Belg. J. Zool. — Volume 125 (1995) — issue 2 — pages 315-327 — Brussels 1995

(Manuscript received on 27 January 1995)

ON THE HOMOLOGY OF THE INCISOR TEETH IN THE RABBIT (*ORYCTOLAGUS CUNICULUS*)

by

PAUL SIMOENS (1), HENRI LAUWERS (1), WALTER VERRAES (2) and ANN HUYSSEUNE (2)

(1) University of Ghent, Department of Morphology, Casinoplein 24, B-9000 Ghent (Belgium)

(2) University of Ghent, Institute of Zoology, Ledeganckstraat 35, B-9000 Ghent (Belgium)

SUMMARY

The homology of the rabbit incisors has remained controversial despite abundant phylogenetic, developmental and morphological research. In this study, development and morphology of the incisors were investigated by means of serial histological sections and by stereomicroscopy in 10 fetal, 25 juvenile and 3 adult New Zealand White rabbits. A vestigial and a major incisor develop in both the upper and lower jaw, while a diphyodont minor incisor is located caudal to the major incisor in the upper jaw. Additionally, a unique case of incisor polydonty in an adult wild rabbit was investigated. The left incisive bone of this case bore a large supernumerary medial incisor which had all characteristics of a typical atavistic expression of the vestigial primordium of the first incisor. From this case the concept was deduced that the major incisor in the rabbit is monophyodont and corresponds to the second incisor, while the minor incisor in the upper jaw represents the diphyodont third incisor.

Key words : Rabbit, incisor teeth, polydonty, dentition, homology.

INTRODUCTION

Lagomorphs have been distinguished as an order separate from the rodents because of their duplicidentate upper jaw dentition (HOROWITZ *et al.*, 1973, THENIUS, 1989). In the rabbit, four upper and two lower incisors are formed bilaterally during fetal development. In adult dentition, a major and minor incisor are present in each upper jaw, and a major incisor in each mandible.

This situation is a vast reduction of the basic diphyodont dentition of adult eutherian mammals presenting bilaterally three upper and lower incisors (BECKER, 1970 ; MILES and GRIGSON, 1990). The regression of one upper and two lower incisors in the rabbit has puzzled scientists for more than 150 years. Despite

numerous phylogenetic, developmental and morphological studies, the homology of the remaining incisors is still controversial. Different hypotheses about the homology of these incisors have been reviewed by HIRSCHFELD *et al.* (1973), OOË (1980) and THENIUS (1989).

In the present study, the literature data were checked against morphological and developmental observations in perinatal rabbits and confronted with a unique finding of incisor polydonty in an adult wild rabbit (*Oryctolagus cuniculus* L., 1758).

MATERIAL AND METHODS

Along with the macerated skull of an adult wild rabbit with incisor polydonty and hypertrophy, 38 rabbits of the New Zealand White breed of *Oryctolagus cuniculus* L., 1758 were studied. The latter animals ranged in age from 21 and 28 days *in utero* (6 and 4 specimens, respectively), 1 through 35 days postnatally (20 specimens), 2 months (5 specimens) and older than 6 months (3 specimens). Size and position of all incisors were determined for each animal. Gestation period in the rabbit is 31 days.

