Ecology and systematics of the Mononchid nematodes from wood-and grassland areas in wet temperate climate. II. The genus *Prionchulus* Cobb, 1916

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SUMMARY

The validity of the characters used to separate the two related species *Prionchulus muscorum* (Dujardin, 1845) Wu & Hoeppli, 1929 and *P. punctatus* (Cobb, 1917) Andrássy, 1958 was studied in a large collection of *Prionchulus* specimens. Until now, only qualitative criteria were used, namely the shape of the denticulate subventral ridges and the structure of the outer layer of the eggshell. A correspondence analysis has shown that other characters, such as the size of the buccal cavity and the position of the tip of the dorsal tooth are more reliable because they can be quantitatively and objectively interpreted. After a detailed study of those characters new diagnoses were proposed for the two species. For any identification, the size of the buccal cavity expressed as a function *d*, of its length and width and the position of the apex of the dorsal tooth in relation to *d*, has to be considered first ; then the structure of the outer layer of the egg-shell and the aspect of its margin and qualitative characters such as the shape of the buccal cavity, the shape of the denticulate subventral ridge and the shape of the tail, can be used to precise the identification.

RÉSUMÉ

Ecologie et systématique des nématodes Mononchides des zones forestières et herbacées sous climat tempéré humide. II. Le genre Prionchulus *Cobb, 1916*

A partir d'une collection importante de *Prionchulus*, les auteurs ont statué sur la validité des critères employés pour la séparation de deux espèces voisines, *P. muscorum* (Dujardin, 1845) Wu & Hoeppli, 1929 et *P. punctatus* (Cobb, 1917) Andrássy, 1958. Les critères utilisés jusqu'à présent, essentiellement basés sur une approche qualitative, sont la forme de la crête denticulée et la structure de la coque des œufs. A l'aide d'une analyse des correspondances il a été mis en évidence d'autres caractères plus fiables car quantitatifs et objectivement interprétables : taille de la cavité buccale et position de l'apex de la dent dorsale. L'étude détaillée de ces derniers caractères amène les auteurs à proposer une nouvelle définition pour séparer les deux espèces. Dans tous les cas, il faudra envisager en premier la taille de la cavité buccale exprimée par la valeur d'une distance, *d*, la position de l'apex de la dent dorsale associée à *d*, puis la structure de la coque associée à l'aspect du contour de l'œuf et enfin les caractères qualitatifs (forme de la cavité buccale, aspect de la crête denticulée, forme de la queue).

During surveys of woodlands around Paris many *Prionchulus* specimens were collected and provisionnally identified as belonging to the species *P. muscorum* (Dujardin, 1845) Wu & Hoeppli, 1929. A definitive assignment of the specimens to *P. muscorum* or *P. punctatus* (Cobb, 1917) Andrássy, 1958 was not possible because of the morphological and morphometrical variations found among the observed populations. Identification of these two related species has caused problems for the past 70 years. Only qualitative criteria were traditionnally used, namely the shape of the denticulate subventral ridges and the structure of the outer layer of the egg-shell (Tab. 1).

Andrássy (1958) considered *P. punctatus* as a synonym of *P. muscorum*, while Clark (1960) and Mulvey (1967) held the opposite view stating that the difference in structure of the outer layer of the egg-shell was sufficient to separate the two species. If their conclusions are accepted it will be impossible to identify non gravid females. The present study was initiated to reconsider critically the criteria used to separate the two species.

Materials and Methods

This study was based on the analysis of 138 gravid females from several biotopes as detailed below :

Table 1

Main differences between *P. muscorum* and *P. punctatus*

	Size of ridge denticles	*Disposition of the ridge - denticles*	*Tail shape*	*Structure of the egg-shell*
P. muscorum	medium to large	regular	long tapering	smooth or scaled
P. punctatus	relatively fine	somewhat irregular	short, more or less conoid	echinulate

— France, forests around Paris ; 105 females ; (Arpin, 1979)
— Mount Kenya, 12 females ; (Coomans & Khan, 1980)
— England, Swanpool (Moss) ; 4 females ; (Rothamsted Collection, 1960)
— England, Winches-Farm pasture ; 13 females ; (Rothamsted Collection, 1946)
— Neotypes of *P. punctatus*, Germany, Bürgerpark, Bremen ; 4 females ; (Riemann, 1979).

The specimens from Kenya were collected in highland region (above 2 500 m) with habitat similar to those from wet temperate climates.

The buccal cavity was studied with additional specimens from the same origin, to a total of 435 females. Observations and measurements were made on animals fixed with hot 4% formaldehyde and mounted on slides in pure glycerine. Drawings made under Leitz stereomicroscope with camera lucida. All the characters measured (see list), the shape of the denticulate subventral ridge, the structure and margin of the shell of intra-uterine eggs were studied in a correspondence analysis of Benzecri (Lebart, Morineau & Fénelon, 1979). This analysis has been largely used for biometrical studies at the species level, for example in botany (Blaise, Briane & Leblanc, 1973) and zoology : *Thecamoeba* (Coûteaux, Munsch & Ponge, 1979) and nematodes (Fortuner, Merny & Roux, 1981). Closely related methods (canonical analysis) have been used for studies on nematodes (Luc & Southey, 1980 ; Baeza-Aragon & Tarjan, 1982). Correspondence analysis has a double advantage over the other methods in that it does not make any preliminary hypothesis on the assignment of individual to a given group and that it permits the simultaneous representation of individuals (specimens) and the variables used to describe them.

