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Habitat tracking, range dynamics and palaeoclimatic significance of Eurasian giant salamanders (Cryptobranchidae) — indications for elevated Central Asian humidity during Cenozoic global warm periods

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ABSTRACT

Environmental fluctuations are a driving force in vertebrate evolution, but cryptobranchids (giant salamanders) show little morphologic change since the Jurassic. Here we analyze their fossil distribution in the Cenozoic of Eurasia and show that morphologic stasis is also maintained by stable environments, making giant salamanders an ideal proxy-group for environmental and palaeoclimatic studies. The climate space of recent and fossil cryptobranchids is best characterized by high humidity with mean annual precipitation values over 900 mm. The recorded patchiness of their fossil record can be explained by habitat tracking and/or range expansion from higher altitudes into lowland settings during humid periods with increased basinal relief. In Central Asia cryptobranchids are recorded from five intervals, four of them are global warm periods: Paleocene–Eocene Thermal Maximum, Late Oligocene warming, Miocene Climate Optimum, and Mio-Pliocene transition. This distribution suggests that during global warmth the Asian cold high pressure zone during winter months may be weak or absent, thus moist westerly winds penetrate far into the continent. The presence of cryptobranchids also indicates that the aridification across the Eocene–Oligocene boundary as reported from Mongolia and northwestern China, does not occur in the Zaysan Basin, probably due to increased upslope precipitation in the rising Altai Mountains.

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1. Introduction

Cryptobranchids represent a group of large sized (up to 1.8 m), paedomorphic basal salamanders known since the Middle Jurassic (Gao and Shubin, 2003; Frost et al., 2006). The group has experienced so little morphological change over the last 160 Myr (Gao and Shubin, 2003) that the two extant genera, the North-American *Cryptobranchus* and the East-Asian *Andrias*, can be regarded as living fossils. This observed morphologic stasis may be attributed to their high degree of behavioral, physiological, and developmental plasticity (Wake et al., 1982; Gao and Shubin, 2003). Here we analyze the fossil cryptobranchid distribution in Eurasia during the last 60 myrs and suggest that morphologic stasis in giant salamanders may also be maintained by relatively stable long-term environmental conditions, which reduce the adaptive plasticity in populations (Masel et al., 2007). We argue that cryptobranchid populations maintained stable environments by habitat tracking or habitat restriction to mountainous refuges during unfavorable conditions in lowland basins. By these, giant salamander fossils can be regarded as very useful palaeoclimatic and palaeoenvironmental proxy organisms.

2. Eurasian cryptobranchids during the Cenozoic

Two extant species of cryptobranchids can be found in eastern Eurasia: *Andrias davidianus* (China) (Fig. 1) and *A. japonicus* (Japan) (Fig. 2). Both are strictly aquatic amphibians and confined to clear, well-oxygenated, cold mountain streams and rivers. They might occur also in lowland rivers earlier in the Holocene (Thenius, 1954), where they are absent now probably due to increased human hunting pressure.

Cenozoic giant salamanders are known from the mid-latitudes of Eurasia with four genera and five or six species from 53 localities, ranging from the Late Paleocene to the Pleistocene (Table 1, Fig. 3). Besides *Aviturus exsecratus* and *Ulanurus fractus* from the latest Paleocene of Mongolia (S-Mongolia, 43°N, 100°E), the Late Eocene species *Zaissanurus beliajevae* is restricted to the Central Asian Zaysan Basin (SE-Kazakhstan, 50°N, 85°E), whereas the Late Oligocene to Early Pliocene species *Andrias scheuchzeri* is widely distributed from

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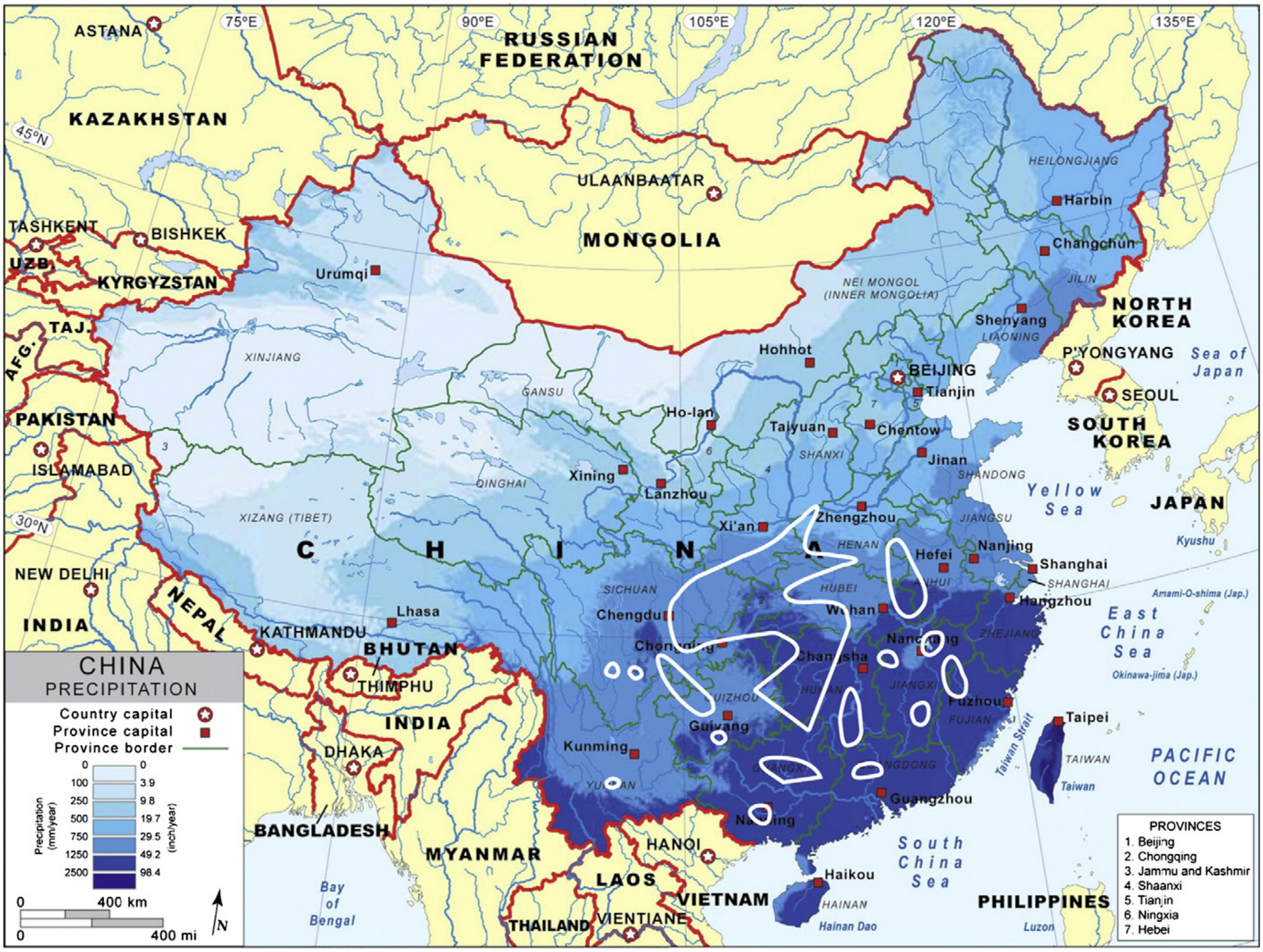

