A NEW PROTEID SALAMANDER (URODELA, PROTEIDAE) FROM THE MIDDLE MIOCENE OF HAMBACH (GERMANY) AND IMPLICATIONS FOR THE EVOLUTION OF THE FAMILY

by LOREDANA MACALUSO[1],* ⓘD, ANDREA VILLA[2] ⓘD *and* THOMAS MÖRS[3],* ⓘD

[1]Dipartimento di Scienze della Terra, Via Valperga Caluso 35, 10125, Turin, Italy; loredana.macaluso@unito.it
[2]Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICTA-ICP, c/ Columnes s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain; andrea.villa@icp.cat
[3]Department of Palaeobiology, Swedish Museum of Natural History, PO Box 50007, SE 10405, Stockholm, Sweden; thomas.moers@nrm.se
*Corresponding author

Abstract: Members of the urodele family Proteidae currently account for eight extant species within two genera and at least four extinct species within three genera. The clade has a clear disjunct geographical range, with the extinct *Paranecturus* and the extant *Necturus* in North America and the extinct *Mioproteus* and the extant *Proteus* in Europe and Asia. A recent phylogenetic analysis supported a Eurasian clade including both fossil and living species found east of the Atlantic Ocean. However, the finding of a new proteid salamander, herein named *Euronecturus grogu*, from the Miocene of western Germany sheds new light on the evolution of this family, challenging the idea of all Eurasian members of the group deriving from a single lineage separated from the North American ones at least prior to the Oligocene. This new proteid taxon is based on five isolated atlases found in late Orleanian (MN 5) sediments in Hambach 6C, and displays features that are unknown in any other proteid, such as the presence of secondary dorsal crests, small and posteriorly-directed postzygapophyses, and (in at least some specimens) a wide and deep ventral fossa between the anterior cotyles. A phylogenetic analysis recovered the new taxon in an early-branching position within Proteidae, sister to all other proteids but the late Maastrichtian *Paranecturus*. It thus suggests the presence in Europe of a second proteid lineage, currently known only in the middle Miocene, that appears unrelated to the *Mioproteus–Proteus* clade.

Key words: Proteidae, *Necturus*, *Mioproteus*, biogeography, Miocene, Hambach.

PROTEUS *anguinus* Laurenti, 1768 is the only living representative of Proteidae in Europe, showing extreme troglobiont adaptations and a distribution limited to the Dinaric Alps, in the Balkans Peninsula (Sket 1997). The other extant proteid genus, *Necturus* Rafinesque, 1819 (including seven extant species), is commonly found in the surface waters of a large part of the eastern United States and Canada (Vitt & Caldwell 2014). The fossil record testifies to the deep roots of the disjunct geographical range of this family and shows both the existence of various extinct genera and species and a wider past distribution. The oldest proteid remains are from the upper Maastrichtian of the Hell Creek Formation in the USA, where atlases and trunk vertebrae were attributed to the early-branching species *Paranecturus garbanii* DeMar, 2013, that shows affinities with *Necturus*. Rare fossils are also attributed directly to this latter genus, being limited to some vertebrae described as the extinct species

Necturus krausei Naylor, 1978 from the upper Paleocene (Tiffanian) of Canada and remains of an unidentified species from the upper Pleistocene of Florida (Naylor 1978; Webb & Wilkins 1984). In Europe, the extant genus *Proteus* has a very scarce fossil record, limited only to an isolated parasphenoid from the Pleistocene of Germany attributed to the extinct species *Proteus bavaricus* Brunner, 1956. However, the validity of this species was questioned by different authors (e.g. Estes 1981; Bailon 1995). On the other hand, several Neogene European localities yielded remains attributed to the extinct genus *Mioproteus* Estes & Darevsky, 1977, that a recent phylogenetic analysis detected as the sister taxon of the extant *Proteus*, together forming therefore a monophyletic Eurasian group of proteids (Venczel & Codrea 2018). *Mioproteus* counts three species described up to now: *M. caucasicus* Estes & Darevsky, 1977, *M. gardneri* Venczel & Codrea, 2018, and *M. wezei* Młynarski *et al.*, 1984. *Mioproteus*

gardneri is the oldest species, being known from the lower Oligocene of Romania (Venczel & Codrea 2018), whereas remains attributed to *M. caucasicus* (or *M.* cf. *caucasicus*) are common in Miocene sites, mostly in Germany (Heizmann *et al.* 1980; Sach & Heizmann 2001; Böttcher *et al.* 2009; Ivanov & Böhme 2011), but also in Austria (Bachmayer & Szyndlar 1985) and Hungary (Bernor *et al.* 2004). Occurrences of this latter species reach western Asia, including the Caucasus (where it was first described) and Kazakhstan (Estes & Darevsky 1977; Malakhov 2003; Vasilyan *et al.* 2017). Published remains attributed to *M. wezei* are from the upper Pliocene of Poland, France, and Russia (Młynarski *et al.* 1984; Bailon 1995; Syromyatnikova *et al.* 2021) and from the lower Pleistocene of Moldova (Averianov 2001). Roček (2004) questioned the validity of this species, considering that the diagnostic features established by Młynarski *et al.* (1984) are in fact intraspecifically variable within *Mioproteus*. Syromyatnikova *et al.* (2021), on the other hand, recently supported its taxonomic status based on a large sample of vertebrae from Russia, even though acknowledging variation in most of the characters. Remains of unidentified *Mioproteus* have also been found in the upper Oligocene and Miocene of Kazakhstan (Malakhov 2003; Lopatin 1996, 2004; Vasilyan *et al.* 2017), the Miocene of Czech Republic, Germany and Greece (Prieto *et al.* 2009; Vasileiadou *et al.* 2017; Ivanov *et al.* 2018; Böhme *et al.* 2019), and in the upper Pliocene of Germany (Mörs 2002). Another extinct genus, *Orthophyia* Meyer, 1845 from the upper Miocene of Germany, was suggested as a synonym of *Mioproteus* (Averianov 2001). However, the holotype was destroyed by fire in 1943, so this synonymy is impossible to confirm (Estes 1981; Venczel & Codrea 2018).