Choice and coding of the variables

In addition to the previously mentioned qualitative characters (subventral ridge weakly or strongly developed, echinulate or scaled eggs-shell) the analysis includes thirteen measurements. Only the position of the apex of the dorsal tooth against the base of the buccal cavity was used as a ratio. The absolute value was used for all the other characters.

The following variables have been used (all measurements in mm, except buccal cavity in μm) :

LONG = total body length (L).
LARG. = body width at oesophago-intestinal junction. Normally the greatest width is measured at vulva but the enlargement of the body due to presence of eggs and/or flattening requires a correction (Geraert, 1961). This corrected value shows only small differences with the width here measured.
CBLO = length of buccal cavity.
CBLA = width of buccal cavity, including the walls.
APEX = distance tip of the dorsal tooth to base of buccal cavity.
OEAN = length of oesophagus.
OEPO = length of body posteriorly to oesophagus.
VUAN = distance anterior end to vulva.
VUPO = distance vulva to posterior end.
QUAN = distance anterior end to anus (= L').
QUPO = tail length.
2 = distance posterior end of oesophagus to vulva.
3 = distance vulva to anus.
CRETE = denticulate subventral ridge, large (coded 1) or fine (coded 2).
OEUF = egg scaled (coded 1), echinulate (coded 3) or smooth (coded 2). Individuals coded 2 are effectively neutralized for the analysis, because only the difference to the mean value is used.

Tranformation of the data

All the variables have been transformed according to the method of Coûteaux, Munsch and Ponge (1979). Their mean has been set equal to ten and their variance to one. All the measurements are of the same magnitude and have the same variability.

Each transformed variable x, has also been coupled with a variable $x' = 20 - x$ that varies in the opposite way. Each measurement will thus be represented on the graph by two point-variables : one corresponds to high values of the variable and is marked $^+$, the other one corresponds to low values and is marked $^-$; between these two points there is a probability gradient from the lowest to the highest values of the variable under consideration. This method, which gives a better legibility of the graphs, makes it possible to interpret directly the factorial coordinates of the variables in terms of their absolute contribution. The more distant a point-variable is from the origin, the greater its contribution to the studied axis or plane will be. Except for this transformation of the data, the method uses the characteristic algorithms of the correspondence analysis.

Results

STUDY OF THE PLANE OF AXES ONE AND TWO (Fig. 1)

Axis 1 accounts for 75% of the whole variance, axis two for 15% and axis three for 2.7%. The plane defined by axes one and two accounts for 90% of the variance (138 individuals and 30 coupled variables) which is most of the information contained in the data. For an easier discussion, the directions on the graph will be referred to as North, South, East and West, as on a map. The specimens are segregated in two clusters separated along a direction NE-SW. In each cluster, a large individual variability results in a scattering of the representative points along a NW-SE direction.

Explanation of the axis one

Axis one can be interpreted as a factor of general size separating the smaller from the bigger specimens, because this axis separates mostly point-variables related to size. All the lower values of the body measurements are situated to the West and all the higher values to the East. The individuals of the SW cluster are on the average smaller than those of NE cluster : 2.11 ± 0.03 mm against 2.43 ± 0.08 mm. The same difference is present in all the measurements related to size, for instance the body width : 0.071 ± 0.001 mm for SW cluster against 0.087 ± 0.004 mm for NE cluster. However variability is larger in the last group : this is seen in the

