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Perspective

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Guidance to Study Salamander Unique Fossil Record

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Abstract
Fossils are commonly preserved impressions, remains or traces of ancient organisms used for the paleontological study of life origins and evolution. However, some fossils such as salamanders are unique and with a relevant role in these studies. To approach this challenge, in this study information was provided of fossil salamander records of body and footprint to guide the study of these fossil records.

Keywords: *amphibian; evolution; fossil; footprint; paleontology; salamander.*

1. Introduction

Salamanders are a special model for the study of organism's evolution and development (Fröbisch and Shubin 2011, Maddin et al. 2020, Bonett et al. 2022). In particular, cranial and palatal morphology are relevant for the study of amphibian paleobiology (Zhou et al. 2017, Jia et al. 2022). Salamander fossil remains have been previously described not only in limestones, but also in amber (e.g., Baltic amber, Eocene, ca. 47-34 million years ago, Mya) (e.g., de la Fuente 2026a).

To advance in these studies, herein fossil salamander remains and impressions in limestone from Paleozoic Era (ca. 280-275 Mya) and Middle-Late Jurassic (165-160 Mya) were used to guide the study of salamander fossil records.

2. Salamander fossil records

2.1. Salamander Fossil Record 1 (Fig. 1)

Specimen: Primitive salamander-like footprints (Animalia: Chordate: Amphibia: Caudata: Urodela, Duméril 1806).
Location: Coconino Sandstone, Arizona, U.S.A.
Geological Formation: Permian geological formation.
Age: Permian, Paleozoic Era (ca. 280-275 Mya).
Size: Matrix, ca. 25.5 x 10 x 1 cm.
Provider: Acquired by the author at OSCMS Spring Rock Swap in Oklahoma State University, Stillwater, Oklahoma, U.S.A., fossil REF.: #501023 - 73(NA).

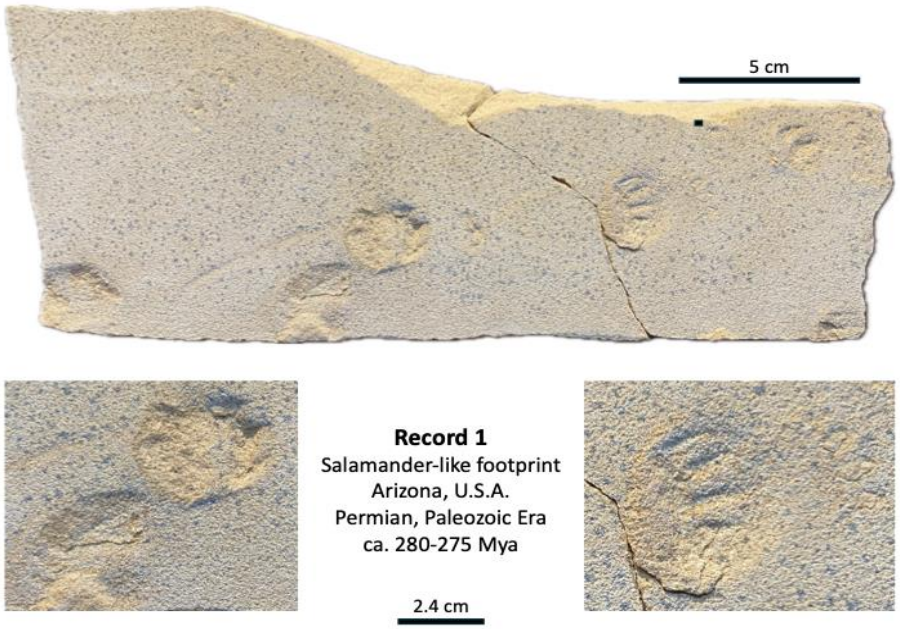


Figure 1: Fossil Record 1 of salamander-like footprints.

2.2. Salamander Fossil Record 2 (Fig. 2)

Specimen: Extinct salamander (Animalia: Chordate: Amphibia: Caudata: Urodela: Cryptobranchoidea: *Jeholotriton paradoxus*†, Wang 2000) (Wang and Rose 2005, Wang and Evans 2006, Carroll and Zheng 2012).

