

# The fossil record of deinotheres in the Jura Mountains and the specific diversity of European deinotheriids

**Lionel Hautier** based on peer reviews by **Martin Pickford** and 1 anonymous reviewer

Fanny Gagliardi, Olivier Maridet, Damien Becker (2021) The record of Deinotheriidae from the Miocene of the Swiss Jura Mountains (Jura Canton, Switzerland). Missing preprint\_server, ver. 4, peer-reviewed and recommended by Peer Community in Paleontology. https://doi.org/10.1101/2020.08.10.244061

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Proboscideans belong to the Afrotheria, a superorder of mammals with an African origin, which was recently recognized based on molecular data (see review in Asher et al., 2009). The fossil record of Proboscidea is well documented and shows that an important part of their evolutionary history took place in Africa, with their representatives inhabiting the continent for at least 60 million years (Gheerbrant, 2009). However, proboscideans also proved to be great travellers, and a flourishing diversity of proboscidean forms colonized most of the continents of the planet, including Europe, from where they have since completely disappeared. Nowadays, Loxodonta africana, L. cyclotis, and Elephas maximus are flagship species of the African and Asian faunas, but they only represent a minor part of the modern mammalian diversity. In contrast, their ancient relatives seemed to be relatively abundant in past ecosystems (Sanders et al., 2010), which raised a number of interesting, but challenging, questions relative to the structure and evolution of ancient megaherbivore communities (Calandra et al., 2008).

Among proboscideans, deinotheres represent a special case. Their morphology clearly departs from that of other groups, notably in displaying distinctive downward curving lower tusks. Compared to their successful sister group the elephantiforms (i.e., all elephant-like proboscideans closely related to modern elephants; sensu Tassy, 1994), deinotheriids are often regarded as the poor sibling of the Proboscidea for showing a relatively low specific diversity and displaying a reduced morphological variability. In fact, many grey areas still exist regarding the evolution of this unique family.

In their article, Gagliardi et al. (2021) revised the material of deinotheres recovered in the Miocene sands of the Swiss Jura Mountains. They described for the first time the material attributed to Prodeinotherium

bavaricum and Deinotherium giganteum from the Delémont valley, and reported the presence of a third species, Deinotherium levius, from the locality of Charmoille in Ajoie. Based on comparisons made on specimens recovered from middle to the late Miocene localities, the authors discussed the potential link between the mode and tempo of deinothere dispersions and the evolution environmental and climatic conditions in Western and Eastern Europe during the Miocene. They also considered the evolution of ecological specializations in the group, especially with regard to size increase.

Gagliardi et al. (2021) proposed to follow the two genera/five species concept (i.e., P. cuvieri, P. bavaricum, D. levius, D. giganteum, and D. proavum), which implies the co-existence of several deinothere species in Europe. The latter hypothesis contrasts with the recognition of a single African Deinotherium species (i.e., D. bozasi) in deposits dated from the late Miocene to the early Pleistocene (Sanders et al., 2010). Such a co-existence of European species was and still is debated; it was here questioned by both reviewers. However, as acknowledged by the authors, only an extensive revision of the material of all recognized species, in Europe and worldwide, will enable to shed more light on the deinothere morphological variability and specific diversity. There is no doubt that such a revision would have a profound impact on our view of the evolution of this enigmatic group.

### References:

Asher, R. J., Bennett, N., & Lehmann, T. (2009). The new framework for understanding placental mammal evolution. BioEssays, 31(8), 853–864. doi: 10.1002/bies.200900053

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Gagliardi, F., Maridet, O., & Becker, D. (2021). The record of Deinotheriidae from the Miocene of the Swiss Jura Mountains (Jura Canton, Switzerland). BioRxiv, 244061, ver. 4 peer-reviewed by PCI Paleo. doi: 10.1101/2020.08.10.244061

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### Reviews

### **Evaluation round #2**

DOI or URL of the preprint: 10.1101/2020.08.10.244061

Version of the preprint: 2

### Authors' reply, 19 March 2021

Answers to the second review:

- 1) "D. giganteum should be referred to D. cf. giganteum because it is based on a single tooth". We have to disagree, more teeth would be better to secure the species-level identification; however, the tooth perfectly fits D. giganteum size and morphology so the use "cf." would not be appropriate. We have slightly modified the text to avoid the confusion.
- 2) We have homogenized the periods spelling, but as opposed to the reviewer's suggestion, without capital letters for early, middle, late to follow the spelling used in Gradstein et al. 2012.
- 3) The figure 6 has been modified to compare the teeth sizes with other well-dated European localities which have yielded deinotheres. Additionally a new figure has been added (Fig. 7) for the comparison of the deciduous premolar only. The discussions on systematics have been updated to include the information provided by these two figures. The manuscript contains now 11 figures.
- 4) The synonymy between P. bavaricum and P. hungaricum is now explained and taken in account, and the appendix and figures 10 and 11 have been corrected accordingly.
  - 5) Other minor corrections proposed by the reviewer have been made accordingly. **Download tracked changes file**

# Decision by Lionel Hautier, posted 17 February 2021

## Decision on your preprint: the preprint merits a revision

Dear authors,

I decided to send again your manuscript to one of the reviewers who recommended major revisions before publishing. Also (s)he acknowledged that this new version is much improved, (s)he also pointed out several issues regarding molar measurements that still need to be carefully considered (see below and the attached file). Until this is done, the manuscript is not ready to be recommended by PCI Paleo.