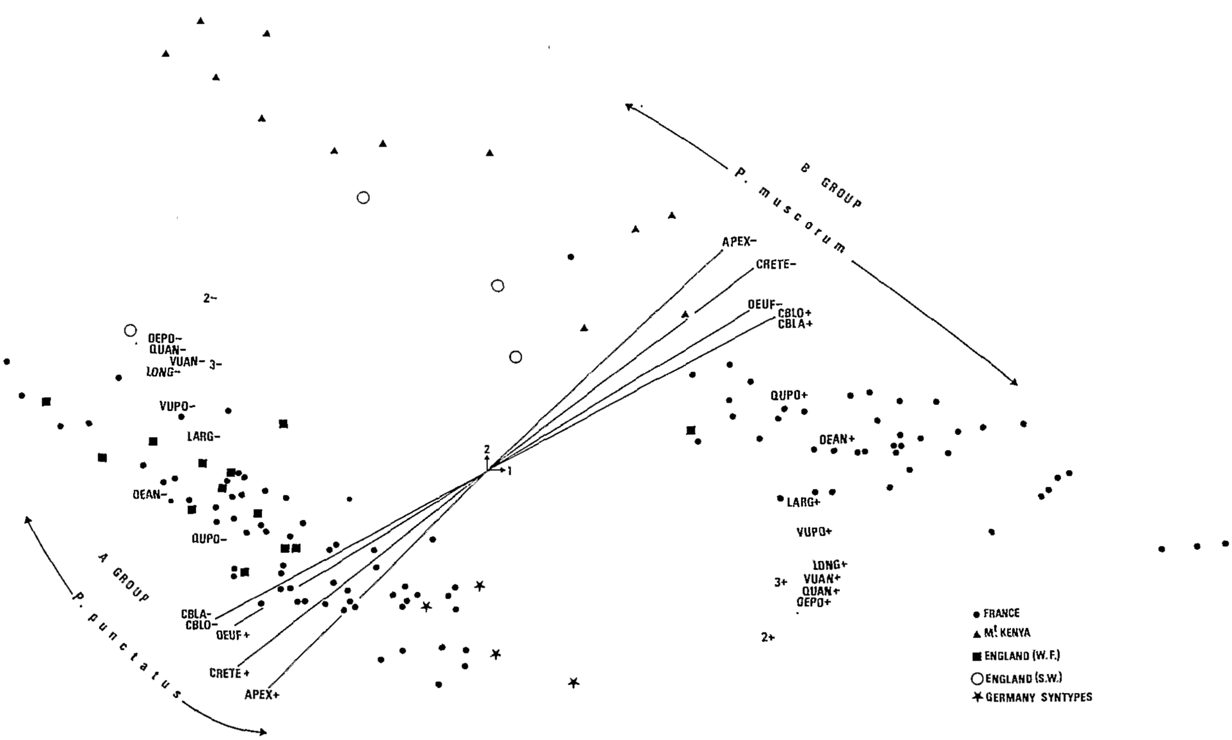

Fig. 1. Correspondence analysis : Projection of the clusters of variables and specimens (n = 138) in the plane of axes one and two.

bigger diffrences in the value of the standard deviation of the mean as well as in the scattering of individual values in the NE cluster. Some specimens of this cluster (mainly the Kenya material and some of the French material) have a size similar to that of some specimens in the other cluster. All the animals of the SW cluster have fine ridges and echinulate eggs (if the egg-shell is not smooth); the animals of the NE cluster have on the contrary strongly developed ridges and scaled eggs.

Explanation of the axis two

Axis two also participates in the segregation between the two clusters. However none of the variables contributes in a strong absolute way to this axis and moreover none seems to be specifically related to it. An interpretation has to be found which does not deal with differences in size between the two groups (because this axis is linearly independent from axis one) but gathers the informations from the respective position of the point-variables in the direction of the axis two. In this direction the point-variables APEX+, CRETE+, KUF+ are opposed to their coupled points marked by−. In other words differences exist in the position of the apex of the dorsal tooth (82.9 ± 0.4% for SW cluster against 75.4 ± 0.4% for NE cluster) and in the structure of egg-shell and denticulate subventral ridges (scaled eggs and strongly developed ridges for NE cluster, echinulate eggs and weakly developed ridges for SW cluster). But the opposition of the measurements of some part of the body reflects differences in proportion, especially between the posterior and anterior body parts against the intermediate parts: The variables QUPO + and OEAN + opposed along the axis 2, not only to QUAN + and OEPO + but also to 2 + and 3 + indicate that oesophagus and tail are relatively longer in NE cluster than in SW cluster. The comparison of the usual ratios b and c for the two species confirms these differences:

SW : b = 4.28 ± 0.04 (oesophagus relatively short)
c = 18.5 ± 0.8 (tail relatively short)

Table 2

Mean values of the variables (characters) for the two species studied.
For buccal cavity and "*d*": *P. punctatus* n = 303, *P. muscorum* n = 132

Variable	*P. muscorum* n = 58			*P. punctatus* n = 80		
	Minimum	*Maximum*	$M \pm t_{0.05}$ µm	*Minimum*	*Maximum*	$M \pm t_{0.05}$ µm
Body length (mm)	1.71	2.94	2.43 ± 0.08	1.75	2.47	2.11 ± 0.03
Body width (mm)	0.060	0.123	0.087 ± 0.004	0.057	0.083	0.071 ± 0.001
Length of pharynx (mm)	0.49	0.71	0.59 ± 0.01	0.42	0.59	0.49 ± 0.01
Vulva position (%)	60.5	67.2	63.5 ± 0.4	58.3	68.1	64.6 ± 0.4
Tail length (mm)	0.131	0.223	0.174 ± 0.005	0.072	0.160	0.118 ± 0.005
Ratio a	23.50	37.33	28.32 ± 0.81	23.98	33.67	29.75 ± 0.45
Ratio b	3.41	4.42	4.09 ± 0.07	3.81	4.71	4.28 ± 0.04
Ratio c	11.27	16.80	14.0 ± 0.3	13.95	27.86	18.5 ± 0.8
Length buc. cav. (µm)	45.39	55.10	49.60 ± 0.63	34.69	44.39	39.50 ± 0.41
Width buc. cav. (µm)	25.76	34.70	29.30 ± 0.61	19.32	26.45	22.20 ± 0.27
Apex (%)	70.9	77.9	75.4 ± 0.4	78.3	87.0	82.9 ± 0.4
d	44.5	58.9	50.3 ± 0.5	32.2	42.7	38.1 ± 0.2
Egg-shell	scaled — egg contour diffuse			echinulate — egg contour sharp		
Buccal cavity	oval shaped			more or less rectangular shaped		
Subventral ridge	prominent with medium to large denticles			low with small denticles		
Tail shape	long, tapering			short, conoid		

NE : $b = 4.09 \pm 0.07$ (oesophagus relatively long)
$c = 14.0 \pm 0.3$ (tail relatively long)

