The nature of the fossil record of Neogene insectivores*

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ABSTRACT: The Working-group on Insectivores from the Neogene of Eurasia (WINE) recently published an overview of the fossil record of insectivores from various European countries. The data thus gathered gives a good impression of the Neogene fossil record of this group. Although most localities are known from Spain, the Central European record has been studied in more detail. The lowermost and late Miocene are as yet relatively poorly documented, particularly in Central Europe. Throughout the Neogene the Central European record is geographically biased, most of our knowledge for a particular timeframe coming from one particular area. Overall the documentation of the fossil record appears to be adequate. Countries for which the fossil record has not been recorded in the WINE-project are, however, needed to complete the picture, providing a challenge for future work.
Key-words: *Mammalia, insectivora, Neogene, Eurasia.*

ΠΕΡΙΛΗΨΗ: Η ομάδα εργασίας στα εντομοφάγα από το Νεογενές της Ευρασίας (WINE) πρόσφατα δημοσίευσε το απολιθωμένο αρχείο των εντομοφάγων από διάφορες Ευρωπαϊκές χώρες. Οι πληροφορίες που συλλέχθηκαν δίνουν μια καλή εικόνα της ομάδας αυτής στο Νεογενές. Αν και οι περισσότερες θέσεις είναι γνωστές από την Ισπανία, είναι η Κεντρική Ευρώπη που έχει μελετηθεί με λεπτομέρεια.
Λέξεις-κλειδιά: *Mammalia, εντομοφάγα, Νεογενές, Ευρασία.*

INTRODUCTION

Insectivores (a mammalian group known under several different order names: Insectivora, Lipotyphla or Eulipotyphla) are an integral part of small mammal associations in the fossil record. Yet, as a result of historical developments and caused by their superficial uniformity, insectivores have always been less well studied than rodents (order Rodentia). As a result, the science of insectivore morphology, systematics and evolution is not nearly as developed as is the case with rodents or several groups of larger mammals. An RCMNS (Regional Committee on Mediterranean Neogene Stratigraphy) working group on mammal zonation concluded as late as 1992 that the Insectivora were insufficiently known to be included in stratigraphical schemes (DE BRUIJN *et al*., 1992). In spite of a tremendous amount of work done to clarify the taxonomy of the insectivores, and the description of dozens of new species, about ten years later the insectivores still held the reputation of being relatively unknown. Thus, even within the recently terminated EEDEN (Environments and Ecosystem Dynamics of the European Neogene) program, studies on small mammals still focused on rodents, mostly ignoring the insectivores.

We felt uncomfortable about this situation, and in November 2002 we started WINE: an acronym for Working-group on Insectivores from the Neogene of Eurasia (VAN DEN HOEK OSTENDE *et al*., 2005b). Our principal goal was to show the adequacy of the fossil record of insectivores, and to show its potential usefulness in biostratigraphical studies and for making palaeoenvironmental reconstructions.

The first WINE meeting (and the only one so far, as most of the work is efficiently done through email contacts) instigated and organized by Constantin Doukas, took place in November 2002 in Frankfurt am Main, Germany, and was hosted by the Forschungsinstitut und Naturmuseum Senckenberg. Participants, in addition to the three authors of this paper, were: Gerhard Storch (D), Reinhard Ziegler (D), Valentin Nesin (U), Oldřich Fejfar (CZ), Burkart Engesser (CH), Marc Furio (E), Hans De Bruijn (NL), and Assi Antonarakou (GR) acted as secretary. It was decided to start a common effort in order to assemble all data so far available on Neogene insectivores. As a result, an overview appeared recently on the fossil record of insectivores from Eurasia (VAN DEN HOEK OSTENDE *et al*., 2005a). This publication, the first in a planned series of two or three such volumes, is a listing of no less than 295 pages, with data from twelve different countries: Austria, Bulgaria, China, Czech and Slovak Republics, Germany, Greece, the Netherlands,

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Fig. 1. The first WINE meeting, November 2002. Left to right: J. Reumer, O. Fejfar, B. Engesser, V. Nesin, H. De Bruijn, A. Antonarakou, C. Doukas, L. v. d. Hoek Ostende, G. Storch, R. Ziegler. M. Furio took the photograph.