Fig. 1. Current distribution (white lines) of recent *Andrias davidianus* and mean annual precipitation map of China.

Central Europe to Western Siberia and the Zaysan Basin. The fossil record from their present-day distribution area in East Asia starts late (Early Pliocene) and is so far restricted to Japan (Table 1, Fig. 3).

2.1. Palaeoclimatic significance of cryptobranchids

To assess the palaeoclimatic significance of giant salamanders we analyzed climate parameters in their present-day distribution area in East Asia and North America (Table 2) and at selected fossil localities from Europe and Central Asia with an independent palaeoclimate record (Table 3). Humidity turns out to be the key parameter in defining the climate space for cryptobranchids, whereas temperature has a lesser role. All recent and all investigated extinct cryptobranchid species exclusively occur in humid areas, without a distinct dry season and with mean annual precipitation (MAP) exceeding 900 mm (900–1.900 mm), irrespective of the related climatic zone, which ranges from warm subtropical to temperate (Tables 2 and 3). This strongly suggests that fossil cryprobranchids are a useful proxy for significantly elevated levels (MAP > 900 mm) of past humidity. We denote this concordance of ancient and extant humidity requirement as environmental stability, which is remarkable, because recent investigation shows that unlike cryptobranchid salamanders other ectothermic vertebrates display a broad environmental plasticity during their evolution (e.g., the anguin lizard *Pseudopus*, Klembara et al., 2010).

2.2. Explaining the fossil cryptobranchid distribution in Eurasia

In all regions over Eurasia, the fossil distribution is stratigraphically patchy (Fig. 4). In Central Asia cryptobranchids occurred only during five periods; the latest Paleocene, the Late Eocene to earliest Oligocene, the latest Oligocene, the late Early to early Middle Miocene and the Miocene–Pliocene transition (grey bars in Fig. 4). All fossils are found in lowland habitats, within deposits of distal meandric rivers as well as in lake sediments. The occurrence in basinal lacustrine deposits stands in contrast to their recent habitats (Thenius, 1954; Westphal, 1958). However, juvenile individuals have thus far been found only in fluvial sediments, which suggest a habitat shift in ontogeny. To explore their patchiness in stratigraphic distribution, as well as their past habitat extension into lakes in distal basinal settings, the temporal evolution of the palaeoclimate and basin topography can provide key-information.

The Neogene humidity evolution in Central Europe is highly variable (as it was probably also in Central Asia), with frequent changes between humid and semi-arid climates (Böhme et al., 2008, 2011). However, cryptobranchids are not recorded in each and every humid period. The patchiness of their fossil record suggests that elevated humidity is a necessary, but not sufficient condition to explain their past distribution. To understand the dependency relationship between this full-aquatic salamanders and humidity we analyze the hypothesis that relatively cool, oxygenated rivers and rivulets, which are a prerequisite for cryptobranchid larval development and typically occur in mountainous

