The simplex and other forms of the upper third molar (M^3) in the common vole (*Microtus arvalis*) in Zeeland, the Netherlands

Jan Piet Bekker

Zwanenlaan 10, NL-4351 RX Veere, the Netherlands, e-mail: jpbekker@zeelandnet.nl

Abstract: The frequencies of the various forms of M^3 (simplex, transient and normal) in common (*Microtus arvalis*) voles were determined in different regions (all former islands) in the province of Zeeland, the Netherlands. A possible higher incidence of left-sidedness of simplex and transient M^3 forms was also investigated. The frequency of simplex forms of M^3 has not apparently been studied in any other part of the Netherlands, except for the north. Common vole specimens (1254 skulls) from owl pellets that were collected between 1995 and 2010 were studied. The M^3 on both sides was assessed and the length of the left molar row was measured. This article presents an analysis of the prevalence of the simplex, transient and normal forms. Based on the measured molar lengths, an age-dependent bias in the classification of the morphotypes is unlikely. In the sample the simplex form of M^3 occurred 4.9% on the left hand side and 6.7% on the right. Breaking the sample down into regions almost all the statistical limits of confidence for the left side remain within these limits of that region at the right side and vice versa. The only exceptions were for the regions of Schouwen-Duiveland and Zeeuws-Vlaanderen where the confidence limits on both sides exceeded each other.

Keywords: Common vole, *Microtus arvalis*, upper third molar M^3, morphotype, simplex form, normal form, comparing percentages, left-right differences, province of Zeeland, the Netherlands.

Introduction

In herbivores the patterns of occlusional enamel ridges on the molars, used to grind vegetable food, vary greatly: from transversely or semilunatic pleated in elephants and bovids, to voles (Arvicolidae) where the molars are covered with triangular enamel ridges around a dentin field. Guthrie (1973) mentioned that most microtine species prefer the vegetative parts of plants (stem, leaves and roots). In the same article Guthrie also pointed out that the jaw movements of microtines differ from many other grazers as they have a high antero-posterior component. In rodents in general, the extreme positions of the lower jaw are: A. Upper and lower rows of molars that cover each other; B. A lower jaw that is pulled forward until the incisors come into contact. The movement between A and B corresponds to the 'powerstroke' when chewing, in the direction of the origin of the superficial masseter muscle (Niethammer 1980). During chewing the third upper molar (M^3) and the first lower molar (m_1) are less involved than the other molar teeth which may be an explanation for the evolution of microtoid molar patterns in which the molar rows are lengthened by an extension of M^3 and m_1 (Niethammer 1980).

In all vole species a superficial dental comparison of the enamel triangles is striking, but close observation reveals differences. In

Figure 1. M^3 (left side) of common vole (*Microtus arvalis*) with various forms: simplex (S), transient (T), normal (N) and normal+ (N^+) (according to Niethammer & Krapp (1982), with alterations).

Microtidae m_1 is often conclusive in helping to identify the species (e.g. Balkan snow vole (*Dinaromys bogdanovi*), snow vole (*Chionomys nivalis*) and root vole (*Microtus oeconomus*). In several Microtidae species, the third upper molar (M^3) is more or less identical as far as the triangular enamel ridges are concerned. This is not only true for the common vole, but also Günthers vole (*M. guentheri*) (Niethammer 1982a), Cabrera's vole (*M. cabrerae*) (Niethammer 1982b), field vole (*M. agrestis*) (Krapp & Niethammer 1982) and