Location: East Asia, Daohugou village of Ningcheng County, Inner Mongolia Autonomous Region, northern China. Restricted to this deposit.

Geological Formation: Daohugou Beds, a set of fossil-rich terrestrial sedimentary strata closely linked to the Middle-Late Jurassic Tiaojishan Formation.

Age: Middle-Late Jurassic (165-160 Mya).
Size: Matrix, 14 x 8 x 0.4 cm. Salamander body, 7.5 cm length.
Provider: Jurassic Dreams (https://www.jurassic-dreams.com/blogs/jurassic-dreams-the-fossils-blog?page=2&srsltid=AYCX9vLHKAnlHpj5HWg3usxLApMTV2QEhGVkJZc49ThZKl5QqoQe7nO5), Spain, fossil REF.: #J719.

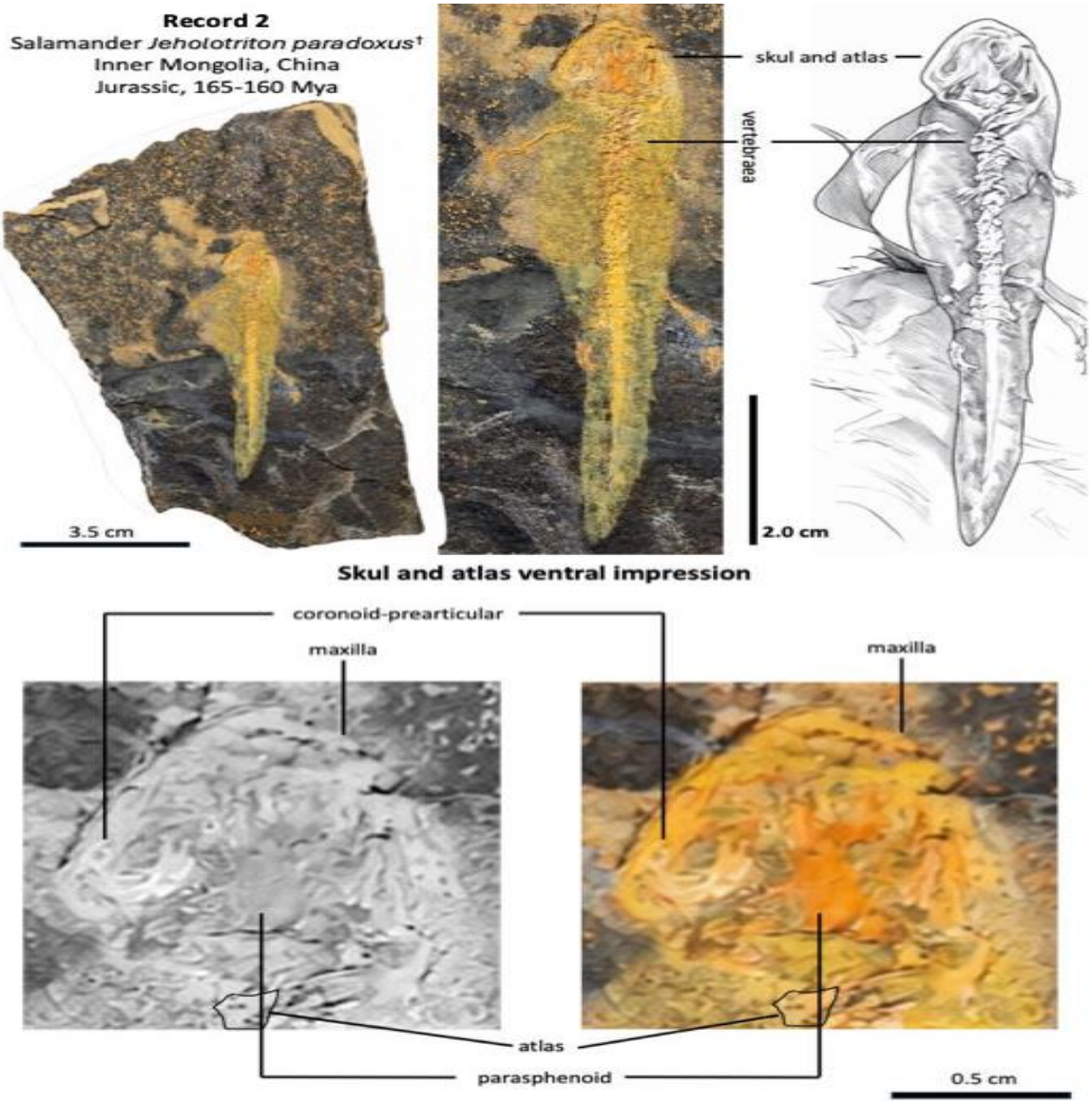


Figure 2. Fossil Record 2 of extinct *Jeholotriton paradoxus*†. Body sketch was generated with ImageToSketch application (https://imagetosketch.com). Higher resolution image disclosed in Supplementary Information (Appendix 3).

2. Analysis

The analysis was based on the fossil records of salamanders with relevant references to previous scientific studies.

2.2. Putative salamander-like footprints in Fossil Record 1 (Fig. 1)

Putative salamander-like footprints were identified in the Coconino Sandstone attibuted to ancient, dry desert sand dunes with tracks left by small reptiles or early tetrapods walking across dry or damp sand (Middleton et al. 2002) (Fig. 1).

The analysis of salamander trackways made **underwater on sloped sand** replicates the footprint impressions with irregular alignments, and abrupt starts/stops seen in the Coconino fossils (Brand and Tang 1991). These results suggested that salamanders were swimming, buoyant, or walking along submerged underwater dunes pushed by water currents.

However, despite these evidence, paleontological analyses of these footprints should consider the possibility that belonged to early tetrapods or diadectomorphs representing advanced amphibians rather than true modern reptiles navigating ancient environments. Nevertheless, the analysis supports the suggested salamander-like footprints (Fig. 1).

2.3. Body of extinct salamander *Jeholotriton paradoxus*† in Fossil Record 1 (Fig. 2)

The *Jeholotriton* is a genus of primitive, neotenic (retaining larval features) salamanders from the Middle-Late Jurassic (approx. 164-155 Ma) of Inner Mongolia, China. Found in the Daohugou Beds, it is a key fossil for early urodele evolution, with specimens often showing well-preserved, soft-tissue impressions, short limbs, and 16-17 presacral vertebrae (Fig. 2).