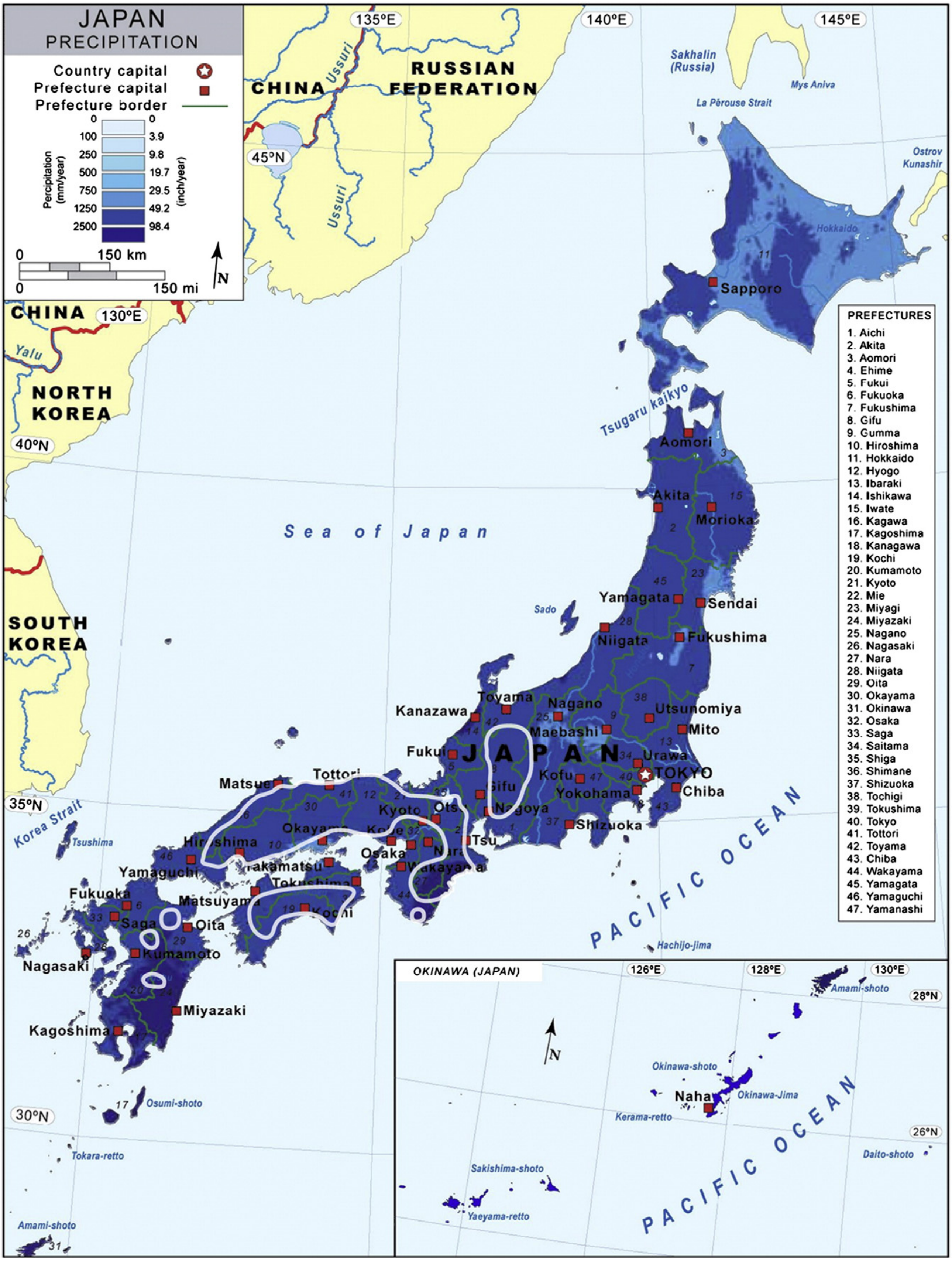

Fig. 2. Current distribution (white lines) of recent *Andrias japonicus* and mean annual precipitation map of Japan.

Table 1
Localities, coordinates, ages, taxon and references for giant salamanders (Cryptobranchidae) from the Cenozoic of Eurasia. Country information of localities are abbreviated and in brackets: Au — Austria, Cz — Czechia, Ge — Germany, Gr — Greece, Jp — Japan, Ka — Kazakhstan, Mo — Mongolia, Ru — Russia, Uk — Ukraine.

