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Review of the enigmatic Eocene shark genus *Xiphodolamia* (Chondrichthyes, Lamniformes) and description of a new species recovered from Angola, Iran and Jordan

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ABSTRACT

Little is known about the extinct *Xiphodolamia*, a peculiar lamnid shark which inhabited the Eocene seas. The reexamination of a large set of fossilized teeth specimens from the Ypresian of Kazakhstan has enabled the reconstitution of the tooth series of this enigmatic taxa of lamnid shark. Five distinct tooth morphologies seem to occur in *X. ensis* Leidy [Leidy, J., 1877. Description of vertebrate remains, chiefly from the phosphate beds of South Carolina. Journal of the Academy of Natural Sciences of Philadelphia 8, 209–261] species revealing a weak ontogenetic variation. Such specific variation in tooth shape means that the other described species may be their junior synonyms. Dental morphology perfectly conforms with a Lamniforme but does not prove the current attribution to the Lamnidae family due to some inconsistent dental features observed, such as the presence of symphysial teeth. This genus could be regarded as an old lineage branched from the stem group of Lamnidae, close to the Isuroids sharks. Several *Xiphodolamia* teeth, originating both from old collections and new acquisitions, are reported and illustrated in order to provide information about a new species described here: *Xiphodolamia serrata* nov. sp. This species, currently limited to deposits in Angola, Jordan and Iran and dated at the Late Eocene, is easily distinguishable from the Early-Middle Eocene material belonging to the genus by the presence of serrated cutting edges. Adding to the type species considered here as the only valid taxa during the Early-Middle Eocene period, the temporal range of this genus extends to the Late Eocene, thus setting its upper stratigraphic limit prior to its disappearance as enigmatic as its appearance in the Early Eocene was.

1. Introduction

Numerous Eocene deposits with records of fossil selachians have revealed some teeth of an extinct shark genus: *Xiphodolamia*, an enigmatic shark from the Atlantic and Tethyan waters, often reported as *Xenodolamia,* a junior synonym. Although the teeth of this genus are easily identifiable and leave no doubt as to their generic attribution, very little is known about this extinct taxon. Its systematics, for example, has long been unclear, the difficulty to recognize distinctive characteristics having led paleoichthyologists to ascribe this genus to several taxonomic groups: the Hexanchiformes (Leriche, 1905; Casier, 1958, 1966), Isuroidea (Lamniformes: Glückman, 1964; Zhelezko and Kozlov, 1999 as Isuridae) and Lamnidae (Lamniformes: Cappetta, 1987; Kent, 1994; Case and Borodin, 2000). Among these families, Lamnidae has, however, reached a consensus, despite the absence of conclusive evidence**.** In fact, the abovementioned different placements have been based on an imperfect study of the genus dental morphology. Dentition is, indeed, quite peculiar in a lamnid shark, showing highly twisted anterior teeth unknown in other extant or fossil lamnid specimens.

Originating in the Ypresian period, this genus spread widely and rapidly during the Early-Middle Eocene. It has been reported throughout Atlantic palaeocoasts, in a wide latitudinal range: from eastern USA and Caribbean seas (e.g. Leidy, 1877; Casier, 1958) to western Kazakhstan (e.g. Glückman, 1964) and a latitudinal range from Denmark (Cappetta, 1987) to Angola (e.g. Dartevelle and Casier, 1959). It disappeared by the end of the Middle Eocene, apparently leaving no descendants.

Such brief time-span and the scarcity of large assemblages (except in the London Clay where teeth of the type species can be found) have not allowed a close observation of the dental

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morphology of this taxon and has limited further research on the phylogenetic relationships within Lamniformes. Only the discovery of numerous teeth or tooth sets did seem really effective to explore such question**.** This report is on such abundant material of isolated teeth recovered by Kozlov from the Early Eocene Aktologay, Western Kazakhstan, all of which belonged to adult or juvenile *X. ensis* (Leidy, 1877) type species. To our knowledge, no other paleogene deposits have revealed as numerous teeth of *Xiphodolamia ensis*.

Moreover, five teeth were collected in several sites in Angola, Jordan and Iran (Fig. 1) between 1950 and 2007, by Antunes, Cappetta, and Hosseinzadeh, respectively and were tentatively reported as *Xiphodolamia*, awaiting further studies or material. The teeth show a slight but entirely serrated cutting edge, a feature never observed in other reported teeth of *Xiphodolamia*. As this was a small and poorly preserved sample (especially the Jordanian and the Iranian materials), the abovementioned authors reported them as *Xiphodolamia*, cautiously suggesting, however, that they could belong to a new species. A comparative review of new and old available samples presented below aims to evaluate the phylogenetic relationships of the enigmatic genus *Xiphodolamia* and to describe a new species.