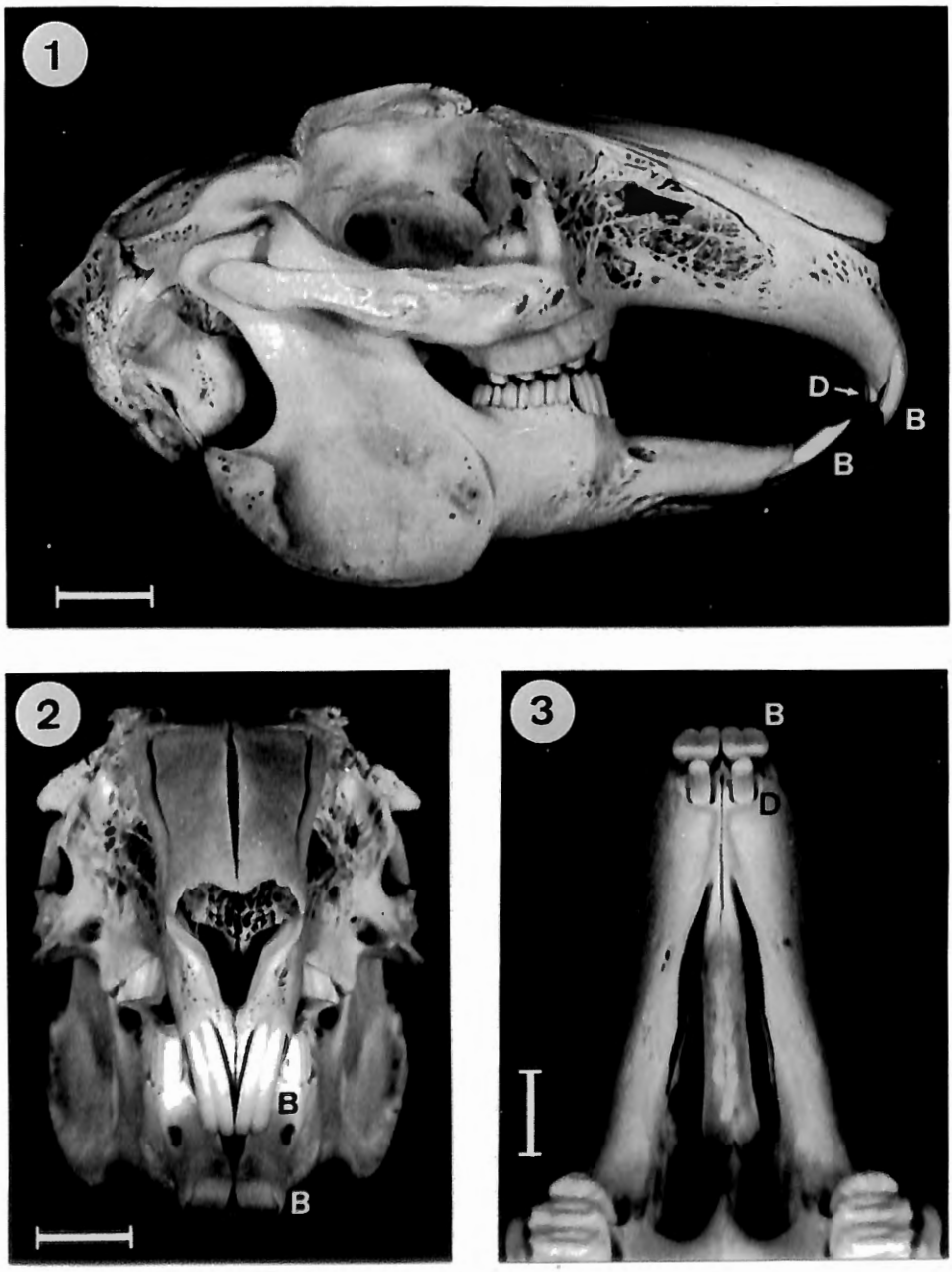
Dental development was investigated histologically in 7 fetal heads embedded in hydroxyethylmethacrylate (Technovit 7100, Kulzer) or paraffin, by means of 10 µm thick transverse and horizontal serial sections coloured with a trichrome or haematoxylin-eosin staining. Early postnatal dentition was examined histologically in two heads of 8 day old rabbits, embedded in paraffin and cut sagittally in serial sections that were subsequently stained with haematoxylin-eosin. Serial histological sections were digitalized for three-dimensional reconstruction of dental arrangement by means of a HP-program as described by VANDEN BERGHE *et al.* (1986). The incisors of all other rabbits were studied stereomicroscopically, both *in situ* and after extraction, using a Zeiss OPMI-FC Epitechnoscope.

The polydontic skull was examined macroscopically and radiographically (exposure settings : 44 KV, 350 mA, 0.02 sec, Trimax T2-HD screen).

RESULTS

Dentition in the adult rabbit (Figs 1-3)

The *major incisors* (B) are long, curved and hypsodont, *i.e.*, continually growing and open-rooted. The clinical roots of the upper and lower major incisors have a wide open root canal, and are deeply implanted in the incisive bones and the



General legend : A = vestigial incisor, B = major incisor, C = deciduous minor incisor, D = permanent minor incisor.

Figs 1-3. — Dentition in the adult rabbit. — 1. Right lateral view (bar = 1 cm). - 2. Rostral view (bar = 1 cm). - 3. Ventral view of the upper incisors (bar = 5 mm).

mandibulae, respectively. The clinical crowns of the upper major incisors converge ventromedially and are strongly curved. They bear a deep longitudinal groove along the convex vestibular surface, and a shallow oblong groove on the concave lingual surface. The clinical crowns of the lower major incisors are less strongly curved and converge dorsomedially. They present a longitudinal lingual groove but no vestibular groove.

The *minor incisors* (D) lie along the caudomedial surface of the upper major incisors. They are much shorter and thinner than the latter, slightly curved and open-rooted.