We herein report on a new proteid from the middle Miocene of Hambach 6C, in western Germany, which gives new information on the past diversity of the European members of this clade.

GEOLOGICAL SETTING AND FAUNAL CONTENT

The large-scale Hambach lignite mine is situated in western Germany about 35 km west of Cologne (50° 54′ 44″ N, 6° 29′ 51″ E; Fig. 1). Geologically, the mine is situated on the tectonic Erft block within the Lower Rhine Embayment, a graben structure that has cut into the Palaeozoic Rhenish Massif since the Oligocene. The mine exposes the Miocene Ville Formation that contains the paralic Rhenish Main Seam, intercalated in a succession of interlocking beach sands of the transgressing North Sea and fluvial sediments of the Palaeo-Rhine and Meuse river system (Boenigk 2002; Schäfer *et al.* 2004). The material described here is derived from channel fill and floodplain deposits (horizon 6C according to the local lithostratigraphy) within the middle Miocene Frimmersdorf lignite seam (Mörs *et al.* 2000; Schäfer *et al.* 2004).

Sedimentological, palaeobotanical and palaeontological evidence indicates an estuarine environment, containing extensive paralic coal swamps and a large fluviatile system (Mörs 2002; Utescher *et al.* 2002; Schäfer *et al.* 2004). Accordingly, the Hambach 6C locality has produced many aquatic and semiaquatic vertebrates, including cyprinid fishes, a cryptobranchid salamander, a discoglossine anuran, trionychid, carettochelyid, chelydrid and emydid turtles, alligatorid crocodylians, chamaeleonid, lacertid and anguid lizards, aniliid, boid, tropidophiid, colubrid, elapid and viperid snakes, anhingid, anseriform and rallid birds, desmanine and dimylid insectivorans, mustelid carnivorans, beavers and tragulid deer (Mörs *et al.* 2000; Ziegler & Mörs 2000; Mörs 2002; Hierholzer & Mörs 2003; Klein & Mörs 2003; Joyce *et al.* 2004; Dalsätt *et al.* 2006; Stefen & Mörs 2008; Mörs & Stefen 2010; Čerňanský *et al.* 2017).

Based on the rich association of more than 70 mammalian taxa, including about 30 rodent species (sciurids, petauristids, glirids, eomyids, cricetids and castorids) the

FIG. 1. Location of the Hambach opencast lignite mine in western Germany (from Mörs & Stefen 2010).

Hambach 6C local fauna can be correlated with the upper part of mammalian Neogene unit MN 5, indicating an absolute age-range of 16.0–15.2 Ma for this late Orleanian, early middle Miocene fauna (Mörs *et al.* 2000; Mörs 2002; Mörs & Kalthoff 2004). The age of the fauna and the high vertebrate diversity, including 'tropical' elements, fits well with the *c.* 2 myr greenhouse interval (the Miocene Climatic Optimum (MCO); Steinthorsdottir *et al.* (2021) and references therein). Paratropical (humid, warm, and with distinct seasonality) climate conditions during deposition of the Ville Formation is also evidenced by palaeofloras found in the Lower Rhine Basin. For Hambach 6C, mean annual precipitation is estimated to have been between 897 and 996 mm, mean annual temperature between 15.7 and 18.0°C, coldest month mean between 9.6 and 11.7°C, and warmest month mean between 25.2 and 28.3°C (Utescher *et al.* 2000).

MATERIAL AND METHOD

Material

The new taxon is described based on material stored in the Steinmann Institute of the Rheinische Friedrich-Wilhelms-Universität Bonn, Germany. Comparisons were made with representatives of all extant families of urodeles, based on both published literature (Estes 1981; Ratnikov & Litvinchuk 2009; Venczel & Codrea 2018; Vasilyan & Yanenko 2020) and personal observations. These latter include comparisons with specimens from the Hungarian Natural History Museum of Budapest, the Museum of Geology and Palaeontology of the University of Turin, the National Museum of Natural Sciences of Madrid and Paris, and from the Staatliche Naturwissenschaftliche Sammlungen Bayerns-Bayerische Staatssammlung für Paläontologie und Geologie of Munich (see Appendix S1 for a complete list of the observed specimens). For families that were not represented in the above collections and for which no literature sources were available, specimens in online repositories (MorphoSource and DigiMorph) were used, including all available cryptobranchids, ambystomatids, dicamptodontids and rhyacotritonids (Appendix S1). If not differently stated, the anatomical terminology follows DeMar (2013).

Phylogenetic analysis

To evaluate the phylogenetic position of the new taxon, we conducted an analysis based on the matrix published by Venczel & Codrea (2018), which in turn was an update of the one originally created by DeMar (2013).

We added three new characters (see Appendix S2; chars 15–17). The new taxon was scored using Mesquite v3.61 (Maddison & Maddison 2017; the matrix is reported in Appendix S3 and available as Nexus and TNT files in Macaluso *et al.* 2021) and the phylogenetic analysis was run using TNT v1.5 (Goloboff *et al.* 2008) using the New Technology search with all options selected, the consensus stabilized five times with a factor of 75, and 1000 trees in memory. A second round of tree bisection and reconnection was run after the first New Technology search.

