The genus Hydrocharis L. (Hydrocharitaceae): distribution features and conservation status

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ABSTRACT

The genus Hydrocharis L. includes three geographically isolated species. Analysis of the actual data (32 thousand geographical locations and 1946 herbarium sheets) covering the period 1765–2019 made it possible to clarify the nature of the distribution of these species and its changes. Hydrocharis morsus-ranae L. has disjunctive Eurasian – North American temperate range, with a massive North American enclave, the formation of which began in the 1930–1940s. The range of Hydrocharis dubia (Blume) Backer is disjunctive Southeast Asian – Australian sub-boreal-tropical, Australia enclave began forming in the 1850–1870s. Hydrocharis chevalieri (De Wild.) Dandy is a macrothermal Central African equatorial endemic. Current threat status of all species may be estimated as Least Concern. The mean annual temperature is the most contrasting feature of the distribution areas of the species, water depth, bottom soil type and hydrochemical composition have lower impact. Prognostic models of the potential distribution of the tagged species have been made.

Keywords: Hydrocharis, Hydrocharitaceae, range, protection status, ecology, invasion

The genera Hydrocharis L. and Limnothium Rich., united in the subfamily Hydrocharitoidae, diverged from the main part of the family Hydrocharitaceae in the Miocene (Chen et al. 2012). The genus Hydrocharis includes three geographically isolated species: Hydrocharis chevalieri (De Wild.) Dandy, Hydrocharis dubia (Blume) Backer and H. morsus-ranae L. (Cook & Liönd 1982). Hydrocharis dubia and H. morsus-ranae have formed extensive secondary ranges, causing significant damage to local ecosystems (Cook & Liönd 1982, Bean 2011). On the other hand, H. morsus-ranae has declined or has been extirpated and it is considered a conservation concern in several areas (e.g. South and Western Europe, Western Asia). Hydrocharis chevalieri is a Central African endemic, morphologically and ecologically significantly distinguished from other species. All species of the genus can be dominant or subdominant in the formation of aquatic vegetation (Cook & Liönd 1982, Lubini 1983).

The purpose of this study is to clarify features of the genus Hydrocharis distribution in the world. The solution to this problem required the implementation of the following main tasks: (a) to thoroughly analyze the relevant information and known locations of the species of the genus Hydrocharis in the world, (b) to determine basic environmental characteristics that can limit the distribution of the species, (c) evaluate the current protection status.

MATERIAL AND METHODS

The data collection on Hydrocharis distribution was performed by analytical generalization of web (Appendix 1) and published information sources (qv. Literature Cited), the analysis of herbarium collections (Appendix 2) and the authors’ original database (hereinafter “AD”). Due to the specificity of the research, below there are references to the oldest herbarium specimens of the region and references.
covering the widest specimens’ geography (Appendix 3). The data includes web sources, records of 1946 herbarium specimens and references covering the period 1765–2019. Web sources were used only if they correspond to the criteria of reliability i.e. not deviating from the known range of the spreading, accompanied by indications of the exact location.

The distribution map, containing over 32 thousand locations, was created using “GBIF occurrences” add-on for QGIS 3 and standard QGIS tools for placing the locations; some of the data was plotted manually. The extent of occurrence (IUCN 2012) was calculated based on the polygons created by joining the outside points on the map that match known locations of the specimens. For computing the area of occupancy (IUCN 2012) we used the sum of areas of water bodies, vector data provided by Natural Earth (2019). The world elevation data was taken from ETOPO1 map (Amante 2009) and basic materials used for global assessment of the distribution of aquatic plants (Murphy et al. 2019).

We extrapolated species distribution data on the entire surface of Earth using standard set of bioclimatic variables (Hijmans et al. 2005). As a supervised learning algorithm, the random forest classifier from Scikit-learn package (Pedregosa 2011) has been applied. We followed the recursive feature elimination with cross-validation procedure RFECV (Pedregosa 2011) to get the best set of features yielding highest accuracy scores. After the RFECV procedure was applied we got three most important features that provided the best prediction accuracy. These are BIO15 (importance = 0.36) – precipitation seasonality (coefficient of variation), BIO3 (importance = 0.35) – isothermality (mean diurnal / annual temperature range), BIO2 (importance = 0.28) – mean diurnal range (mean of monthly, max temperature – min temperature); other features have significantly lower influence on the prediction and were not accounted when creating the map.

