not extend inward to the lingual crown border, although on the anterior inner angle of the crown there are three enamel pillars that may have become confluent with the talon upon further wear, and has a concave wear facet in the middle third of its anterior surface.

Because of the excessive development of cement on this specimen the width of the enamel plates at the crown base and the boundary between crown and root cannot exactly be determined. The width of the enamel figures shown on the masticatory surface varies from 76 to 89 mm, but this is not the greatest width of the crown. If the intermediate lingual conule between the third and second plates from behind is included, the width of these plates amounts to 97 mm, while the maximum width of the molar, including the cement buccally, is not less than 115 mm; the same width we found for the foregoing M^3 dext. exclusive of cement. The laminar frequency on the masticatory surface is $4\frac{1}{2}$; intermediate between that of crown base and apex in the foregoing specimen. Further measurements cannot be given.

Like the former, the latter molar fragment is by far too incomplete for its ridge-plate formula to be determined, but its great width points to a last upper molar. As such, the two above described molar fragments are well within the variation limits of the last upper molar of *Archidiskodon meridionalis* (NESTL) as determined by WETHOFER (1890) on the base of specimens from the Val d'Arno in Italy; the Italian M^3 's vary in width from 100 to 120 mm (a width less than 100 mm is rare), and in height of the crown from 120 to 140 mm (WETHOFER, 1890, p. 171). The laminar frequency, which has been thought to be of value in separating "primitive" from "progressive" stages in the Eurasiatic archidiskodonts, will be discussed after the remaining molars in the present collection have been described.

A fragment of an upper or lower molar, containing half of a worn plate, a cement-filled valley, and a portion of another plate (Zieriksee Museum, no. 9.0) has the plate and the adjoining valley contained in 25 mm of antero-posterior length and thus has a laminar frequency of 4, slightly lower even than that in the two M^3 fragments.

A heavily worn upper left molar (Zieriksee Museum, no. 5.0) bears seven plates, all worn down to single transverse enamel figures and somewhat curved backward at either end, in an anteroposterior length of 107 mm; one plate may be lost in front. The buccal and lingual sides have a thick cement coating, and the width is 87 mm inclusive of this cement; the enamel figures are at most 75 mm wide. The enamel thickness of the plates is at most 2 mm, and the laminar frequency, measured on the masticatory surface, amounts to not less than $7\frac{1}{2}$.

Although the exact length and the number of plates cannot be deter-

mined, the width of the present molar points to the first upper molar; the M^1 of *Archidiskodon meridionalis* varies from 64 to 88 mm in width (POHLIG, 1888—91, pp. 130 and 131).

Much better preserved is an M^1 dext. (Zieriksee Museum, no. 4.0) which is complete from front to back; it has seven plates as well as anterior and posterior talons. Wear has progressed to the fourth plate only, and the enamel rings on the apices of the worn plates shows them to have had five or six conelets. The second plate from the front is somewhat expanded in the median line posteriorly; this is not seen in the plates in front or behind. Cement fills up the valleys completely but does not extend over the buccal or lingual edges of the plates although it covers up the unworn conelets of the plates in the back half of the tooth. The plates diverge slightly from base to their apices and are superficially injured laterally. Roots are missing but the crown base with the ridges representing the transverse valleys is preserved well enough for the height of the crown to be taken. The total length of the crown is 143 mm, the greatest width (at plates 4 and 5 from the front) is 74 mm, which makes the width-length index 52. The total height at the same level is 98 mm, which makes the height-width index of this molar 132. Thus, the present molar is distinctly higher than wide, in contradistinction to the M^3 above described. However, the present M^1 is not even too high for *Archidiskodon planifrons* from the Upper Siwaliks of India (OSBORN, 1942, p. 954, cites an M^1 80 mm wide and 107 mm high, giving a height-width index of 134), while it is also fully within the variation limits of the European *Archidiskodon meridionalis*; two specimens of M^1 cited by POHLIG (1888—91, p. 130) are 88, resp. 68 mm wide, and 83, resp. 97 mm high, giving height-width indices of 94 and 142 respectively. It should be added that the laminar frequency of the present East Schelde M^1 is $5\frac{1}{2}$ at the apex of the crown against 6 at the base, while OSBORN's *A. planifrons* M^1 's from the Siwaliks are stated to have laminar frequencies ranging from $3\frac{1}{2}$ to $4\frac{1}{2}$ only (OSBORN, 1942, p. 954). This would exclude *A. planifrons* were it not that OSBORN (l.c.) further lists an M^3 with a laminar frequency of $5\frac{1}{2}$ —6 as belonging to *A. planifrons* too; if last molars with so high a laminar frequency are found in the Upper Siwaliks we can certainly expect a laminar frequency of $5\frac{1}{2}$ —6 for first molars, too, for the laminar frequency is normally higher in the first than in the last molars. The number of plates observed in the present complete M^1 , seven (plus the talons), is consistent both with *A. planifrons* (LYDEKKER, 1880, p. 277) and *A. meridionalis*, in which latter this number ranges from seven (POHLIG, 1888—91, p. 130) to nine (WETHOFER, 1890, p. 154).