The systematics and dental terminology follow Cappetta (1987). Teeth from the Angolan sample, which includes the type specimens of the new species, are currently housed at Science Academy of Lisbon, Portugal. Institutional abbreviations are as follows:

UMC-AKT: Material from Aktologay (Kazakhstan) comprising the collections of the University of Montpellier, France; UMC-DAH: Material from Dahikiya (Jordan), comprising the collections of the University of Montpellier, France; UMC-EGE: Material from "Egemkapel Clay member", Egem Sand Member (Belgium) "Steenbakkerij Ampe", comprising the collections of E. Collier hosted by the University of Montpellier, France; ACL-ANG: Material from Angola, in the collections of Science Academy of Lisbon, Portugal; UTR-ILA: Material from Iran. Personal collection of Rohallah Hosseinzadeh which is currently hosted by the Geology Museum of the Faculty of Science, University of Tehran, Iran.

2. Review of the genus *Xiphodolamia*v

ORDER: Lamniformes Berg, 1958
Lamnidae *incertae sedis*
Genus *Xiphodolamia* Leidy, 1877

Type species: X. ensis (Leidy, 1877, p. 252, pl. 34, fig. 25–30) – from New Jersey marls. Early Eocene.

The species of *Xiphodolamia* were usually attributed to the genus *Xenodolamia* Leidy, 1877 by most authors until the 1980s (e.g. Leriche, 1905; Casier, 1958). As discussed by Cappetta (1987: 97), confusion has arisen because Leidy (1877) had simultaneously described the new genus *Xiphodolamia,* based on the analysis of anterior teeth from the Eocene New Jersey marls, and the new genus *Xenodolamia,* based on the observation of teeth from the Neogene Ashley Phosphate beds of South Carolina, USA. The type species of *Xenodolamia* (*X. pravus*, Leidy, 1877, pl. 34, fig. 33–34) is represented by two Lamnid teeth that could not be determined at the generic level, a fact that, therefore, prevented this latter genus from being considered valid. Notwithstanding, Leriche (1905) insisted that the teeth Leidy had described under the names *Xenodolamia* and *Xiphodolamia* belonged to the same genus and unlikely chose *Xenodolamia.*

Three species are commonly recognized as *Xiphodolamia* (or *Xenodolamia* as abovementioned):

- The type species *X. ensis*, currently known at type locality, Ypresian (Leidy, 1877), the Early-Middle Eocene of Central Asia (Menner, 1928; Glückman, 1964 as *X. eocaena*; this report) and Jordan (Qasr Ouzaykhim: Cappetta et al., 2000; Jebel eth Thuleithuwat: Mustafa et al., 2005).
- *X. barbadica* (Casier, 1958) is known in Scotland Fm only (Lower Lutetian, West Indies: Casier, 1958). The author distinguished this species based on the rectangular-shaped root of a single tooth from Spa Peak, stating, however, that it was very similar to *X. eocaena.* In fact, *X. barbadica* is sometimes referred to as *X. eocaena* (Cappetta, 2006).

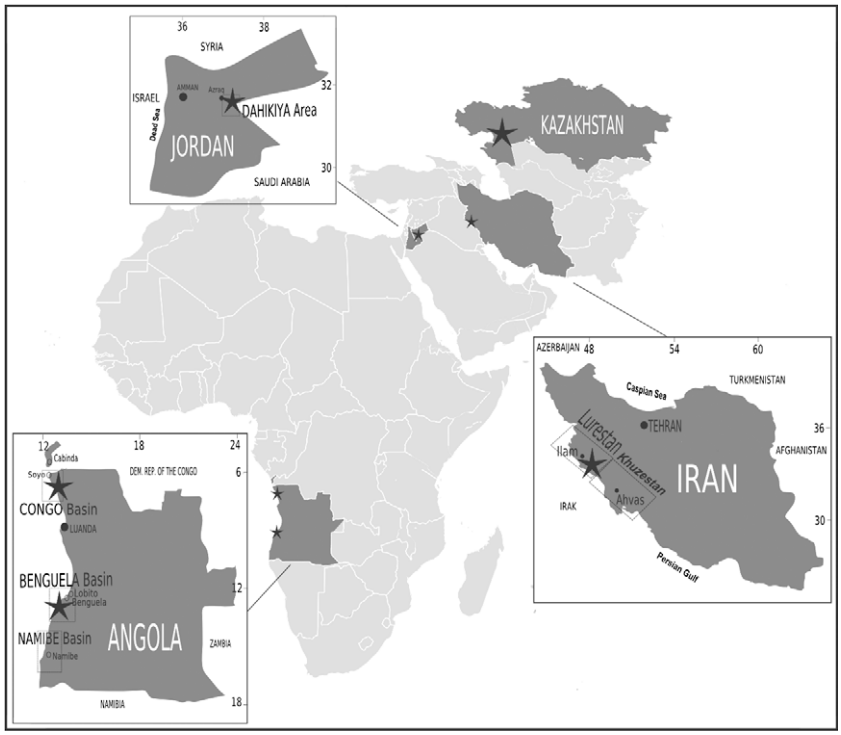

Fig. 1. General map of sites that delivered *X. ensis* and new species figured in this work (star symbol), see text for details.