	Locality	Coordinates	Stage	Age (Ma)	Taxon	Reference
1	Shikimizu quarry (Jp)	N 33.4667 E 132.717	Late Pleistocene	0.012–0.126	*Andrias japonicus*	Shikama and Hesegawa, 1962
2	Ajimu-Chro (Jp)	N 33.4362 E 131.37	Piacencian	2.80–4.30	*Andrias* sp.	Matsui et al., 2001
3	Willershausen (Ge)	N 51.7833 E 10.10	Zanclean	3.60–5.30	*Andrias scheuchzeri*	Westphal, 1967
4	Kuchurgan (Uk)	N 46.75 E 29.9833	Zanclean	4.85–5.25	*Andrias* sp.	Chkhikvadze, 1982
5	Antipovka (Ru)	N 50.7019 E 40.0167	Zanclean	4.896–4.997	Cryptobranchidae indet.	Averianov, 2001
6	Maramena (Gr)	N 41.1791 E 23.4711	Zanclean	5.25–5.50	Cryptobranchidae indet.	this paper
7	Pavlodar 2A (Ka)	N 52.2759 E 79.9897	Messinian	5.30–5.60	Cryptobranchidae indet.	Chkhikvadze, 1984, this paper
8	Götzendorf (Au)	N 48.0167 E 16.5833	Tortonian	9.78–9.94	*Andrias scheuchzeri*	Miklas, 2002
9	Vösendorf-Brunn (Au)	N 48.20 E 16.36	Tortonian	10.25–10.45	*Andrias scheuchzeri*	Westphal, 1958
10	Hammerschmiede 1 (Ge)	N 47.9258 E 10.5989	Tortonian	11.08–11.28	*Andrias* sp.	this paper
11	Gritsev (Uk)	N 49.975 E 27.16	Tortonian	11.10–11.50	*Andrias scheuchzeri,* Cryptobranchidae gen. et sp. nov.	this paper
12	Mörgen (Ge)	N 48.1521 E 10.5059	Tortonian	11.10–13.30	*Andrias scheuchzeri*	Böhme, 2003
13	Tiefenried (Ge)	N 48.20 E 10.4833	Tortonian	11.10–13.30	*Andrias scheuchzeri*	this paper
14	Derndorf (Ge)	N 48.183 E 10.4717	Tortonian	11.20–12.50	*Andrias scheuchzeri*	Böhme, 2003
15	Eppishausen (Ge)	N 48.1669 E 10.5211	Tortonian	11.20–12.50	*Andrias scheuchzeri*	Böhme, 2003
16	Mataschen (Au)	N 46.903 E 15.9555	Tortonian	11.30–11.45	*Andrias scheuchzeri*	Tempfer, 2004
17	Wartenberg near Erding (Ge)	N 48.4013 E 11.9993	Serravallian	12.00–13.00	*Andrias* sp.	Westphal, 1970
18	Zeilarn (Ge)	N 48.2834 E 12.8942	Serravallian	12.50–12.70	*Andrias scheuchzeri*	this paper
19	Oehningen oberer Bruch (Ge)	N 47.6667 E 8.90	Serravallian	12.50–13.20	*Andrias scheuchzeri*	Westphal, 1958
20	Kirchheim in Schwaben (Ge)	N 48.1833 E 10.4833	Serravallian	13.00–14.00	*Andrias scheuchzeri*	Böttcher, 1987
21	Poltinik (Ka)	N 47.45 E 84.47	Langhian	13.00–15.00	*Andrias karelcapeki*	Chkhikvadze, 1982
22	Hambach 6 C (Ge)	N 50.90 E 6.45	Langhian	14.50–14.90	*Andrias scheuchzeri*	Böhme, 2003
23	Tri Bogatirya (Ka)	N 47.60 E 83.80	Langhian	15.00–18.00	*Andrias karelcapeki*	Chkhikvadze, 1982
24	Vympel (Ka)	N 47.45 E 84.47	Langhian	15.00–18.00	*Andrias karelcapeki*	Chkhikvadze, 1982
25	Illerkirchberg 1 (Ge)	N 48.31 E 10.046	Burdigalian	16.70–17.00	*Andrias scheuchzeri*	Sach and Heinzmann, 2001
26	Illerkirchberg hor. 3a (Ge)	N 48.31 E 10.04	Burdigalian	17.20–17.40	*Andrias scheuchzeri*	Böttcher, 1987
27	Reisensburg near Günzburg (Ge)	N 48.462 E 10.314	Burdigalian	17.30–17.60	*Andrias* sp.	Westphal, 1970
28	Ringingen-Frontal 2 (Ge)	N 48.35 E 9.8167	Burdigalian	17.70–17.80	*Andrias scheuchzeri*	Sach and Heinzmann, 2001
29	Langenau 1 (Ge)	N 48.5003 E 10.1219	Burdigalian	17.75–17.80	*Andrias scheuchzeri*	Böttcher, 1987
30	Hochberg near Jungnau (Ge)	N 48.1513 E 9.24447	Burdigalian	17.75–17.85	*Andrias* sp.	Westphal, 1970
31	Ringingen-Frontal 1 (Ge)	N 48.35 E 9.8167	Burdigalian	17.75–17.85	*Andrias scheuchzeri*	Sach and Heinzmann, 2001
32	Břešt'any near Bilina (Cz)	N 50.5667 E 13.75	Burdigalian	18.00–19.00	*Andrias scheuchzeri*	Kvacek et al., 2004
33	Eggingen-Mittelhart (Ge)	N 48.3523 E 9.8598	Burdigalian	17.85–17.90	*Andrias scheuchzeri*	Sach and Heinzmann, 2001
34	Merkur North, Ahnikov (Cz)	N 50.45 E 13.4333	Burdigalian	20.00–20.00	*Andrias* sp.	Böhme, 2003; Kvacek et al., 2004
35	Rott near Hennef (Ge)	N 50.7833 E 7.2833	Chattian	23.80–24.50	*Andrias scheuchzeri*	Westphal, 1958
36	Altyn Shokysu (Ka)	N 47.2724 E 61.025	Chattian	23.80–24.70	*Zaissanurus beliajevae*	this paper
37	Oberleichtersbach (Ge)	N 50.35 E 10.05	Chattian	24.00–24.00	*Andrias scheuchzeri*	Böhme, 2008
38	Pancirny Sloy (Ka)	N 48.2158 E 84.3248	Priabonian	33.80–35.00	*Zaissanurus beliajevae*	Chkhikvadze, 1982
39	Maylibay (Ka)	N 47.4833 E 84.7183	Rupelian	31.00–33.80	Cryptobranchidae indet.	Chkhikvadze, 1984
40	Talagay, Tayzhuzgen section (Ka)	N 47.5984 E 84.00	Rupelian	31.00–33.80	*Zaissanurus beliajevae*	Chkhikvadze, 1982, 1984
41	Korablik (Ka)	N 48.00 E 84.50	Priabonian	33.80–34.60	Cryptobranchidae indet.	this paper
42	Korsak B (Ka)	N 47.4733 E 85.51	Priabonian	35.00–37.00	*Zaissanurus beliajevae*	this paper
43	Sopka obo (Ka)	N 48.2158 E 84.3248	Priabonian	35.00–37.00	*Zaissanurus* sp.	this paper
44	Konur-Kura (Ka)	N 47.4401 E 84.4981	Priabonian	36.20–37.00	*Zaissanurus beliajevae*	Chkhikvadze, 1982
45	Kusto-Kyzylkain section (Ka)	N 47.6137 E 84.1009	Priabonian	35.00–37.00	*Zaissanurus beliajevae*	Chkhikvadze, 1982
46	Lager Biryukova (Ka)	N 48.2158 E 84.3248	Priabonian	35.00–37.00	*Zaissanurus* sp.	this paper
47	Pod Chernim (Ka)	N 48.2158 E 84.3248	Priabonian	35.00–37.00	*Zaissanurus* sp.	this paper
48	Yakor (Ka)	N 48.2158 E 84.3248	Priabonian	33.80–35.00	*Zaissanurus* sp.	this paper
49	Belye Salamandry (Ka)	N 48.2158 E 84.3248	Priabonian	35.00–37.00	*Zaissanurus* sp.	this paper
50	Tsagan-Khushu, Naran member, top (Mo)	N 43.455 E 100.37	Thanetian	55.80–56.00	*Aviturus exsecratus*	Gubin, 1991
51	Aguy-Dats-Bulak, Naran member, top (Mo)	N 43.455 E 100.50	Thanetian	55.80–56.00	*Aviturus exsecratus*	Gubin, 1991
52	Aguy-Dats-Bulak, Naran member, top (Mo)	N 43.455 E 100.50	Thanetian	55.80–56.00	*Ulanurus fractus*	Gubin, 1991
53	Aguy-Dats-Bulak, Naran member, layer 6 (Mo)	N 43.4667 E 100.445	Thanetian	56.02–56.04	*Aviturus exsecratus*	Gubin, 1991