It seems evident that the above mentioned M^1 could be identified as *A. planifrons* or as *A. meridionalis* with equal justice, and this makes it important to decide where exactly the boundary between the two species should be drawn. There is no doubt that the skulls are distinct, but in the absence of cranial material the distinction between the Siwalik and the European species becomes a matter of dispute, as there appears to be a great overlap in dental characters between the two. LYDEKKER, for one, states that the molars of *A. planifrons* usually so closely resemble those of *A. meridionalis*, "that if they both occurred in the same area it is more than doubtful if they could be specifically distinguished" (LYDEKKER, 1886, p. 107). The only difference LYDEKKER observed in the molars is the rather higher average figures for the ridge-plate formulas in *A. meridionalis* as compared with *A. planifrons*. Another primitive feature in the Siwalik species is the pres-

ence of premolars (FALCONER and CAUTLEY, 1845, pl. 6 figs. 4—6, pl. 12 figs. 8—11) not found in *A. meridionalis* of Europe but recorded in *A. imperator* LEIDY from Chapala, Mexico (PONTIER and ANTHONY, 1933). If this observation is correct, and if the American Pleistocene *Archidiskodon* is a direct descendant of *A. meridionalis* as held by OSBORN (1942, pp. 982, 996, 1037); we might of course expect to find premolar succession in the latter species also.