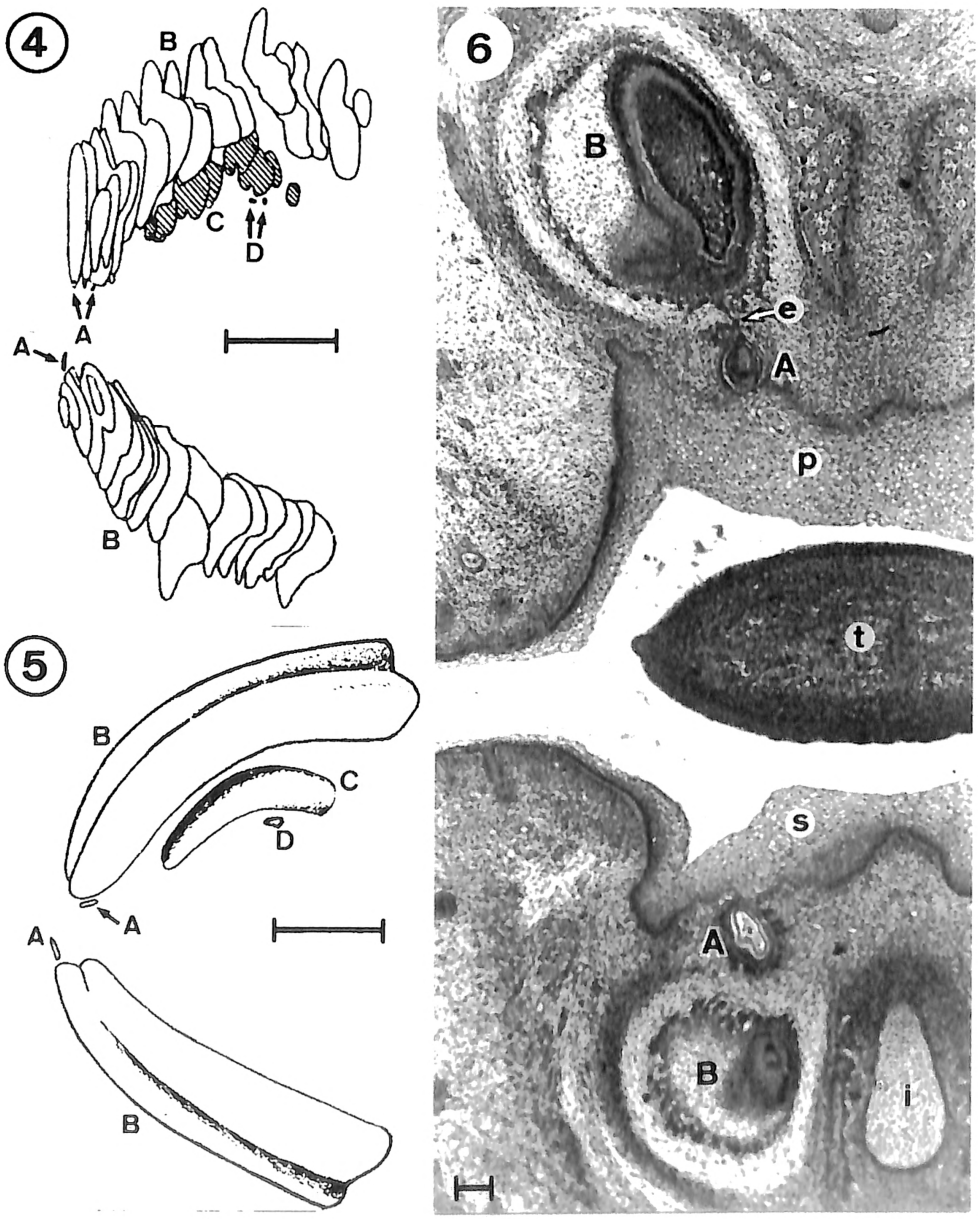
Development of the incisor teeth
(Figs 4-14)

A *vestigial incisor* (A) was present in both the upper and lower jaws at day 21 of fetal life. This rudimentary tooth was closely adjacent to the rostral oral mucosa and was located rostromedial to the major incisor (B) (Figs 6, 7, 9 and 10). It was connected with the enamel organ of the latter tooth through an epithelial cord (Figs 6 and 9). At day 28 of fetal life, the vestigial incisor was either erupting or effectively erupted (Figs 11 and 12), and it was no longer seen in neonatal rabbits.

The *major incisor* (B) was present in the upper and lower jaws of all fetal and postnatal rabbits investigated. This long bicuspidal tooth was still covered by the oral mucosa at day 28 of fetal life, but was erupted at birth in both the upper and lower jaws.

The *deciduous minor incisor* (C) was observed in the upper jaw at day 21 of fetal life, lying ventromedial to the caudal segment of the major incisor (Fig. 7). During further development, the dental root of this incisor became distinctly bifurcated. At birth (day 1), this incisor could be palpated through the oral mucosa, but its eruption only occurred at day 4 postnatally. This tooth was shed early in the second month of life; in one case it was already lost unilaterally at the end of the first month (Figs 13-14).

The *permanent minor incisor* (D) of the upper jaw was not yet visible at 21 days of fetal life. The germ stage of this tooth was apparent at fetal day 28 (Figs 4 and 5). It lay ventral to and closely associated with the enamel organ of the deciduous minor incisor. Eighteen days after birth, the permanent minor incisor could be palpated caudal to the major incisor through the bulging oral mucosa. Eruption of the permanent minor incisor was observed 23 days after birth, *i.e.*, before shedding of the deciduous minor incisor. Consequently, at the end of the first month of life, three incisor teeth were aligned rostro-caudally in each upper jaw, *i.e.*, the major incisor (B), the deciduous minor incisor (C) and the permanent minor incisor (D) (Figs 13-14).



Figs 4-5. — Rostrolateral view of the left incisors in a fetal rabbit of 28 days post conception (bar = 1 mm) — 4. Compiled transverse serial sections. - 5. Dental outline reconstruction.