The extinct *Jeholotriton paradoxus*† (Wang 2000) is a salamander with a distinctively shaped "paradoxical" skull, from which it derives the species name (Figure 2). It shows well preserved impression of soft parts and paedomorphic features retaining juvenile traits into adulthood such as larval-like skull structure and unossified carpal/tarsal elements.

Studies of fossilized guts show that *Jeholotriton* along with *Chunerpeton* fed on aquatic invertebrate prey such as juvenile clam shrimp of branchiopod crustaceans conchostracans (*Euestheria luanpingensis*), indicating a specialized, lacustrine (lake-dwelling) diet. *Jeholotriton* is associated with the Jehol Biota, although the Daohugou fossils are actually older than the main Jehol fauna.

Regarding to its preservation, it is exceptional as it corresponds to a "Konservat-Lagerstätten" fossil. Coined by Adolf Seilacher in 1970, Lagerstätte means "storage place" or "site" and thus Konservat implies high-quality preservation (Kimmig and Schiffbauer 2024). Focus on quality (exceptional preservation of soft parts).

According to provider Jurassic Dreams, during the excavation of the fossil, the final slab broke into various fragments which were subsequently glued and filled, making the piece stable again. Considering these restorations in the matrix, the fossil in itself does not pose any type of restoration other than the fractures that cross it and were glued and filled.

In the Jurassic environment, *Qiyia jurassica* gen. et sp. nov. from China represents a stem group of the tabanomorph family Athericidae aquatic ectoparasitic insect that probably fed on blood of salamanders (Chen et al. 2014).

3. Conclusions

The integrated analysis of two salamander fossil records provides information for the representation of the ancient environments for these organisms (Fig. 3). Based on Thomas (2018), fossil salamander footprints represent reptile tracks and guide the study of these organisms with unique fossil record. The interest in fossil records is illustated with Sebastian Münster book Cosmographia Universalis published in 1550 (Fig. 3).