The point-variables LARG $^+$ and LONG $^+$, though being both on the side of the negative values of axis two, are not close to each other. When going from South to North one passes, in terms of mean values, from rather thin specimens to rather stout ones. The value a reflects this difference between both groups : $a = 29.8 \pm 0.5$ for SW cluster, relatively thin specimens, against $a = 28.3 \pm 0.8$ for NE cluster, relatively stout specimens. While the variables APEX, CRETE, ŒUF are those for which the distance to the origin (along the axis 2) is relatively large, they do not exactly explain this axis. Axis two corresponds to the difference in proportions between the anterior end or the posterior end of the body and the parts in between (2 + 3). No variable reflecting this phenomenon was present in the analysis. The fact that the point-variables which correspond to lengh measurements (OEAN, OEPO, etc.) are stratified along axis two, whereas they have similar coordinates along axis one, supports this interpretation of axis two. Moreover this stratification reflects a phenomenon other than differences in size and is independent of them.

Two facts must be stressed in the interpretation of axis two : first the results along axis two are interpreted in terms of ratios although these are absent in the analysis. It is thus unnecessary to incorporate ratios in such an analysis. Axis two, as axis one, reflects the variability of all the specimens together and not only the differences between the two groups, which, for the body proportions, are very small but significantly different on the average. It is mostly intraspecific variation : (variation both in size and in proportion) that is represented by axis one and two when they are treated separately. This explains the large scattering of the points of the two clusters, that are well separated in this plane.

Study of the variables segregating between the two clusters

The variables that give the best segregation between the two clusters will not be found among those related to size (axis one) nor among those reflecting body proportion (axis two), but rather among those for which the opposition between the two poles $^+$ and $^-$ corresponds the best with the opposition of the two clusters. The clusters are opposed mostly along an oblique direction NE-SW. The variables that are arranged along the same direction are the two qualitative variables previously listed (denticulate ridge and egg-shell structure) and three quantitative variables : APEX (position of the tip of the dorsal tooth), CBLO (lengh of buccal cavity) and CBLA (width of the buccal cavity). For these variables the segments linking the poles $^+$ and $^-$ are drawn on the graph of Figure 1. The position of the tip of the dorsal tooth differs clearly in the two groups : $82.9 \pm 0.4\%$ for SW cluster against $75.4 \pm 0.4\%$ for NE cluster. A similar difference is found in the length and the width of the buccal cavity : 39.5 ± 0.4 µm × 22.2 ± 0.3 µm for SW cluster against 49.6 ± 0.6 µm × 29.3 ± 0.6 µm for NE cluster. The individual values of these three characters do not overlap between the two groups even when all the measured specimens are considered (Tab. 2). However the extreme values come close to each other. The correspondence analysis thus proposes three quantitative variables that can be used for a clear separation of the two species.

According to the presence in the NE and SW clusters of qualitative variables corresponding to previous definition of the two species of *Prionchulus*, we propose to name the individuals of SW cluster *P. punctatus* and the individuals of NE cluster *P. muscorum*. An emended diagnosis for these two species will be given after the study of the differentiating characters.

Study of the differentiating characters

The denticulate subventral ridge

Several intermediate forms exist between a strongly developed ridge (subventral ridge prominent, with strong developed denticles, evenly spaced and variable in number from eight to seventeen and a fine one (subventral ridge weak, with small denticles, sometimes almost invisible, mostly unevenly spaced and from four to fifteen in number). Figure 2 shows most of the observed variation of the subventral ridges in *P. muscorum* and *P. punctatus*. This variation not only concerns the number of denticles on the two subventral ridges of the same buccal cavity but also the proportion of the ridge that is denticulate. The denticulate area can vary from about half to the whole of the ridge. Two types of buccal cavity occur : large ones with a length above the 45 µm and small ones with a length under 41 µm. The prominent subventral ridges seem to be associated with a large buccal cavity (Fig. 2 H, I, K) and the fine and low subventral ridges are mostly found in small buccal cavities (Fig. 2 A-C). However, the great variation in development of the denticles in each species is remarkable. A strongly developed denticulate ridge can sometimes occur in *P. punctatus* (Fig. 2 E, F, G) while the opposite is true for *P. muscorum* (Fig. 2 J). In such cases this character is difficult to use.

