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Evolution (Extinctions)

Latest Oligocene–Early Miocene in Europe: Dark Period for booid snakes

Jean-Claude Rage^{a,*}, Zbigniew Szyndlar^b

^a UMR CNRS 5143, département « Histoire de la Terre », Muséum national d'histoire naturelle, CP 38,
57, rue Cuvier, 75231 Paris cedex 05, France

^b Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Sławkowska 17, 31-016 Kraków, Poland

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Abstract

The diversity of booid snakes strongly decreased during the Latest Oligocene (zones MP 29–30) and Early Miocene (zones MN 1–2, and perhaps MN 3) in Europe. Moreover, the few remaining taxa were all small and displayed fossorial trends. This crisis is referred to as the Dark Period of booid snakes. The outset of this event probably resulted from cooling and aridization that were prevailing during the Late Oligocene. The period ended when a warm and humid climate was restored; aside from direct effect, the latter change caused the arrival of immigrants that probably contributed to the elimination of the booids of the Dark Period. **To cite this article:** J.-C. Rage, Z. Szyndlar, C. R. Palevol 4 (2005).

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Résumé

Oligocène terminal–Miocène inférieur en Europe : l'énigme des serpents boïdes. En Europe, la diversité des serpents boïdes a fortement chuté pendant l'Oligocène terminal (zones MP 29–30) et le début du Miocène (MN 1–2, et peut-être MN 3). Les quelques boïdes qui subsistaient étaient petits et de tendances fouisseuses. Cette crise a été qualifiée de *Dark Period* des boïdes. Elle a probablement été déclenchée par l'aridification et le refroidissement qui se sont renforcés vers la fin de l'Oligocène. Cette période de crise s'est terminée avec le retour de l'humidité et de la chaleur ; en plus d'un effet direct, ces changements ont aussi entraîné l'arrivée d'immigrants, qui ont certainement contribué à l'élimination des boïdes de la *Dark Period*. **Pour citer cet article :** J.-C. Rage, Z. Szyndlar, C. R. Palevol 4 (2005).

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* Auteur correspondant.

E-mail address: jcraige@mnhn.fr (J.-C. Rage).

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Introduction

Les Booidea vivent actuellement dans les régions intertropicales essentiellement. En Europe, ce groupe n'est représenté que par *Eryx* (Boidae, Erycinae). Au Tertiaire, la situation était très différente, puisque les Booidea ont très largement dominé les faunes de serpents, y compris en Europe, jusqu'à la transition Miocène inférieur/Miocène moyen. Ils ont ensuite été remplacés par les Colubroidea en tant que formes dominantes.

Deux événements bien marqués ont touché les booides en Europe. Le premier est la 'Grande Coupure' (limite Éocène/Oligocène), qui a profondément affecté les faunes de squamates [8,10,21]. Le second est d'âge Oligocène terminal/Miocène inférieur ; il fait l'objet du présent article. Il a été observé en Europe occidentale et centrale, étant entendu que ce travail n'a pas pu être étendu à l'Europe orientale, en raison de l'absence de gisements.

Composition des faunes successives de Booidea en Europe

Les Booidea de l'Oligocène

Après la Grande Coupure (zone MP 21), les faunes de serpents sont très pauvres en Europe. Elles se sont progressivement enrichies et, de MP 25 à MP 28, les booides comprennent des Boidae (Boinae, Erycinae) et des Tropidophiidae. De grosses espèces sont alors présentes, la longueur de leur centrum vertébral (dimension utilisée comme référence) atteignant 7,3 mm chez *Bavarioboa crocheta* (Boinae). Mais, dans les deux dernières zones de l'Oligocène (MP 29 et MP 30), ne subsistent que de petits booides, dont la longueur du centrum atteint au plus 4,6 mm (Fig. 1). Les booides de ces deux zones sont l'éryciné *Bransateryx* et les tropidophiidés *Platyspondylia* et *Rottophis*. *Bransateryx* et *Platyspondylia* sont des survivants des niveaux plus anciens, alors que *Rottophis* n'est connu que dans un seul gisement.