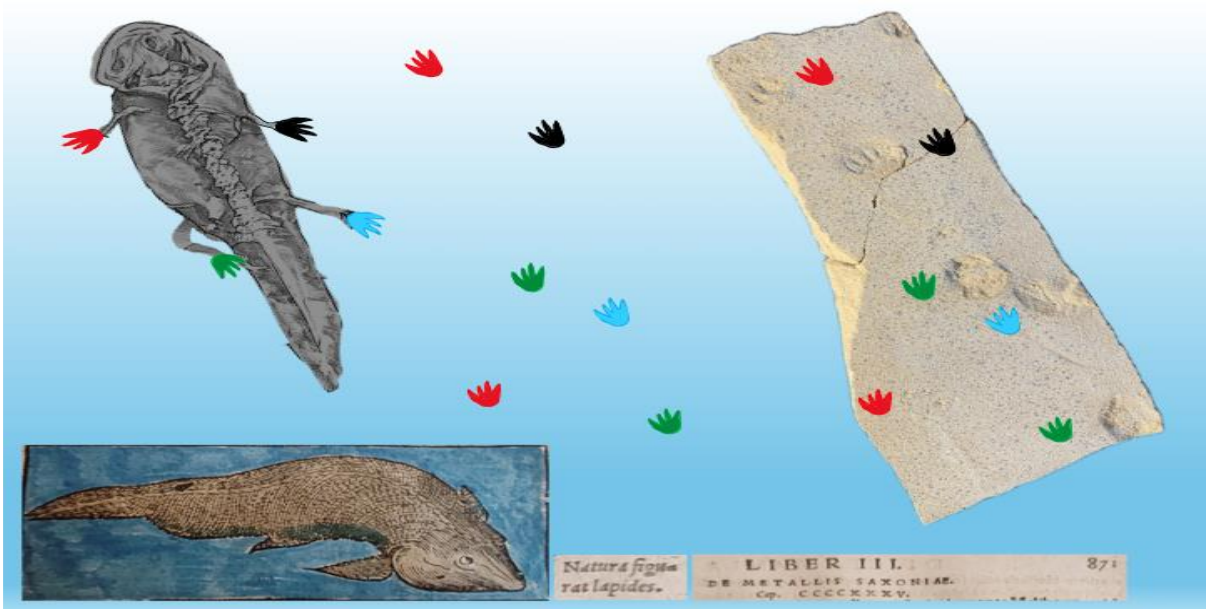


Figure 3: Representation of salamander footprints in fossil environment. The environment is illustrated with a fossil stone "Nature form stones" ("Natura figurat lapides") from Münster (1550). Additional information disclosed in Supplementary Information (Appendix 4).

4. Acknowledgments

Fossils were certified as authentic with Certificate of Legal Origin (CLO) and Certificate of Authenticity (COA) for Salamander Fossil Record 2 (Supplementary Information, Appendixes 1 and 2). Fossils and images included in the study derived from KGJ Collection (Ciudad Real, Spain) (de la Fuente 2026b).

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Supplementary Information

Appendix 1. Declaration of Legal Origin (DLO) provided by Jurassic Dreams. Fossil Record 2 of extinct *Jeholotriton paradoxus*† (Fig. 2).

DECLARATION of LEGAL ORIGIN

Object Information

Item	FOSSIL SALAMANDERS	**Culture**	JURASSIC PERIOD
Dimensions	SEVERAL INDIVIDUALS / SPECIMENS	**Century/ TimeFrame**	160 MILLION YEARS

Provenance Information

Acquired in (year)	1980's	**From** EX- PRIVATE FOSSIL COLLECTION	☒ **Private** ☐ **Fair** ☐ **Gallery / Antique shop** ☐ **Auction** ☐ **Other** .....
Acquired in (city/country)	JAPAN	**Initials** previous Seller/Owner	JAPAN MINERAL & GEM SHOW PRIVATE OWNER

Previous ownership history

Acquired in (year)	☒ **Private collection** ☐ **Auction/Gallery/Antique shop** ☐ **Excavated** ☐ **Other,**	**From** EX - PRIVATE FOSSIL COLLECTION	☒ **Private** ☐ **Fair** ☐ **Gallery / Antique shop** ☐ **Auction**
In collection since (year)	1980's	**In collection since**	1980's