habitats, developed in basinal settings only during periods of increased basinal relief and/or very humid climates. Elevated ground-water levels and increased uplift and erosion will strengthen alluvial springs, whose discharge is regulated mainly by precipitation. This hypothesis can be tested in two well-studied and sampled Cenozoic basins: the European North Alpine Foreland Basin (NAFB) bounded by the Alpine orogene in the south, and the Central Asian Zaysan Basin in southeastern Kazakhstan, bounded by the Altai Mountains in the northeast and the Tian Shan, respectively Tarbagatai Mountains in the south (Fig. 3).

In the NAFB, *Andrias* fossils are known from 16 localities (Table 1, Fig. 4; Böttcher, 1987; Böhme and Ilg, 2003) within two narrow time periods: between 17.8 and 17.4 Ma (8 localities from the Brackishwater Molasse and the earliest part of the Upper Freshwater Molasse — UFM), and between ~13 and ~11.5 Ma (8 localities from the Younger Series of the UFM, including the famous site of Oehningen, the type locality of *Andrias scheuchzeri*). In hundreds of fossil localities analyzed, not a single cryptobranchid was found in the time-interval between the two periods (Böhme, 2010). The cryptobranchid-bearing intervals of the NAFB differ significantly in respect to temperature and vegetation (paratropical evergreen forests versus subtropical/warm temperate deciduous forests, Böhme et al., 2007), but show analogies in terms of basinal relief. Both times are characterized by erosion and hiatuses at the basin margin (Grimm, 1957), moderate alpine topography (Kuhlemann, 2007) and the incision of major valleys (e.g., Graupensand valley, Reichenbacher et al., 1998; Palaeo-Inn valley, Frisch et al., 1998) to which most cryptobranchid localities are bounded (Fig. 5).

From the Zaysan Basin, cryptobranchid salamanders are also known from two time periods only (Fig. 4). From the older period, ten localities derive from the Late Eocene (Late Aksyr and Kusto Formations) and two localities from the earliest Oligocene (Buran