Les Booidea du Miocène

Dans les deux premières zones du Miocène (MN 1 et MN 2), comme dans les deux dernières de l'Oligocène, seuls des booides de petite taille sont présents

(longueur du centrum inférieure à 5 mm ; Fig. 1). La diversité s'est encore réduite. Il ne reste que l'éryciné *Bransateryx* et surtout des formes indéterminées ; les tropidophiidés ont disparu.

La zone MN 3 pose un problème, car il est impossible d'établir si des formes de grande taille ont existé à cette période. Le grand pythoniné *Python euboicus* [15] vient d'un gisement grec qui pourrait être daté de MN 3, mais sans aucune certitude [21]. Par ailleurs, *Bavarioboa* (genre qui inclut des espèces de grande taille) est de retour, mais n'est représenté dans MN 3 que par une petite forme.

MN 4 se caractérise par la richesse et la diversité de sa faune de serpents. En ce qui concerne les herpétofaunes, ce renouvellement a été assez général et a aussi affecté les amphibiens anoures [14] et probablement les lézards. Les booides sont de nouveau diversifiés et comprennent des Boidae (Boinae, Pythoninae, Erycinae) et le boiné ou tropidophiidé *Falseryx*. Deux genres de grande taille, *Bavarioboa* (Boinae) et *Python* (Pythoninae) sont présents. La longueur du centrum atteint 11,1 mm chez *Python europaeus*.

MN 5 conserve de grands booides mais, à partir de MN 6, seules de petites formes subsistent ; ces dernières appartiennent uniquement aux érycinés, à l'exception possible de l'énigmatique *Falseryx*, qui est peut-être présent dans MN 7+8.

La Dark Period

La période MP 29–MN 2 (et peut-être MN 3) se caractérise donc par une diminution de la taille et une baisse de la diversité des booides ; ils sont alors représentés essentiellement par des érycinés. De plus, les faunes ne sont, ni riches (exceptée celle de Coderet ; Oligocène terminal), ni nombreuses. Le début du Miocène avait été qualifié de *Dark Period* des booides [21] ; nous étendons ici ce qualificatif à toute la période MP 29–MN 2 (MN 3 ?) ; nous y incluons donc la fin de l'Oligocène.

Les causes des changements

Le changement entre MP 28 (dont la faune peut être qualifiée de « normale ») et MP 29 (début de la *Dark Period*) est brutal. Seuls de petits booides, montrant tous des adaptations à la vie fouisseuse, ont survécu. Ce changement est certainement lié à l'aridification et

au refroidissement qui se sont développés pendant l'Oligocène et se sont accélérés vers la fin de la période [12,16,18]. Toutefois, les modifications climatiques ont certainement été plus ou moins progressives, alors que le changement de faune a été abrupt. Le changement entre MN 2 (MN 3 ?) et MN 4 est lui aussi très marqué. Une faune riche et diversifiée succède à une faune très pauvre, très peu diversifiée, et aucun booïde de la *Dark Period* n'a survécu. Ce changement résulte probablement du retour de l'humidité et du réchauffement du début du Miocène, ce dernier ayant atteint un maximum durant MN 4 [1,17]. Ces modifications climatiques ont probablement eu un effet direct sur les booïdes de la *Dark Period*, mais avec, en plus, l'établissement de la connexion terrestre entre l'Afrique et l'Eurasie ; elles ont aussi amené en Europe une vague d'immigrants, incluant des colubroïdes, qui a certainement contribué à l'élimination des derniers booïdes de la *Dark Period*. Pendant la *Dark Period*, divers serpents (dont les plus anciennes vipères) sont arrivés en Europe. Pourtant, bien que des niches écologiques se soient certainement trouvées vides, aucun booïde n'a participé à ces immigrations ; les causes qui ont empêché la pénétration des booïdes en Europe à cette époque restent inconnues.