Institutional abbreviations. IPB-HaH, Institute of Palaeontology Bonn, Germany (Hambach Hauptflöz (or main seam) = Hambach 6C).

SYSTEMATIC PALAEONTOLOGY

AMPHIBIA Linnaeus, 1758
URODELA Duméril, 1806
PROTEIDAE Bonaparte, 1831

Genus †EURONECTURUS nov.

LSID. urn:lsid:zoobank.org:act:0F121BFF-676B-44CC-8152-48F595B261C1

Derivation of name. *Euro* in reference to its European distribution, and *necturus* to recognize its closer resemblance and probable phylogenetic affinity to forms such as *Paranecturus* and *Necturus* rather than to *Proteus* and *Mioproteus*. Gender is masculine.

Type species. *Euronecturus grogu* (by monotypy).

Diagnosis. As for the type and only known species.
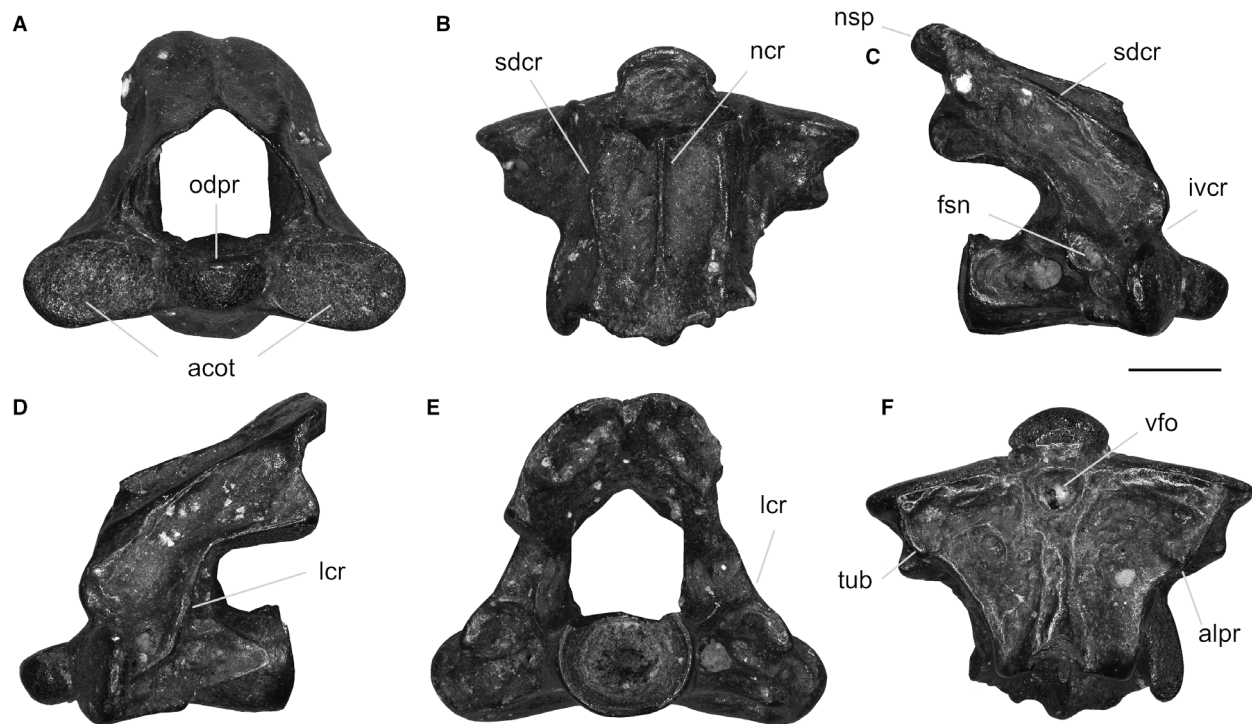
†*Euronecturus grogu* sp. nov.
Figures 2, 3

LSID. urn:lsid:zoobank.org:act:5FC5AE62-16AA-4A16-BF5D-4818988FBD95

Derivation of name. Specific epithet refers to Grogu, the Child in the popular Star Wars series 'The Mandalorian'. This recalls the fact that, like the new taxon herein described, Grogu is a member of an ancient lineage we know nothing or almost nothing about, which appears in an unexpected place at an unexpected time.

Holotype. IPB-HaH 2121, an almost complete atlas (Fig. 2).

Paratypes. IPB-HaH 2120 and IPB-HaH 2150, two atlases (Fig. 3A, B) missing the dorsal portion of the neural arch.

FIG. 2. Holotype atlas (IPB-HaH 2121) of *Euronecturus grogu* gen. et sp. nov. from Hambach 6C in: A, anterior; B, dorsal; C, right lateral; D, left lateral; E, posterior; F, ventral view. *Abbreviations*: acot, anterior cotyles; alpr, alar process; fsn, foramen for the first spinal nerve; ivcr, incisura vertebralis cranialis; lcr, lateral crest; ncr, neural crest; nsp, neural spine; odpr, processus odontoideus; sdcr, secondary dorsal crest; tub, tuberculum; vfo, ventral fossa. Scale bar represents 1 mm.

Other referred material. IPB-HaH 2119 and IPB-HaH 2165, two atlases (Fig. 3C, D) missing the dorsal portion of the neural arch. In IPB-HaH 2119, the left anterior cotyle is broken as well.