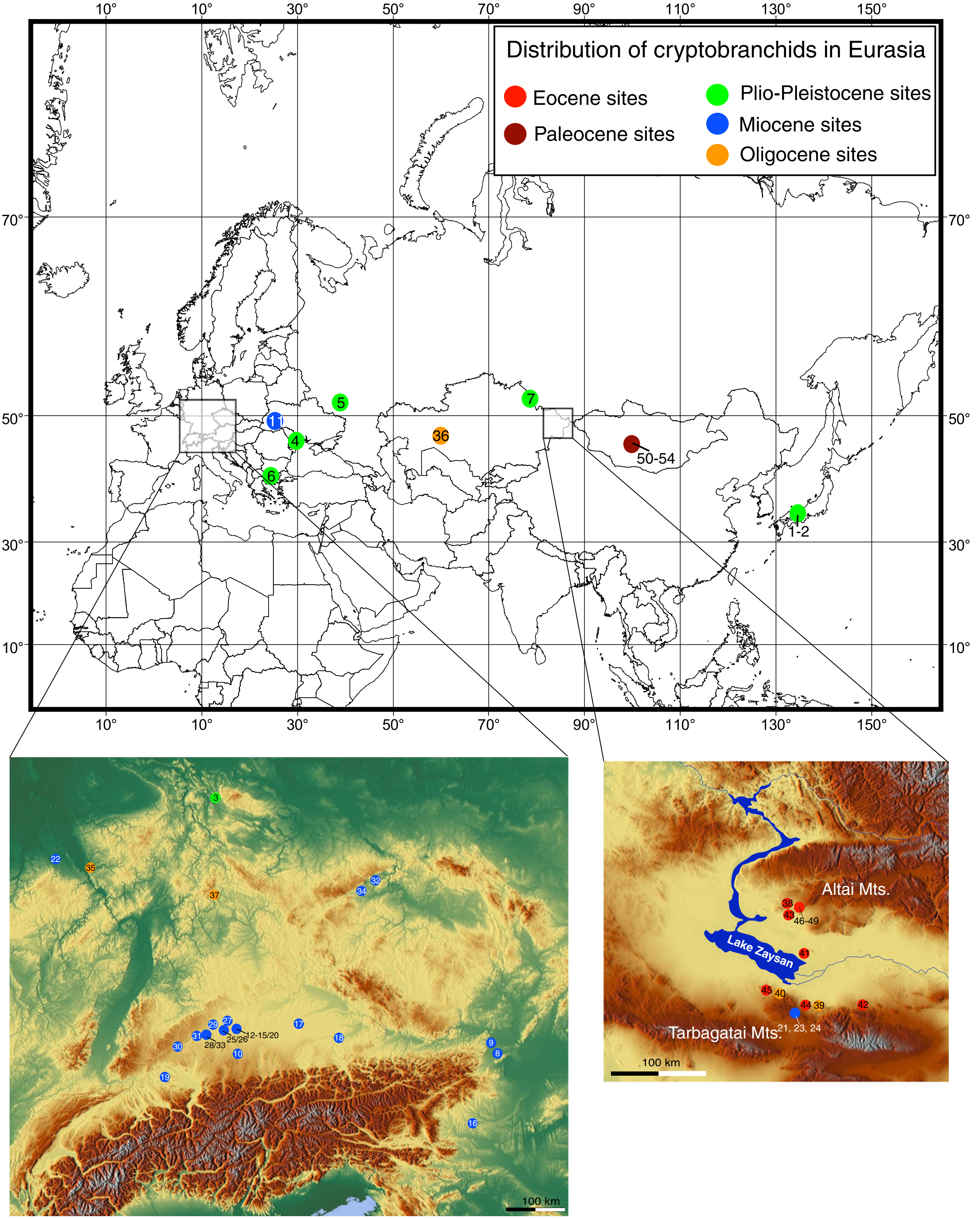

Fig. 3. Map of Eurasia showing the Cenozoic localities of giant salamanders. The dense record in Central Europe and the Zaysan Basin is shown in separate topographic maps. Numbers refer to localities in Table 1.

Table 2
Mean annual precipitation (MAP) from climate stations within the distribution area of extant Eurasian and North American cryptobranchids.

Climate station	Species	MAP	Reference
Hiroshima	*A. japonicus*	1.597	Müller and Hennings, 2000
Osaka	*A. japonicus*	1.360	Müller and Hennings, 2000
Kyoto	*A. japonicus*	1.585	www.weather.com, 2010
Matsue	*A. japonicus*	1.895	www.wunderground.com, 2010
Tottori	*A. japonicus*	1.950	www.wunderground.com, 2010
Kobe	*A. japonicus*	1.314	www.wunderground.com, 2010
Yamaguchi	*A. japonicus*	1.844	www.wunderground.com, 2010
Chongqing	*A. davidianus*	1.090	Müller and Hennings, 2000
Guilin	*A. davidianus*	1.967	Müller and Hennings, 2000
Chengdu	*A. davidianus*	1.146	Müller and Hennings, 2000
Changsha	*A. davidianus*	1.531	Müller and Hennings, 2000
Nanchang	*A. davidianus*	1.864	Müller and Hennings, 2000
Wuhan	*A. davidianus*	1.194	Müller and Hennings, 2000
Savannah River (GA, SC)	*C. a. alleganiensis*	1.220	www.wrcc.dri.edu, 2010
Tennessee River (VA, TN, KY)	*C. a. alleganiensis*	1.170–1.420	www.wrcc.dri.edu, 2010
Ohio River (PA, OH, IN)	*C. a. alleganiensis*	990–1.200	www.wrcc.dri.edu, 2010
Black River (MO)	*C. a. bishopi*	1.140	www.wrcc.dri.edu, 2010
White River (AR)	*C. a. bishopi*	1.140	www.wrcc.dri.edu, 2010

Formation), suggesting that giant salamanders were present in the basin over a significant time span (Late Aksyr to Buran Formations) between 37 and 33 Ma. The second period (17 to 15 Ma) includes three localities crossing the Early to Middle Miocene boundary (Shamangora and Zaysan Formations). The regional tectonic evolution suggests that after a period of stability and regional peneplainization during the late Cretaceous to Paleocene a first period of tectonic deformation occurred in the Zaysan basin during the Late Eocene to Early Oligocene, including a regional uplift of the Altai Mountains (Buslov, 2004). A second period of tectonic movements along reactivated accretion–collision zones and faults is documented from the Middle Miocene (Buslov, 2004; DeGrave et al., 2007).

Therefore, the fossil distribution and tectonic data from both basins support the hypothesis that, besides elevated humidity increased basinal relief is necessary to provide spawning habitats for giant salamanders in lowland settings. Given these circumstances it is reasonable to assume that Central European giant salamanders lived permanently during the Neogene in mountain habitats of the Alpine orogene and colonized lowland basins only during periods of significantly elevated humidity and increased basinal relief (Fig. 6). We hypothesize the same for cryptobranchids of Central Asia where the Altai Mountains may act as a refuge for giant salamander populations. In both cases, environmental stability will be maintained by habitat restriction to mountainous refuges during dry climates, and/or periods without suitable spawning habitats in the lowland basins. This model explains the high patchiness of giant salamander distribution in densely sampled basins and illustrates

