

MARINE AND TERRESTRIAL VERTEBRATES FROM THE MIDDLE MIOCENE OF GRUND (LOWER AUSTRIA)

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Abstract: The Grund assemblage comprises 45 vertebrate species from marine and terrestrial ecosystems. A whale, sharks, rays, bony fishes, and sea-birds hint at marine conditions, whereas a salamander, a pheasant bird, turtles, snakes and land-mammals indicate various terrestrial paleoenvironments. Biostratigraphically the upper part of MN5 (mammals) and the upper part of the Lower Lagenidae Zone (foraminifers) are indicated. The assemblage of Grund therefore serves as a reference point for the continental/marine correlation in the Central Paratethys.

Key words: Badenian, Central Paratethys, fishes, amphibians, reptiles, birds, mammals.

Introduction

In Grund near Hollabrunn in Lower Austria, extended excavations were carried out by the University of Vienna's Institute of Paleontology in the field seasons 1998–2000.

The geological setting of the type area of the Grund Formation and the sedimentology of the Grund sections are investigated and discussed in detail by Roetzel & Pervesler (2004) (Fig. 1). The sediments are dominated by yellowish fine sands and silts; the channels are filled with coarser sand, fine gravel, and with molluscan debris, occasionally intermixed with vertebrate remains. For localization of the vertebrate-bearing layers in the sections (GRU-B1-1, GRU-B1-3, GRU-F-11) see Roetzel & Pervesler (2004: Fig. 4a–d).

In addition to the excavations, three large bulk samples were washed by members of the Natural History Museum Vienna and by students, focusing on smaller molluscs and vertebrates. For wet screening sieves with mesh sizes of 0.5, 2.5 and 5.0 mm were used. These investigations yielded a vertebrate assemblage that is expectedly poor in specimens (180) but surprisingly

diverse in species (45). The scarce, disarticulated terrestrial fossils are strongly eroded. They hint at long-distance transport from the hinterland, at reworking and dislocation, and at a final deposition in channels filled with sand and molluscan debris.

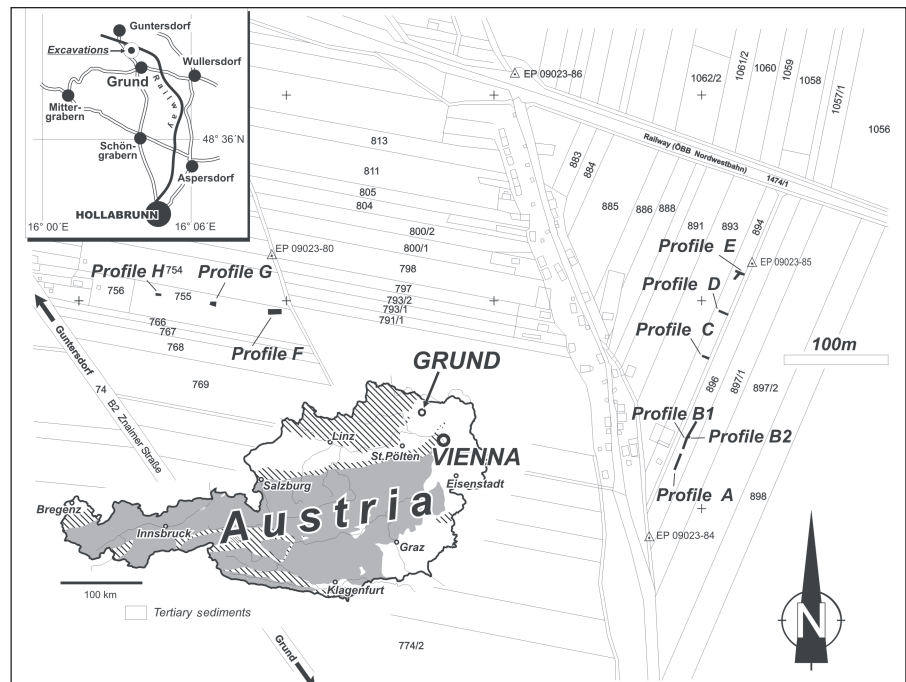


Fig. 1. Geographical and geological position of the locality Grund (slightly modified from Roetzel & Pervesler 2004).