The structure of the egg-shell

Among 58 gravid females of *P. muscorum*, 20% have smooth or almost smooth eggs and 80% have eggs with well developed scaled protuberances. In *P. punctatus* among 80 gravid females, 11% have smooth eggs or almost so and 89% have echinulate eggs. The presence of smooth eggs can therefore no longer be maintened as a unique feature of *P. muscorum*. The structure of the egg-shell can only be studied on eggs present in the uterus and not on those present in the *pars dilatata*, where eggs can be found in different stages of egg-shell formation. The variations of the structure of the outer layer of the egg-shell as well as the structure of the subventral ridges have been studied in detail on cultures animals collected from the different sample sites (Samsoen *et al.*, 1984). Two egg-shell structures are recognized : echinulate eggs and scaled eggs. The echinulate eggs *(P. punctatus)* are characterized by a sharp contour of the egg bearing individualized sharp to blunt protuberances. The sharpness of the contour of the egg is due to the thick chitinous layer of the shell on which an outer layer is deposited that consists mainly of cylindrical to sharp echinulate protuberances (Fig. 3 F-I). These protuberances in surface view (Fig. 3 B,D,E) look as flattened evaginations with fine inner striae, but in optical section they look pointed (Fig. 3 F), hooked (Fig. 3 G) or cylindrical (Fig. 3 A, H) and sometimes slightly rounded (Fig. 3 I). The scaled eggs *(P. muscorum)* do not show a clear egg contour, because the scaled protuberances cover the chitinous layer sometimes partially (Fig. 3 O-Q) but mostly totally (Fig. 3 K, L, M). These protuberances cover each others and mask the egg margin which results in a diffuse egg contour (Fig. 3 K-M). In surface view (Fig. 3 J, N) the protuberances appear as rounded ridges, well developed (Fig. 3 K) or more or less flattened (Fig. 3 P). Thus the echinulate or scaled egg-shell is a sound criterion to separate the two species. The species differ in the sharp or diffuse contour of the egg, regardless of the variation of the protuberances.

The buccal cavity

Fig. 4 presents the relation of the length (L) and the width (W) of the buccal cavity of 435 females,

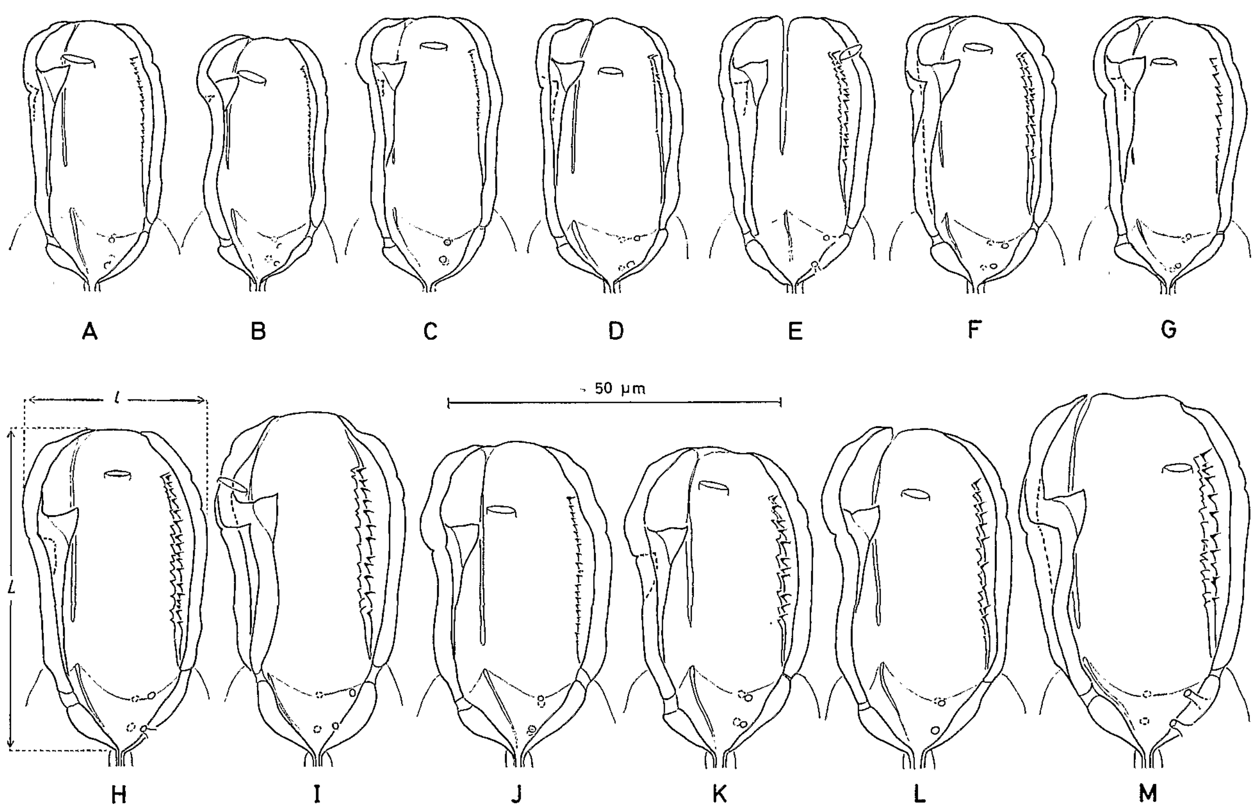

Fig. 2. Variation in the buccal cavity. A-G : *Prionchulus punctatus*. H-M : *P. muscorum*.