Archidiskodon planifrons has come to be recognized in Europe since 1912, when SCHLESINGER (1912) described a fragment of an M_3 sin. from Dobermannsdorf, Austria, as belonging to this species. The primitive characters stressed by SCHLESINGER, notably the widely spaced plates, the presence of enamel loops forming median expansions of the plates, the prominence of the enamel figures above the level of the cement, and the relatively low crown, are well taken; in all these points the Austrian specimen resembles the Siwalik molars of *A. planifrons* closely. In a subsequent paper (SCHLESINGER, 1913) a more perfect specimen of M_3 sin., originating from Laaerberg, Austria, is ascribed to *A. planifrons* too. The latter species furthermore is indicated among the material from the Upper Val d'Arno described as *A. meridionalis* by WEITHOFER (1890, pl. XI figs. 2 and 4, see SCHLESINGER, 1912, p. 101; 1913, p. 731). Again, there is nothing in these specimens that differentiates them from the Siwalik specimens of *A. planifrons* with which SCHLESINGER (1912, 1913, 1916) very carefully compared them; of special interest is the presence of median posterior loops to the enamel figures of the lower molars, characteristic of *A. planifrons* (SCHLESINGER, 1913, figs. 5—6) and not seen in typical *A. meridionalis* (SCHLESINGER, 1912, pp. 101 and 106), and the height of the crown, which is less in *A. planifrons* (up to 116.5 mm. in M_3) than in *A. meridionalis*. Passing mention is made by SCHLESINGER (1916, p. 129) of the fact that the length-lamella quotient of M_3 (length of molar divided by number of lamellae, thus indicating the average thickness of one plate plus one cement interval) is always over 25 in *A. planifrons*, and less than 25 in *A. meridionalis*, in other words, that the laminar frequency (number of plates in 10 cm of anteroposterior length) is less than 4 in *A. planifrons* and over 4 in *A. meridionalis*. This dividing line was taken up again by DEPÉRET and MAYET (1923), who separated last molars with laminar frequencies of $3\frac{1}{2}$ —4 as *A. planifrons* (as occurring in a skeleton from Chagny, France), and further distinguish a number of ascending mutations of *Archidiskodon meridionalis*, beginning with the archaic mutation (laminar frequency of M_3 $4\frac{1}{2}$), followed by the typical mutation (laminar frequency of M_3 5), the Saint Prestian mutation (laminar frequency of M_3 $5\frac{1}{2}$), and finally the Forest Bed form or Cromer mutation (laminar frequency of M_3 6— $6\frac{1}{2}$). The archaic form of *A. meridionalis*, no ridge-plate formula of which is given, is barely differentiated from *A. planifrons*, however, which latter species reaches laminar frequencies higher than 4 in a number of last upper as well as lower molars. We do occasionally find *A. planifrons* M^s 's and M_3 's having length-lamella quotients below 25 (SCHLESINGER, 1913, pp. 728—729) or laminar frequencies even up to $5\frac{1}{2}$ and 6 (OSBORN, 1942, p. 954), and there evidently is a broad zone of overlap in these figures between the two species. One might even argue that if in Europe we identify any M^s or M_3 with a laminar frequency up to and including 4 as *A. planifrons*, we should by the same principle identify any Siwalik M^s or M_3 that has a laminar frequency higher than 4 as *A. meridionalis*. This is, in fact, what OSBORN (1942, pp. 949 and 954) did when

he placed the Siwalik molars described by FALCONER (1868) and those of the Barnum Brown Siwalik collection in the American Museum under the head: "*Archidiskodon planifrons*, ascending to *A. meridionalis*". Following DEPÉRET and MAYET (1923) it was PONTIER (1924) who identified a molar from the Red Crag of England as *A. planifrons*. STEHLIN (1923) observed that the archidiskodon from Senèze odontologically resembles the most primitive *A. meridionalis* from the Val d'Arno referred to *A. planifrons* by DEPÉRET and MAYET, but is against the application of the latter name for European archidiskodonts as long as a stratigraphical separation between the primitive and the more progressive types has not been proved to exist. In this he is followed, e. g., by SCHAUB (1948, p. 109, footnote), who points out further that premolar succession, the most distinctive *A. planifrons* character, has never been observed in Europe as yet.

In the opinion of DIETRICH (1942, p. 74), *Archidiskodon* is a difficult genus, in which isolated molars can hardly be correctly identified as to the species. *A. planifrons*-like molar fragments have been recorded under many different names from South, East, and North Africa (see ARAMBOURG, 1938, p. 17; DIETRICH, 1942, p. 72; OSBORN, 1942, p. 986; ARAMBOURG, 1948, p. 270). In these cases it is more doubtful even than it is with the material from Europe whether *A. planifrons* or perhaps some other equally primitive archidiskodont species is actually represented. ARAMBOURG has recently separated the Lower Villafranchian, *A. planifrons*-like molars from North Africa as *Elephas africanavus* (ARAMBOURG, 1952, p. 407); this form is succeeded in the Upper Villafranchian by *Elephas* aff. *meridionalis* (ARAMBOURG, l. c., pp. 410 and 417). In the former the last lower molar is about as high as wide, and has a laminar frequency of $3\frac{1}{2}$, while the Upper Villafranchian form has last molars that are distinctly higher than wide, and laminar frequencies of 4, and $4\frac{1}{2}$ —5. Thus, there is a parallel to the series of ascending mutations as distinguished in Europe by DEPÉRET and MAYET (1923). At any given time and locality, however, there must have been a number of individuals that vary in molar structure and size among themselves, and for this reason it seems more than doubtful whether such fine distinctions as proposed by DEPÉRET and MAYET can really be made to any advantage, or whether they are stratigraphically separate. In the Red Crag of England, beside *A. planifrons*, we find last molars in which the laminar frequency is $5\frac{1}{2}$ (OSBORN, 1942, p. 981), figure supposedly typical of the Saint Prestian mutation. Third molars from the Cromer Forest Bed, according to BERNSEN (1930), vary in laminar frequency from 4—6, and thus include even the archaic mutation of DEPÉRET and MAYET. It is evident that a single molar is not a safe indication for the stratigraphic relationships of the horizon from which it came, the differences between the archidiskodont molars from successive strata being rather of an average sort. There is no definite break in the series, either in India or in Europe, at which the boundary line between *A. planifrons* or *A. meridionalis* can conveniently be placed.