Kind regards,

Lionel Hautier **Download recommender's annotations** 

### Reviewed by anonymous reviewer 1, 12 February 2021

The authors have done a good work and improved significantly the manuscript in the revised version. Most of the issues raised for the original version were corrected/applied. However, I still recommend to add length-width diagrams for each tooth position, so that the specimens described are plotted and compared with other localities. The diagrams that the authors have added (Fig. 6) from the previous version are not informative. I suggest to include only well-dated localities with secure species identification (see for example datasets in Böhme et al., 2012 and Göhlich, 2020). Dental dimensions play an important role in the evolutionary history of deinotheres and contribute significantly for taxonomic determinations, as well as for biostratigraphic conclusions, and therefore this addition is deemed crucial. This is indeed important because some specimens here attributed to D. levius fit well also within the size variation known for D. giganteum. Accordingly, the single m2 attributed here to D. giganteum has similar dimensions to specimens of D. levius from Hinterauerbach in Germany (Gräf, 1957). All these affect of course the biostratigraphic range provided by the authors in Figure 9. Several other corrections and suggestions for improvement are noted in the attached pdf file.

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### **Evaluation round #1**

DOI or URL of the preprint: 10.1101/2020.08.10.244061

### Authors' reply, 04 February 2021

Answer to reviewers comments:

Concerning the validity of genera and species There are indeed different concepts, different combination of systematic points of view including one or two genera and from two to five species; as an example, the points of views of the two reviewers differ on that matter. As explained in the text we consider the morphological differences between Prodeinotherium and Deinotherium as reliable. Without general revision of this group we consider that the five species P. cuvieri, P. bavaricum, D. levius, D. giganteum and D. proavum are valid. We consequently made clearer now that we follow the 2 genera / 5 species concept.

Terminology One the reviewer suggests changing the term 'labial' by 'buccal' throughout the manuscript. As far as cheek teeth are concerned both terms are really equivalent, so such a change is not relevant. Additionally, the term 'labial' has often been used in previous publication focusing on dinotheres; we consequently didn't follow this recommendation.

Concerning the co-existence of species Both reviewers question the co-existence of Deinotherids species in Europe. At local scale, we agree that the occurrence of more than one species needs to be supported by a study of morphological and size variability, which is usually not the case. The co-existences within a same locality are rare in the literature and possibly doubtful (although not necessarily wrong). At European scale, some publications have proposed that co-existences of several species are also not possible (e.g. Pickford & Pourabrishami 2013; Konidaris et al. 2014). However, these studies are not based on a revised systematic of the family, and question or disregard any occurrence that doesn't fit this hypothesis. We disagree with this point of view and, based on the most recent systematic studies, we have simplified our dataset and deleted all occurrences that are not based on a solid systematic work. However, there are still contemporaneous localities where identified specimens can be referred to different species (i.e. fit the diagnosis and size range of different species). At this point, and unless a revision of the family proves otherwise, we have to follow the evidences and accept that different species can co-exist at European scale.

Concerning the age of the localities of the studied specimens Although some specimens included in our study have been discovered a long time ago, the origin and age of the sediment that yielded them is well established. As explained in detail in the text, the Bois de Raube Formation (OSM; Upper freshwater molasse) is subdivided into three members differing by a markedly different heavy mineral spectrum and pebble content: a basal Montchaibeux Member (Origin of the Montchaibeux specimens), a middle conglomeratic Bois de Raube Member (Origin of the Bois de Raube specimens) and an upper Ajoie Member (Origin of the Charmoille specimens). The succession and ages of these sedimentary members are well established thanks to recent biochronologic revisions (see Kälin 1997, Choffat & Becker 2017 and Prieto et al. 2017).

Concerning the dataset and the distribution of species We have simplified the dataset, deleted all the occurrences which are not based on a systematic study and deleted all co-occurrences within a same locality. Additionally, identifications which were erroneous based on the published descriptions and measurements have been corrected (new identification is indicated following the 5 species concept). The localities of the dataset of which the age was uncertain have also been removed. As a result, fewer occurrences are included in the last figure. We have also corrected the dataset to insure that all occurrences fit the 5-species concept and void mixing with other systematic concepts. Nonetheless, the results and conclusions remains the same showing the progressive change in the geographical distribution of the family through time.

Other comments: - We have added a diagram to illustrate the size differences between the different populations included in our study; - We have included more references according to the reviewer suggestions; - All other minor modifications in text and figures have been done according to reviewers' comments. This included a correction of the English according to reviewers' suggestion.