Fig. 6. — Transverse section of the left vestigial (A) and major (B) incisors in a fetal rabbit of 21 days post conception. e = epithelial connection between the enamel organs of the vestigial and major incisors, i = intermandibular cartilage, p = palatal mucosa, s = sublingual mucosa, t = tongue (bar = 100 μm).

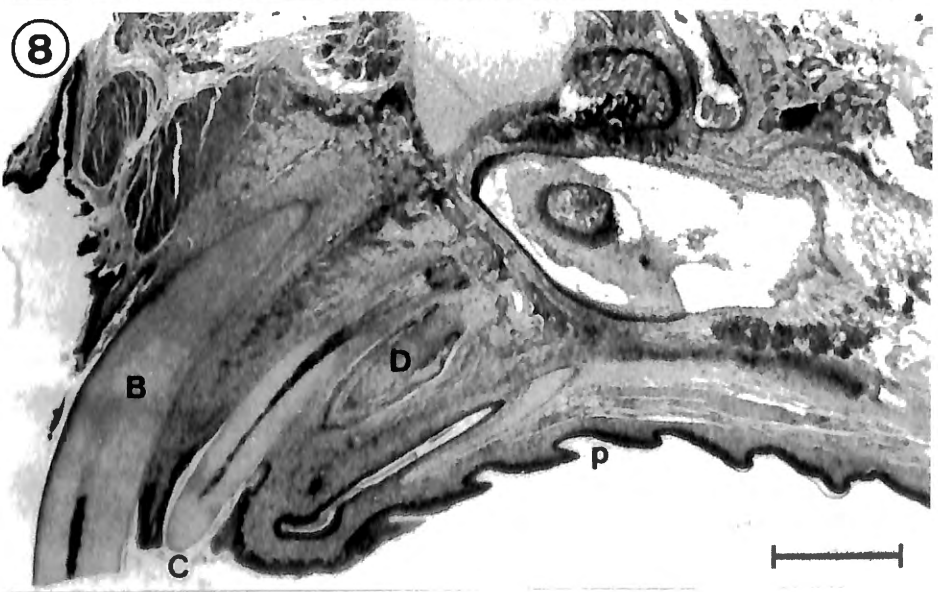
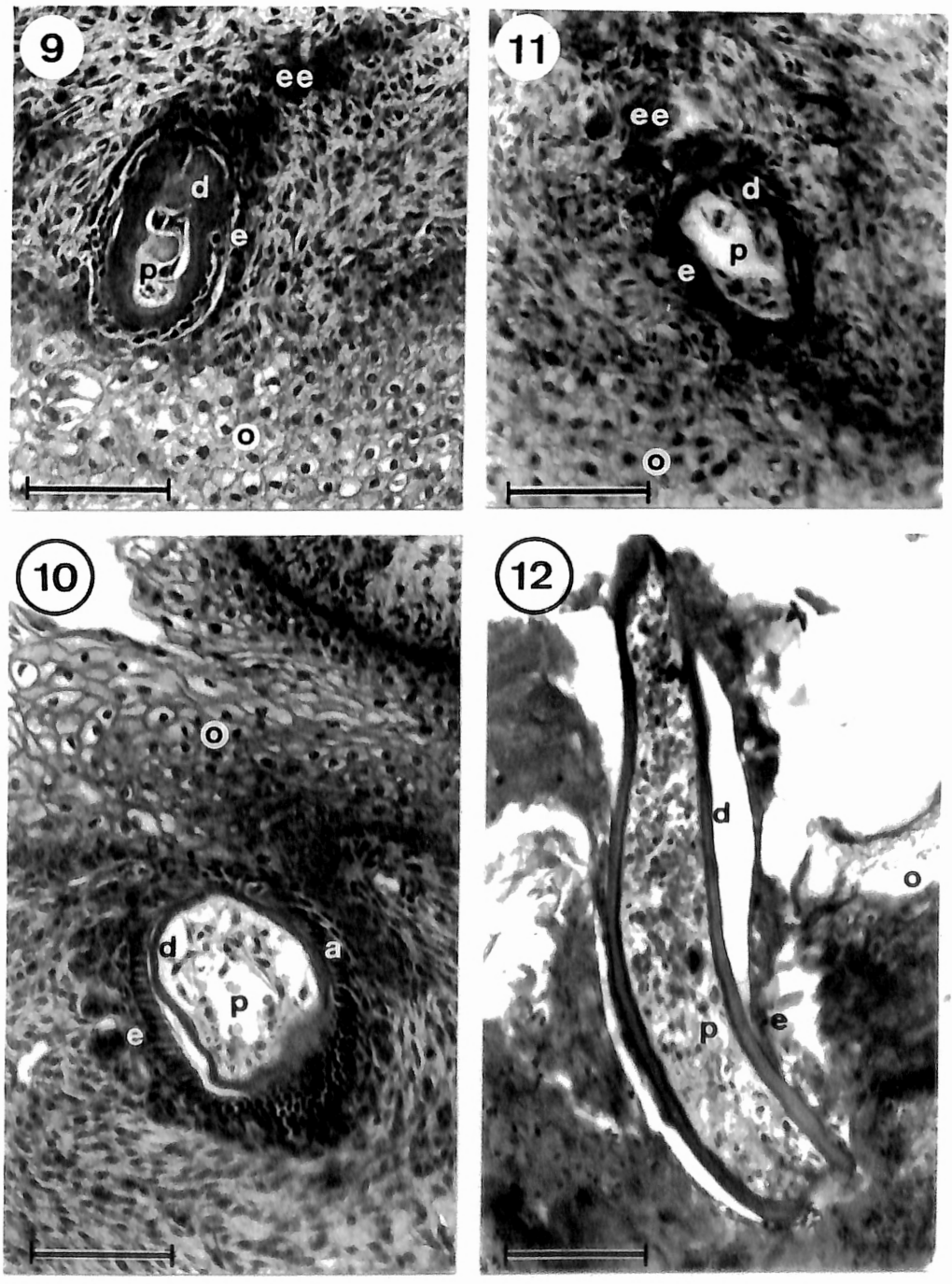
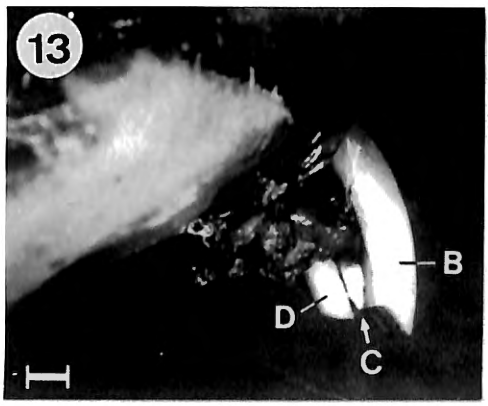