The conservation status was determined using methodology proposed by the International Union for Conservation of Nature (IUCN 2012).

RESULTS

The description of the Hydrocharis species spreading within the global range can be found further, the map of the present range is shown in Fig. 1.

Distribution of Hydrocharis morsus-ranae

The modern H. morsus-ranae range is disjunctive Eurasian – North American temperate. The main part of the range in Eurasia is from 51 (Asia) and 36 (Europe) to 63–64°N, with the northern border reaching 69°N in Fennoscandia and 66.5°N in Western Siberia, and the southern borders reaching 32°N in the Arabian Peninsula and northern Africa. The secondary range includes a significant North American enclaves between (28)42 and 48°N and small stands in Eurasia (Fig. 1). A more detailed description of the distribution by macroregions is given below.

Hydrocharis morsus-ranae is a sporadically distributed species in the Western Europe, but population sizes are decreasing in certain territories. The plants flower and occasionally bear fruit (e.g. in Britain (Appendix 1: Mountfor 2019)). In the United Kingdom of Great Britain and Ireland it is quite common, but is rare in Scotland. This species has declined in Britain in the last century, but some populations have been reported in canals outside of its native range (Cook & Lüönd 1982, Preston & Croft 1997, Appendix 1: Mount-

Figure 1 World distribution of the species of Hydrocharis L.
ford 2019, GBIF 2019, E, W). In France the species is quite common, although it is rare in the south (Appendix 1: Inventaire 2019, GBIF 2019, Z+ZT, W) and is absent from Pyrenees, Massif Central, French Alps. In Belgium and Luxembourg it has disappeared from many previously known habitats (Appendix 1: IUCN 2019, Belgian 2019, Z+ZT, W). In the Netherlands *H. morsus-ranae* is commonly found across the country (Appendix 1: FLORON 2019, IUCN 2019, Invasive 2019, GBIF 2019, Z+ZT, W), and often forms dense thickets.

*Hydrocharis morsus-ranae* is generally a widespread species, it is rare in mountain areas of the Central Europe. The population sizes are declining and it has disappeared from some areas. On the other hand, the building of reservoirs and increasing eutrophication contribute to the distribution of *H. morsus-ranae* in secondary habitats. In the Czech Republic *H. morsus-ranae* occurs mainly in Central and Eastern Bohemia, southern Moravia. It is rare in southwestern and southern Bohemia, North-Eastern Moravia and Silesia and the population sizes show a declining trend. This species has vanished from many of its sites due to habitat destruction or changing (Danhelka et al. 2012, Kaplan 2018, Appendix 1: GBIF 2019, PRC). In Slovakia it is found in the Pannonian region and is extinct in the Carpathians (Turis et al. 2014). In Hungary the plant is quite common in Magyar Középhegység (Transdanubian Mountains, North Hungarian Mountains), Great Hungarian Plain and is rare in Southern Transdanubia (Király 2007, BP). In Poland it is common (Zając & Zając 2001, Toma 2013). In Germany and Liechtenstein (IUCN 2019) *H. morsus-ranae* is rare, it is mainly found in the lowlands of north (Western Pomerania, North Rhine-Westphalia, Saxony-Anhalt, Schleswig-Holstein) and Bavaria (Schiell & Krautkrämer 2019, Appendix 1: GBIF 2019). In Austria it occurs in all regions except Tirol and Vorarlberg, however, it is highly endangered (Schiell & Krautkrämer 2019, W, Z+ZT). The species is absolutely protected in the cantons of Thurgau and Waadt in Switzerland (Appendix 1: Info flora 2019, GBIF 2019, W, Z+ZT, LE). It is occasionally found in Slovenia (Borska lowland, Danubian plain, East Slovakian plain) (Martinčič & Susnik 1969, Kochjarová et al. 2013, Appendix 1: GBIF 2019, LE, BP).