Terrestrial and marine vertebrates

The vertebrate fossil from two localities of the Grund Beds in the Molasse Basin of Lower Austria, that is the fossil sites of Mühlbach and Grund, were recently investigated and published in a special volume (104 A) of the *Ann. Nat. Hist. Mus. Wien* (2003). These two seemingly unspectacular assemblages merit special attention because terrestrial and marine organisms occur together in isochronous marine sediments. They not only provide insight into various ecosystems, but also allow a correlation to be established between continental and marine biozonations.

The present paper summarizes our present knowledge of the vertebrates from the Grund sections, from some wine cel-

lars in Grund, and from the neighbouring village of Guntersdorf (Table 1). A total of 45 taxa were described and figured in the above-mentioned special volume (104 A): 19 fishes (Schultz 2003), 1 amphibian and 6 reptiles (Miklas-Tempfer 2003), 4 birds (Göhlich 2003), 1 insectivore (Ziegler 2003), 2 rodents (Daxner-Höck 2003), 4 carnivores (Nagel 2003), 5 ruminants (det. Roessner), 2 proboscideans (Huttunen 2003) and 1 whale (det. Kazár).

Pisces — Schultz (2003): The fish fauna is poor, even though the Grund area has been sampled for over 150 years. The total yield is 19 marine fish-taxa: 8 sharks/Squalomorphii, 6 rays/Batomorphii and 5 bony fishes/Osteichthyes. The small-sized sharks as well as the rays and the bony fishes indicate a shallow sea. The habitat can be classified as neritic. The shark

Table 1: Middle Miocene vertebrates from the locality Grund (sections GRU-B1 and GRU-F) and Guntersdorf. The specimens are housed in the collections: Natural History Museum Vienna, Geol.-Paleontol. Department (Nat. Hist. Mus. Vienna), Institute of Paleontology, University of Vienna ¹⁾, Niederösterreich. Landesmuseum ²⁾, H. Schaffer ³⁾, Geological Survey Vienna ⁴⁾, A. Kroh ⁵⁾.

	GRU-B1-1 (1998)	GRU-B1-3 (1998)	GRU-F-11 (1999)	Nat. Hist. Mus. Vienna	Uni Vienna ¹⁾ NÖ Land. Mus. ²⁾ CollSCHAFER ³⁾ Geol. Surv. ⁴⁾	GRU-KROH ⁵⁾
Pisces (Schultz 2003)						
Squalomorphii indet.		2 vertebrae				
<i>Notorynchus primigenius</i> (Agassiz, 1843)			2 teeth			
<i>Carcharias acutissimus</i> (Agassiz, 1844)		9 teeth	22+3? teeth			
<i>Carcharias cuspidatus</i> (Agassiz, 1844)			9 teeth			
<i>Carcharias</i> sp.		2 teeth				
<i>Scyliorhinus distans</i> (Probst, 1879)			1 tooth			
<i>Carcharhinus priscus</i> (Agassiz, 1843)	1? tooth	1+2? teeth	11 teeth			
<i>Galeocerdo aduncus</i> Agassiz, 1843				2 teeth		
<i>Sphyrna?</i> sp.		1 tooth				
<i>Dasyatis</i> cf. <i>rugosa</i> (Probst, 1877)		1 tooth	1 tooth			
<i>Dasyatis</i> sp.		1 tooth		1 tooth		
<i>Myliobatis</i> sp.				1 toothplate		
<i>Rhinoptera</i> sp.			1 toothplate			
<i>Myliobatis/Rhinoptera</i> sp.	1 toothplate	2 toothplates	5 toothplates			
<i>Aetobatus arcuatus</i> Agassiz, 1843		1 toothplate		2 toothplates		
Myliobatidae/Dasyatidae		2 tail spines	1 tail spine			
<i>Diplodus incisivus</i> (Gervais, 1852)		2 teeth				
<i>Sparus umbonatus</i> (Münster, 1846)			6 teeth	10 teeth		
<i>Pagrus cinctus</i> (Agassiz, 1836)		1 tooth	1+?1 teeth			
Sparidae indet.		13 teeth	10 teeth			
<i>Sphyræna</i> sp.		1 tooth				
Amphibia (Miklas-Tempfer 2003)						
<i>Salamandra sansaniensis</i> Lartet, 1851	1 vertebra					
Reptilia (Miklas-Tempfer 2003)						
<i>Testudo</i> sp.					1 humerus ²⁾ 1 shellfrag. ¹⁾ shellfrag. ³⁾	
<i>Ptychogaster grundensis</i> Bachmayer et Schaffer, 1959		2 shellfrag.		cast of Holotypus	1 carapax (Holotypus) ³⁾ shellfrag. ³⁾	1 shellfrag.
<i>Trionyx vindobonensis</i> Peters, 1855						
Anguidae indet.			1 vertebra			
<i>Elaphe kohfidischi</i> Bachmayer et Szyndlar, 1985	1 vertebra		1 vertebra			2 vertebrae
<i>Naja romani</i> Hofstetter, 1939	1 vertebra		3 vertebrae			1 vertebra