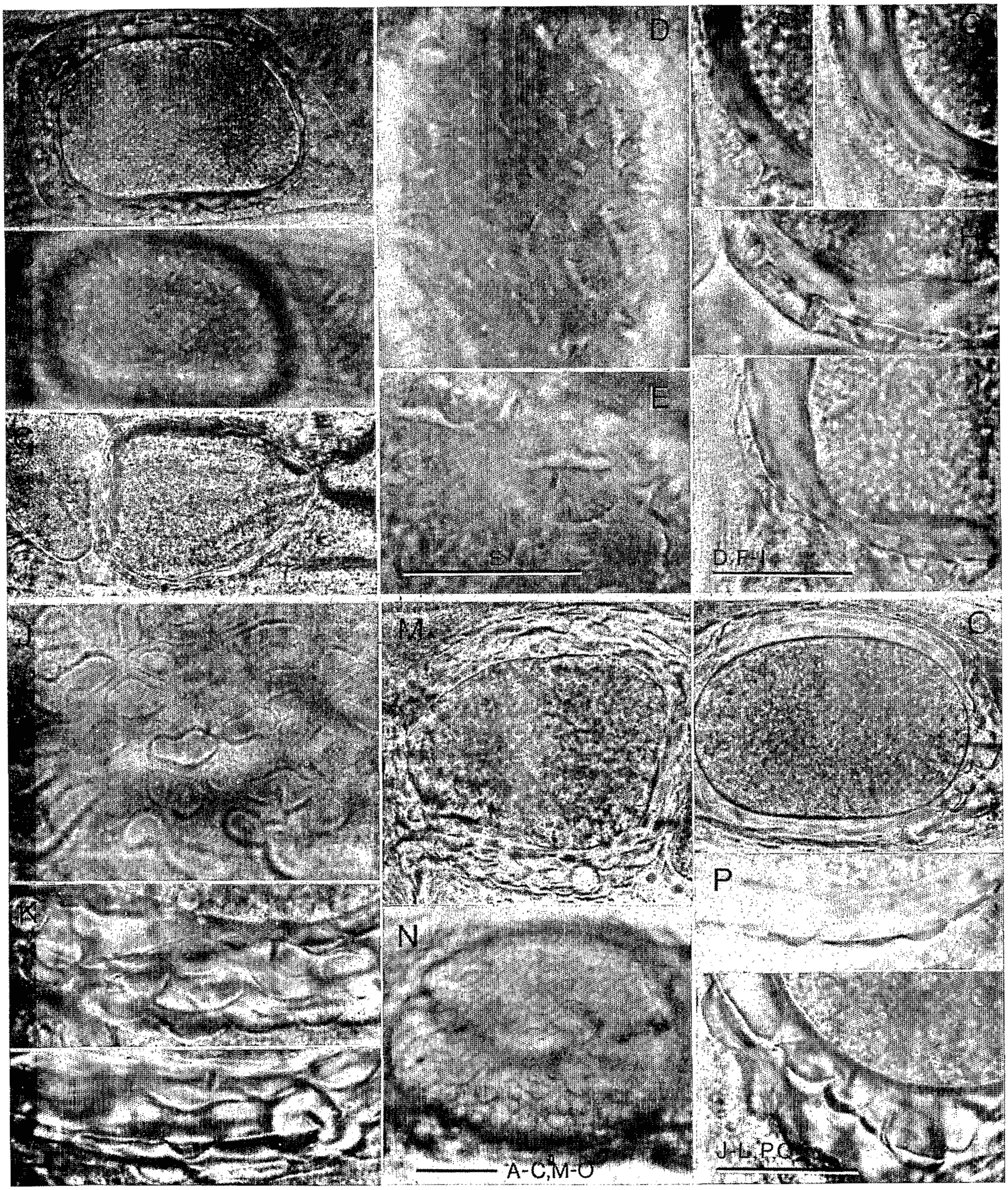

Fig. 3. Intra-uterine eggs. A-I : *Prionchulus punctatus*. J-Q : *P. muscorum*. A, C, M, O : optical median section. C, B, D-E, J, N : surface view. F-I, K, L, P, Q : detail of the egg contour in median section. (Bar = 20 μm.)

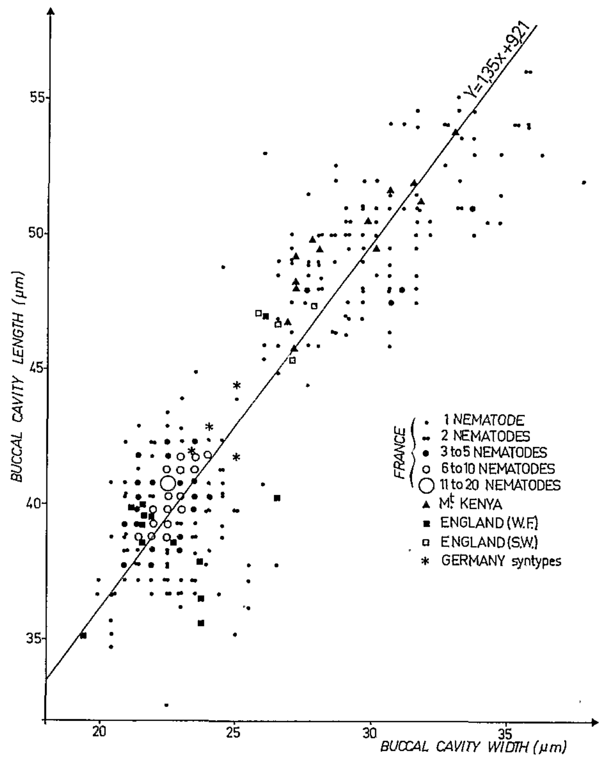

Fig. 4. Relationship between length (L) and width (W) of the buccal cavity for the two populations considered (n = 435), with the regression line.