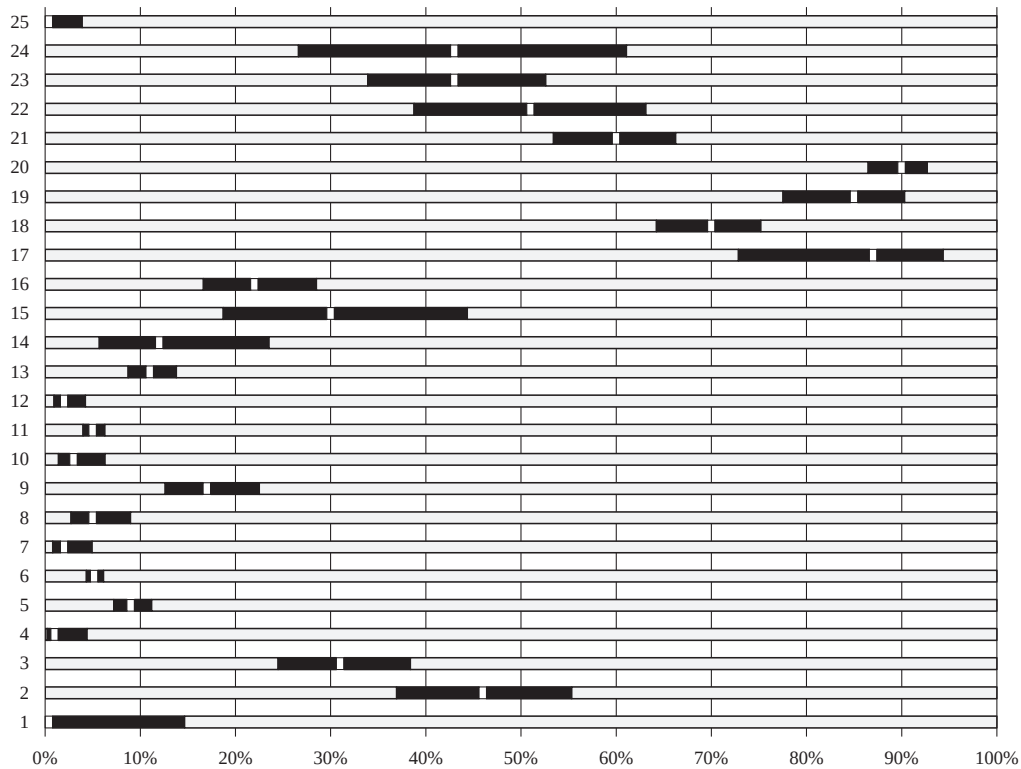

Figure 2. Percentages (white) of simplex forms of M^3, with limits of confidence (black), of common vole (*Microtus arvalis*) in regions or countries in Europe (after table 72 in Niethammer & Krapp (1982); not included: multiple percentages); 1: Island Guernsey (Great Britain); 2: Yeu Island (France), 3: Spain, 4: a National Park in Switzerland, 5: Bohemia (Czech Republic), 6: Thüringen (Germany), 7: Hannover and Braunschweig (Germany), 8: Köln (Germany), 9: the north of the Netherlands, 10: Vorarlberg (Austria), 11: Silesia (Poland), 12: Mähren (Slovakia), 13: Sachsen and Lausitz (Germany), 14: Ostpreuszen (Poland/Kaliningrad/Lithuania), 15: Danzig (Poland), 16: Ostpommern (Poland), 17: Westpommern (Germany), 18: Stettin (Poland), 19: N. Mecklenburg (Germany), 20: Schleswig (Germany), 21: Berlin (Germany), 22: E-Brandenburg (Germany), 23: Geestmünde-Frelsdorf (Germany), 24: Oldenburg (Hammelvarden) (Germany), 25: Krim (Russia); Subspecies of *Microtus arvalis*: 1 (*M. a. sarnius*), 2 (*M. a. oayensis*), 3 (*M. a. asturianus*), 4 (*M. a. rufescentefuscus*), 5-10 & 24 (*M. a. arvalis*), 11-23 (*M. a. duplicatus*) and 25 (*M. a. iphigeniae*).

root vole (Tast 1982). Surprisingly, in each of these species, M^3 can have three (or even more) different forms: 'simplex', 'normal' and an intermediate form, referred to as 'transient' in this paper (figure 1).

Stein (1931) was first to describe the anatomical features of the M^3 variations, when he found that northern subspecies have a much higher incidence of the simplex form than subspecies in the south. Zimmermann (1935) later confirmed this cline in a study of common voles (*Microtus arvalis*) from 17 central European sites. Niethammer & Krapp (1982) compiled an overview of simplex M^3 forms of populations from Zimmermann's sites, supplemented with results of islands and other remote places. Figure 2 shows the percentages of the presence of simplex M^3 forms with the limits of confidence, based on the number of observations (for the calculations of these limits, see Materials and Methods). Figure 2 shows a diverse spectrum of percentages, especially for the subspecies *M. a. duplicatus* (10-18) and *M. a. arvalis* (4-9). For the first subspecies the percentages and confidence limits vary widely and show hardly any overlap. For the second subspecies these limits reveal two percentages that form an exception on the low values, lower than 10%: in Oldenburg (24) 43% of the sample had simplex M^3 variations, while amongst a population from the north of the Netherlands (9) the figure was 17%, with confidence limits well above 10% (see figure 2).

The provisional outcome of a preliminary investigation of dentition in common voles in Zeeland indicated low values of simplex M^3 forms. Also it appeared that both simplex and transient variations occurred more frequently on the left side than on the right (J.P. Bekker, unpublished data).

As mentioned before and shown in figure 2, apart from the north of the Netherlands and including the recently studied specimens

Table 1. Selected sites in Zeeland of owl pellets containing the remnants of common voles (*Microtus arvalis*); Regions: SD: Schouwen-Duiveland, Th: Tholen, NB: Noord-Beveland, W: Walcheren, ZB: Zuid-Beveland and ZV: Zeeuws-Vlaanderen.

Coll. nr.	Coll. Date	Region	Place	M^3 complete	M^3 incomplete
#09	14-11-1998	SD	Westenschouwen	32	11
#12	4-12-2008	SD	Brouwershaven	130	44
#33	24-12-2008	SD	Brouwershaven	85	39
#01	mid 1997	Th	Tholen	46	18
#10	June 1999	Th	Tholen	74	16
#15	Jan. 1999	Th	Tholen	68	12
#06	June 1999	Th	Hollarepolder	27	6
#39	13-2-1999	NB	Wissenkerke	138	31
#18	11-2-1995	W	Arnemuiden	67	17
#03	18-6-1998	W	Arnemuiden	65	19
#29	9-8-1997	W	Middelburg	78	27
#27	1998	ZB	Bath	129	33
#14	10-3-1999	ZB	Bath	52	18
#22	30-10-1999	ZB	Wolphaartsdijk	36	6
#17	Feb. 2007	ZV	Axel	61	4
#26	5-11-1999	ZV	Axel	26	7
#13	17-7-1997	ZV	Sluiskil	92	27
#32	25-6-2007	ZV	Hoek	48	11
Total				1254	346