*Locality & age.* Hambach 6C, Germany; early middle Miocene (late Orleanian, MN 5).

Diagnosis. Euronecturus grogu is diagnosed by the following combination of features: (1) anterior cotyles dorsoventrally compressed and not confluent medially; (2) processus odontoideus with an unseparated articular surface; (3) presence of secondary dorsal crests; (4) postzygapophyses small and directed ventrolaterally. Our phylogenetic analysis recovers features 3 and 4 as possible unambiguous autapomorphies of the new taxon. The presence of a deep ventral fossa on the ventral surface of the atlas, between the anterior cotyles, is also known only in *E. grogu*, even though IPB-HaH 2165 clearly shows that it is not unequivocally present in all atlases referred to the taxon.

Description of the holotype. IPB-HaH 2121, a moderately small atlas (Fig. 2), is rather well preserved. It has strongly dorsoventrally compressed anterior cotyles, the articular surface of which is flat. The joints are separated by a rather narrow, short, and not gutter-shaped processus odontoideus, which has an unseparated and round articular surface. It is the only specimen referred to the new taxon preserving the dorsal part of the neural arch. The processus odontoideus is distinctly narrower than

both the posterior cotyle and the neural canal. In anterior view, the neural canal has an asymmetrically-rhomboidal section. It is as wide as each anterior cotyle and twice as high as them. The neural canal clearly narrows posteriorly. Still in anterior view, the ventral edge of the processus odontoideus lays in a horizontal plane dorsal to the one containing the ventral edges of the anterior cotyles.

In dorsal view, the anterior margin of the neural arch is slightly concave. The dorsal surface carries a sharp and distinct longitudinal ridge in the middle (the neural crest; ncr in Fig. 2) and two distinctly-developed and parallel secondary dorsal crests (sdcr in Fig. 2), which are more robust and located laterally to the median one. The neural crest is low and narrow, enlarging only slightly at its posterior end. Contrariwise, the secondary crests are anteriorly enlarged and posteriorly narrower. None of these ridges touches the posterior margin, even if they get close to it. The posterior margin of the neural arch in dorsal view appears wavy and bears no notch; moreover, it extends slightly posterior to the end of the postzygapophyses with a short neural spine. The posterior cotyle is not visible in dorsal view.

In lateral view, the lateral walls of the neural arch show an anterior convexity, flanked ventrally by a small notch (incisura vertebralis cranialis; ivcr in Fig. 2) close to the anterior cotyles. The convexities partially cover the anterior cotyles in dorsal view. Still in lateral view, the dorsal surface of the neural arch is strongly anteriorly inclined. The posterior margin of the lateral walls is deeply concave and it does not reach the posterior edges
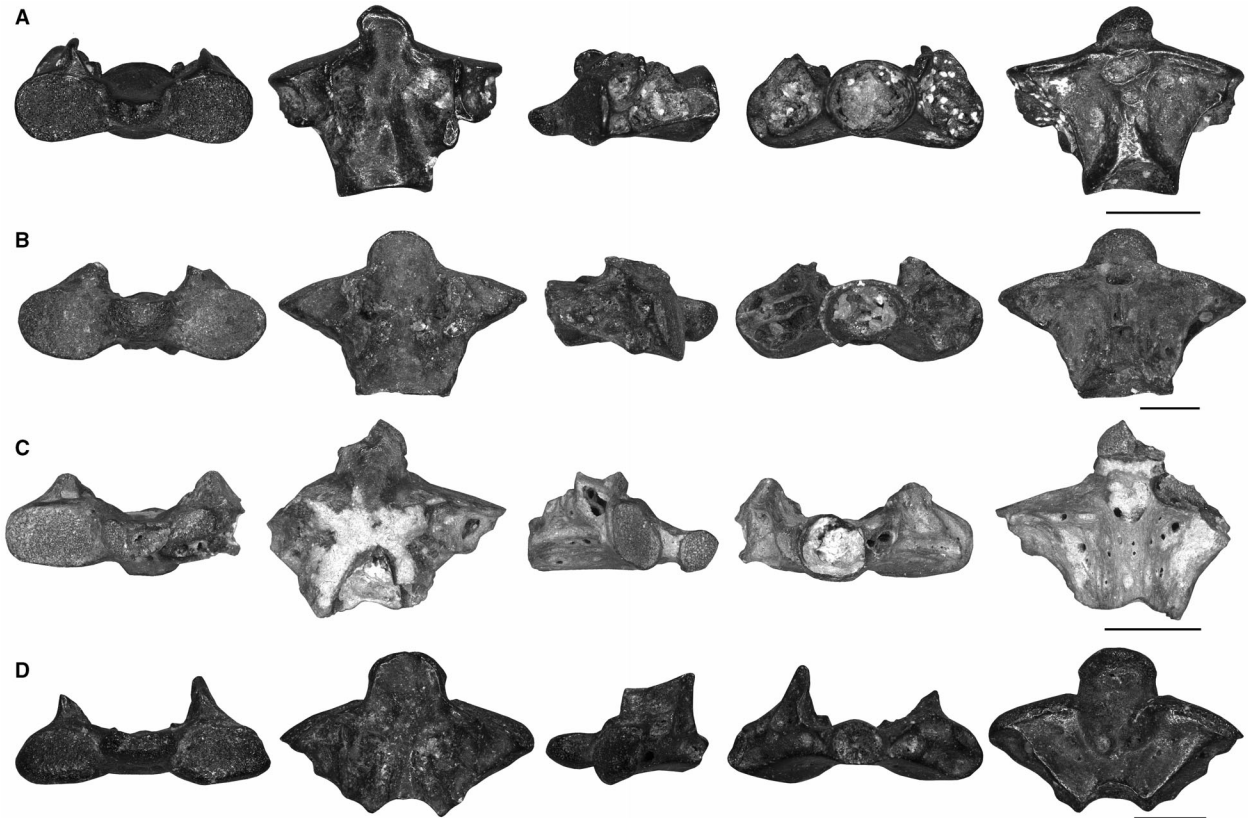
FIG. 3. Paratype (A, B) and referred (C, D) atlases of *Euronecturus grogu* gen. et sp. nov. from Hambach 6C. A, IPB-HaH 2120. B, IPB-HaH 2150. C, IPB-HaH 2119. D, IPB-HaH 2165. Each row from left to right in: anterior, dorsal, lateral, posterior and ventral view. Scale bars represent 1 mm.