There is a noticeable decrease in the number of known populations and habitats in the Southern Europe. The species is found in the west of Portugal (Beira Litoral, Estremadura, Ribatejo) and in the northeast and south of Spain (Huelva, Gerona, Lugo). The species is endangered in the Iberian Peninsula (Talavera 2010, ILISP, ВС, VAL). It is frequently and very frequently (Gusev 1979, Papchenkov 1987, Dubina 1993, Appendix 1: GBIF 2019, LE, MW). In Romania it is occasionally found across the territory with the exception of the Carpathians (Tota 1966, Z+ZT, W). In Moldova it is reported for the entire territory, but is rare in the Central Moldavian plateau (Geideman et al. 1986, W, PR). In Bulgaria *H. morsus-ranae* was previously more widely distributed, it is now occasionally found in the valleys of the Danube, Maritsa and Struma Rivers (Jordanov 1963, BP).

In the North of European Russia the plant is commonly found (Miyade et al. 1981, Appendix 1: GBIF 2019, LE, MW, IBIW). It is sporadically distributed in Karelia, in the far south (Pryladozhie and Prionezhie) it occurs frequently enough, in the rest of the south it is rare. The most northern locality in the macroregion is 63.5°N (Kravchenko 2007). In Central Russia and the Black Soil Zone *H. morsus-ranae* is widespread, in the Non-Black Soil Zone it occurs somewhat more often (Kamyshov 1978, Gusev 1979, Maevsky 2014, Bulohov & Vyalichkin 1998, Appendix 1: GBIF 2019, LE, MW, IBIW). In the Upper and Middle Volga it is found frequently and very frequently (Gusev 1979, Papchenkov 2001, Appendix 1: GBIF 2019, LE, MW, IBIW). In the Lower Volga region it is common, but only occasionally found in the Caspian Lowland (Swordtsov 2006, Gusev 1979, Appendix 1: GBIF 2019, LE, MW, IBIW, SARAT, RWBG).

Sporadically distributed in the Caucasus and the Ciscaucasia species, the most numerous habitats are found in the basins of major rivers (Don, Kuban), but it is rare in mountain areas. *Hydrocharis morsus-ranae* forms dense thickets in eutrophicated water bodies, abundant in irrigation canals and ditches. The species is rare in Georgia (Samegrelo and Upper Svaneti, vicinity of Poti; probably Imere) and Ab-
khazia (Gagnière 2005, LE, ERA, TBI, TGM). The first collections for Azerbaijan are dated the year 1897 (Lenkoran and Astara districts); at present it is probably extinct. It is not known from Armenia (Gatilyan & Oganyan 2001). In the Southern Russia and the Ciscaucasia the species is distributed irregularly. It is more common in the Western Ciscaucasia and is occasionally found in the Eastern Ciscaucasia, the Western and Eastern Transcaucasia, it is rare in the Western Caucasus (Novosad 1992, Zernov 2006, Ivanov 2019, Shvanova 2006, LE, MW, TGM). In the Crimean Peninsula *H. morsus-ranae* is an introduced species which was found in the 2011 in the vicinity of Sevastopol (Appendix A: All flowers 2019).

*Hydrocharis morsus-ranae* is quite common in the Ural and the Cis-Ural. In the Middle Urals the species is quite common, though less so in the Northern and Southern Urals (Ose nov 1997, Ryabinina & Knazyev 2009, Kulikov 2010, Appendix 1: GBIF 2019, LE, MW, IBIW). The northern border of its distribution lies in the south of the Komis Republic, and thus in the taiga zone (Martyrenko & Gruzdev 2008).

In the Western Siberia and the Altai the plants regularly and abundantly bear fruit, although fruiting in the North is rare. There are numerous paleontological records, the earliest of them are dated Miocene (Nikitin 2006, LEPAL). The species is widespread in Western Siberia; it is sporadically distributed in the Central Ob Lowland, in the south *H. morsus-ranae* is quite common. The northern border of its distribution almost reaches the Gulf of Ob (ca. 66°N) (Dobrokhотова 1956, Timokhina 1988, Appendix 1: GBIF 2019, LE, NS, NSK, TK, PD). In the Altai region it is unevenly distributed, common in the Northwest Altai; occasionally found on the Salair Ridge, rarely on the Western and Northern Altai, Kuznetsk Basin, Kuznetsk Alatau (Timokhina 1988, Ebel 2012, Appendix 1: GBIF 2019, LE, NS, TK).