Sphyrna and the rays *Rhinoptera* and *Aetobatis* indicate tropical to subtropical conditions. Living relatives of all remaining taxa inhabit tropical to temperate waters.

Amphibia and Reptilia — Miklas-Tempfer (2003: Figs. 2–14; Plates 1–5): The herpetofauna points to a wooded paleoenvironment and partly to some standing or slowly flowing freshwater habitats. The reptiles are: 3 tortoises (*Ptychogaster grundensis*, *Testudo* sp. and *Trionyx vindobonensis*), 1 species of Anguidae indet. and 2 snakes (*Elaphe kohfidischi* and *Naja romani*). The amphibians are represented by only one member of the salamanders, *Salamandra sansaniensis*. Its living relative is *Salamandra salamandra*,

which prefers hilly or mountainous wooded habitats up to 2000 m. This terrestrial salamander needs damp environments with bushes and deciduous woods, but can also be found in semiarid environments. While modern herbivorous Testudinidae live in dry environments, members of the fossil turtle *Ptychogaster* were terrestrial-aquatic animals inhabiting bushes and woods near water bodies. Terrapins of the genus *Trionyx* require standing or slowly flowing, shallow freshwaters with some sandy ground for burrowing. The ecological requirements of living Anguidae span from dry (e.g. *Pseudopus apodus*) to moist (e.g. *Anguis fragilis*). The snakes from Grund definitely point to ecologically dry conditions, such as

Table 1: Continued

	GRU-B1-1 (1998)	GRU-B1-3 (1998)	GRU-F-11 (1999)	Nat. Hist. Mus. Vienna	Uni Vienna ¹⁾ NÖ Land. Mus. ²⁾ Coll. SCHAFFER ³⁾ Geol. Surv. ⁴⁾	GRU-KROH ⁵⁾
Aves (Göhlich 2003)						
<i>Microsula pygmaea</i> (Milne-Edwards, 1874)	1 femur		1 humerus			
<i>Phalacrocorax intermedius</i> (Milne-Edwards, 1867) cf. <i>Palaeortyx intermedia</i> Ballmann, 1969	1 carpometa-carpus					1 coracoid
<i>Laridae</i> indet.			1 ulna			
Aves indet.			1 carpometa-carpus			
Insectivora (Ziegler 2003)						
<i>Schizogalerix pristinus</i> Ziegler, 2003	1 M2 sin.					
Rodentia (Daxner-Höck 2003)						
<i>Cricetodon meini</i> Freudenthal, 1963	1 maxilla		1 jaw 1 M1 sin.			
<i>Democricetodon mutilus</i> Fahlbusch, 1964			1 M2 dext.			
Carnivora (Nagel 2003)						
<i>Semigenetta sansaniensis</i> (Lartet, 1851)	maxilla P3-4					
Caniformia gen. et spec. indet.	1 phalange					
Mustelidae gen. et spec. indet.	1 caput femoris					
Carnivora indet.	1 vertebraefrag.					
Ruminantia (det. Rössner)						
Ruminantia indet.	1 atlas 1 frag. vert. 1 intermediale					1 m inf. 1 humerus-frag.
Pecora indet.	1 ulna prox.		2 phalanges			2 phalanges
<i>Micromeryx</i> sp.						1 M2 dext.
<i>Micromeryx</i> aff. <i>flourensianus</i> Lartet, 1851			1 M1 sin. 1 M2 dext. 1 m1 sin. 1 P4 dext.			
<i>Palaeomeryx eminens</i> von Meyer, 1847					1 p4 sin. ⁴⁾	
Proboscidea (Huttunen 2003)						
<i>Gomphotherium angustidens</i> Cuvier, 1817				1 incisorfrag.* 1 maxillafrag.*		
<i>Prodeinotherium bavaricum</i> von Meyer, 1841				1 d4 sin.		
Proboscidea indet.						1 sesamoid
Cetacea (det. Kazár)						
Mysticeti indet.	1 mandiblefrag.					