gravid or not gravid. The combined study of the two measurements gives a better segregation between the two species than each character alone. The graph of Fig. 4 shows a good separation of the two species, and a greater scattering of the higher values. However some points of the graph, i.e. some animals, present an intermediate position and cannot be identified with certainty. To remove this doubt the regression line between length and width is drawn ; its equation is $L = 1.35\ W + 9.21$. A projection of each point of the graph onto the regression line enables us to calculate the value of distance d, which is the distance from the y-intercept to the project point on the regression lines :

$$d = \frac{W + a\ (L - b)}{\sqrt{W + a^2}}$$

a, the regression coefficient, is equal to 1.35 and b the y-intercept is equal to 9.21 ; d becomes :

$$d = 0.804\ L + 0.594\ W - 7.409$$

The histogramm (Fig. 5) of the values of d (Tab. 2) shows the two groups of measurements clearly separated. The size of the buccal cavity represented by the values d seems to be a very good criterion to separate the two species.

Position of the tip of the dorsal tooth

The mean values of the position of the dorsal tooth as a percentage of the buccal cavity length (APEX) are statistically different for the two

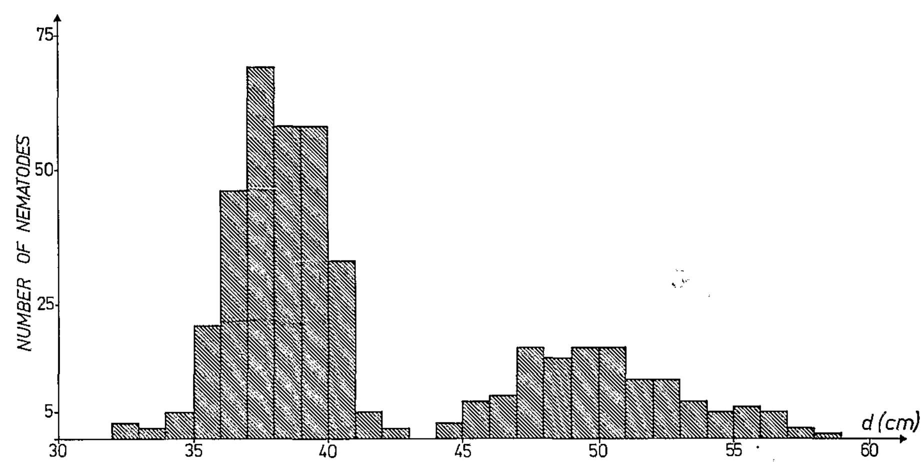

Fig. 5. Histogram of d for the two populations considered (n = 435).

species. The ranges of individual values for both species almost overlap and identification will be difficult for some specimens. However, when used with another measurement, *d* for instance, APEX permits a definite identification. Fig. 6 shows the relation between the position of the tip of the dorsal tooth and *d* for the 138 females used in the factorial analysis. A specimen with a value for APEX of 78.3% and a value *d* of 33 clearly belongs to *P. punctatus*, while a specimen with APEX = 77.9% and *d* = 47.3 is typical of *P. muscorum*, Conversely, any specimen that cannot be identified by the value of *d* only is immediately characterized by the value APEX.

In conclusion one character alone (CBLO, CBLA or APEX) is never differentiating between the two species ; two combined characters (CBLO and CBLA combined in value *d*) are more likely to be so and three characters (APEX together with *d*) are always able to provide a definite identification.

Other characters

The two other characters used by different authors (Tab. 1) are sometimes difficult to define. The buccal cavity appears somewhat differently shaped in the two species : more oval-shaped in *P. muscorum* and more rectangular in *P. punctatus* (Fig. 2). Intermediate shapes exist (Fig. 2, E and L) that make it very difficult to use this character.

The measurements of the tail in both species are statistically different. The interpretation of axis two pointed to the relative difference in lengths and ratios of the tails between the two species. However, the ranges of individual values overlap (Tab. 2) and neither the C ratio nor the tail length can be used satisfactorily to separate the species. Each species tends to have a typical shape of tail (Fig. 7). In *P. muscorum* the tail tends to be more elongate with rounded tip and mostly terminal rounded projection (Fig. 7 H-K). In *P. punctatus* the tail is short, strongly conoid with acute to rounded terminus (Fig. 7 A-D) and rarely with a well differentiated projection. However similar tail shapes do occur in both species (compare Fig. 7 E with J, F with L and G with H).

Conclusion

The separation of the two related species of *Prionchulus* has traditionnally been founded on qualitative characters (namely the structure of the denticulate subventral ridge and of the shell of intra-uterine eggs), poorly described and with unknown intra-specific variability. A better definition of the scaled or echinulate structure of the egg-shell and of the clarity of the outline of the egg makes this character a more useful criterion to separate the two species. But in any case, and especially with