In the Middle Siberia it is occasionally found in the Upper Yenisei floristic region (the south of Krasnoyarsky Territory) and in the Cisyersiressy Sayans (Timokhina 1988, Antipov 2012, Stepanov 2016, LE, NS, TK), the northern distribution border reaches ca. 66.5°N.

The eastern border of the distribution range in Eastern Siberia lies in Irkutsk Oblast (is quite common along the Birusa River valley but is very rare east of the valley – in the basins of rivers Angara, Iya, Oka, Nizhnyaya Tunguska) and Zabaykalsky Krai (vicinity of Nerchinsk) (Timokhina 1988, Chepinoga et al. 2008, MW, NSK). Initially recorded for Irkutsk Oblast in 1908 (Appendix 3), rather than in 1989 (Chepinoga et al. 2008). Probably an invasion species, rare in Eastern Siberia.

The species is common in the Central Asia, it is found in the North and the Center of Kazakhstan (mainly throughout river valleys), less common in the west and southwest. In the North Kazakhstan *H. morsus-ranae* often forms dense stands in watershed and valley lakes (Dobrokhотова 1956, Sviridenko 2000, LE, TK, MWG, AD). The southern border of its distribution reaches the Cisbalkhash, at ca. 43°N. Records for Uzbekistan (Appendix 1: Invasive 2019, IUCN 2019) require clarification.

In Western Asia *H. morsus-ranae* is a rare species. In Turkey it is known from a few seaside regions: Strandja, Catalca-Kocaeli, Western Black Sea, Middle Black Sea, Antalya (Appendix 1: Ekim 2012, EW, Z+ZT). In Israel it is reported from Upper Galilee (Danin 2016), but is probably extinct in the wild (Sapir 2003). It is not known for Palestine (Ali-Shtayeh & Famous 2018). The species was reported for north and northwest Iran (Cook & Lüönd 1982, Yousefi & Toranj 2015, W), Iraq (Appendix: Iraqi 2010) and Syria (Flora Syria 2019). It is a neophyte, which was first reported for the region in 1977 (Assadi & Wendelbo 1977).

Recently a few invasion sites were discovered in the Indian subcontinent (Jammu and Kashmir Himalaya). *Hydrocharis morsus-ranae* and *H. dubia* grow sympatrically in Miragund and Haigam wetlands (Ganie et al. 2016).

The species’ status in North Africa (Algeria, Morocco, presumably Tunisia) (García et al. 2012, Appendix 1: IUCN 2019, Conservatoire 2019) is not clear, probably it is a neophyte. It is protected in the macroregion (García et al. 2010). In the South the species’ distribution is supposedly limited by the Atlas Mountains, ca. 31°N.

*Hydrocharis morsus-ranae* was first brought to North America in 1932 at the Ottawa botanic garden from Zurich and later noticed as an escapee in 1939 in the Rideau Canal (Dore 1968). This species then spread into the Ottawa and the St. Lawrence Rivers in 1974. By the early 1990s it had spread to the marshes and bays of Lake Ontario's south shore. In the USA, it is present in Michigan, Wisconsin, Vermont, New York, Washington and Florida states (Catling & Dore 2003, Zhu et al. 2018, Appendix 1: INaturalist 2019, GBIF 2019). Recently, it was found further south and has been observed in Maine, Ohio and Pennsylvania states (Jacobo & Berent 2019). In Canada *H. morsus-ranae* is currently found in the southeastern part of the country (Ontario and Quebec) (Catling & Dore 2003, Zhu et al. 2018). The species has become a source of concern due to its high invasion success (Zhu et al. 2018).