Conclusion

Les faunes de booïdes de la période MP 29–MN 2 (MN 3 ?), ou *Dark Period*, se distinguent nettement des faunes précédentes et suivantes. Parmi les faunes du Tertiaire, elles se reconnaissent aisément. Il convient de noter qu'un phénomène similaire, et peut-être en partie contemporain, le 'Cricetid Vacuum', a touché les rongeurs [2]. Cependant, il a été de durée beaucoup plus courte que celui qui a affecté les booïdes, puisqu'il ne s'étend que sur la moitié supérieure de MN 3 [4]. Toutefois, en raison de la concomitance partielle de ces deux phénomènes, cette période de transition Oligocène/Miocène mérite une certaine attention.

1. Introduction

Today, booid snakes are comprised of the Boidae (about 20 genera), Xenopeltidae (1 genus), Loxocemidae (one genus), Tropidophiidae (four genera) and Bolyeriidae (two genera). They mainly inhabit tropical

areas; only the erylinae boids extend markedly out of this range (in Eurasia and North America). In Europe, only the genus *Eryx* (Erycinae, Boidae) represents the Booidea. It is restricted to the southeastern part of the continent [3,24].

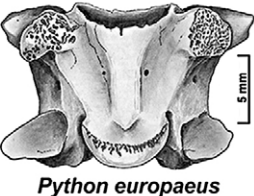









During the Cainozoic, the Booidea were the ruling forms within snakes up to the Early/Middle Miocene transition, whatever the continent may be [11]. They have been replaced, as dominant snakes, by the Colubroidea. Two marked events affected the group in Europe. The first event corresponds to the 'Grande Coupure', i.e. the Eocene/Oligocene transition, which deeply altered the faunas of most terrestrial vertebrates. Most of the European snakes died out at that time and they were replaced mainly by immigrants [8,10,21]. The 'Grande Coupure' resulted from a worldwide event, the effects of which were increased by palaeogeographic changes in Europe. The second event took place by Late Oligocene/Early Miocene times. Szyndlar and Rage [21] touched on this event, but did not develop its study. This event is the subject of the present article; it has been observed in western and central Europe, it being understood that contemporaneous faunas are unknown in Eastern Europe.

The biostratigraphic units used here are the zones MP (for the Palaeogene) and MN (for the Neogene). They are based on appearances, disappearances, and evolution of lineages of mammals.

2. Compositions of the successive faunas of booids in Europe

2.1. The Booidea from the Oligocene

After the Grande Coupure, the snake faunas of the beginning of the Oligocene (zone MP 21) are very poor. They include only undescribed non-erylinae booids of small size and perhaps the tropidophiid *Dunnophis*. After MP 21, immigrations (probably of Asiatic origin) and probably local evolution progressively increase the faunas. Among immigrants, are the Colubridae which first appear in Europe in MP 22. Apart from the Colubridae, the post-MP 21 Oligocene includes rare Aniliidae and Tropidophiidae, but mainly Boidae; the snake faunas are of Euro-Asiatic nature [8]; they are not as rich and diverse as those of the Eocene (which were of Euro-American origin). Up to MP 24 the size

	Ventral view of a typical vertebra	Centrum length of largest vertebra (in mm)
MN 5	 <i>Python europaeus</i>	10.8 (<i>Python europaeus</i>)
MN 4	 <i>Bavarioboa hermi</i>	11.1 (<i>Python europaeus</i>)
MN 3	 Boidae indet. (? <i>Eryx</i> sp.)	4.6 (<i>Bavarioboa</i> sp.)
MN 2	 Boidae indet. (? <i>Eryx</i> sp.)	4.4 (<i>Bransateryx vireti</i>)
MN 1	 <i>Bransateryx vireti</i>	4.7 (<i>Bransateryx vireti</i>)
MP 30	 <i>Bransateryx vireti</i>	4.6 (<i>Bransateryx vireti</i>)
MP 29	 <i>Bransateryx vireti</i>	3.6 (<i>Bransateryx vireti</i>)
MP 28	 <i>Bavarioboa crocheti</i>	7.3 (<i>Bavarioboa crocheti</i>)
MP 27	 <i>Bavarioboa</i> sp.	6.7 (<i>Bavarioboa</i> sp.)
MP 26	 <i>Bavarioboa bachensis</i>	>5.9 (<i>Bavarioboa bachensis</i>)