of the cotyle. Only the left postzygapophysis is preserved, extending posteriorly beyond the cotyle for half of its total length. Dorsally to the latter, the posterior margin of the dorsal surface of the arch is slightly S-shaped in lateral view, with a posterior convexity starting from the posterior margin of the postzygapophyses and a concavity more dorsally. The short and thick neural spine (nsp in Fig. 2) is visible between the lateral flanges of the neural arch. The lateral crests (lcr in Fig. 2) of the atlas are well developed; they are sigmoid, being weakly inclined (20–30°) close to the anterior cotyles, highly inclined in the middle part (70–80°), and horizontal in the posterior trait, where they form the lateral margin of the postzygapophyses. The foramen for the first spinal nerve is present on the external surface of the lateral walls of the neural arch (fsn in Fig. 2).

The posterior cotyle is circular. Due to the accumulation of sediment inside it, it is not possible to state whether a notochordal foramen is present or not. The neural canal is roughly ogival in posterior view and as wide as the cotyle. The dorsal surface of the neural arch is rounded in posterior view, with an inverted U-shape and the thick neural spine quite evident in the middle. The preserved postzygapophysis does not project laterally in a significant way compared to the dorsal portion of the neural arch.

In ventral view, the anterior cotyles are almost perpendicular to the processus odontoideus, forming an angle of slightly more than 180°. The ventral surface of the centrum displays a large

fossa at the base of the processus odontoideus (vfo in Fig. 2). The rest of the surface does not bear significant foramina, but two symmetrical and slightly sunken areas on the sides. The ventral surface is marked laterally by well-developed alar processes ('alar-like processes' in DeMar 2013; alpr in Fig. 2), starting from the posterior edge of the posterior cotyle and defining the ventral margin of each processus lateralis (*sensu* Ratnikov & Litvinchuk 2009). Laterally, the latter processes have some more or less large foramina and a well-developed ridge running posterodorsally. In both ventral and lateral view, the alar processes show a tuberculum (tub in Fig. 2) not far from the anterior cotyles. In ventral view, the processus odontoideus is not much extended anteriorly. A short neck separates its articular surface from the rest of the atlas, including the anterior cotyles.

Description of the paratypes. Both paratypes are almost entirely missing the neural arch but the centrum is generally well preserved. IPB-HaH 2120 and IPB-HaH 2150 (Fig. 3A, B) show similar morphologies to the holotype, except for the anterior cotyles that are oval and less dorsoventrally compressed. IPB-HaH 2150 also displays a less-distinct neck compared to the holotype.

Description of the referred material. IPB-HaH 2119 (Fig. 3C) is also missing the neural arch. The preserved centrum is ruined in

its left part, missing the left anterior cotyle and the left half of the articular surface of the processus odontoideus. The overall morphology is similar to the holotype, but the neck of the processus odontoideus is longer so that the articular surface of the processus is further away from the anterior cotyles. Moreover, the articular surface of the single preserved joint is slightly concave instead of flat. IPB-HaH 2165 (Fig. 3D) also has a morphology of the occipital area similar to the holotype, but ventrally the alar processes are less laterally extended, and they show no tuberculum close to the anterior cotyles. Moreover, in this specimen, the deep fossa at the base of the processus odontoideus on the ventral surface is absent, whereas two smaller foramina are present more posteriorly. As in IPB-HaH 2119, the neck is slightly longer than in the type material. Most of the posterior cotyle of IPB-HaH 2165 is broken off.

Remarks. The peculiar morphology of the studied urodele atlases allows their attribution to a new genus and species. The flat and dorsoventrally compressed anterior cotyles and the rounded, anteriorly projecting processus odontoideus distinguish the new taxon from most of the extant families of urodeles (including sirenids, ambystomatids, salamandrids, amphiumids, plethodontids, dicamptodontids and rhyacotritonids; Estes 1981; Ratnikov & Litvinchuck 2009; Vasilyan *et al.* 2013; pers. obs.) and from fossil atlases attributed to cryptobranchids (e.g. Georgalis *et al.* 2019). Sirenids further possess a narrower neural canal and highly developed secondary dorsal and lateral crests, whereas ambystomatids have an expanded neural crest, forming a dorsal bulge. Similarly, a dorsal bulge is visible in the atlas figured by Herre (1955) of the extinct genus *Bargmannia*, reported from the upper Miocene of Slovakia, and in extant representatives of hynobiids, dicamptodontids, rhyacotritonids and plethodontids. In the three latter families, as well as in ambystomatids, the secondary dorsal crests are absent. The Hambach taxon further differs from hynobiids because of the dorsal margin of the neural arch rising caudally and the neural arch extended posterior to the postzygapophyses (Ratnikov & Litvinchuck 2009; Jia *et al.* 2019). It cannot be referred to salamandrids due to not having a gutter-shaped processus odontoideus with separated articular surfaces and due to the neural arch extending posterior to the postzygapophyses. Amphiumids have a thicker neural crest and a larger size. As far as fossils urodeles are concerned, the Hambach taxon differs from the Mesozoic taxa of Europe (mentioned and described by Evans & McGowan 2002) in having flat anterior cotyles (except perhaps in IPB-HaH 2119) and a thick processus odontoideus with a well-defined neck. The main differences between the Hambach taxon and the extinct family Batrachosauroididae are the flat articular surface of the anterior cotyles and the more rounded and developed processus odontoideus (Naylor 1983; Evans & McGowan 2002). A single species belonging to this family, *Palaeoproteus miocenicus* Vasilyan & Yanenko, 2020 from the upper Miocene of Europe, has a very long processus odontoideus, which is however much longer than that of the new Hambach taxon. The latter differs from *P. miocenicus* also in the more dorsoventrally compressed anterior cotyles, the relatively longer centrum, and the shape of the processus odontoideus, that is lip-shaped and anteroventrally bent in *P. miocenicus* and rounded and knob-like in *E. grogu*.