Documents that corroborate this ownership or provenance

I am able to demonstrate the (legal) origin with	☐ **Invoice** ☒ **Certificate of Authenticity** ☐ **Provenance statement** ☐ **Photos** ☐ **Export license** ☐ **Other,**	**Copy of it will be sent to the buyer**	☐ **Yes** ☒ **No**
Dated	16 - 04 - 1996		

The seller ensures

☑	**Seller** familiarised himself that in line with the laws and regulations in his own country it is allowed to sell/export this object. https://en.unesco.org/cultnatlaws/
☑	**Seller** ensures that any necessary permits are/will be arranged.
☑	**Seller** will give to the buyer all provenance information known about the piece.

Place: TUCSON, ARIZONA, USA Date: 06/02/2026

Name: JURASSIC DREAMS LLC Signature: Jurassic Dreams LLC

Appendix 2. Certificate of Authenticity (COA) provided by Jurassic Dreams. Fossil Record 2 of extinct *Jeholotriton paradoxus*† (Fig. 2).



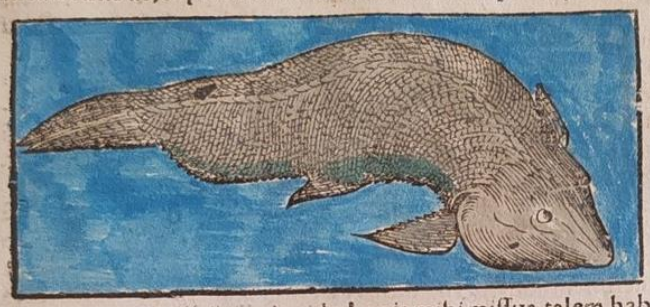
Appendix 3. Fossil Record 2 of extinct *Jeholotriton paradoxus*†. High resolution image.



Appendix 4. Münster, S. (1550). Cosmographia Universalis. Latin edition. Publisher Heinrich Petri, Basel, Old Swiss Confederation. pp. 871-872.

DE METALLIS SAXONIAE.
Cap. CCCCXXXV.

HAbet hodie Saxonia uaria & multa metalla: præsertim in monte Meliboco, qui à Chattis extenditur ad Saxones. Nam apud Eislebam, Mansfeldum & Hostedam est lapis fissilis, quem Germani *Schiffer* uocant, qui niger bituminosus, æroſus primum ex puteis extractus in aream effunditur, atq; ita ex ista coaceruatione oritur tumulus: deinde inferior tumuli pars circundatur sarmentis, in quæ similiter injiciuntur id genus lapides: Tum sarmentis admoto igni accensis, ignem etiam concipiunt lapides super ea coniecti. Hi proximis quibusq; impartiunt ignem, atq; omnino omnes qui iam ardent, eis proximè adiunctis. Et cum ardent, talem odorem emittunt, qualem carbones bituminosi cum flagrant, emittere solent. Præterea si quando in ardentes mediocris pluuia decidit, magis ardent & citius mollescunt, quod declarat eos esse lapides bituminosos. Atq; id genus lapidum crustæ, interdum scintillis pyritæ aurei coloris adhærentibus & discurrentibus, exprimunt uarias animantium species, ut in genere piscium passeres marinos, lucios, percas: in auium, gallos gallinaceos, nonnunquam salamandras, imò Pontificis Romani barbati & triplicem coronam in capite habentis effigies reperta est, quam multi uiderũt. Sunt qui aiunt uicinum esse lacum, & qualia ille nutrit animantia, talia pingit natura in fissili illo lapide. Lapis mihi missus, talem habet piscis figuram, ære ueluti manu pictoris expressam. Collegerunt autem Mansfeldenses comites maximum fructum ex uenis suæ terræ, unde æs & argentum conflant. Apud Goslariam Otto Imp. argenti dicitur inuenisse mineras, quarum magni fuerunt redditus, ex quibus Imp. duo construxit sacerdotum collegia & regium pallatium nobilis operis. Abutentibus autem ciuibus suppeditatis diuitijs, offensus Deus permisit puteum unum corruere, quo casu mille homines & supra oppressi fuerunt. Et post illud tempus neq; argentum, neque aurum fuit amplius inuentum in eo loco, sed plumbum nigrum. Fit autem primò attramentum sutorium, quod uulgò uitrillum uocant, deinde ex eo excoquitur aliquid plumbi & argenti. Perhibent autem metallum Goslariæ sic natum: Quidam nobilis homo equum cui nomen erat Ramelus in monte ad ramum arboris alligauit. In ungulis, quibus ferreæ soleæ inductæ, terram quatit, uerrit, atque ita recõditam plumbi nigri uenam integumentis nudauit, non aliter ac Pegasus alatus, ut poëtę fingunt, aperuit fontem, dum ungula ferit saxum. Vt autem fons iste ex eo nominatur Hippocrene, ita montem Saxones Ramelum uocarunt, qui hodie maximè floret, atque admirabilem plumbi copiam suppeditat. Goslariæ tantum inuenitur galenæ & pyritarum, ex quibus plumbum nigrum excoquitur, ut mons quidam ferè nihil nisi galena & pyritæ esse uideatur. Principes quoq; uici Brunonis cumularunt bona magna ex Cellerfeldensibus alijsq; fodinis. Nec Brandenburgenses qui imperant Francis, caruerunt fortunis metallicis. Nam Gold cranach auri metallum septimo quoque die dedit ipsis mille & quingentos aureos Rhenanos.