of all European booids is small (the centrum length of vertebrae, i.e. the reference measurement, is not over 5 mm). From MP 25 to MP 28, large booids are present in Europe. Most of them are assigned to the boine *Bavarioboa* [21]. In MP 25 and MP 26, the centrum length of the largest vertebrae approaches or exceeds 6 mm. In MP 28, it reaches 7.3 mm in *Bavarioboa crocheti*. But, in the last two zones of the Oligocene (MP 29 and MP 30), only small snakes occur. Non-erycine Boidae are no longer present, the Booidea being represented by only an erycine boid (*Bransateryx*), which is the predominant taxon, and by the tropidophiids *Platyspondylia* and *Rottophis*. In the largest vertebrae of booids from MP 29 and MP 30, the centrum length does not exceed 4.6 mm (Fig. 1).

Fig. 1. Variation of the size of vertebrae of Booidea from the Middle Oligocene to the Middle Miocene. Provenances: MP 26, Espeyrasse, France (USTL, ESP 601); MP 27, Ehrenstein 7, Germany (SMNS 57624–5); MP 28, Pech-du-Fraysse, France (MNHN, PFR 11041); MP 29, La Milloque, France (MNHN, uncatologued); MP 30, Coderet, France (ZZSiD, uncatologued); MN 1, Weisenau, Germany (SMNS, uncatologued); MN 2, Marcoin, France (MNHN, MRC 1); MN 3, Stubersheim 3, Germany (SMNS 57709–2); MN 4, Petersbuch 2, Germany (BSP, 1976 XXII 5859); MN 5, La Grive P&B, France (MNHN, LGA 34). (BSP: 'Bayerische Staatssammlung für Paläontologie und historische Geologie', Munich, Germany; MNHN: 'Muséum national d'histoire naturelle', Paris, France; SMNS: 'Staatliches Museum für Naturkunde', Stuttgart, Germany; USTL: 'université des sciences et techniques du Languedoc', Montpellier, France; ZZSiD: Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, Poland). Figures of the vertebrae from MP 26–28 and MN 2–5 after Szyndlar and Rage [21].

Variation de la taille des vertèbres des Booidea de l'Oligocène moyen au Miocène moyen. Provenances : MP 26, Espeyrasse, France (USTL, ESP 601) ; MP 27, Ehrenstein 7, Allemagne (SMNS 57624–5) ; MP 28, Pech-du-Fraysse, France (MNHN, PFR 11041) ; MP 29, La Milloque, France (MNHN, non numéroté) ; MP 30, Coderet, France (ZZSiD, non numéroté) ; MN 1, Weisenau, Allemagne (SMNS, non numéroté) ; MN 2, Marcoin, France (MNHN, MRC 1) ; MN 3, Stubersheim 3, Allemagne (SMNS 57709–2) ; MN 4, Petersbuch 2, Allemagne (BSP, 1976 XXII 5859) ; MN 5, La Grive P&B, France (MNHN, LGA 34). (BSP : Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Allemagne ; MNHN : Muséum national d'histoire naturelle, Paris, France ; SMNS : Staatliches Museum für Naturkunde, Stuttgart, Allemagne ; USTL : université des sciences et techniques du Languedoc, Montpellier, France ; ZZSiD : Instytut Systematyki i Ewolucji Zwierząt, Polska Akademia Nauk, Cracovie, Pologne). Figures des vertèbres de MP 26–28 et MN 2–5 d'après Szyndlar et Rage [21].