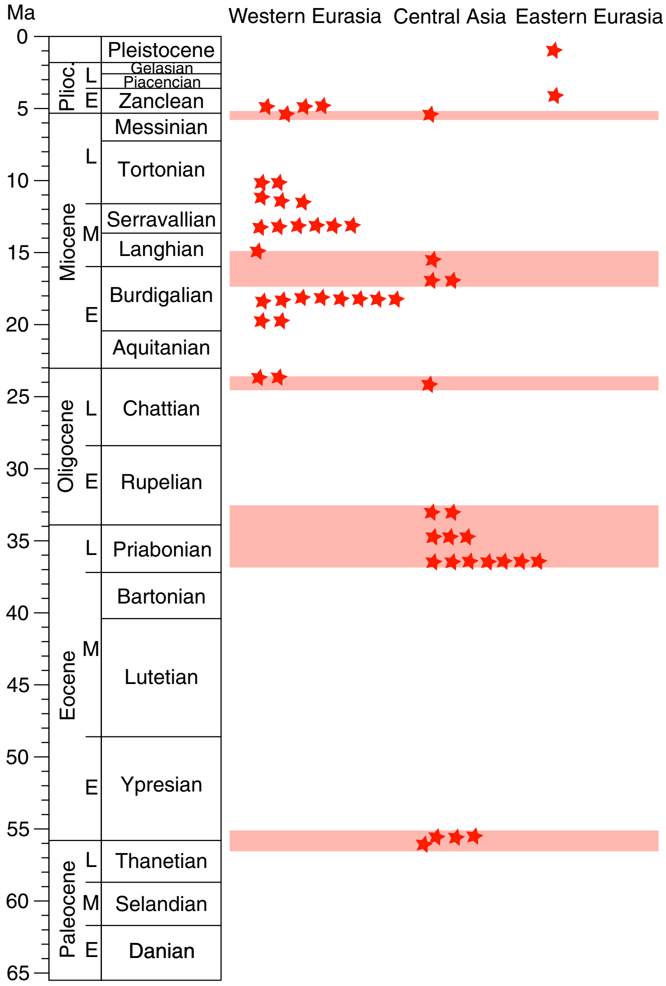

Fig. 4. Stratigraphic distribution of cryptobranchids in Eurasia during the Cenozoic. Western Eurasia covers Europe and the European part of Russia, Central Asia covers Kazakhstan, the Asian part of Russia and Mongolia, and East Asia document Japanese localities. The five periods when cryptobranchids are present in Central Asia are highlighted in grey.

Table 3
Mean annual precipitation (MAP) values of giant salamander localities from the Oligocene and Neogene of Europe and Asia.

Locality	Country	Age (in Ma)	Stage	Species	MAP (in mm)	Reference
Willershausen	Germany	5.3–3.6	Zanclean	*A. scheuchzeri*	897–1.151	Thiel et al., 2012*
Kuchurgan	Ukraine	5.25–4.85	Early Zanclean	*Andrias* sp.	1.425 ± 273	Böhme, pers. comm.**
Maramena	Greece	5.5–5.25	Messinian/Zanclean	*Andrias* sp.	994 ± 257	Böhme, pers. comm.**
Götzendorf	Austria	9.94–9.78	Early Tortonian	*A. scheuchzeri*	1.303 ± 267	Böhme et al., 2008**
Vösendorf	Austria	10.45–10.25	Early Tortonian	*A. scheuchzeri*	918 ± 255	Böhme et al., 2008**
Hammerschiede 1	Germany	11.28–11.08	Earliest Tortonian	*Andrias* sp.	974 ± 256	Böhme et al., 2008**
Oehningen	Germany	13.5–13.0	Early Serravallian	*A. scheuchzeri*	1.159–1.237	Mosbrugger et al., 2005*
Hambach 6 C	Germany	15.0–14.5	Late Langhian	*A. scheuchzeri*	1.174 ± 262	Böhme, pers. comm.**
Reisensburg	Germany	17.5–17.3	Late Burdigalian	*A. scheuchzeri*	1.648 ± 285	Böhme et al., 2011**
Langenau	Germany	17.9–17.75	Late Burdigalian	*A. scheuchzeri*	1.112 ± 260	Böhme et al., 2011**
Oberleichtersbach	Germany	23.5–23.0	Latest Chattian	*A. scheuchzeri*	1.131 ± 261	Böhme, 2008**
Rott	Germany	23.5–23.0	Latest Chattian	*A. scheuchzeri*	843–1.281	Utescher et al., 2000*
Altyn Shokysu	Kazakhstan	23.8–24.7	Late Chattian	*Z. beliajevae*	897–1.028	Bruch and Zhilin, 2007*

* Estimated by botanical proxy-method (Coexistence Approach, Mosbrugger and Utescher, 1997).
** Estimated by herpetofaunal proxy-method (Böhme et al., 2006).

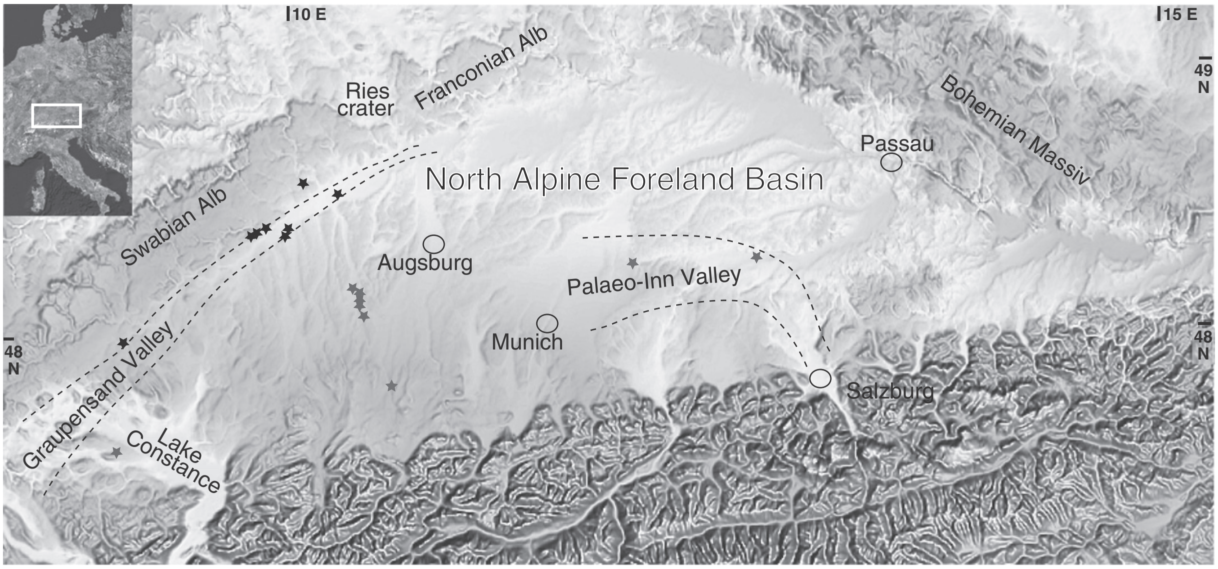

Fig. 5. Digital elevation model of Southern Germany (from Kuhlemann et al., 2006, 2007) showing the location of all crypobranchid occurrences in the North Alpine Foreland Basin (black stars — Burdigalian localities; grey stars — Serravallian localities) in relation to the two main incised valleys of the Upper Freshwater Molasse: the Burdigalian Graupensand valley (according to Reichenbacher et al., 1998) and the Serravallian Palaeo-Inn valley (according to Frisch et al., 1998).

biogeographic patterns during 20 million years of cryptobranchid residence in Central Europe and Central Asia.