Lapides fissiles.

Natura figurat lapides.

Minera Goslariæ.

Atramentum sutorium.

Galena.

DE DIVISIONE MODERNAE SAXONIAE.
Cap. CCCCXXXVI.

ETiam si Saxonia olim comprehenderit Vuestphaliam & Ostphaliam atq; Brunsuicensem ditionem, hoc est, totam regionis illius tractum usq; ad Albim fluuium, est tamen hodie longè alia ratio diuisionis, ubi non secundum flumina, sed secundum dominia principum, terrarum fiunt partitiones. Sicque nostro tempore duplex est Saxonia, superior & inferior. Superior habet electuram, cuius præcipua oppida sunt Vuittenbergum & Torga. Inferior uerò est prope Luneburgum & Lebenburgum iuxta Albim complecturque Holsatiam, quæ olim fuit Vuagria, Stormariam & Dithmarsiam.

Saxoniæ superior & inferior.

marſiam. Holſatia olim fuit comitatus, hodie uerò eſt ducatus, & habitatio primogẽniti Danorum regis, ſicut Delphinatus in Gallia principatus eſt quem ſucceſſor regis Franciæ poſsidet, Hamburgũ eſt in Stormaria aut Nordalbingia, & Brema in Diethmarſia.

DE DVCIBVS SAXONIAE ET EORVM genealogia. Cap. CCCCXXXVII.



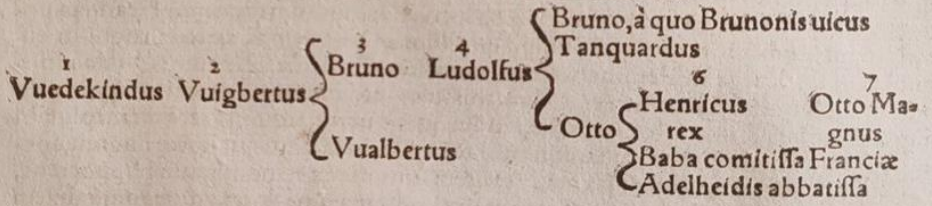
Vuitikindus.

TEmpore illo quo Carolus Magnus oppugnabat Saxoniam, fuit Saxoniæ dux Vuitikindus, quem Krantzius uocat Vuedekindum, & quidam alij uocant eum regem Saxonum, præſertim autem Angriæ, quæ eſt in Vueſtphalia. Et hi ferunt, ante regis Caroli aduentum, Saxoniæ prouinciam adminiſtrari ſolitam per duodecim proceres alternis uicibus: quem uerò grãde bellum in adminiſtratione apprehenderet, eum regem habuere ad finem uſq; belli. Inde factum eſt, ut ueniente Carolo in prouinciam Vuedekindus dux Anglariæ (Angriam uocant) in adminiſtratione erat, & ideo pro rege illis fuit durante bello, fuitq; tunc ſumma Saxonum poteſtas in Anglaria, Vuedekindus itaq; anno Chriſti 785. uiſitatus à Domino, Chriſti baptiſmum ſponte depoſcens, manibus Caroli regis leuatus eſt honoris gratia ex ſacro fonte. Inde Saxonia iam pacata quieuit, & ſemel ſuſceptam fidem nunquam reiecit.