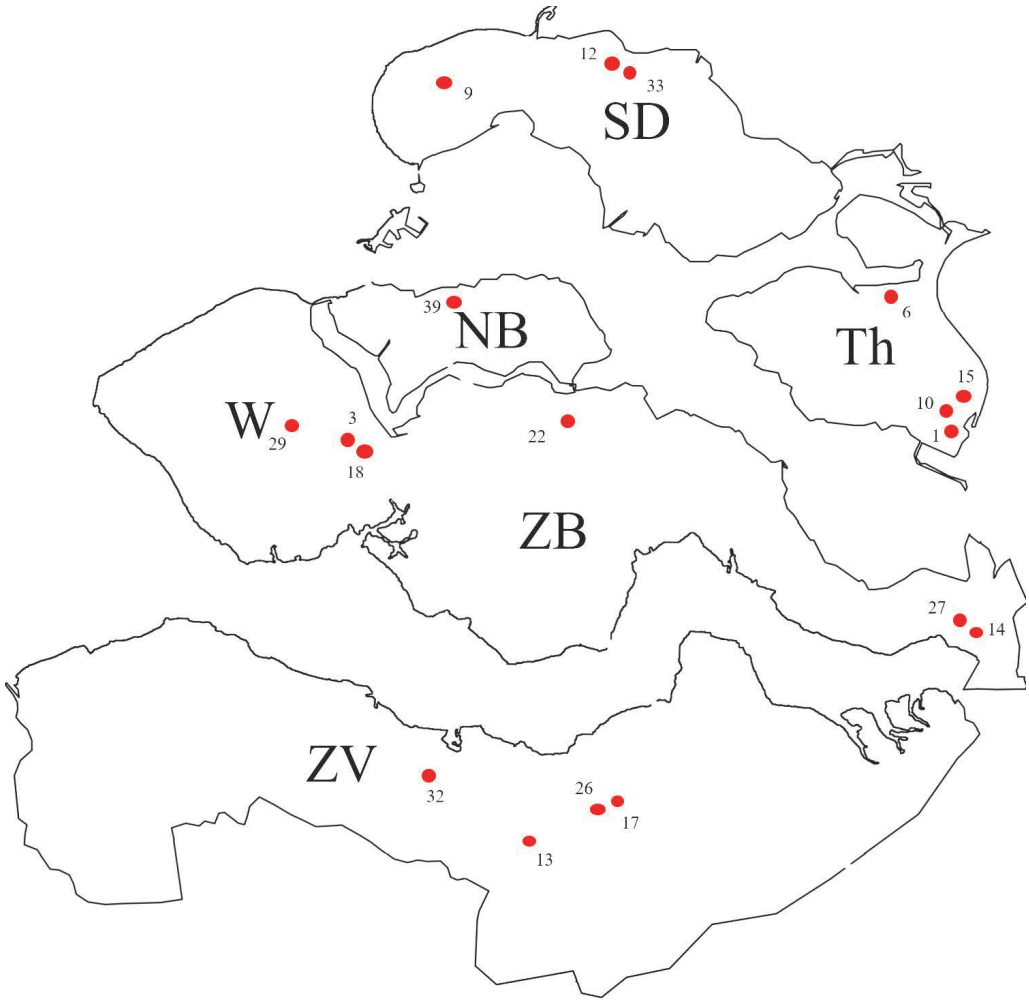

Figure 3. Map of the province of Zeeland with regions and sites where owl pellets were collected (red dots). For abbreviations of the regions see the caption in table 1, for sites see the rows with the corresponding collection numbers (author's own elaboration).

(*n*=180) from the Wieringermeerpolder by Markova et al. (2010), there seem to have been no other studies from other parts of the country into the frequencies of simplex M^3 forms in common voles.

In this paper the frequencies of simplex, transient and normal M^3 forms in this species are determined in different regions of the province of Zeeland, in the southwest of the Netherlands. These regions of Zeeland are a cluster of former islands and peninsulas that became interconnected, in some cases centuries ago (e.g. Zeeuws-Vlaanderen), in others just decades ago (e.g. Schouwen-Duiveland). The article also investigates the existence of a possible left-sided bias towards simplex and transient M^3 forms.

Materials and methods

Preserved common vole specimens, predominantly from barn owls' pellets, collected and identified between 1995 and 2010, were avail-

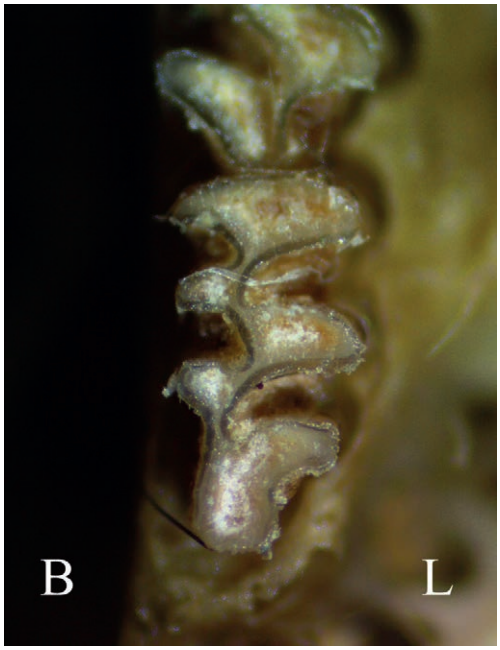

Figure 4. M^3 (right side) of common vole (*Microtus arvalis*) with forma simplex (S); B: buccal side, L: lingual side.