Poland, Romania, Spain, and Switzerland. Data from a total of 511 fossil mammal localities are included. However, it is directly clear that the total listing is still incomplete, as several important countries are missing (e.g. France, Hungary, Italy, Turkey, Kazakhstan, and Pakistan). Therefore, the volume was designated as being part 1, and WINE intends to produce a second volume that will fill in the gaps.

ADEQUACY OF OUR RECORDS

The data set assembled in the WINE project can be seen as a test case for how well the fossil record of small mammals actually is. Questions about the adequacy of the fossil record for mammals are most easily answered by pointing out the inadequacy. Anyone familiar with the Mesozoic record of the class will admit that it is patchy. And as is the case in practically every palaeontological discipline, the fossil mammal record is strongly biased towards Europe and North America, these being the continents with the longest history in natural sciences and the highest density of active researchers. Yet, few questions are usually raised about the adequacy - or better: the quality - of the fossil record on these continents. Since it is used in the reconstruction of ecosystems of the past (as has been done in the EEDEN program), it is of the utmost importance to know the quality of the record. Without knowing how good our basic dataset is, we cannot make a reasonable assessment on how good our interpretations based on these data are.

Before answering, we have to realize that we do not in fact study the whole fossil record itself. For most taxonomical groups there are simply too many specimens spread out over too many collections for one person to have seen them all. So, if we study any particular taxon, most of our knowledge will not come from the fossils themselves, but from descriptions in the literature. This implies that we do not only depend upon the quality of the fossil record, but also on the quality of the published record.

A third factor to consider is what can be called the quality of the readership. We need to know for whom we intend our representation of the fossil record. Specialists in any taxon may experience literature to be sufficient, whereas a layman (including specialists in other taxa) would find it highly confusing. Thus, paleontologists familiar with subsequent revisions will not mind the use of different names for the same taxon, as they know what is implied. An example: whether the Turolian desmans from Europe are listed under the genus names *Dibolia*, *Ruemkelia* or *Archaeodesmana* does not make a difference, since the specialist knows they represent one and the same taxon. But those not familiar with talpid classification will surely recognize three different genera in these names.

We intend to work on our WINE project for the sake of showing the adequacy of the fossil record of insectivores. This task we do not perform for ourselves, but for a more general readership of paleontologists. Hence, the need was felt to use a classification that was as consistent as possible with the current state of our knowledge. One of the main goals of the EEDEN program was the in-

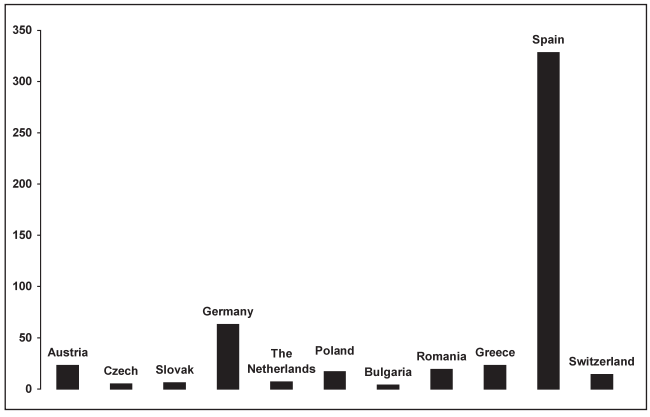

Fig. 2. Histogram of the number of localities in European countries (Eurasia minus China).