Furthermore, the Hambach taxon can be distinguished from Mesozoic scapherpetontids by the presence of alar processes on the ventral surface and by the relatively lower and more robust neural arch (Naylor & Krause 1981; Gardner 2012). On the other hand, these same features, together with the dorsoventrally-compressed anterior cotyles, are shared between this taxon and members of the Proteidae. Within European fossil proteids, atlases have been referred to the species *M. caucasicus* and *M. gardneri* and described by Estes & Darevsky (1977), Miklas (2002), and Venczel & Codrea (2018). All descriptions and figures agree in *Mioproteus* atlases having the 'cotylar surface … confluent across the tiny intercotylar process' (Estes & Darevsky 1977, p. 165). This character allies *Mioproteus* with the extant species of *Necturus* and *Proteus*, distinguishing all of them from the Hambach urodele. Furthermore, the anterior cotyles forming a 225° anterior angle in *Mioproteus* in ventral view (Venczel & Codrea 2018) further exclude a possible attribution of the Hambach atlases to this genus. The processus odontoideus is also wider and placed differently in *E. grogu* than in both extant proteids and *Mioproteus*, being set at mid-height of the anterior cotyles rather than in the upper half as in the latter (see char. 13 of DeMar 2013; Venczel & Codrea 2018). The general morphology of the atlases described herein closely resembles the North American taxon *Paranecturus garbanii*, from the upper Maastrichtian of Montana. However, atlases attributed to this species (including the holotype) show a neural canal that is partly flanked laterally by the anterior cotyles, rather than being completely above them as in the Hambach urodele. Also, the latter shows a deep ventral fossa at the base of the processus odontoideus and dorsoventrally compressed anterior cotyles, both features lacking in *Paranecturus*. *Euronecturus grogu* also differs from all known extant proteids (and extinct scapherpetontids; J. Gardner pers. comm. 2021) in the presence of secondary dorsal crests. However, this character is unknown for *Mioproteus*, *Paranecturus*, and most fossil urodeles, because the dorsal part of the neural arch is very rarely preserved.

PHYLOGENETIC ANALYSIS

Our phylogenetic analysis resulted in a single tree of 59 steps (Fig. 4). Consistency (CI) and retention (RI) indexes are 0.593 and 0.676, respectively. The analysis was able to recover a monophyletic Proteidae, with *P. garbanii* as the most early branching taxon. *Euronecturus grogu* is then sister to a clade including the extant *Necturus maculosus* (Rafinesque, 1818) and all other European proteids. *Mioproteus* species form a monophyletic group, which is sister to *P. anguinus*. Bremer support is, however, low for all nodes (Fig. 4).

DISCUSSION

Although most of the extant species of Proteidae are currently widespread in the eastern part of North America, the fossil record of this group there is limited, with only

FIG. 4. Phylogenetic relationships of *Euronecturus grogu* gen. et sp. nov. from Hambach 6C. Numbers at nodes show Bremer support.
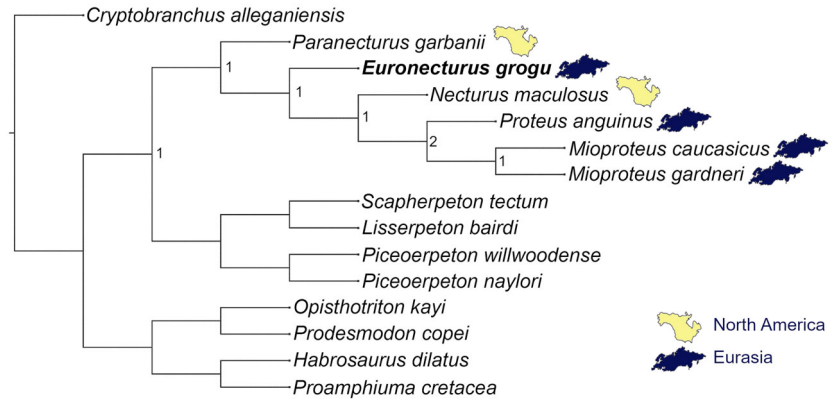