HOPWOOD (1935, p. 88) diagnoses *A. planifrons* as follows: "An *Archidiskodon* with nine to ten plates in the third upper molars; lamellar frequency 3—4". We should bear in mind, however, that if we restrict *A. planifrons* to last molars with a laminar frequency up to 4, we do so completely arbitrarily, as no sharp distinction between the molars of *A. planifrons* and *A. meridionalis* can be made, and all we observe is a gradual transition from low-crowned to high-crowned molars that have more plates per 10 cm than the former. On the base of the molars, it seems justified to speak of the

Archidiskodon planifrons-meridionalis phyletic line, or lines, observed in the Upper Siwaliks as well as in Europe and North Africa.

The incomplete M_3 sin. dredged from the East Schelde near Ierseke described by SCHREUDER (1944) and identified by her as *A. planifrons* has the greatest crown height (126 mm) only slightly exceeding its width (117 mm), and the laminar frequency is 4 (SCHREUDER, l. c., p. 51); the total number of plates is estimated to be nine. Thus, this last lower molar is just on the arbitrary limit between *A. planifrons* and *A. meridionalis*. The two fragmentary last upper molars from the East Schelde South of Schouwen Island above described are slightly more advanced in that the laminar frequency of the unworn specimen is just over 4 at the apex, and 5 at the crown base, and that of the worn specimen is $4\frac{1}{2}$, i. e., the figure for DEPÉRET and MAYET's archaic mutation of *A. meridionalis*. The relative crown height of the unworn M_3 of the present collection is very much the same as that of the M_3 described by SCHREUDER (1944), however. These specimens, the ridge-plate formula of which cannot be given, could be either *A. planifrons* or *A. meridionalis*, and the same holds for the anterior molars (M^1), as we have already stated above. As the present material is not sufficiently characteristic to make a decision one way or the other, it has been thought advisable to leave it specifically undetermined, and to record it under the head *A. meridionalis* or *A. planifrons*.

Equus cf. *robustus* POMEL.

Among the remains of horses dredged from the East Schelde South of Schouwen island and preserved in the Zieriksee Museum there are two third metatarsals which differ from the other bones in being heavily fossilized and thoroughly black in colour. These bones may, therefore, be taken to represent the "black" fauna. Unfortunately, neither of the bones is complete. The distal end of the left specimen (Zieriksee Museum, no. 36.0) is lost, and the right (Zieriksee Museum, no. 39.0) is injured proximally and distally; its length, however, can be approximately given as most of the distal sagittal ridge is preserved behind. Although this seems somewhat inadequate material on which to base a specific determination of the horse from the "black" fauna, it appears that the dimensions of the bones in question agree well with those of *Equus robustus* POMEL, olim *E. stenorhis* race *major* BOULE (1900, p. 539), and exceed those of true *Equus stenorhis* COCCHI, with which the larger species is associated in the Villafranchian of France and Italy (HOPWOOD, 1936, p. 909). In the Upper Villafranchian

TABLE 2

Metatarsal III	<i>Equus</i> cf. <i>robustus</i> Zieriksee Museum nos. 36.0 39.0	<i>Equus robustus</i> SCHWARZ, 1927, pp. 435—436.	<i>Equus stenorhis</i> MAJOR, 1880, pp. 74—75.
Total length	— ca. 285	271—320	229—281
Proximal width	59 59	—	41.5—53.5
Least width	41 39	34.5—42.5	—

fauna of Tegelen only the larger of the two species had thus far been found (BERNSEN, 1931; SCHREUDER, 1945b, p. 192; HOOLJER, 1947, p. 40), and the same is true for the Norwich Crag in England with which the Tegelen fauna has been correlated. Thus, the horse of the "black" fauna appears to be the same as that of the Tegelen fauna.