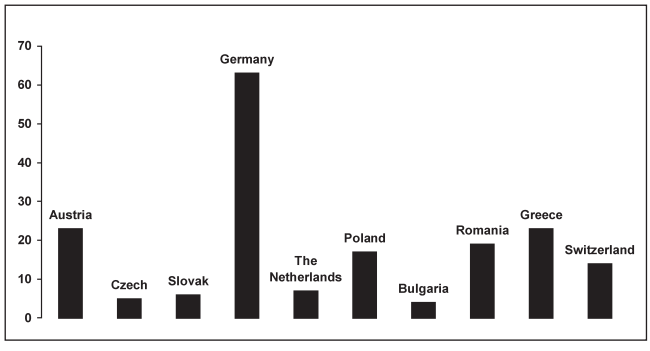

Fig. 3. Histogram of the number of European localities minus Spain.

tegration of data from various disciplines. In order to do so, it is vital that specialists present their data clearly. Simply gathering data from literature to build an overview of the fossil record is not enough. It might cause a mingle of redundant and new names, and it may even include misidentifications long since put straight. We thus considered it our task to make sure that the fossil record is presented consistently.

This sometimes required a decision. If the authors of the various contributions did not reach unanimity about some taxonomical problem, the help of an umpire was needed. For this task we selected Dr. Burkart Engesser of the Naturhistorisches Museum in Basel, Switzerland, not so much for the reason of the famous Swiss neutrality, but for his great knowledge of all groups covered in our study. One example of this is the ongoing debate on the systematic status of the shrews belonging to the Heterosorici(d/n)ae VIRET & ZAPFE, 1951. This group was coined as a subfamily of shrews by REPENNING (1967), hence Heterosoricinae. REUMER (1987, 1998) raised them to the family rank (Heterosoricidae), basing himself on the different masticatory musculature and the presence of a zygomatic arch. This was followed by, e.g. VAN DEN HOEK OSTENDE (2003) and RZEBIK-KOWALSKA (1998), but it was not accepted by STORCH *et al*. (1998) who retained the subfamily status of the taxon. For the framework of our WINE project, we thought it more important to stick to uniformity than to hold on to our own opinions. Burkart Engesser then decided that for the purpose of these WINE volumes the taxon should be referred to as a subfamily, which is why we consistently use the name Heterosoricinae even though some of us do not agree with that view.

RESULTS

Within the context of the WINE project, we have so far assembled data from 511 localities in 12 Eurasian countries (Austria, Bulgaria, China, Czech and Slowak Republics, Germany, Greece, the Netherlands, Poland, Romania, Spain, and Switzerland). Here, we will try to make an assessment on the nature and on the adequacy of the fossil record of the insectivores as it is so far published. All countries so far studied are from Europe, except for China (QIU & STORCH, 2005) which is situated at the other extreme of the Eurasian continent and which is only fragmentarily known. Thus, for the purpose of this study we will concentrate on the better-known European record, and leave out the Chinese faunas. In addition, stratigraphic and faunistic correlations across Eurasia (i.e., between Europe and China) are still very tentative, which provides a problem in itself.

GEOGRAPHICAL DISTRIBUTION

The most apparent bias in the fossil record becomes clear when we look at the number of localities per country (Fig. 2). The contribution of Spain is by far the largest, consisting of 64 % of the total record. Of the remaining countries, Germany has the largest record with 12 % of the localities. If we do not take the Spanish record to account, the German record makes up over one third of the remaining countries, the contribution of the others varying between 4 % and 13 % (Fig. 3). Although the Spanish record is quantitatively the best (that is, has the majority of localities), the amount of taxonomic work done in Spain is far less than in countries such as Germany or Poland.