Habuerant Saxonum principes pro inſigni armorum in militaribus ſignis pullum equinum, atrum ante baptiſmum, poſt uerò candidum. Poſt multos uerò annos, quum ducatus Saxoniæ peruueniret ſubinde ad alios & alios dominos, arma ſæpius fuerunt mutata, uel leonibus ex Anglia allatis per Henricum ducem, cognomento Leonem, uel ſtratorijs in clypeo lignis, quę rutæ ſertum ex obliquo condecorat, per Bernhardum prius comitem de Anhold, inde uerò ſurrogatum Henrico Leoni in ducatum Saxoniæ, cum ille per Fridericum primum ſolenni imperij conuentu per ſententiam deponeretur.

Genealogia Vuedekindi ducis Saxoniæ.



Rabodus dux Friſonum.



Brunſuicum unde.

Vuigbettus 2. dux Angriæ accepit uxorem filiam Rabodi ducis illius Phriſonũ, qui baptiſandus rogauit, quo nam conceſsiſſent patres eius, & ubi audiuit omnes à Chriſto alienos in perditionẽ abiiſſe, pedẽ è baptiſmo retraxiſſe, ſecq; eò profecturum conteſtans, quo maiorum ſuorũ cœtus demigraſſet. Fuerat iſte Vuigbertus Chriſto ualde deuotus ab adoleſcentia uſq; ad ſupremam ætatem, ſepultus in Vuildeshuſen oppido Bremenſis diocœſis, ubi & poſtea Vualbertus in Chriſti religione obdormiens ſepultus fuit. Bruno à q̃ Brunſuicum nomẽ accepit, uir inſignis, glorioſo fine pro fide Chriſti occubuit. Nam

The front of the page 871 bearing the heading LIBER III delves into the mineral riches and the political geography of central Germany, hosting the chapters DE METALLIS SAXONIAE (Cap. CCCCXXXV) and DE DIVISIONE MODERNAE SAXONIAE (Cap. CCCCXXXVI). The Latin text offers a mineralogical discussion of the ore deposits of Eisleben, Mansfeld, and Goslar (Minera Goslariana), describing bituminous schists, pyrite, and fossil fuels. Münster also describes the prodigy of fossils, stones on which nature has impressed figures of fish, lizards, or even birds. The central portion of the front hosts a splendid woodcut that shows in detail a fossil fish enclosed in rock. Below, the next chapter analyzes

the geographic and riverine division of modern Saxony (Saxoniae superior and inferior). Of great historical-collecting significance are the contemporary marginal notes (Lapides fissiles, Natura figurat lapides, Galena, Saxoniae superior and inferior).

Turning to the page 872, the back bearing the heading DE GERMANIA concentrates on medieval Saxon history and dynastic matters with the opening of the chapter DE DVCIBVS SAXONIAE ET EORVM genealogia (Cap. CCCCXXXVII). The Latin text recounts the historic wars between Charlemagne and the ancient Duke of the Saxon s Vitichindo (Vuitikindus), describing the fierce resistance of the latter in Angria and in Westphalia, until his submission and conversion to Christianity in the year 785 with baptism. The façade is exceptionally rich iconographically. It features at the top left two woodcut heraldic shields attributed to Vitichindo, followed in the center by the branched scheme of the Genealogia Vuedekindi ducis Saxoniae. At the bottom stands a large narrative woodcut illustrating a solemn encounter or an act of feudal submission between a sovereign on his throne and a dignitary, flanked by marginal typographic glosses (Vuitikindus, Babardus dux Frisonum, Brunsuicum unde) which highlight the historical origins of the houses and of the city of Braunschweig.

Page dimensions 30 x 20 cm.

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