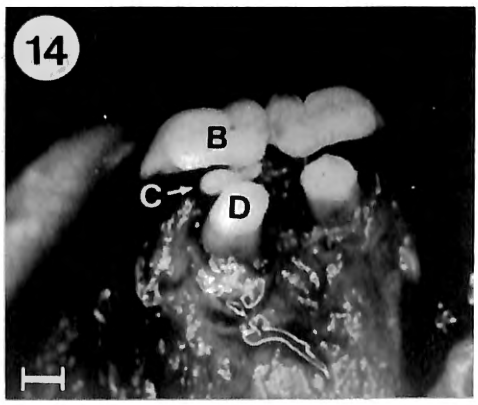
Fig. 7. — Horizontal section of the vestigial (A), major (B) and deciduous minor (C) upper incisors in a fetal rabbit of 21 days post conception. p = philtrum, v = vomeronasal organ (bar = 100 μm).

Fig. 8. — Sagittal section of the major (B), deciduous minor (C) and permanent minor (D) upper incisors in a 8 days old rabbit. The permanent minor incisor (D) has developed into the bell stage. p = palatal mucosa (bar = 1 mm).



Figs 9-12. — Legend on p. 322.





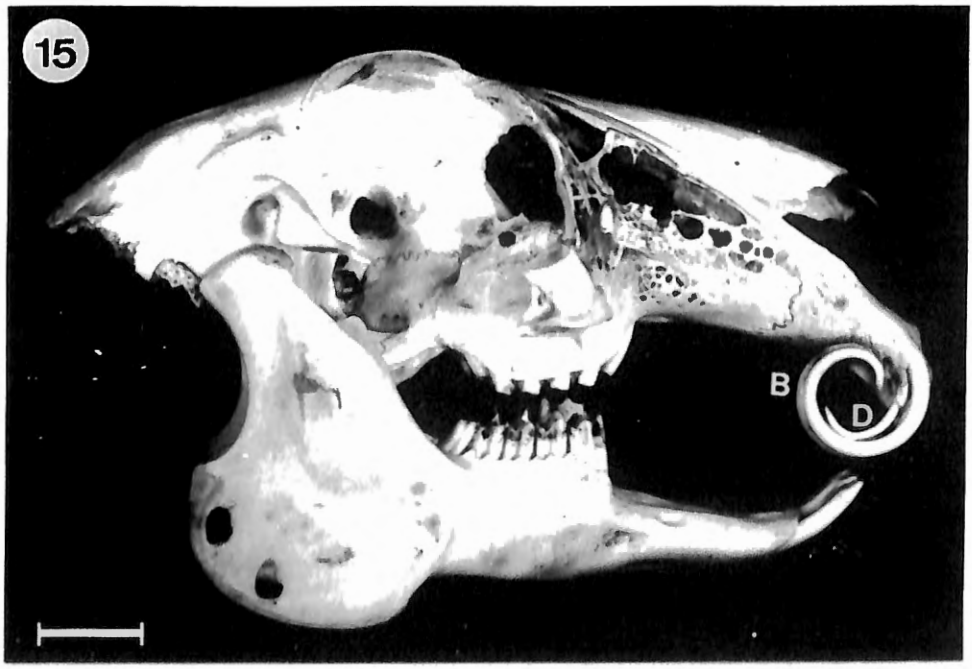
Figs 13-14. — Upper incisors in a 1 month old rabbit with deciduous minor incisor (C) still present between the major incisor (B) and the permanent minor incisor (D) on the right side (bars = 1 mm). — 13. Right lateral view. - 14. Ventral view.