Figure 5. M^3 (right side) of common vole (*Microtus arvalis*) with forma normal+ (N^+) and note the fourth salient angle at the buccal side; B: buccal side, L: lingual side.

able. A selection of these was made from several sites, resulting in 1600 specimens, distributed over different parts of the Province of Zeeland (table 1, figure 3). In 1254 skulls the M^3 on both sides were intact and on at least one side the length of the molar row could be measured. This was done using a calliper with an accuracy of within 0.02 mm.

Up to almost 40% of the premaxillas, predominantly of young specimens, were missing from the studied skulls, making it impossible to measure the diastema length in these skulls. Although Niethammer and Krapp (1982) show the diastema length to be a fair indication of age, this constraint led this study to focus on the length of the upper molar row rather than the diastema length, in an attempt to optimise the numbers of skulls that could be included in this study. The length of the upper molar row was used to control any bias in the presence of the simplex, transient or normal M^3 forms, by different age categories.

A schematic assessment of the morphotypical characteristics of the dental system of arvicolines, developed by Markova (2014) was used to assign and to rank the forms by the degree of complexity. The most common forms of M^3 (some of which are illustrated in figure 1) are described below:

Simplex: There are three lingual, salient angles and the last backward bend shows no (lingual) angle or bulge (figure 4).

Transient: There are three lingual, salient angles and the last backward bend shows a lingual bulge, but no salient angle.

Normal: There are four lingual, salient angles; the last angle may be slightly shorter than the other lingual salient angles.

Normal+: There are four lingual, salient angles; the last angle may be slightly shorter than the other lingual salient angles. In addition, there is a backward-facing bulge with a dent (convexity) on the lingual side (figure 5).

Complex Typ3/5 and Complex Typ4/5: There are five lingual, salient angles; the last angle may be slightly shorter than the other lingual

salient angles. There are three or four labial, salient angles respectively, with the last angle sometimes slightly shorter than the other labial salient angles. In addition, there is a backward-facing bulge with a dent (convexity) on the lingual side. We adopted Markova's (2014) suggestion of combining the categories "Normal+" and "Normal" and to include the first in the last category.

A chi-squared test (Green et al. 1979) was used to test bilateral trait correlation for independence. The frequencies of M^3 forms and the absolute numbers are presented in tables 2 and 3. Key statistics (*M*, Sd) of the length of the upper molar rows are presented for each form. To determine the statistical significance of the difference between percentages, a 95% confidence interval was calculated around the measured difference in percentages (Wilson's formula, RIVM 2020). This 95% confidence interval indicates that it is 95% probable that the true value of the difference is in the interval (Rothman & Greenland 1998). This interval decreases when the measured percentages are based on more observations. In the case of zero observations, the upper limit of the 95% confidence interval is calculated using Byar's formula (RIVM 2020).

Results

The percentages of simplex forms of M^3 from all sites in Zeeland combined, were 4.9 % (left) and 6.7 % (right); this indicates a difference in the prevalence in favour of the right side. For the transitional forms the prevalence is in favour of the right side (left: 10.9%, right 14.0%). For the normal forms (left: 84.2% resp. 79.3%) the prevalence is in favour of the left side (see table 2).

The coherence between left and right sided forms is presented in table 3. The percentage of common vole specimens with at least one simplex form on both sides is 72.1. For the transient and normal forms these values are 53.3% and 89.7% respectively.

Table 2. M^3 forms: simplex (S), transitional (T) and normal (N) in Zeeland; the difference between the left and right side is significant (chi-squared test; *: P=0.0064).

Side	Left*	Right*	total
S	61	84	145
T	137	175	312
N	1056	995	2051
Total	1254	1254	

The lengths of the molar row in the 1254 common vole specimens are presented in figure 6, in clusters of 0.1 mm. 1204 skulls were measured on the left side while for the remaining 50 skulls they were taken on the right side. The outcome is a slightly left-skewed distribution with a kurtosis of -0.46 (M=5.34; SD=0.29).

The standard statistical values for molar row lengths in the simplex form can be summarised as n=44, M=5.35 and SD=0.24; for transient and normal forms these values are n=73, M=5.36 and SD=0.32 and n=947, M=5.40 and SD=0.29 respectively. Considering the values of the molar lengths, an age depended bias in the classification of the forms is not probable.

Of all the sites in Zeeland from where barn owl pellets were analysed (see table 4), the percentage of the simplex M^3 left (M=4.49; SD=3.15) was lower than the percentage of simplex M^3 right (M=6.09; SD=3.66); the difference was at the edge of significance (t (18) = -1.59; P=0.05). The percentages of transient forms on the left side (M=10.56; SD=5.04) was lower than that on the right (M=14.25; SD=4.66). This difference was significant (t (18) = -4.47, P<001). The percentages of normal forms on the left side (M=84.89; SD=6.51) was higher than that on the right side (M=79.61; SD=6.33). This difference was extremely significant (t (18) = -3.69, P<0.00005).

The percentages of the simplex M^3 forms on the left and right sides varies moderately by region. All the left side percentages remain within the limits of confidence of that region on the right side and vice versa. If the regions

Table 3. Coherence between left and right forms of M^3 in common voles (*Microtus arvalis*) in Zeeland.