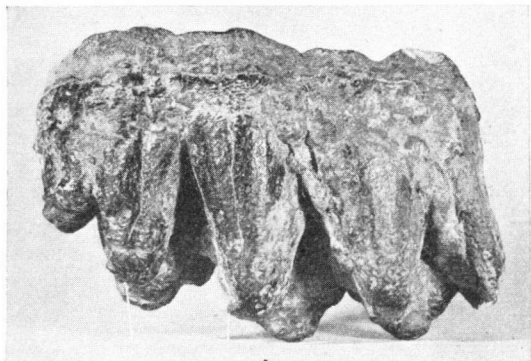
The purpose of the present paper has been to put on record the "black" mammalian fossils dredged from the East Schelde since Miss SCHREUDER's latest (1949) paper on the subject. There is every reason to abstain from a precise age determination of the "black" fauna from the East Schelde as long as it consists of isolated dredged specimens whose association is uncertain. The *Anancus* molars could be of any age from the post-Pontian upward into the Villafranchian, and the *Archidiskodon*, although characteristically Villafranchian, gives no clue to which subdivision of the Villafranchian it belongs. *Equus robustus* occurs in the Red Crag, Norwich Crag, and in the Cromer Forest Bed of England (HOPWOOD, 1936), and thus could be Villafranchian as well as Saint Prestian in age. The metatarsals referred to above are the first *Equus* remains to be recorded from the "black" Schelde fauna.

It has also been shown that the *Anancus* and *Archidiskodon* molars of the present collection are less thoroughly black than those first described by Miss SCHREUDER. The molars dredged near Ierseke are black not only on the enamel surface but also on that of the cement, while the specimens from South of Schouwen Island have only the enamel black, while cement and dentine are brown. There appear to be local differences in degree to which the fossils are affected by this black staining, which makes us even more careful in using the black coloration as evidence of contemporaneity. If the "black" fossils thus far described are really unified as to age, they would make up an assemblage that is to be dated as Lower Villafranchian, correlative with Chagny, Perrier, and the Red Crag of England, as already stated by SCHREUDER (1949, p. 413).

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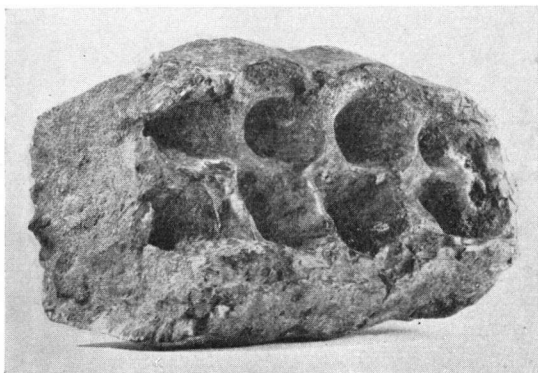
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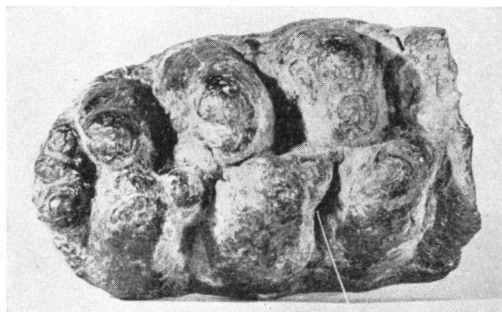
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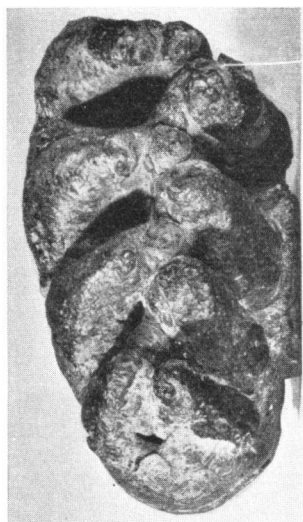
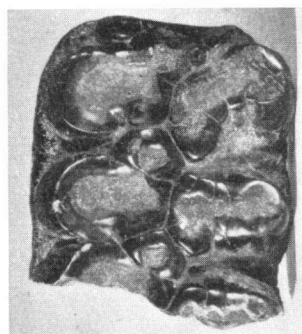