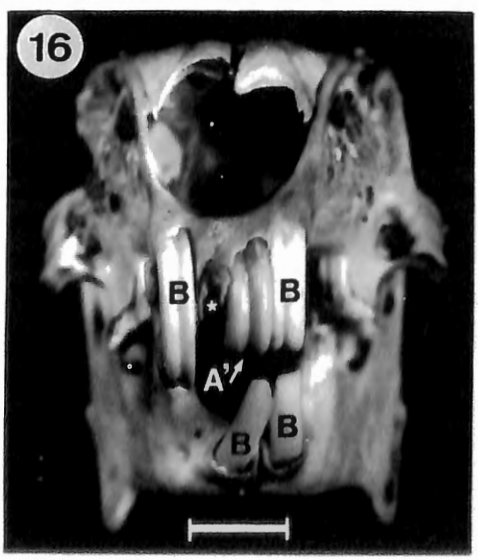
Incisival polydonty in a wild rabbit
(Figs 15-17)

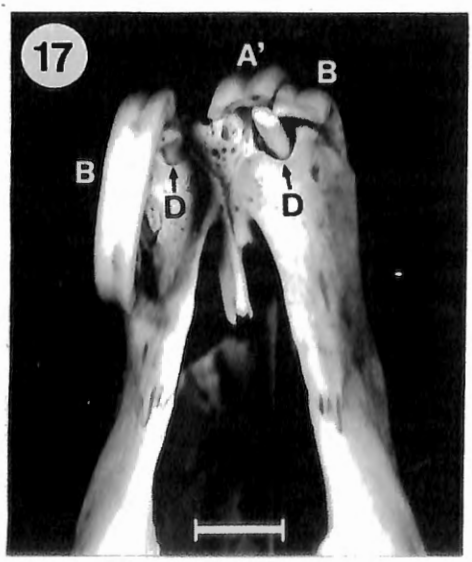
The mandibular incisors, as well as the upper and lower premolars and molars of this adult skull were normal in size and shape. In the upper jaw, however, the incisors presented manifest positional deviation, hypertrophy and polydonty.

In the left upper jaw, three incisors were present. Size, shape and intraosseous position of the major incisor (B) were normal, but the orientation of the crown segment of this tooth was sagittal instead of rostromedial. This deviation was caused by the presence of an additional large medial incisor (A'). The general shape of the latter tooth was very similar to that of a regular major incisor, although its root was shorter and its crown broader. The root of this additional incisor was embedded in the incisive bone and the crown curved rostromedially, forming occlusal contact with the incisor of the right mandible. A normal minor incisor (D) lay caudal to the large incisors. It emerged from the incisive bone at the level of the medial lobe of the major incisor (B) and its crown was directed rostroventrally along the caudal surface of the additional major incisor (A'). Medial to the major and additional major incisors lay a mass of active osteosclerotic tissue (Fig. 16). The latter enclosed a central excavation that was ventrally opened. Contents of the excavation were not present in this macerated specimen.

Figs 9-12. — Histology of the vestigial incisors (bars = 100 µm). a = ameloblasts, d = dentin, e = enamel organ, ee = epithelial extension between enamel organs of the vestigial and major incisors, o = oral mucosa, p = dental pulp. — 9. Upper vestigial incisor in a fetus of 21 days post conception. - 10. Lower vestigial incisor in a fetus of 21 days post conception. - 11. Upper vestigial incisor in a fetus of 28 days post conception. - 12. Lower vestigial incisor in a fetus of 28 days post conception.







Figs 15-17. — Skull of an adult wild rabbit with polydonty and hypertrophy of the incisors. — 15. Right lateral view showing coiled upper incisors (B and D) (bar = 1 cm). - 16. Rostral view demonstrating the position of the major incisors (B), the large additional incisor (A') and a medial osteosclerotic tissue mass (asterisk) in the upper left incisive bone (bar = 1 cm). - 17. Ventral view of the upper incisors (bar = 5 mm).

The right upper jaw contained two hypertrophied incisor teeth. The major incisor (B) was sagittally oriented and formed no contact with the lower incisors. Its crown was coiled for 360°, the apical part of the crown being more strongly curved than the basal segment. The minor incisor (D) was also elongated, forming a semicircle along the inner curvature of the major incisor.

Both the left and right mandibles bore a large incisor (B), the size and shape of which were normal (Fig. 16). The lower left incisor formed occlusal contact with the major incisor of the left upper jaw (B). The crown of the lower right incisor was deviated dorsally to the left and thus made contact with the additional incisor of the left upper jaw (A'). This arrangement had caused normal attrition and length of the left upper incisors and both lower incisors.

DISCUSSION

The exact homology of the rabbit incisors has remained uncertain, because only four upper and two lower incisor primordia are found in the rabbit during development.