2.2. The Booidea from the Miocene

In the first two zones of the Miocene (MN 1 and MN 2), as in the last two zones of the Oligocene, only small snakes are present; the centrum length of booids does not reach 5 mm (Fig. 1). Moreover, the faunas are neither rich nor diverse; they are known only from France and Germany. In France, booids have been found at Paulhiac, Pyrimont (MN 1), Marcoin, and some localities of the area of Saint-Gérard-le-Puy (Poncenat, Chavroches, Montaigne-le-Blin) (MN 2). In Germany, only Weisenau (MN 1) and Ulm-Westtangente (MN 2) have produced Booidea [5,21]. These booids from MN 1 and MN 2 are represented by almost only trunk vertebrae that look like those of Erycinae, more specifically *Bransaterix*. Astonishingly, caudal vertebrae, i.e. the most reliable elements in Erycinae, have been found only at Paulhiac. Szyndlar and Rage [21] referred the booids from Paulhiac, Chavroches, Montaigne-le-Blin and 'Saint-Gérard-le-Puy' to *Bransaterix vireti* and Szyndlar and Böhme [18] assigned the form from Weisenau to the latter species. But, the absence of caudal vertebrae in these localities (except Paulhiac) casts doubts on the referral of these booids to the Erycinae because Szyndlar and Böhme [19] shown that erycine-like trunk vertebrae may be present in non-erycine Booidea. Consequently, *B. vireti* is identified at Paulhiac, but the booids of the other localities cannot be securely referred to this species and even to the Erycinae. The booids from Poncenat (unpublished) and Weisenau pose the same problem, although at Poncenat rare skull bones appear to support assignment to *Bransaterix* [9]. The booids from Marcoin and Ulm-Westtangente remain indeterminate [21]. Finally, Pyrimont yielded a single vertebra that cannot be identified within the Booidea (unpublished). But, whatever the precise taxonomic assignment of the Booidea from MN 1 and MN 2, it should be noted that they are small and not numerous.

The zone MN 3 represents a peculiar problem, because it is not possible to establish definitely whether large booids are present in this level. At Kimi (Island of Euboea, Greece) was found a boid described as *Python euboicus* by Roemer [15]. The age of the locality appears to be MN 3, but this cannot be definitely accepted [21]. The single specimen that represents *P. euboicus* is probably lost, but from the illustration and text it may be deduced that this snake was large

(centrum length over 10 mm [21]). On the other hand, *Bavarioboa*, a genus of generally large booids present in the Oligocene, is back in MN 3. But, from this zone, *Bavarioboa* is known only in the Czech locality Merkur-North (*Bavarioboa* sp. [7]), where it is represented by a rather small form whose centrum length does not reach 5 mm. Other booids from MN 3 are small indeterminate Boidae [21].

MN 4 is characterized by a rich and diverse fauna of snakes. The presence of *Bavarioboa* and *Python* in this zone marks the return of large booids in Europe. Several localities from MN 4 yielded *Bavarioboa hermi* (Petersbuch 2, Germany, and Dolnice, Czech Republic), *Bavarioboa* sp. and cf. *Bavarioboa* [21]. *Python europaeus* has been found only in France, at Béon 1 and at Vieux-Collonges (in fact, the age of the latter site is transitional between MN 4 and MN 5). In *B. hermi*, the centrum length reaches 6.8 mm, whereas it amounts to 11.1 mm in *P. europaeus*. Moreover, in an indeterminate booid from Ivancice (Czech Republic) this measurement reaches 6.8 mm. Aside from large forms, MN 4 produced small booids: erycine Boidae and the Boinae or Tropidophiidae *Falseryx*.

MN 5 retains large booids. The largest ones are *Bavarioboa* sp. from L'Isle d'Abeau (France) and *Python europaeus* from the old level of La Grive (France). In these two snakes, the centrum length reaches 6.6 mm and 10.8 mm respectively. Astonishingly, the presence of small booids from MN 5 cannot be confirmed. The 'old collections' of La Grive include the small erycine *Albaneryx depereti* that might come from the old level (MN 5) of the locality, but this stratigraphic provenance remains doubtful. *A. depereti* is the only possible small booid from MN 5.

After MN 5, large Booidea are no longer found in Europe. Only small species persist beyond the MN 5/MN 6 transition: the enigmatic *Falseryx* is perhaps present in MN 7+8 [21] and the Erycine have survived up to the present.