	M^3 simplex R	M^3 transient R	M^3 normal R	Totals
M^3 simplex L	44	7	10	61
M^3 transient L	26	73	38	137
M^3 normal L	14	95	947	1056
totals	84	175	995	1254

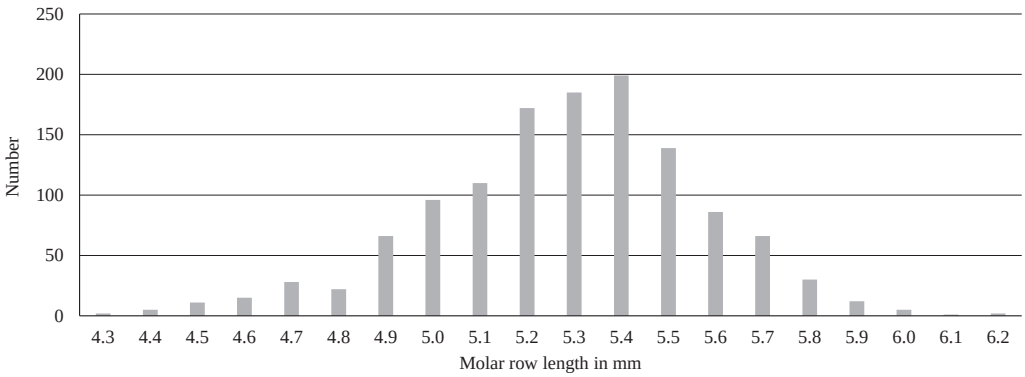

Figure 6. Distribution of molar row length in 1254 specimens of common vole (*Microtus arvalis*) in Zeeland.

themselves are compared, only Schouwen-Duiveland (SD) and Zeeuws-Vlaanderen (ZV) exceed each other's confidence limits (on both sides, see figures 7 resp. 8).

Discussion and conclusions

The percentages of simplex forms of M^3 in common voles found in the province of Zeeland were 4.9% (left) and 6.7% (right): substantially lower than the 17% that Zimmermann (1935) reported for the north of the Netherlands, but quite close to the 8%, Markova et al. (2010) found for the Wieringermeerpolder. They noted that the proportion of simplex M^3 in their sample was quite low (Markova et al. 2010). The values for the province of Zeeland are also in line with other findings for the subspecies *M. a. arvalis* in the western parts of Germany, including values from Leubnitz-Neuostra and Kleinzschachwitz, based on the number of molars (5.4% (*n*=353), 5.3% (*n*=642 respectively)) (Kapischke 1997). The only exception is a high value (43%) of simplex molars reported from Oldenburg (see figure 2).

The difference with respect to the percentages of the simplex M^3 forms between the regions of Schouwen-Duiveland (SD) and Zeeuws-Vlaanderen (ZV) might be explained by the long-term isolation of Schouwen-Duiveland from the other islands and the rest of the Netherlands whereas Zeeuws-Vlaanderen has for centuries had a partial or a permanent connection to the mainland. *M. arvalis* has been reported from Schouwen-Duiveland in catches and in owl pellets (van Wijngaarden et al. 1971), but its population of common voles is undoubtedly isolated. With the construction of the almost 6 km long Grevelingendam in 1964, Schouwen-Duiveland became connected to Goeree-Overflakkee on the east side with a lock on the side of the former. Since 1971 the west side of Schouwen-Duiveland has also been connected to Goeree-Overflakkee with the construction of the Brouwersdam, without any bridges or locks.

The last region in Zeeland where *M. arvalis* was missing appeared to be Noord-Beve-

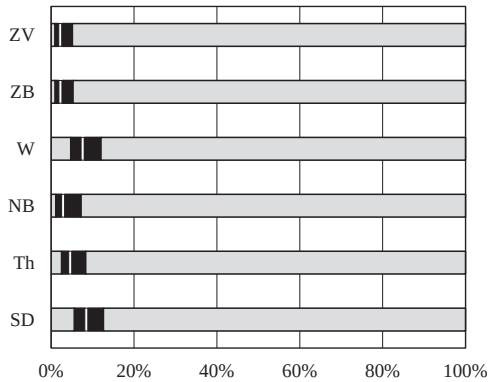

Figure 7. Regional percentages (white) of simplex M3 forms (left), with limits of confidence (black). For abbreviations of regions see caption in table 1.

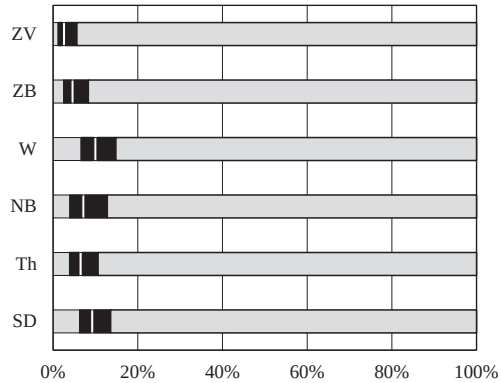

Figure 8. Regional percentages (white) of simplex M3 forms (right), with limits of confidence (black). For abbreviations of regions see caption in table 1.

land (van Wijngaarden 1959). The remains of common voles which Wilmink (1944) found in pellets in 1938 must therefore have been caught elsewhere (van Wijngaarden 1959). The dykes between Noord-Beveland and Walcheren and Zuid-Beveland (built in 1961 and 1960, respectively, the latter with a lock) connected the three former islands (Anonymus 1984). In 1967 *M. arvalis* was caught on Noord-Beveland at the western side (after 5 years) and at the eastern side (after 7 years) (Ligtvoet & van Wijngaarden 1994). Given the origin of the *M. arvalis* population (Zuid-Beveland and Walcheren) it is not surprising that the percentages of M^3 simplex forms found in Noord-Beveland are within the reliability margins of those of the neighbouring regions (see figures 7 and 8).

