

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 (foraminiferas) 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 (this volume) (Fig. 1). The sediments are dominated by yellowish fine sands and silts; the channels are filled with coarser sand, fine gravel, and with mollusc 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 (this volume: 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 mollusc debris.

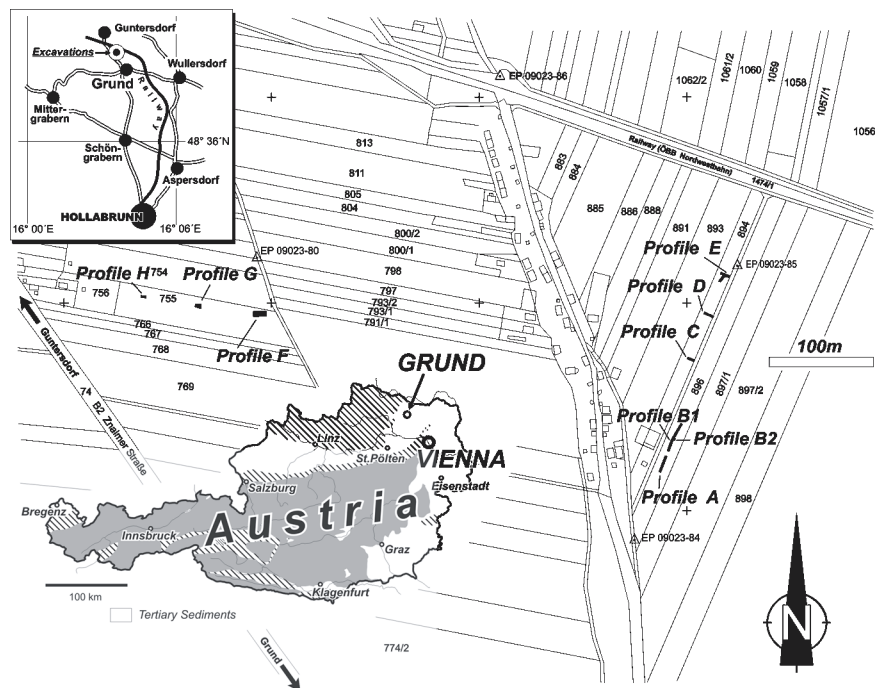


Fig. 1. Geographical and geological position of the locality Grund (slightly modified from Roetzel & Pervesler, this volume).

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 cellars in

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. Wien), Institute of Paleontology, University of Vienna ¹, Niederöstrerr. 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 Coll. SCHAFFER 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+?1teeth			
Sparidae indet.		13 teeth	10 teeth			
<i>Sphyaena</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 & Schaffer, 1959		2 shellfrag.		cast of Holotypus	1 carapax (Holotypus) ³⁾	1 shellfrag.
<i>Trionyx vindobonensis</i> Peters, 1855					shellfrag. ³⁾	
Anguidae indet.			1 vertebra			
<i>Elaphe kohfidtschi</i> Bachmayer & Szyndlar, 1985	1 vertebra		1 vertebra			2 vertebrae
<i>Naja romani</i> Hofstetter, 1939	1 vertebra		3 vertebrae			1 vertebra

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

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)	1 carpometacarpus					
cf. <i>Palaeortyx intermedia</i> Ballmann, 1969						1 coracoid
<i>Laridae</i> indet.			1 ulna			
Aves indet.			1 carpometacarpus			
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.					

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 *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 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”-horizon (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; Plate1: 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 cetother (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 sea-

birds, 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

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	Switzerland	Switzerland	Germany	MN Zones
			Czech Republic Slovakia		Bentonites		
14	C5ABn	Black					13.5
	C5ABr	White		▶ Bachtel-Ornberg		Laimering 4b, 5	MN6
	C5ACn	Black	Apfelberg	▶ Mettlen 4 ▶ Oeschgraben ▶ Wieshölz ▶ Rümikon	▶ Leimbach 14.15-14.22 ▶ Waldkirch-Mollen 14.4	Göttschlag	
	C5ACr	White				Laimering 2, 3, 4a	
	C5ADn	Black				Unterzolling 1a	
C5ADr	White	Neudorf-Spalte Strakonice	▶ Katzenstebel ▶ Chatzloch ▶ Aspibobel	▶ Künsnacht 14.84-14.94	Gallenbach		
15	1n	Black				Ziemetshausen 1b	14.9
	C5Bn 1r	White	Mühlbach Grund	▶ Frohberg	▶ Urdorf 15.22-15.31	Unterneu 1c	
	2n	Black	Göriach	▶ Vermes 2		Wannenwaldtobel 2	
16	C5Br	White		▶ Tobel Hombrechtikon		Ziemetshausen 1a, 1c	MN5
	1n	Black		▶ Vermes 1		Edelbeuren-Maurerkopf	
	1r	White		▶ Hüllistein		Ebershausen Unterneu 1a	
	C5Cn 2n	Black		▶ Martinsbrünneli		Eberstetten Altstadt	
	2r	White				Oggenhof Affalterbach	
17	C5Cr	White	Teiritzberg Obergänserndorf Franzensbad			Betlinshausen Gisselshausen	MN4
	C5Dn	Black	Wies Eibiswald Dolnice 3 Orechov	▶ Hubertingen ▶ Tägernausraße		Sandelzhausen Maßendorf	
	C5Dr	White	Oberdorf			Puttenhausen Schönenberg	
	Dolnice 1, 2					Langenmoosen Engelswies Bellenberg	
18	C5Dr	White				Rauscheröd Rembach	16.8
						Günzburg Langenau	
						Erkertshofen Petersbuch 2	18.0

- marine correlation
- radiometric dating
- GPTS correlation

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						
		C4Ar					9.88			MN10	9.7	NN9b	
		C5n								MN9	11.1	NN8/9a	
		C5r					11.54			11.5	Bessarabian	M12	NN7
	15	MIDDLE MIOCENE	C5An		Serravallian	Sarmatian	Volhynian	MN 8-7	M11-M8	NN6			
			C5Ar								13.0	Konkian	M7
			C5AAn										
			C5ABn		Bolivina/Bulimina	Tschokrakian	MN6						
			C5ABr		Spiroplectammia Zone								
C5ACn				Langhian	Upper Lagenid Zone	Tarkhanian	14.9	M6	NN5				
C5ADn													
C5ADr													
C5Bn				Burdigalian	Lower Lagenid Zone	Karpatian	MN5	M5b	M5a	NN4			
C5Br											16.4	Otnangian	Kotsakhurian
C5Cn		16.8	M4a								17.3		
C5Cr		18.0	M3								18.3		
C5Dn													
C5Dr													
C5En		Eggenburgian	Sakaraulian	MN3	M2	NN3							
C5Er													
C6n													
20	E. MIOCENE	C6r					20.0		NN2				

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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