**Distribution of Hydrocharis dubia**

*Hydrocharis dubia* has a disjunctive Southeast Asian – Australian subboreal-tropical range. The northern border reaches 46.5°N, while the southern border – 35.2°S, most of the known locations are situated 39–40°N and 7–10°S. The western border goes along the Indo-Gangetic Plain, 35.3°N. *Hydrocharis dubia* is widely distributed in South-Eastern Asia, but is sporadically dispersed. In Indochina there are known localities in Bangladesh (Jessore, Manda Rajshahi (W, LE)), Thailand (Bangkok, Chaing Mai, Nakhon Ratchasima, Nakhon Sawan (QBQ), Ang Thong, Saraburi, Sukhothai (Z+ZT), Rayong (probably in culture, QBG)). There are a few occurrences in Myanmar (Shan; distribution in other states requires clarification), Vietnam (mainly the southern part of the country – Long An Province, Dong Thap Province etc., Hanoi) and Laos (distribution pattern requires clarification) (Cook & Lüönd 1982, Haynes 2001, Kress at al. 2003, Newman 2007, Ito & Barfod 2014, Appendix 1: IUCN 2019, GBIF 2019). There is no reliable data on occurrences in Cambodia.

In the Malay Archipelago it is scattered and somewhat sparingly represented and apparently absent from several larger land masses (Malayan Peninsula, Sumatra and the Is-

In the Indian subcontinent H. dubia occurs only in the north-west along the Himalayas (Jammu and Kashmir, north-east Uttar Pradesh, north Bihar, West Bengal, probably C'hhattisgarh) (Cook 1998, Guha & Maonald 2005, Appendix 1: Barooah & Ifukhier 2014, GBIF 2019, WAG, W, Z+ZT). In Pakistan it is reported from the north-east, but the distribution pattern requires clarification (Appendix 1: Ghafoor 2019). It is quite a rare species in the macroregion, the number of habitats is reducing.


In the Russian Far East the species is found on the northern border of its range. The distribution is limited by the south of Primorsky Territory; it sporadically grows near Lake Khanka (LE, VLA). It was successfully introduced from Primorsk Power Station to the city of Khabarovsk and its vicinity in 2009–2013 (AD).

Hydrocharis dubia has a secondary enclave which includes the southern shore of Australia (Queensland and the north-eastern part of New South Wales) (Cook & Liou 1982, Appendix 1: IUCN 2019) and, possibly, some islands of Oceania. The species was first recorded for Australia by Bentham in 1873 under the misapplied name H. morsus-ranae. The record was based on a specimen collected by J. Bidwill, from “Wide Bay” between 1848 and 1853. There is a strong evidence to support an alien status for H. dubia with regard to its occurrences in Australia; it was recorded as naturalized for Australia (Bean 2011, Jacobs & McColl 2011). Currently in Australia its distribution area stretches along the Great Dividing Range with most occurrences in the coastal area and a few specimens found west of the mountain range. The southern border of the distribution area is at 35.2°S. The eastern border reaches North Stradbroke Island (27.5°S 153.5°E).

**Distribution of Hydrocharis chevalieri**

Hydrocharis chevalieri range is continuous Central African (Guineo-Congolean) equatorial, extending northwards to 11.9°N 14.8°E and southwards to 5.0°S 18.8°E. From the west coastal region of the Cameroons (7.4°N 2.6°E) it extends eastwards to the Great Rift Valley (3.7°N 29.8°E). Most of the known habitats are located in the Congo River basin. The area of distribution is widely separated from that of the other species of Hydrocharis.

**Hydrocharis chevalieri** is known from Cameroons (mainly southwestern regions) (BR, K, WAG, YA, Z+ZT), Gabon (Ngounié, l’Ogooué-Ivindo, l’Ogooué-Lolo, Woleu-Ntem) (WAG), Equatorial Guinea, Central African Republic (BR), Democratic Republic of the Congo (sporadically occurs in western and central regions but is rare in the east), Republic of the Congo (Z+ZT), there are also a few occurrences in Benin (West Africa) and in the north of Cameroons (Cook & Liou 1982, Symoens 1984, Akoegninou et al. 2006, Symoens 2015, Symoens 2017, Appendix A: Conservatoire 2019, GBIF 2019). The species is not found in Eastern Africa – Rwanda and Burundi (Symoens 2015).