All evidence available indicates that the minor incisor is diphyodont, as two teeth are successively formed from the enamel organ within the same dental alveole (POUCHET and CHABRY, 1884 ; FREUND, 1892 ; HIRSCHFELD *et al.*, 1973 ; SYCH and READE, 1987). The tooth that develops first has all features of being deciduous as it is smaller, lies more rostral and erupts earlier than the subsequent tooth by which it is replaced (KRAUSE, 1884 ; HIRSCHFELD *et al.*, 1973 ; HOROWITZ *et al.*, 1973). The latter incisor persists throughout life and is therefore truly permanent.

In contrast, the nature of the vestigial and major incisors is still uncertain. The major incisor is generally considered as permanent because it persists throughout life, but it is still controversial whether or not this tooth has a deciduous predecessor. Most authors consider the vestigial incisor as the deciduous predecessor of the major incisor, because the germs of both teeth are closely adjacent and present epithelial contiguity, while the vestigial anlage is smaller, develops earlier and erupts faster than the large incisor (HUXLEY, 1880 ; POUCHET and CHABRY, 1884 ; FREUND, 1892 ; PETERS and STRASSBURG, 1968 ; HIRSCHFELD *et al.*, 1973 ; SYCH and READE, 1987). According to ADLOFF (1910), however, the positional contiguity of the vestigial and the major incisors merely results from the large outgrowth of the latter, and both dental germs develop separately as the first and second incisors, respectively. A similar opinion is held by NISHIYAMA (1932) who considered the epithelial connection between the germs of both teeth as a secondary link. More recently, even the permanent nature of the major incisor has been challenged by OOË (1980) who considered this tooth as deciduous because it develops distal (*i.e.*, lateral) instead of lingual (*i.e.*, caudal) to the vestigial incisor.

The controversial nature of the vestigial incisor, combined with the reduced number of incisors, has entailed differing numerical classifications of the rabbit incisors (Table 1).

TABLE 1

Homology of the vestigial (A), major (B), deciduous minor (C) and permanent minor (D) incisors of the rabbit as proposed by various authors.
*(I : incisor ; d : deciduous ; p : permanent ; * : see discussion)*

A	*B*	*C*	*D*	*Authors*
Id1	Ip1	Id2	Ip2	WOODWARD (1892)
- (*)	Id1	Id3	Ip3	WEBER (1928)
I 1	I 2	—	I 3	ADLOFF (1910), NISHIYAMA (1932)
Id1	Id2	Id3	Ip3	OOË (1980)
I 1	I 2	Id3	Ip3	*This article*

For the reasons described above, ADLOFF (1910), NISHIYAMA (1932) and OOË (1980) conclude that regression has reduced the first incisor to a vestigial remnant, and that the major and minor incisors therefore correspond to the second and third incisors, respectively. More evidence for this probability is offered by the case of polydonty described here. This case presents indeed all characteristics of a typical atavistic polydonty, *i.e.*, development of a supernumerary dental primordium that is normally found lingering in the reduced dentition of a particular species (BECKER, 1970). Several decades ago, NISHIYAMA (1932) pointed out the possibility that the phylogenetically reduced dental primordium in the rabbit might occasionally come to expression, but to our knowledge such a case has never been reported hitherto. The additional large incisor present in this aberrant dentition could be interpreted as the outgrowth of either a deciduous predecessor of the major incisor or a monophyodont first incisor. The former possibility seems unlikely, however, because the supernumerary incisor was similar in size and morphology to the major incisor. Therefore the supernumerary and the major incisors most likely correspond to the first and the second monophyodont incisors, respectively, and consequently the minor incisor is equivalent to the third incisor. It is evident that the interpretation of such aberrant morphological findings remains always speculative, even when it seemingly offers the missing link that has long been sought. One cannot completely overlook the possibility that the supernumerary incisor could also be the expression of atypical polydonty, *i.e.*, a casual variation that has no phylogenetic basis but results from malformations such as dichotomy of teeth primordia or transposition of the dental lamina (BECKER, 1970 ; MILES and GRIGSON, 1990).

A completely different interpretation of the numerical reduction of the rabbit incisors is provided by WEBER (1928), who designates the deciduous incisors as Id1 and Id3, adding that the latter is replaced by the permanent minor incisor I3. This description states that the second incisor is lost, but no arguments or facts are given to document that presumption. This record is ambiguous as it does not state clearly whether the first deciduous incisor corresponds either to the vestigial or the major incisor. This ambiguity was not uncommon in older records in which the vestigial

incisors were overlooked and the major teeth were considered to be deciduous because they happen to be formed very early (see WOODWARD, 1892). This interpretation has therefore been used in compiling Table 1.