The simplex M^3 forms of *M. arvalis* on islands along or off the coasts of Britain and France have been found to be very different from on the mainland (see also table 1). Orkney voles (*M. a. orcadensis*) on the Orkney mainland form a distinct group with affinities more to south western Europe, while those from Guernsey are closer to the continent (Corbet & Wallis 1977). According to Berry and Rose (1975) it seems probable that *M. arvalis* came to Orkney with some of the earliest human colonizers about 4000 years ago, and then radiated to the different islands. A population originating from a small number of founders will differ from its original group and will display its genetical basis through for example selection or genetical drift (Berry 1972). Zimmermann (1959) described fertile young of voles from Orkney and Germany, as did Crowcroft and Godfrey (1962) of voles from Orkney and Guernsey, indicating the segregation between the different subspecies is relatively recent.

There have been disagreements between Stein and Zimmermann over M^3 forms, in particular the issue of the north-south cline in the simplex form of *M. arvalis* (Guthrie 1971). Stein (1931) found that the northern subspecies had a much higher prevalence of the simplex form than those in the south. Zimmermann (1953) proposed that the cline of the molar variation in *M. arvalis* represented an accumulation of a recessive gene on the periphery of the species' range. Stein (1958) argued that the simplex form has a selective advantage in a poor environment; and since the climate in Eurasia is more favourable in the north, simplex is most abundant in the north and e.g. in fir forests. Zimmermann (1958) proposed three arguments to oppose Stein's theory: 1. In a number of places the populations of *M. arvalis* have predominantly simplex M^3 forms, although the conditions they endure could not described as being

Table 4. Percentages of M^3 forms, left (L) and right (R), simplex (S), transient (T) and normal (N) of common vole (*Microtus arvalis*) from 18 sites in Zeeland. For abbreviations of the regions see the caption in table 1.

Site No.	Region	Site name	*n*	S L	S R	T L	T R	N L	N R
#09	SD	Westenschouwen	32	3.1	0	9.4	15.6	87.5	84.4
#12	SD	Brouwershaven	130	11.5	11.5	13.1	16.2	75.4	72.3
#33	SD	Brouwershaven	85	5.9	9.4	5.9	9.4	88.2	81.2
#01	Th	Tholen	46	6.5	8.7	26.1	23.9	67.4	67.4
#10	Th	Tholen	74	5.4	8.1	18.9	18.9	75.7	73
#15	Th	Tholen	68	1.5	4.4	7.4	13.2	91.2	82.4
#06	Th	Hollarepolder	27	7.4	3.7	3.7	14.8	88.9	81.5
#39	NB	Wissenkerke	138	2.9	7.2	10.1	8	87	84.8
#18	W	Arnemuiden	67	9	9	10.4	13.4	80.6	77.6
#03	W	Arnemuiden	65	4.6	6.2	10.8	7.7	84.6	86.2
#29	W	Middelburg	78	9	14.1	11.5	19.2	79.5	66.7
#27	ZB	Bath	129	2.3	4.7	10.9	15.5	86.8	79.8
#14	ZB	Bath	52	1.9	3.8	7.7	9.6	90.4	86.5
#22	ZB	Wolphaartsdijk	36	2.8	5.6	8.3	22.2	88.9	72.2
#17	ZV	Axel	61	4.9	3.3	4.9	11.5	90.2	85.2
#26	ZV	Axel	26	0	7.7	7.7	7.7	92.3	84.6
#13	ZV	Sluiskil	92	2.2	2.2	12.9	15.1	83.9	81.7
#32	ZV	Hoek	48	0	0	10.4	14.6	89.6	85.4

poor. 2. Under poor conditions, where there is high winter mortality there is no increase of simplex M^3. 3. The higher prevalence of the simplex form in woodlands is inconsistent with a greater degree of inbreeding. Guthrie (1971) contributed to this debate by offering two possible explanations for the *M. arvalis* molar cline: 1. The demands of the food itself. 2. Differences in competition between other related species (e.g. *M. agrestis*) or genera (e.g. *Clethrionomys glareolus*).

Molar forms in *M. arvalis* show a pattern of spatial variability with an increase in the proportion of complex forms with longitude and latitude. This pattern of molar complication is strongly correlated with geographic variables; a negative correlation with longitude was found in the frequencies of simple forms (Markova et al. 2010). Simple patterns of dentition in, *M. a. arvalis* are found in Spain, along the Atlantic coast of France and on islands thereabout, in north-eastern Germany and the Kirov region in European Russia (Markova 2014). Kryštufek (2017) questions the formal recognition of infraspecific entities as there is a lack of consensus among authorities on ways to classify and enumerate the numbers and distributions of *M. arvalis*.

Despite clear definitions and descriptions of the morphotypes, the allocation of M^3 forms remains a subjective decision. Therefore it seems that a completely certain classification was not possible in every case. This uncertainty about the allocation of M^3 forms has already been mentioned by Görner (1973).