3. Implications for Cenozoic palaeoclimatology of Central Asia

Applying the relationship between giant salamander occurrences and humidity indicates that the five Central Asian cryptobranchid intervals (Fig. 4) are characterized by humid to very humid climates, with MAP above 900 mm. Interestingly all but one interval represent global warm periods. Cryptobranchids from the oldest interval derive from the top of the Naran Member of the Naran Bulak Formation in south-central Mongolia (Tolstikova and Badamgarav, 1976: Fig. 4), which can be correlated to the late Gashatan Asian Land Mammal Age and the late Clarkforkian North American Land Mammal Age (Meng and McKenna, 1998; Luterbacher et al., 2004; Secord et al., 2006), very near or contemporary with the Paleocene–Eocene Thermal Maximum. For both the Naran Member and the contemporary nearby Chinese Nomogen Formation humid environments have been already suggested (Tolstikova and Badamgarav, 1976; Van Itterbeeck et al., 2007). The second Central Asian cryptobranchid period covers not only the Late Eocene warming, but also the latest Eocene and the earliest Oligocene cooling periods (see Villa et al., 2008: Fig. 9). The third Central Asian cryptobranchid period is documented in latest Oligocene strata near the present-day Lake Aral (Aral Formation) and may correspond to the Late Oligocene warming, whereas the fourth cryptobranchid period is documented in the Zaysan basin again (Shamangora and Zaysan Formations). This period falls within the Miocene Climatic Optimum (Flower and Kennett, 1994; Böhme,

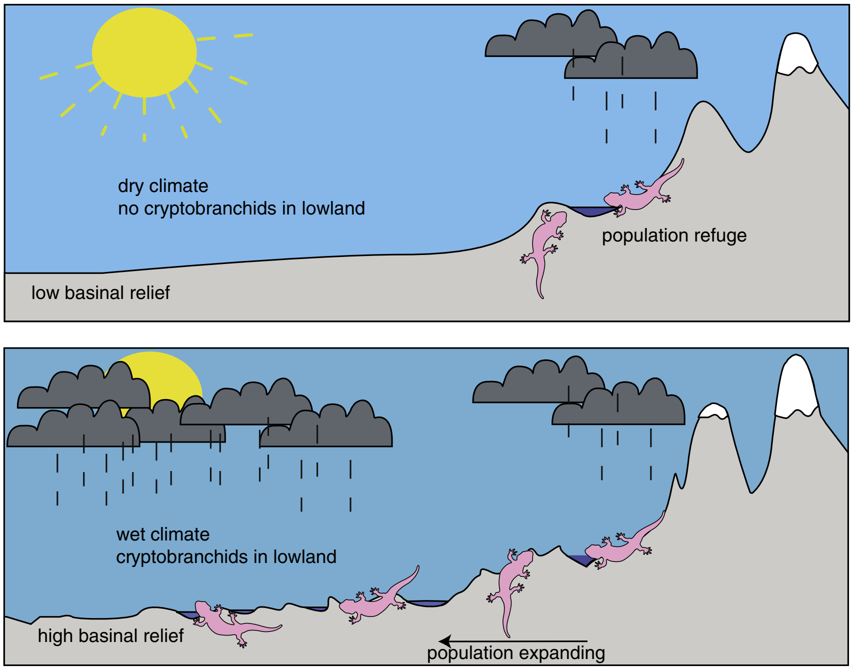

Fig. 6. Altitudinal distribution model of giant salamanders during dry climate and low basinal relief (above) and wet climate and high basinal relief (below).

2003). The last Central Asian cryptobranchid populations are found at the Miocene/Pliocene transition, when giant salamanders are recorded from bio-magnetostratigraphically dated (5.6 to 5.3 Ma) sediments near Pavlodar (West Siberia).

4. Conclusion

Based on their environmental stability fossil cryptobranchids are excellent palaeoclimate proxies, indicating humid to very humid climates with MAP exceeding 900 mm. Their fossil distribution in Eurasia is shown to be highly patchy and we hypothesize that they occur in basinal habitats only during humid periods of increased regional uplift. In Central Asia giant salamanders occur during five intervals, four of them are characterized as global warm periods (Paleocene–Eocene Thermal Maximum, Late Oligocene warming, Miocene Climate Optimum, Mio-Pliocene transition), suggesting a direct (positive) relationship between global temperature and Central Asian humidity evolution. The elevated and probably less seasonal humidity in Central Asia during global warm periods may be explained by a weak or absent Asian cold high pressure zone during winter months, allowing moist westerly winds (low-pressure systems) to penetrate far into the continent. The presence of cryptobranchids in the Zaysan Basin across the Eocene–Oligocene transition indicates that, unlike in Mongolia and northwest China where an intense aridification is recorded at this time (Böhme, 2007; Dupont-Nivet et al., 2007; Xiao et al., 2010), the Zaysan Basin exhibits a humid climate during this stepwise global cooling period. This may be explained by the contemporary uplift of the easterly bordering Altai Mountains and an increase in upslope precipitation.

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