More investigators share the opinion that the phylogenetic reduction of the rabbit incisors has affected the third incisor, whereby the functional major and minor incisors are considered as the first and second incisors, respectively (FREUND, 1892 ; WOODWARD, 1892). For a long time this viewpoint was based upon the erroneous belief that, of the three incisors present in the upper jaw of young rabbits, the third or outer one was lost (WOODWARD, 1892). More recently, THENIUS (1989) has also referred to some statements claiming that a third incisor might be formed but is lost soon after birth. FRIANT (1957 and 1961) has described a similar case of exceptional dentition in the upper jaw of a 20 days old rabbit, having a third incisor that lay behind the major and deciduous minor incisors. The caudal tooth allegedly erupted around the twentieth day of life and was shed soon afterwards without replacement. The description further claimed that the permanent minor incisors erupt after their deciduous predecessors are lost. However, this description and the iconographic evidence of this case contain controversial data, and most probably they actually refer to the normal situation of three aligned teeth (major, deciduous minor and permanent minor incisor) that are present in rabbits at that age. Therefore we feel that no conclusive evidence is given for claiming that regression of the incisors in rabbits has focused on the third incisor.

In view of the literature reports and our histological findings, the unique case of polydonty that is described in this study endorses the concept that in the rabbit (1) the vestigial incisor is monophyodont and corresponds to the first incisor, (2) the major incisor is also monophyodont and corresponds to the second incisor, and (3) the deciduous and permanent minor incisors in the upper jaw represent both stages of the diphyodont third incisor.

ACKNOWLEDGEMENTS

The authors express their gratitude to Dr. A. Van Wassenhove for procuring the polydontic rabbit skull, to Prof. F. Verschooten for radiographic analysis, and to the technicians R. De Moor, G. De Wever and M. De Volder for meticulous histological processing.

REFERENCES

ADLOFF, P. (1910) — Zur Entwicklungsgeschichte des Nagetiergebisses. *Anat. Anz.*, **37** : 257-271.

BECKER, E. (1970) — Zähne : In : *Handbuch der speziellen pathologischen Anatomie der Haustiere*, Band V : Digestionsapparat, I. Teil, 3. Aufl., Verlag Paul Parey, Berlin : 83-313.

FREUND, P. (1892) — Beiträge zur Entwicklungsgeschichte der Zahnanlagen bei Nagethieren. *Arch. mikrosk. Anat.*, **39** : 525-555.

FRIANT, M. (1957) — La morphologie des dents temporaires du lièvre commun *(Lepus europaeus pallas)* au stade cuspidé. *Acta anat.*, **31** : 572-576.

FRIANT, M. (1961) — La formule incisive des Lagomorphes. *Actualités odontostomatiques*, **35**, 481-484.

HIRSCHFELD, Z., M.M. WEINREB and Y. MICHAELI (1973) — Incisors of the rabbit : morphology, histology, and development. *J. Dent. Res.*, **53** : 377-384.

HOROWITZ, S., S.H. WEISBROTH and S. SCHER (1973) — Deciduous dentition in the rabbit *(Oryctolagus cuniculus)*. A roentgenographic study. *Arch. oral Biol.*, **18** : 517-523.

HUXLEY T.H. (1880) — Evolution and the arrangement of the vertebrata. *Proc. Zool. Soc. London*, 655.

KRAUSE, W. (1884) — *Anatomie des Kaninchens*, 2. Aufl., Verlag von Wilhelm Engelmann, Leipzig : 197-199.

MILES, A.E.W. and C. GRIGSON (1990) — *Coyler's variations and diseases of the teeth of animals*. Cambridge University Press, Cambridge : 1-18, 133-139, 355-369.

NISHIYAMA, Y. (1932) — Beiträge zur Kenntnis der Morphologie, Bedeutung und Entwicklungsgeschichte der Rudimentärzähnchens beim Kaninchen. *Keija J. Med.*, **3** : 138-159.

OOË, T. (1980) — Développement embryonnaire des incisives chez le lapin (*Oryctolagus cuniculus L.*). Interprétation de la formule dentaire. *Mammalia*, **44**, 259-269.

PETERS, S. and M. STRASSBURG (1968) — Zur Frage der ersten Dentition bei Kaninchen und Maus. *Z. Säugetierkunde*, **34** : 91-97.

POUCHET, G. and L. CHABRY (1884) — Contribution à l'odontologie des mammifères. *Journal de l'Anatomie et de la Physiologie, 168-171.*

SYCH, L.S. and P.C. READE (1987) — Heterochrony in the development of vestigial and functional deciduous incisors in rabbits *(Oryctolagus cuniculus L.)*. *J. Craniofacial Genet. Developm. Biol.*, **7** : 81-94.

THENIUS, E. (1989) — Zähne und Gebiß der Säugetiere. In : *Handbuch der Zoologie* by J. Niethammer, H. SCHLIEMANN and D. STARCK (eds.), Vol. 8, Walter de Gruyter Verlag, Berlin : 221-232.

VANDEN BERGHE, W., P. AERTS, H. CLAEYS and W. VERRAES (1986) — A microcomputer-based graphical reconstruction technique for serial sectioned objects, with hidden line removal. *Anat. Rec.*, **215** : 84-91.

WEBER, M. (1928) — *Die Säugetiere*. Vol. 2, Fischer Verlag, Jena : 253-257.

WOODWARD, M.F. (1892) — On the Milk-dentition of *Procavia (Hyrax) capensis* and of the rabbit *(Lepus cuniculus)*, with remarks on the relation of milk and permanent dentitions of the Mammalia. *Proc. Zool. Soc. London*, 36-49.