Based on the published WINE-list, an estimate has been made on how well-documented the various assemblages are. Only about 12 % of the Spanish record is well documented, *versus* 83 % in the remaining assemblages. This large difference has various causes. First, because there are so many possible localities in Spain, sampling does not concentrate on one particular locality, but rather on a number of localities within a section. Thus, sample sizes are often smaller than in other European faunas. Secondly, the insectivore assemblages in Spain also seem to constitute a lower percentage of the total small mammal assemblage, which mainly consists of a plethora of Rodentia. Many Spanish insectivore assemblages consist of a few dental elements only. Thirdly, so far only few

specialist papers have appeared on Spanish insectivores, and more often than not these papers focused on particular taxa: e.g. Desmaninae (RÜMKE, 1985); *Desmanodon* (VAN DEN HOEK OSTENDE, 1997); *Galerix* (VAN DEN HOEK OSTENDE & DOUKAS, 2003); Anousoricini (VAN DAM, 2004).

Only a few papers have been published on insectivore assemblages as a whole (e.g. DE JONG [1988] on the Late Aragonian from the Daroca-Calamocha area, and VAN DEN HOEK OSTENDE [2003] on the insectivores from the Ramblian type section). This is in sharp contrast to Central Europe, where the insectivores from Southern Germany and Austria were published in a considerable series of papers by ZIEGLER (e.g. 1985, 1989, 1990a, 1990b, 1994, 2000, 2003a, 2003b, 2005), and where the Polish insectivore assemblages were described by RZEBIK-KOWALSKA (1971, 1975, 1976, 1981, 1989, 1990a, 1990b, 1991, 1993, 1994a, 1994b, 1996).

STRATIGRAPHICAL COVERAGE

Fig. 4 shows the number of localities in the list per MN zone. The Spanish and Central European record is plotted separately. As can be seen, the record outside of Spain is relatively constant in comparison to the Spanish situation. Most MN zones are represented by 10-20 non-Spanish localities. The earliest Miocene (MN 1-3) is represented by less than 10 localities, as is the Vallesian (MN 9-10) and the Turolian (MN 11-13). The latter stage in particular is remarkably poorly represented, with a total of only twelve localities. Peaks in the Spanish record represent the Spanish-Dutch collaboration projects in the Aragonian and Ramblian typesections (e.g. FREUDENTHAL, 1988; VAN DER MEULEN *et al*., 2003) and the Spanish-French and Spanish-Dutch Turolian projects in the vicinity of Teruel (e.g. VAN DAM *et al*., 2001). These peaks are therefore largely an artifact of human effort.

Figure 5 shows the relative number of localities in various geographic areas in Central and South-eastern Europe in relation to the MN zonation. The areas are rather grossly defined. The WINE-list itself was divided in countries; no discrimination is made between smaller (e.g. the Netherlands, Switzerland, Austria) or larger countries (Spain, Germany). Here we have separated Germany in a southern part, in which mostly the localities from the Alpine molasse basin are represented, and a northern part, which lies in the realm of the North Sea basin. To these two groupings we have added the Swiss and Dutch localities, respectively. Furthermore, the Austrian, Slovak, Czech and Polish data is combined, as is the data from the countries in South-eastern Europe (Bulgaria, Romania, and Greece). The groupings were chosen as a gross representation of various sedimentary realms. As fissure-fillings are technically not a part of sedimentary basins, they have been included as a separate grouping, irrespective of their geographical position.

Fig. 5 clearly shows that the fossil record is not evenly distributed over the various realms in time. The earliest