2.3. The Dark Period

The period MP 29–MN 2 (MN 3 ?) appears somewhat strange as far as booids are concerned. Szyndlar and Rage [21] termed 'Dark Period' the beginning of the Miocene (MN 1–MN 3). In fact, the end of the Oligocene (MP 29–MP 30) is part of this peculiar period. On the other hand, it remains uncertain as to whether

or not MN 3 represents the last zone of the Dark Period, the beginning of the revival of snakes in Europe, or a transitional period.

3. Discussion

3.1. Faunal changes

Localities bearing snakes from the Dark Period are not numerous, the snake fauna of each locality (except Coderet, see below) is neither rich nor diverse, and all booids are small. From MP 29 to MN 2, the faunas of booids are almost exclusively comprised of the erycine boid *Bransateryx*. The only non-erycine booids are the Tropidophiidae *Platyspondylia lepta* from the French localities Dieupentale (MP 29) and La Colombière (MP 30) and *Rottophis atavus* from Rott (MP 30; Germany) [21]. Whatever the booid taxon, from MP 29 to MN 2, the centrum length of the largest specimens is not over 5 mm. It should be added that, except *Vipera*, all non-booid snakes are also small.

Coderet (MP 30; France) appears to be somewhat dissonant among the localities from the Dark Period, because it has produced numerous specimens. However, as in the other localities, its fauna is not diverse; it includes hundreds of bones (nearly only vertebrae) referred to *Bransateryx vireti*, the only booid from the locality, and few (less than ten) vertebrae of *Coluber cadurci* (Colubridae). In other words, the composition of the snake fauna from Coderet is similar to that of the other localities of the Dark Period.

These assemblages of small booids from MP 29 to MN 2 are sandwiched between richer and more diverse faunas in which large forms are present.

Two of the identified taxa from the Dark Period (*Bransateryx vireti* and *Platyspondylia lepta*) are survivors from older Oligocene levels, whereas *Rottophis atavus* is known from a single locality. It should be noted that, aside from small size, the vertebrae of all booid taxa from the Dark Period show adaptation to fossorial life (*Bransateryx* [5]; *Platyspondylia* [13]; *Rottophis* [19]).

3.2. The factors of the faunal changes

The changes between MP 28, during which a 'normal' fauna inhabited Europe, and MP 29, i.e. the outset

of the Dark Period, is abrupt. The depauperate fauna of small snakes from MP 29 markedly contrasts with the rich and diverse assemblage from MP 28, which includes large species. It is worth noting that only small fossorial booids survived to the MP 28–MP 29 limit. This event appears to be connected to palaeoenvironmental changes. Aridification, initiated during the Eocene, increased throughout the Oligocene and the aridity was certainly pronounced by the Latest Oligocene, a period that was moreover relatively cold [12,16,18]. Aridification is supported by the predominance of *Bransateryx*; as living Old World erycines, this snake probably lived in desert-like environments. This is probably the cause that led to extinctions and/or withdrawals of several taxa and left only small and fossorial booids after MP 28. However, the climatic change was relatively gradual while the faunal change was abrupt.

From MP 29 to MN 2 (and MN 3 ?), the booid fauna did not evolve notably despite a climatic change at the beginning of the Miocene. At that time, a humid tropical to subtropical climate was restored. However, the tropidophiids that were rare in the Oligocene part of the Dark Period did not survive beyond the Oligocene–Miocene limit. Therefore, in the Miocene part of the Dark Period, only the erycine *Bransateryx* (and indeterminate forms) represented the Booidea. Although most niches were certainly free, no newcomer reached Europe and increased the booid assemblages (and no endemic evolution took place). Nevertheless, snakes were able to enter Europe, since vipers first appeared there in MN 1, probably coming from the east. The factor(s) that precluded the arrival of booids during the Dark Period cannot be determined.