*deciduous dental material from Guntersdorf near Grund

in the case of *Elaphe kohfidischi*, which is a relative to the living Aesculapian snake. As a member of the Colubrinae it prefers dry and wooded environments, even without permanent water nearby. The living Aesculapian snake is a good climber on trees and bushes. Members of the genus *Naja*, a poisonous snake, are restricted to tropical areas today; they inhabit dry places and spend the day concealed in the vegetation and crevices.

Aves — Göhlich (2003: Plate1): The avifauna contains 4 taxa of different ecological habitats: a pheasant, a boobie, a cormorant and a gull. An additional carpometacarpus from an as yet undetermined bird was also found. Whereas the pheasant (cf. *Palaeortyx intermedia*) is a terrestrial bird, the boobie (*Microsula pygmaea*), the cormorant (*Phalacrocorax intermedius*) and the gull (Laridae indet.) are aquatic taxa, most of them probably marine. Modern boobies are sea-birds known worldwide from pelagic to coastal environments. The piscivorous cormorants are also cosmopolitan in marine and freshwater environments, preferring temperate to tropical waters of coasts, lakes, open swamps and slow-flowing rivers. Extant gulls (Laridae) are typically sea-birds, but are also found in inland waters. *Phalacrocorax intermedius* was previously known only from its Early Miocene type locality (Faluns de l'Orléanais, France) and is herewith recorded for the first time in the Middle Miocene (MN5).

Insectivora — Ziegler (2003: Tafel 1-2) and **Rodentia** — Daxner-Höck (2003: Plates 1-3): Small mammal fossils are extremely rare in the Grund fauna. The hedgehog *Schizogalerix pristinus*, the small hamster *Democricetodon mutilus* and the large hamster *Cricetodon meini* are represented by one molar each. Furthermore, one maxilla and a mandible without teeth can be assigned to the large hamster *Cricetodon*. These few small mammal fossils are identical to those of the hedgehog *S. pristinus* and the hamsters *C. meini* and *D. mutilus*, that is the most numerous mammals from Mühlbach. They are not only the dominating mammal species of the Mühlbach assemblage, but also highly relevant for stratigraphic interpretations. As a burrowing rodent, *Cricetodon* points to rather dry woodland and a low groundwater level; *Schizogalerix* is also indicative for a woodland habitat but hints at close-by freshwater habitats.

S. pristinus is the most primitive species of *Schizogalerix*, and Mühlbach is the earliest record of the genus in Central Europe. The large hamster *Cricetodon* migrated from Anatolia to SE-Europe in the Early Miocene (MN4). The first record of *C. meini* is Komotini in Greece (MN5). It reached Central and Western Europe and ultimately became extinct at the end of the Mammal Zone MN5. In Central Europe, *C. meini* marks a short time interval in the upper part of MN5. This is shown by several occurrences immediately below the “Brock”-hori-

Table 2: Stratigraphy and correlation of Early to Middle Miocene vertebrate faunas from Central Europe (slightly modified from Daxner-Höck 2003).