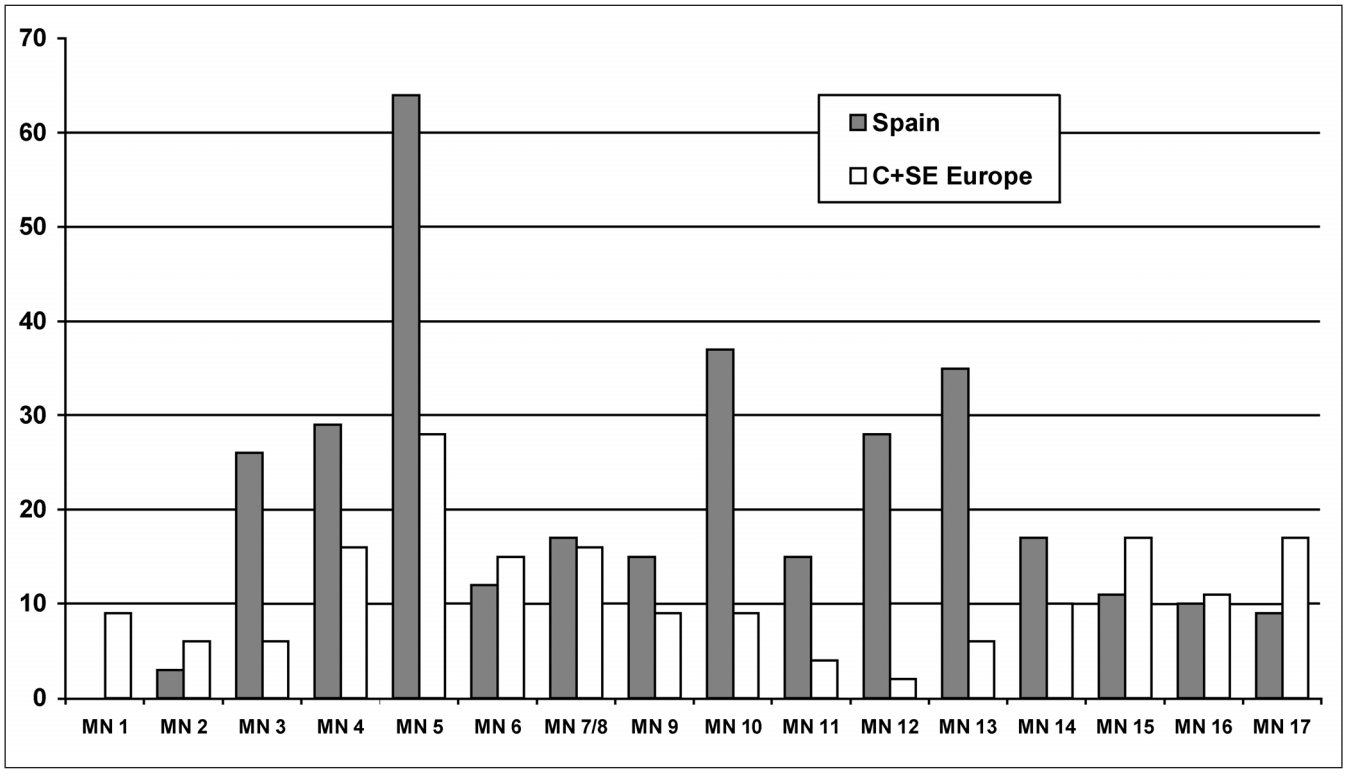

Fig. 4. Number of localities (in Spain and in other European countries) per MN unit.

Miocene (MN 1 + 2) is represented only in the Swiss-S. German localities, which continue to provide the majority of the data up to MN 7/8. The fissure-fillings in this time range are also mainly from Southern Germany, the only exception being two MN 6 fissures from the Slovak Republic. Thus, the German contribution is even larger than is directly apparent from Fig. 5. In the late Middle/early Late Miocene, however, very few localities are found in this realm. The listing of localities in MN 10 and MN 11 is even somewhat artificial, since these localities are from Rheinland-Pfalz, considerably north of the other localities included in this realm.

The Central European record is largely confined from MN 3 to MN 11, its relative importance increasing as that of the western realm decreases. The only two younger non-karstic localities from Central Europe are the loess deposits from Stranzendorf (Austria) and a maar infill at Hajnačka (Slovak Republic). Still, the Central European insectivore record for the Pliocene is rich. Most of the European fissure fillings and cave deposits from that period are found in that area, in particular in the Wielan Upland (Poland) and at Deutsch-Altenburg (Austria). As Hungary was not yet taken into account, the fissures from that country with classical localities such as Villány, Beremend and Csarnota have now not been considered, although these too yielded a rich and well-documented record for insectivores (e.g. REUMER, 1984).