The fauna from MN 3 (the composition of which cannot be accurately established) set aside, a marked change occurs between the faunas from MN 2 and MN 4. That of MN 2 is typical of the Dark Period, whereas the fauna from MN 4 displays a marked renewal. As far as snakes are concerned, the transition between MN 2 and MN 4 represents an important faunal change [6,22]; this event marks the end of the Dark Period. The booid fauna from MN 4 deeply differs from the preceding one because it does not include booids inherited from the Dark Period and because new forms invaded Europe at that time. The erycine *Bransateryx*, the only booid from the MN 1–MN 2 period, definitely died out before MN 3 [21]. In MN 4, erycine booids

were represented by the extant genus *Eryx* [23]. *Bavarioboa*, which withdrew from at least western and central Europe before MP 29, was back and frequent in MN 4. It should be noted that *Bavarioboa* re-appeared before MN 4, in a single locality (Mercur-North, MN 3), but it was represented there by a small form (*Bavarioboa* sp. [7]). Pythonine Boidae (*Python europaeus*) appeared in Western Europe at Béon 1 (Rage and Bailon, in progress). The small and enigmatic *Falseryx petersbuchi* (Boidae or Tropicophiidae?) completed the booid fauna.

This diversity of booids from MN 4 fits into the renewal that affected the whole fauna of snakes, but also anuran amphibians [14] and probably lizards. As far as snakes are concerned, in addition to the above booid newcomers, elapids and large vipers of the 'oriental group' of *Vipera* first appeared in Europe, while colubrids became largely diversified during MN 4 times. These newcomers eliminated the last booid (*Bran-sateryx*) that was present during the Dark Period.

As for the beginning of the Dark Period, this faunal event is probably connected to palaeoenvironmental changes. Humidity and heat were back by the beginning of the Miocene. The warming reached a maximum by the end of the Early Miocene [1], i.e. by MN 4 times [17]. The environmental changes certainly affected directly the last booids present during the Dark Period. But, in addition, the arrival in Europe of new snake taxa certainly contributed to the elimination of these booids. These newcomers probably reached Europe owing to the new conditions. Moreover, the terrestrial connection between Eurasia and Africa that was established during the Early Miocene might have been the cause of the arrival of part of the immigrants in Europe. However, the geographic origin(s) of the MN 4 invaders remain(s) unknown. It was only demonstrated that the elapid that was present at Vieux-Collonges (MN 4/5; France) is probably closely related to *Naja romani*, a member of the Asiatic assemblage of *Naja* [20]. But this does not rule out a possible African origin of part of the invaders.

MN 5, that is poorly documented, appears as a continuation of MN 4 since large representatives of *Bavarioboa* and *Python* were present. After MN 5, European booids have undergone a progressive decay. Apart from one non-erycine booid (*Falseryx*?) from MN 7+8, only erycines have been reported from post-MN 5 levels [21]. This has certainly resulted from both competition with colubroids and climatic degradation.

4. Conclusions

In western and central Europe, the depauperate faunas of small booids that occur from the zone MP 29 (Latest Oligocene) to MN 2 (or MN 3?) (Early Miocene) clearly contrast with older and younger assemblages (Fig. 1). This time interval is referred to as the Dark Period of booid snakes. Booid taxa from the Dark Period are not only small, but they show also trends towards fossorial life. Every booid fauna from that period is characteristic and readily recognizable.

The Dark Period was probably triggered by the aridization and cooling that took place during the Late Oligocene. The end of the Dark Period also resulted from a climatic event (restoration of humidity and warming). In addition to a direct effect on the fauna, the latter climatic change certainly acted indirectly on extinctions, since it favoured the arrival of a wave of immigrants that (probably largely) contributed to the elimination of the last representatives of the Dark Period. During the Dark Period some snake taxa entered Europe but, for unknown reasons, booids did not join these immigrants.

Finally, a parallel may be drawn between the Dark Period and the 'Cricetid Vacuum', an event that affected cricetid rodents. The Cricetid Vacuum is a time interval during which, in western and central Europe, the cricetid *Eucricetodon* was rare or absent, while eomyid rodents increased in number [2]. Its duration is markedly shorter than the Dark Period since it represents only the upper half of the zone MN 3, but it ended at the limit between MN 3 and MN 4 [4], i.e. probably at the same time as the Dark Period. Therefore, further comparisons between these two events might be of interest.

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