Whether all sites in Zeeland are considered combined or apart, the percentages of simplex and transitional forms of M^3 were in favour of the right side. An explanation for this difference and the direction (i.e. on the right side) is not obvious, but it could be of genetic origin. An alternative explanation could be the fixed handling in the evaluation of the molar rows, with the rostrum on the left side and, as a consequence, the left side away from the observer and the right side turned towards the observer. The handling results in a slight difference in the observation angle, and this

might be the cause of the left-right difference. This observer effect could have influenced the allocation of simplex and transitional forms of M^3 in favour of the right side at the expense of normal forms.

To take full advantage of describing the dental morphotypes of *M. arvalis*, we not only need to study M^3 but also m_1. This makes it necessary to collect both the skull and the mandibles of each specimen and to keep these together.

In this study the age categories were estimated by measuring the lengths of the left molar row. This resulted in a drop out number of 346 (21.6%, see table 1), due to missing molars in the preserved skulls. The molar range of M^3 forms simplex-normal-complex, unavoidable led towards greater lengths of M^3 itself and the upper molar row because of added extra loops of that very molar. The option to estimate the age category more precisely by measuring the diastema, will inevitably result in a higher drop out percentage because of missing premaxillas (due to the analysing activity). It can be argued that age doesn't influence the shape of the occlusal plane, as the tip of the root mirrors that shape. However, in young individuals the prisms of M^3 are still closed. Therefore, in measuring the diastema seems to be the best practise, meaning a higher drop out percentage of measured objects will have to be accepted.

Acknowledgements: I express special thanks to the volunteers who collected barn owl pellets in the different regions of the province of Zeeland: Marc Buise, Jos Haak, André Hannewijk, G. v.d. Hel, Rinus van 't Hof, Kees Mostert, Luud Persijn, Piet Stols, Eddy Taalman en Jaap Woets. I also thank Freddy van Nieulande for technical support with taking pictures in the depot of the Zeeuws Museum in Middelburg. Eric Thomassen and Nicholas Parrott kindly helped in improving the English language. Two anonymous referees gave valuable comments, including applicable suggestions to improve the manuscript.

References

Anonymus 1984. Encyclopedie van Zeeland. Koninklijk Zeeuwsch Genootschap der Wetenschappen, Middelburg, the Netherlands.

Berry, R.J. 1972. General approaches to taxonomy. Proceedings of the Royal Society of Medicine 65: 33-34.

Berry, R.J. & F.E.N. Rose 1975. Islands and the evolution of *Microtus arvalis* (Microtinae). Journal of Zoology 177: 395-407.

Corbet, G.B. & S.J. Wallis 1977. Orkney/Guernsey vole *Microtus arvalis*. In: G.B. Corbet & H.N. Southern (eds). The Handbook of British Mammals: 193-195. Blackwell Scientific Publications, London, UK.

Crowcroft W.P. & G Godfrey 1962. Laboratory produced hybrids of the Guernsey vole (*Microtus arvalis sarnius* Miller). Annals and Magazine of Natural History (13) 5: 408-419.

Green R.F., J.M. Suchey & D.V. Gokhale 1979. The statistical treatment of correlated bilateral traits in the analysis of cranial material. American Journal of Physical Anthropology 50: 629–634.

Görner, M. 1973. Ergebnisse von Gewöllenanalysen der Schleiereule (*Tyto alba*) im südthüringischen Grabfeld. Hercynia (Leipzig) N.F. 10: 35-40.

Guthrie, R.D. 1971. Factors regulating the evolution of microtine tooth complexity. Zeitschrift für Säugetierkunde 36: 37–54.

Kapischke, H.J. 2011. Schädel- und Zahnmerkmale von Feldmäusen aus Waldohreulen gewöllen (Dresden im Winter 2009/2010). Mitteilungen für sächsische Säugetierfreunde (2011): 24-28.

Krapp, F. & J. Niethammer 1982. *Microtus agrestis* (Linnaeus, 1761) – Erdmaus. In: J. Niethammer & F. Krapp (eds). Handbuch der Säugetiere Europas. Band 2/I. Nagetiere II: 349-373. Akademische Verlaggesellschaft, Wiesbaden, Germany.

Kryštufek, B. 2017. Common vole *Microtus arvalis*. In: D.E. Wilson, T.E. Lacher, Jr & R.A. Mittermeier (eds). Handbook of the Mammals of the World. Vol. 7. Rodents II: 351-352. Lynx Edicions, Barcelona, Spain.

Ligtvoet, W. & A. van Wijngaarden 1994. The colonization of the island of Noord-Beveland (the

Netherlands) by the common vole *Microtus arvalis*, and its consequences for the root vole *M. oeconomus*. Lutra 37 (1): 1-28.

Markova, E.A. 2014. Assessment of tooth complexity in Arvicolines (Rodentia): A morphotype ranking approach. Biology Bulletin 41 (7): 589-600.

Markova, E., V. Malygin, S. Montuire, A. Nadachowski, J.-P. Quéré & K. Ochman 2010. Dental variation in sibling species *Microtus arvalis* and *M. rossiaemeridionalis* (Arvicolinae, Rodentia): Between-species comparisons and geography of morphotype dental patterns. Journal of Mammal Evolution 17: 121–139.

Niethammer J. 1980. Eine Hypothese zur Evolution microtoider Molaren bei Nagetieren. Zeitschrift für Säugetierkunde 45: 234-238.