three occurrences reported from the area (Fig. 5A). In particular, North America hosts the oldest proteid record: *Paranecturus garbanii* from the upper Maastrichtian of the Hell Creek Formation (DeMar 2013). In this context, the finding of *E. grogu* in the lower middle Miocene of Hambach 6C is of exceptional relevance because of its clear resemblance to this Cretaceous, North American relative. In fact, *E. grogu* and *P. garbanii* share a similar morphology of the atlas, especially in the well-developed processus odontoideus with an unseparated articular surface and a short neck, as well as in the flat anterior cotyles. A comparison between *E. grogu* and *N. krausei* from the upper Paleocene of Canada to evaluate possible affinities was not possible, because the latter is only represented by trunk vertebrae. As a matter of fact, a detailed scrutiny of the amphibian fossils from Hambach 6C looking for skeletal elements other than atlases with a proteid-like morphology that could be attributed to *E. grogu* was unsuccessful. Several extant taxa and groups currently show similarities between North America and Europe (e.g. proteids themselves, or the plethodontid genera *Hydromantes* and *Speleomantes*; see Carranza *et al.* 2007) or showed them in the past (e.g. the extant plant genus *Lycopus*; see Martinetto *et al.* 2021).

However, the new species from Hambach is particularly significant for the evolution of the family Proteidae when considering the result of our phylogenetic analysis (Fig. 4), revealing its early-branching position. This finding has notable biogeographical implications, especially considering the more derived state of the extant *N. maculosus*. According to our analysis, the other European proteids (the extant *Proteus* and the extinct *Mioproteus*) are, therefore, more closely related to the American *Necturus* than to *Euronecturus*. It is interesting to note that proteids were generally widespread during the Neogene in Eurasia (Fig. 5B), even though most of the fossils are attributed to *Mioproteus*, reported from several localities in Europe, Caucasus and Kazakhstan from the Oligocene onwards (Venczel & Codrea 2018). Apart from the dubious *Proteus*

bavaricus, the only other genus of proteid known as fossil from Europe is *Orthophyia*, with the single species *Orthophyia longa* Meyer, 1845 from the upper Miocene of Germany. The holotype of this species is lost and any comparison with *Mioproteus* or *Euronecturus* is thus prevented (Estes 1981; Venczel & Codrea 2018), including the evaluation of a possible synonymy with one of the species of either. *Mioproteus* shares a very close morphological similarity with the extant *Proteus* and they form a monophyletic group in our analysis. Thus, they are most likely to have been derived from a single lineage of proteids widespread in Eurasia since at least the late Palaeogene. Whether this lineage entered the Palaearctic through a land bridge connecting it with the Nearctic (Beringia, the De Geer route, or the Thulean route; see Brikiatis 2014, for an extensive review on the topic) sometime before the Oligocene (when *M. gardneri* was already present in Europe; Venczel & Codrea 2018) or originated in Eurasia from a more ancient stock separated from its North American relatives when the two continents split, is difficult to ascertain at the moment, in particular due to the very scarce record of fossil Palaeogene proteids and especially Asiatic ones.

The phylogenetic distance between the *Mioproteus–Proteus* lineage and *Euronecturus* suggests that the latter is not related to the same colonization or speciation event as the former. Moreover, atlases of *Euronecturus* are the only remains that can be unambiguously attributed to a proteid salamander in Hambach 6C, thus indicating that this genus did not co-occur with any other member of the clade in the only locality where it is currently known. Again, *Euronecturus* could be a relict member of another lineage whose roots have to be sought in the Mesozoic or Palaeogene, when North America and Eurasia still presented shared faunal elements (as is the case for lizards, for example; Rage 2013). Alternatively, it could have originated from another wave of proteids entering Eurasia from North America sometime before
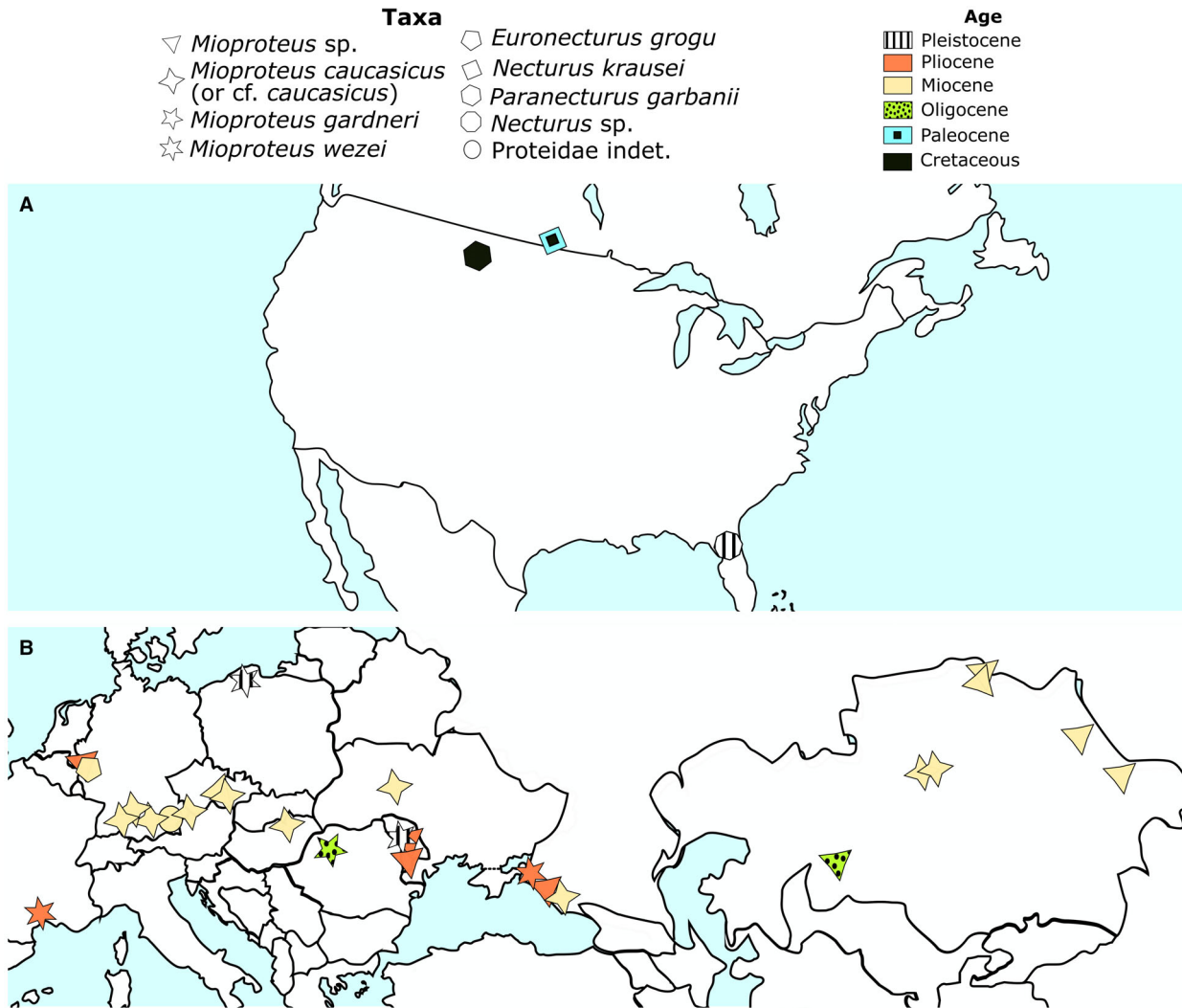
FIG. 5. Fossil record of proteids. A, North American fossil record; from Naylor 1978, Webb & Wilkins 1984, DeMar 2013.
B, Eurasian fossil record; from Estes & Darevsky 1977, Heizmann *et al.* 1980, Młynarski *et al.* 1984, Bachmayer & Szyndlar 1985, Bailon 1995, Lopatin 1996, 2004, Averianov 2001, Sach & Heizmann 2001, Mörs 2002, Malakhov 2003, Bernor *et al.* 2004, Böttcher *et al.* 2009, Prieto *et al.* 2009, Ivanov & Böhme 2011, Vasileiadou *et al.* 2017, Vasilyan *et al.* 2017, Ivanov *et al.* 2018, Venczel & Codrea 2018, Böhme *et al.* 2019, Syromyatnikova *et al.* 2021. Given the uncertain nature of *Orthophyia* Meyer, 1845 (see main text) this specimen is here indicated by 'Proteidae indet.'