This Central African endemic is widespread in the region, but is found rarely enough (Lubina 1983). This species sporadically occurs in lowland rainforest region, but some occurrences are known in savanna region. Mainly it grows in small sedge swamps of rivers and streams. Often H. chevalieri dominates communities of wetland aquatic plants.

**Paleohistory of the genus Hydrocharis**

The stem node age of Hydrocharis–Limnobium was dated around 54.7 Ma, the crown node age of this subclade was dated around 15.9 Ma. From there Limnobium had split from the relatively ancient Hydrocharis in the Miocene (Chen et al. 2012a). At least 10 members of the genus Hydrocharis are known (Kats et al. 1965, Krasilov 1976, Mai 1988, Carrió & Dupré-Olivier 1996, Velichkevich & Zastawniak 2003, Yao et al. 2011, Appendix 1: The International 2019, LEPAL) (Table 1), most of which existed in Oligocene and Miocene.

During the Eocene-Holocene H. morsus-ranae had a European-Siberian boreal distribution, with its Northern border located in the mouth of the river Ob, 66°N. The fossil seeds of H. morsus-ranae occur in interglacial floras of different ages, but are never numerous in Europe, although relatively numerous in Western Siberia. Seeds of the same morphological type were described by Mai (2000) from the Late Miocene of Lusatia, the Pliocene of Thuringia and the Late Pliocene flora of Kholomech in southeastern Belarus (Mai 1988, Mai 2000, Velichkevich & Zastawniak 2003). Seeds similar in description to H. dubia are known from the Tsagayan flora (Amur region, Russia), they are dated to the Late Cenonian – Paleocene (Krasilov 1976). No information on the paleontological findings of H. chevalieri, as well as other species of the genus, in Africa, was found.

**DISCUSSION**

Based on the calculation results we determined that plurizonal Eurasian – North American temperate H. morsus-ranae has the biggest area of the extent of occurrence, and the smallest area is that of equatorial H. chevalieri. Since the distribution pattern of water plants is mostly defined by the presence of suitable waterbodies, the area of occupancy is significantly smaller (Table 2).

Hydrocharis morsus-ranae is a widespread species with numerous and quite stable populations, with irregular sexual reproduction and prevalent vegetative reproduction, so its global threat status is given as LC (IUCN 2019, Table 3). However, in some parts of the range (Central (some regions), Western (some regions) and Southern Europe, Caucasia,
Table 1. Paleontological findings of species of the genus Hydrocharis

<table>
<thead>
<tr>
<th>Species</th>
<th>Fossil status</th>
<th>Stratigraphy</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hydrocharis batrachidigma A. Massal.</td>
<td>leaves</td>
<td>Oligocene</td>
<td>Schiavon (Chiavon), Vicenza, Veneto, Italy</td>
</tr>
<tr>
<td>Hydrocharis longifolii R. Ludw.</td>
<td>leaves</td>
<td>Miocene</td>
<td>Salzhausen, near Nidda, Wetterau, Hessen, Germany</td>
</tr>
<tr>
<td>Hydrocharis lasiata Mai in Mai, H. Walther</td>
<td>seeds</td>
<td>Miocene</td>
<td>Oberoderwitz borehole, Saxony, Germany</td>
</tr>
<tr>
<td>Hydrocharis magna Mai in Mai, H. Walther</td>
<td>seeds, pollen</td>
<td>Oligocene</td>
<td>Haseilbach, Landkreis Altenburg; Thuringia, Germany</td>
</tr>
<tr>
<td>Hydrocharis orbiculata Heer</td>
<td>leaves</td>
<td>Miocene</td>
<td>Öhningen, Landkreis Konstanz, Baden-Württemberg, Germany</td>
</tr>
<tr>
<td>Hydrocharis obtusa R. Ludw.</td>
<td>leaves and flowers</td>
<td>Miocene</td>
<td>Salzhausen, Münzenberg, Wetterau, Hessen, Germany</td>
</tr>
<tr>
<td>Hydrocharis rotundis Weyl.</td>
<td>not available</td>
<td>not available</td>
<td>Rott near Bonn, North Rhine-Westphalia, Germany</td>
</tr>
<tr>
<td>Hydrocharis terticularis Hartz</td>
<td>seeds</td>
<td>Miocene</td>
<td>Sonderskov near Silkeborg, Jutland, Denmark</td>
</tr>
<tr>
<td>Hydrocharis sp. f. dubia (Blume) Backer</td>
<td>leaves</td>
<td>Late Senon – Paleocene</td>
<td>Amur region, South of Russia Far East</td>
</tr>
<tr>
<td>Hydrocharis sp.</td>
<td>not available</td>
<td>Miocene</td>
<td>South China</td>
</tr>
<tr>
<td>Hydrocharis sp.</td>
<td>seeds</td>
<td>Oligocene, Miocene, Neopleistocene</td>
<td>South of Western Siberia</td>
</tr>
<tr>
<td>Hydrocharis sp.</td>
<td>pollen</td>
<td>Upper Pliocene – Caspian Lowland (Baku)</td>
<td>Middle Pleistocene</td>
</tr>
</tbody>
</table>