The Southeast European record starts in MN 4. The oldest localities are from Greece (Aliveri) and probably represent a landmass between the Tethys to the south and the Paratethys to the north. Thus they may represent a somewhat different sedimentary realm than the younger localities. The Southeast European localities become increasingly important in the Late Miocene, although we have to bear in mind that, in general, the Turolian is a relatively unknown period, the record for MN 12 and MN 13 being restricted to a number of Greek localities. The Pliocene record consists, apart from the Central European

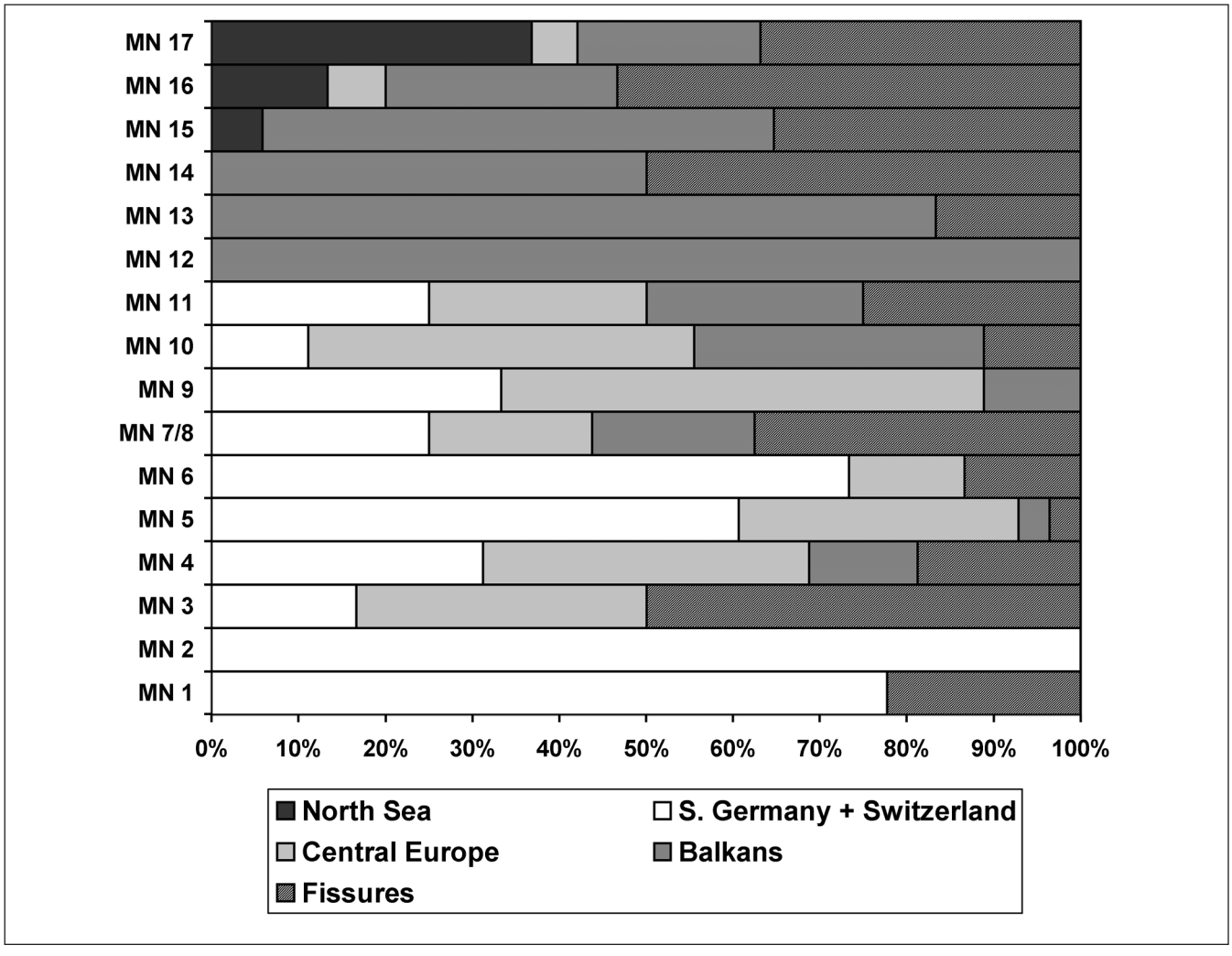

Fig. 5. Provenance of the Neogene Insectivores per area and per MN unit. 'Fissures' combines all karstic localites, grouped irrespective of their provenance area. 'North Sea' combines northern German localities and the Netherlands. 'Central Europe' combines Austria, the Czech and Slovak Republics and Poland. 'Balkans' combines Greece, Romania and Bulgaria.

fissures, mainly of Southeast European localities, such as those from the Ptolemais lignite fields in Greece and the Dranic Basin in Romania. To these are added the localities from the North Sea Basin in the Late Pliocene. The importance of this new basin is somewhat exaggerated in Fig. 5, as it also includes boreholes with a single find only. Nevertheless, it is clear that continental deposits are starting to form in that area, which from then on becomes one of the major areas for the European Pleistocene fossil record.

CONCLUSIONS

As we pointed out earlier, there are various ways in which one can define the adequacy of the fossil record. As the WINE project started of more or less as an off-shoot of the EEDEN program, the main question lies if the end result is sufficient to serve the needs of that program, i.e., whether the insectivore record is sufficiently known to help in the reconstructions of Neogene environments in Europe.

From the sheer number of data, it is clear that the WINE project provided a good overall coverage of the European fossil record of insectivores, even though important countries like France, Turkey, Hungary and Italy are as yet absent from the listings. More important than the quantity, however, is that for the first time the insectivore record is presented using a consistent classification. In terms of number of localities, Spain is by far