the middle Miocene. If the colonization option is true for at least one of the two lineages, the west Eurasian distribution of both extant and extinct taxa in this part of the world, as well as the absence of fossil proteids in eastern Asia, may suggest that these urodeles did not reach the Palaearctic through Beringia. De Geer and Thulean routes may be more plausible. These two routes connected Greenland with west Asia and Fennoscandia, and Great Britain, respectively. However, these considerations should be treated only as speculative at the moment, given how poor our current knowledge of extinct proteids is.

In any case, *Euronecturus* has not been detected in any locality other than Hambach up to now, contrary to *Mioproteus*, whose fossil record is rich and widespread. This disparity could reflect an effective unevenness of the past distribution of the two genera, with *Mioproteus* having a wider geographical range. However, other options should also be considered, including taphonomic or geological biases, such as living habitats with different fossilization chances or different geographical ranges (i.e. *Euronecturus* could have lived in areas of Europe with scarce outcrops from the corresponding age). Be that as it may, more fossil proteids are needed, especially from the Palaeogene, to better understand the dynamics of the group and the origin of the different subclades and lineages.

CONCLUSION

The new proteid *Euronecturus grogu* is herein described based on five atlases from the German middle Miocene locality of Hambach 6C. Atlases belonging to this species are diagnosed by the combination of: anterior cotyles dorsoventrally compressed and not confluent medially; processus odontoideus with an unseparated articular surface; presence of secondary dorsal crests; and postzygapophyses small and directed ventrolaterally. Our phylogenetic analysis recovers the previously-known European clade of proteids (including the genera *Mioproteus* and *Proteus*) as the sister group to the extant American genus *Necturus*, whereas the new Hambach taxon has a more early-branching position within the clade Proteidae. The closest resemblance of the atlases of *E. grogu* is with the oldest known proteid *Paranecturus garbanii* from the upper Maastrichtian of North America. The phylogenetic distance between the *Mioproteus*–*Proteus* clade and *Euronecturus*, as well as the similarity between the latter and *Paranecturus*, suggest that two different proteid lineages lived in Europe during the Cenozoic. One of these two lineages (the *Euronecturus* one) is currently known only from the few fossils from Hambach 6C, and therefore future finds, especially from the Palaeogene, are required to disentangle the evolution and biogeographical origin of this enigmatic group of urodeles.

DATA ARCHIVING STATEMENT

This published work and the nomenclatural acts it contains, have been registered in ZooBank: http://zoobank.org/References/7CAD0EBB-7838-4C86-901C-948AB8B71758. Data for this study are available in MorphoBank: http://morphobank.org/permalink/?P4061

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (https://doi.org/10.1111/pala.12585):

Appendix S1. Specimens observed for comparison.
Appendix S2. Character list.
Appendix S3. Character matrix used for the analyses (NEXUS format), composed of 27 characters and 15 taxa.

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