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Figs. 1, 3 and 4, *Ananous arvernensis* (CROIZET et JOBERT), M³ dext. (Zieriksee Museum no. 2.0); fig. 1, buccal view; fig. 3, basal view; fig. 4, crown view.

Fig. 2, *Archidiskodon meridionalis* (NESTI) or *A. planifrons* (FALCONER et CAUTLEY), M³ sin. (Zieriksee Museum, no. 10.0), crown view.

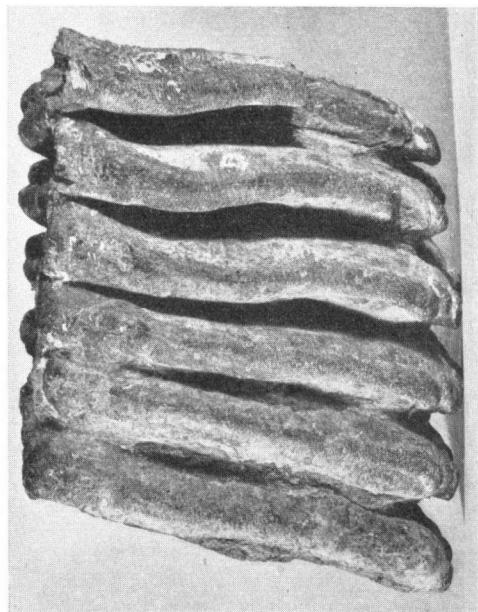
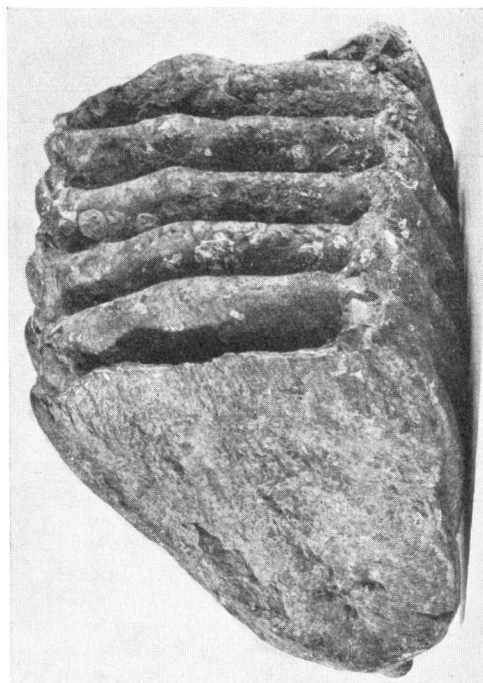
All figures one-half natural size.



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Figs. 1 and 3, *Anancus arvernensis* (CROIZET et JOBERT), M₃ dext. (Zieriksee Museum); fig. 1, crown view; fig. 3, buccal view.
 Fig. 2, *Anancus arvernensis* (CROIZET et JOBERT), MF sin. (Zieriksee Museum, no. 3.0), crown view.
 Figs. 4 and 5, *Archidiskodon meridionalis* (NESTI) or *A. planifrons* (FALCONER et CAUTLEY), M₃ dext. (Zieriksee Museum, no. 1.0); fig. 4, basal view; fig. 5, lingual view.

All figures one-half natural size.