the largest contributor. However, the Iberian insectivore record has not been studied in the same detail as e.g. the German and Austrian record, and the taxonomy of many Spanish faunas still needs to be elaborated. The earliest Miocene (MN 1-2) is poorly represented in the present list. Except for three MN 2 localities from Spain, it only contains data from the Swiss and German molasse localities. The Turolian (MN 11-13) is well represented in Spain only, but not so in the rest of Europe.

For the reconstruction of he Neogene environments in Europe it is particularly interesting to make comparisons between different areas. This way the position of the various vegetational and climatic zones can be reconstructed. The dense Spanish record certainly also allows palaeoenvironmental comparisons between the various continental basins of that country. But the possibilities of comparisons of areas across Europe is somewhat hampered, as the record for a certain period is usually restricted in its geographic range. The lower part of the Miocene is, e.g. primarily known from the western Alpine molasse basin and the fissure fillings of the adjacent Franconian Alb. The early Late Miocene in Central Europe is mainly known from Austrian localities, whereas the Early Pliocene is best represented in South eastern Europe and in the karstic localities from Poland. Of course, for all of these time slices comparisons can be made between the Spanish record and that from Central Europe, which certainly can yield interesting results (e.g. VAN DAM, 2004). However, to ensure such comparisons are useful, a lot of taxonomic work remains to be done on the Iberian faunas.

Thus, the WINE-project has not only yielded a number of promising results, but it also made clear which are the tasks at hand to improve the quality of the published fossil record. Of course, the areas in Eurasia for which the fossil insectivores have not yet been recorded form the major gap in our knowledge at the present. As such, they are the main focus for the workgroup. It is a challenge to see if, and how, the missing countries will give an even better picture of the record. And than, of course, we shall see how this 'complete' fossil record of the insectivores can tell us more about the environmental changes on the European continent over the last 20 million years.

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