Time (Ma)	Chronos	Polarity	Austria	Czech Republic	Slovakia	Switzerland	Switzerland	Bentonites	Germany	MN Zones
14	C5ABn									13.5
	C5ABr									MN6
	C5ACn		Apfelberg		Bachtel-Ornberg			Laimering 4b, 5		
	C5ACr				Mettlen 4		Leimbach 14.15-14.22	Göttschlag		
	C5ADn				Oeschgraben		Waldkirch-Mollen 14.4	Laimering 2, 3, 4a		
C5ADr				Wiesholz			Unterzolling 1a			
15	C5ADr		Neudorf-Spalte		Katzenstebel			Ziemetshausen 1b		14.9
	1n		Strakonice		Chatzloch		Küsnacht 14.84-14.94	Unterneu 1c		
	C5Bn 1r		Mühlbach Grund		Aspitobel			Wannenwaldtobel 2		
	2n		Göriach		Frohberg			Ries Impact 14.9		
	C5Br				Vermes 2		Urdorf 15.22-15.31	Ziemetshausen 1a, 1c		
16	C5Br				Tobel Hombrechtikon			Edelbeuren-Maurekopf		MN5
	1n				Matt			Ebershausen Unterneu 1a		
	1r				Güntisberg			Eberstetten Altenstadt		
	C5Cn 2r							Oggenhof Affalterbach		
	2n							Betlinshausen Gisseltshausen		
17	C5Cn 3n		Teiritzberg		Vermes 1			Sandelzhausen Maßendorf		16.8
	3n		Obergänserndorf		Hüllistein			Puttenhausen Schönenberg		
	C5Cr		Franzensbad		Martinsbrünneli			Langenmoosen		
	C5Cr				Hubertingen			Engelswies Bellenberg		
	C5Dn		Wies Eibiswald		Tägermausraße			Rauscheröd Rembach		
18	C5Dn		Dolnice 3 Orechov					Günzburg		MN4
	C5Dr		Oberdorf					Langenau		
	C5Dr		Dolnice 1, 2					Erkertshofen		
								Petersbuch 2		18.0

Table 3: Early to Late Miocene geochronology and biostratigraphy (Harzhauser et al. 2003). The shaded area indicates the stratigraphic position of vertebrate-bearing samples of the Grund sections.

Time (Ma)	Epoch	Chronos	Polarity	Mediterranean Standard Stages	Western ("Central") Paratethys Stages	Eastern Paratethys Stages	Neogene Mammals	Planktonic Foraminifera	Calcareous Nannoplankton				
10	L. MIOC.	C4r		Tortonian	Pannonian	Maeotian	MN11	M13a	NN10				
		C4An					8.7						
11		C4Ar							9.88	MN10		NN9b	
		C5n								9.7			
11.54		C5r					MN9	M12	NN8/9a				
15	MIDDLE MIOCENE	C5An		Serravallian	Sarmatian	Bessarabian	MN 8-7	M11-M8	NN7				
		C5Ar								11.54	11.5	12.2	NN6
		C5AAn											
		C5ABn		Langhian	Badenian	Konkian	Karaganian	Tschokrakian	MN6	M7			
		C5ABr									13.59	13.0	Bolivina/Bulimina
		C5ACn											Spiroplectammina Zone
		C5ADn											
		C5ADr											
C5Bn													
C5Br													
16.4	E. MIOCENE	C5Cn		Karpatian	Tarkhanian	MN5	MN5	M5b	NN4				
C5Cr											16.1	M5a	
C5Dn			Burdigalian	Ottangian	Kotsakhurian	MN4	MN4	M4b					
C5Dr										16.8	M4a		
C5En											17.3	M3	
C5Er									18.3				
20		C6n		Eggenburgian	Sakaraulian	MN3	MN3	M2	NN2				
	C6r												

zon (indicating the Ries impact at 14.9 Ma) of the Upper Freshwater Molasse in Germany (Table 2). Above the "Brock"-horizon, *C. meini* was no longer present, but was replaced by its larger relative *C. aff. aureus*.

Carnivora — Nagel (2003: Plate 1): The carnivore fossils from Grund are: a maxilla with P4, a caput femori, a phalanx and some postcranial remains. Due to the size and the characteristic premolar, the maxilla could be identified as *Semigenetta sansaniensis*. It is the first record of this species in Austria. The caput femori is probably from a mustelid, while the phalanx could fit into the morphology of an amphicyonid. Some scarce postcranial remains can only be identified as Carnivora indet.

Ruminantia — det. Roessner: The investigated material from Grund sections comprises six isolated teeth and eight postcranial elements. While a species determination of the

teeth is possible, for the time being the postcranials and a strongly worn lower molar were assigned to Ruminantia indet. and to Pecora indet., respectively. *Micromeryx* aff. *flourensianus* is indicated by 4 isolated teeth. One M2 of *Micromeryx* sp. is slightly larger than the former. One P4 of *Palaeomeryx eminens* is listed in Pia & Sickenberg (1934). Detailed investigations on the ruminants are in progress.