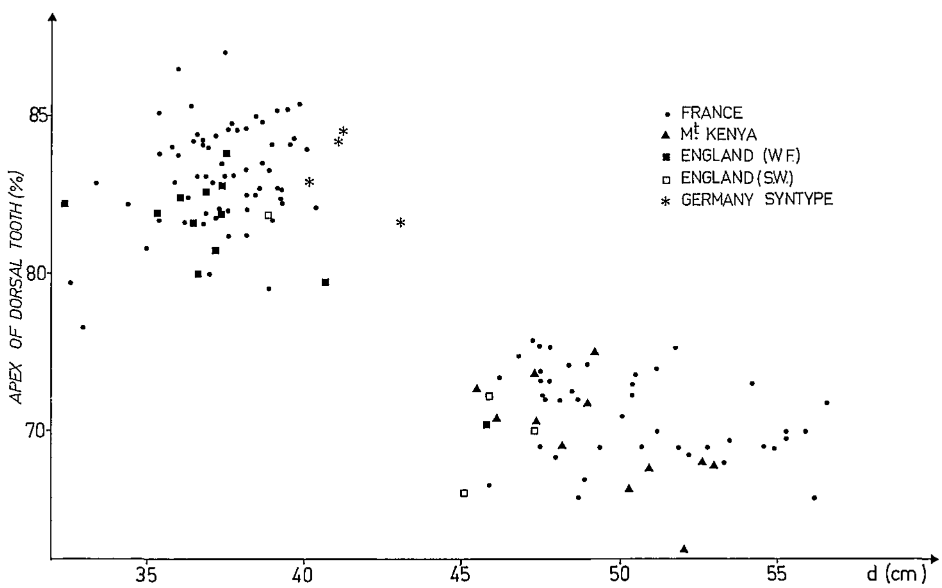

Fig. 6. Relationship between APEX and value *d* for the two populations considered in the correspondence analysis (n = 138).

non gravid females, priority has to be given to the size of the buccal cavity and to the position of the apex of the dorsal tooth, because they are more reliable characters, easy to measure and independent of the judgement of the observer. The value of these quantitative criteria for specific differentiation has been proved by the correspondence analysis. However it is necessary to use several criteria for a safe identification. Table 2 summarizes the values of measurements and morphological characters that can be used for the identification of *P. muscorum* and *P. punctatus*.

The diagnosis of both species must be amended to include the conclusions of our study :

P. muscorum: eggs in gravid females of scaled structure and with egg contour diffuse. Distance from tip of dorsal tooth to base of buccal cavity around 75% of the length of the buccal cavity (70.9% to 77.9%). Buccal cavity large : "*d*" values between 44.5% and 58.9%. Denticulate subventral ridge prominent with medium to large regulary spaced denticles. Tail long and tapering.

P. punctatus: eggs in gravid females of echinulate structure and with egg contour sharp. Distance from tip of dorsal tooth to base of buccal cavity around 83% (78.3% to 87%) of the length of the buccal cavity. Buccal cavity small : "*d*" values between 32.2% and 42.7%. Denticulate subventral ridge low with small and often uneven-spaced denticles. Tail short and conoid.

The European populations studied in the present article show some differences with the populations described as *P. muscorum* from North America especially by Mulvey (1967). The status of these North America populations will be discussed in a future article. On the other hand. the variations observed in the two species and revealed by the correspondence analysis are probably entirely due to the differences of the sample site as will be shown in a next paper ; the specimens were collected from different soil or humus types.

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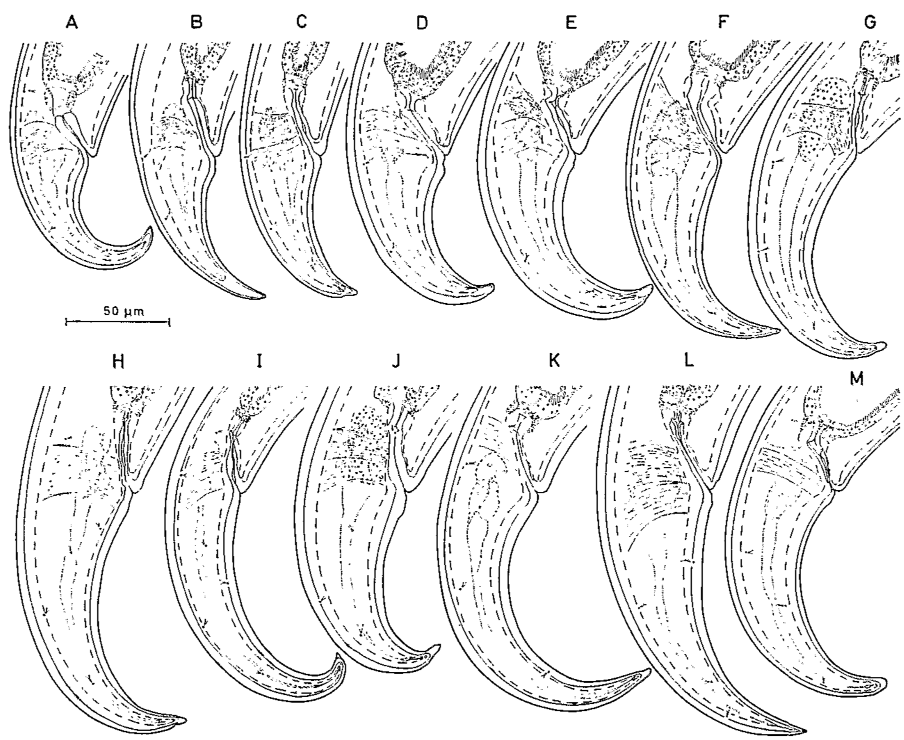

Fig. 7. Variation in shape of tail. A-G : *Prionchulus punctatus*. H-M : *P. muscorum*.

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