Niethammer, J. 1982a. *Microtus guentheri* Dandord et Alston, 1880 – Levante-Wühlmaus. In: J. Niethammer & F. Krapp (eds). Handbuch der Säugetiere Europas. Band 2/I: 331-339. Nagetiere II. Akademische Verlaggesellschaft Wiesbaden, Germany.

Niethammer, J. 1982b. *Microtus cabrerae* Thomas, 1906 – Cabreramaus. In: J. Niethammer & F. Krapp (eds). Handbuch der Säugetiere Europas. Band 2/I: 340-348. Nagetiere II. Akademische Verlaggesellschaft Wiesbaden, Germany.

Niethammer, J. & F. Krapp 1982. *Microtus arvalis* (Pallas, 1779) – Feldmaus. In: J. Niethammer & F. Krapp (eds). Handbuch der Säugetiere Europas. Band 2/I: 285-318. Nagetiere II. Akademische Verlaggesellschaft Wiesbaden, Germany.

RIVM 2020. rivm.nl/prezies/infectiecijfers-betrouwbaar-gebruiken/statistische-betrouwbaarheid-van-infectiecijfers; viewed 23 November 2020.

Rothman, K.J. & S. Greenland 1998. Modern Epidemiology. 2nd. edition. Lippincott Williams & Wilkins, Philadelphia, PA, USA.

Stein, G.H.W. 1931. Beiträge zur Kenntnis einiger mitteleuropäischer Säuger. Mitteilingen aus dem Zoologischen Museum in Berlin 17: 273-298.

Stein, G.H.W. 1958. Über den Selektionswert der simplex-Zahnform bei der Feldmaus *Microtus arvalis* (Pallas). Zoologische Jahrbücher. Abteilung für Systematik 86: 27–34.

Tast, J. 1982. *Microtus oeconomus* (Pallas, 1776) – Nordische Wühlmaus, Sumpfmaus. In: J. Niethammer & F. Krapp (eds). Handbuch der Säugetiere Europas. Band 2/I: 374-396. Nagetiere II. Akademische Verlaggesellschaft Wiesbaden, Germany.

van Wijngaarden, A. 1959. De zoogdieren van Noord-Beveland. De Levende Natuur 62: 211-216.

van Wijngaarden, A., V. van Laar & M.D.M. Trommel 1971. De verspreiding van de Nederlandse zoogdieren. Mammalia: Insectivora, Chiroptera, Rodentia, Lagomorpha, Carnivora, Pinnipedia, Artiodactyla. Lutra 13 (1-3): 1-41.

Wilmink, W.F. 1944. Noordsche woelmuis *Microtus ratticeps* op Noord-Beveland. De Levende Natuur 49: 35-36.

Zimmermann, K. 1935. Zur Rassenanalyse der mitteleuropäischen Feldmäuse. Archiv für Naturgeschichte (N.F.) 4: 258-273.

Zimmermann, K. 1953. Die simplex-Zahnform der Feldmaus *Microtus arvalis* (Pallus). Verhandlungen der Deutschen Zoologischen Gesellschaft, Freiburg, 1952: 492-498.

Zimmermann, K. 1958. Selektionswert der simplex-Zahnform bei der Feldmaus *Microtus arvalis*? Zoologische Jahrbücher Systematik 86: 35-40.

Zimmermann, K. 1959. Über eine Kreuzung von Unterarten der Feldmaus *Microtus arvalis*. Zoologische Jahrbücher Systematik 87: 1-12.

Samenvatting

De simplex en andere vormen van de derde boven-molaar (M^3) bij de veldmuis (*Microtus arvalis*) in de provincie Zeeland

Afgezien van het noorden lijken er geen andere delen van Nederland te zijn onderzocht op frequenties van simplex-vormen van de derde boven-molaar (M^3) bij veldmuizen (*Microtus arvalis*). Frequenties van M^3-vormen ('simplex', 'transient' en 'normaal') in veldmuizen zijn bepaald in verschillende regio's (voormalige eilanden) in de provincie Zeeland. Verder is gezocht naar een mogelijke linkszijdige voorkeur van simplex- en overgangsvormen van M^3. Voor deze studie zijn 1254 schedels van veldmuizen gebruikt, afkomstig van braakbalmateriaal, en geplozen in de jaren

1995-2010. Zowel de linker als rechter M^3 is beoordeeld en tevens is de lengte van de bovenste kiezenrij gemeten. Er zijn definities gegeven van de vormen ('simplex', 'transient' en 'normaal'), aangeduid met het aantal linguaal uitstekende hoeken. De gemeten lengtes van kiezenrijen maken een leeftijdsafhankelijke bias in de indeling van de M^3-vormen niet waarschijnlijk. De percentages simplex-vormen van M^3 in Zeeland waren respectievelijk 4,9% (links) en 6,7% (rechts). Regionale percentages van de simplex M^3-vormen aan de linkerkant blijven binnen de betrouwbaarheidsgrenzen van die aan de rechterkant en vice versa. De gevonden percentages simplex-vormen overschrijden alleen in de regio's Schouwen-Duiveland en Zeeuws-Vlaanderen aan beide kanten elkaars procentuele betrouwbaarheidsgrenzen. Dit kan verklaard worden door de langdurige isolatie van Schouwen-Duiveland als eiland, terwijl Zeeuws-Vlaanderen al sinds eeuwen geheel of gedeeltelijk verbonden is met het continent.

Received: 11 October 2020
Accepted: 19 November 2020