Proboscidea — Huttunen (2003: Plate 1): *Gomphotherium angustidens* is represented by a fragmentary maxilla with left and right deciduous teeth (D2-4), permanent premolars (P2-3) and the M1, and by an isolated deciduous incisor. This exceptional finding from the locality of Guntersdorf near Grund was investigated for the first time by Schlesinger (1917: 17-22; Plate 1: Fig. 2a; Plate 2: Fig. 1). The present study yielded new details of deciduous and permanent tooth morphology and the existence of a permanent P2 of *G. angustidens*. The

second proboscidean, *Prodeinotherium bavaricum*, was identified on the basis of a deciduous lower d4 from the locality Grund. Furthermore, a sesamoid from Grund most likely belongs to a small-sized proboscidean.

Cetacea — det. Kazár: A mandible fragment of a baleen whale from Grund shows marked similarities to lower jaws of the genus *Mesocetus*, an insufficiently known Middle Miocene cetothere (Cetacea: Mysticeti: Cetotheriidae) reported from several localities of the Carpathian and Vienna Basins (Van Beneden 1884; Kadić 1904; Kellogg 1925; Pia 1937). Due to the lack of diagnostic cranial features, however, the fossil cetacean remains from Grund can only be referred to as Mysticeti indet.

Middle Miocene species classified as cetotheres were baleen-bearing, filter-feeding mysticetes structurally close to present-day balaenopterids (Fordyce & Muizon 2001). The most influential factor in baleen whale distribution is food supply: large whales today depend on dense patches of zooplankton or fish swarms (Gaskin 1976). Although the mandible fragment from Grund belonged to a small individual (estimated mandible length: 100–120 cm, and thus the estimated total body length falls well below the size of the smallest recent baleen whale, the minke whale, *Balaenoptera acutorostrata*), the presence of a mysticete in the Grund fauna indicates a high-productivity environment. Living baleen whales are distributed worldwide in pelagic marine environments and it is possible that Middle Miocene forms favoured similar habitats.

Paleoecology, stratigraphy and correlations

Paleoecology

The Grund assemblage combines elements of marine and terrestrial ecosystems. The shallow sea was inhabited by different sharks, rays and bony fishes. The presence of a baleen whale (Mysticeti) points to abundant planktonic organisms and/or fish swarms. Fishes were the food supply for the seabirds, the cormorant (*Phalacrocorax*) and the boobie (*Microsula*), while the gull (Laridae) might have fed on eggs, on small birds and on the fish-prey that was lost by cormorants and boobies. The amphibians, reptiles, the pheasant bird and the land mammals represent different terrestrial environments. More dry areas along the coast and on land — slopes covered with dense bushes, shrubs and smaller trees — were inhabited by the tortoises (*Testudo*), the snakes (*Elaphe* and *Naja*), the pheasant bird (cf. *Palaeortyx*), and by the hamsters (*Cricetodon* and *Democricetodon*). On the other hand, the salamander (*Salamandra*), the terrapin (*Trionyx*), the semi-aquatic turtle (*Ptychogaster*), and the hedgehog (*Schizogalerix*) preferred wooded environments close to standing or flowing freshwater. The musk deer-like (*Micromeryx*) and the large ruminant (*Palaeomeryx*) most probably inhabited swampy forests and floodplains along rivers, as did the proboscideans (*Gomphotherium* and *Prodeinotherium*). All these herbivorous mammals, birds and the reptiles were potential prey of the carnivore-omnivore hunters, that is the viverrid (*Semigenetta*) and the amphicyonid and mustelid carnivores.

Stratigraphy and correlation

According to Daxner-Höck (2003) the terrestrial vertebrate assemblages with *Cricetodon meini* are representative of the late MN5 and are definitely older than the Ries event, which is dated at ~14.9 million years (Table 2). The marine fauna of the Grund Formation corresponds to the foraminiferal Zone Lower Lagenidae Zone. It is interpreted by Rögl et al. (2002) and Rögl & Spezzaferri (2003) to span the upper part of the planktonic foraminiferal Zone M5b (indicated by *Praeorbulina glomerata circularis*) to Zone M6 (FAD of *Orbulina suturalis*) at 15.1 million years (Table 3). The co-occurrence with rodents, indicating the late MN5, agrees with this dating. Therefore, the fauna from Grund serves as a reference tie point for marine/continental correlation in the Central Paratethys.

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