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### Decision by Lionel Hautier, posted 19 August 2020

### Recommender comments on Gagliardi et al. PCI-Paleontology by Lionel Hautier

Dear authors.

We have now received two reviews of your manuscript entitled "The record of Deinotheriidae from the Miocene of the Swiss Jura Mountains (Jura Canton, Switzerland)". The reviewers pointed out that your paper contains interesting material, but raised some critical points and presented substantial suggestions how to further improve the manuscript. Both reviewers questioned the co-existence of European deinothere species. They raised important issues regarding specimen stratigraphic positions and species biostratigraphic ranges. They also carefully discussed the taxonomical views adopted throughout the manuscript. I concur with the reviewers that the English style should be improved.

The comments of the two referees are below. Annoted pdfs (Reviewer1 and 2) are also attached to this decision letter. When submitting your revision, please include a rebuttal letter which indicates in details the changes you have made. Also, indicate which of the suggested changes, if any, you have elected not to make and your reasons.

Kind regards,

Lionel Hautier PCI Paleo recommender

### Reviewed by Martin Pickford, 18 August 2020

I strongly doubt the co-existence of two or more species of deinothere in Europe at any one time. Some of the records published are based on misidentified deciduous teeth, or are based on a mis-understanding of the range of metric variation of the various species. All the sites that are supposed to have yielded two species have yielded only one or two teeth (and there are very few of these sites, in fact only one place in France which is doubtful) and the Deinotheriensande which yielded many specimens (but which is now known to span MN 4 - MN 11). Once a decent sample is found at a site, all the specimens belong to one species.

Also, the characters supposed to differentiate *Prodeinotherium* from *Deinotherium* seem to me not to be constant. I've seen a mandible in which the left side would be classified as a different genus from the right side.

Apart from these comments, the paper is interesting, but it needs alot of effort on the English before it is formally published.

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### Reviewed by anonymous reviewer 1, 18 August 2020

The preprint of Gagliardi et al. is an interesting contribution on the deinotheriid remains (attributed to *Prodeinotherium bavaricum*, *Deinotherium levius* and *D. giganteum*) from several localities of Switzerland, ranging from the late early to the early late Miocene. The specimens are scientifically treated following the standard methodology and the manuscript is well-structured. However, I made several corrections and suggestions for improvement directly in the mansucript (attached pdf file). My major points are the following:

- The authors follow the 5 species concept of European deinotheres (*Prodeinotherum cuvieri*, *P. bavaricum*, *Deinotherium levius*, *D. giganteum*, *D. proavum*). However, when comparing their specimens with published ones, as well as in the discussion and in the list given in the Appendix, the authors do not revise accordingly the older taxonomical view(s), i.e. the 2 species concept (*P. bavaricum-D. giganteum*) usually adopted until recently or even until now. This leads to the mixing of the 2, 4 (without *D. levius*) and 5 species concept, particularly evident in Figure 8, but also in the text (e.g., co-occurrence of 3 deinothere species, or that *D. giganteum* survived until the end of the late Miocene).
- *Prodeinotherium* is not known from the late Miocene. Older publications, which note the presence of *P. bavaricum* during the Vallesian are mainly based on its occurrence in the Dinotheriensande (Eppelsheim

Formation) of the Mainz Basin in Germany. This Fm was generally considered to be of Vallesian age, but see Böhme et al. (2012) and Pickford and Pourabrishami (2013).

- Because dental dimensions play an important role in the evolutionary history of deinotheres and contribute significantly for taxonomic determinations, as well as for biostratigraphic conclusions, I recommend the authors to add length-width diagrams for each tooth position, so that the specimens described are plotted and compared. I suggest to include only well-dated localities with secure species identification (see for example datasets in Böhme et al., 2012 and Göhlich, 2020) in order to avoid the mixing of the 2 species concept, which will result to wrong interpretations or complicate matters.
- I wonder if the stratigraphic positions of several specimens described is secure, as at least some of them concern old discoveries. To be more explicit, the correlation of the Bois de Raube specimen to the middle Miocene (MN6-7/8 in Table 5) and of the Charmoille specimens to the late Miocene (MN 9 in Table 4) is secure? For example, if I understand correctly, the Bois de Raube tooth was found in 1858 and I suppose without precise stratigraphic information. All the above correlations result (see also Fig. 8) that the *D. giganteum*-bearing Bois de Raube locality is older than the *D. levius*-bearing Charmoille locality.
- *Deinotherium proavum* was not present during the middle Miocene, while Pliocene occurrences of deinotheres are questioned (see Markov, 2008).
- I suggested several publications in the pdf that I find necessary to be included, e.g., Tobien (1988) for *D. giganteum* from Montredon (France).
- The correct spelling is "deinothere", not "dinothere".
- The English language should be improved.

To sum up, this is a nice contribution, but I recommend major revisions before publishing. **Download the review**