Table 2. Main characteristics of the range of the species of Hydrocharis

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Hydrocharis chevalieri</th>
<th>Hydrocharis dubia</th>
<th>Hydrocharis morsus-ranae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Extent of occurrence, Mkm²</td>
<td>3.134</td>
<td>6.820</td>
<td>16.030</td>
</tr>
<tr>
<td>Area of occupancy, Mkm²</td>
<td>0.074</td>
<td>0.199</td>
<td>0.785</td>
</tr>
<tr>
<td>Extreme latitudes</td>
<td>11.9°N – 5.0°S</td>
<td>46.5°N – 35.2°S</td>
<td>68.9°N – 33.1°N</td>
</tr>
<tr>
<td>Extreme longitudes</td>
<td>2.6°E – 29.8°E</td>
<td>72.6°E – 153.0°E</td>
<td>90°W – 122.0°E</td>
</tr>
</tbody>
</table>

Table 3. Assessment of the conservation status of the species of Hydrocharis. Note: CR – critically endangered; EN – endangered; EW – extinct in the wild; VU – vulnerable; NT – near threatened; LC – least concern

<table>
<thead>
<tr>
<th>Species</th>
<th>Category for the World</th>
<th>Category for macroregions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hydrocharis chevalieri</td>
<td>LC</td>
<td>BENIN AND CAMEROON (savanna regions); probably NT (A4c, e) (AD)</td>
</tr>
<tr>
<td>Hydrocharis dubia</td>
<td>LC</td>
<td>SOUTH-EAST ASIA; probably NT (AD); JAPAN; NT (Appendix 1: Global 2020); INDIAN SUBCONTINENT; probably NT/ VU (AD); RUSSIAN FAR EAST; NT (AD)</td>
</tr>
<tr>
<td>Hydrocharis morsus-ranae</td>
<td>LC</td>
<td>WESTERN EUROPE: United Kingdom and Ireland – VU (A2c) (Cheffings &amp; Farrell 2005), South France – EN/CR (Appendix 1: Inventaire 2019), Belgia – VU/CR (Belgian 2019); CENTRAL EUROPE: Czech Republic and Slovakia – EN (C2b) (Danihelka et al. 2012, Kaplan 2018), Germany, Austria, Slovenia – EN/CR (Schill &amp; Krauterbrüner 2019, AD); Switzerland – EN (B5ab(iii,iv)) (Appendix 1: Info flora 2019), Slovenia – EN (AD); Southern Europe: Italy – NT, Portugal and Spain – CR, other country – EN/CR (Beck von Mannagetta 1904, Talavera 2010, Dýigurski et al. 2010, Dimopoulos 2013, Nikolić 2015, Barina 2017); CAUCASUS: Georgia, Azerbaijan – probably EW (AD); MIDDLE AND EASTERN SIBERIA: NT (A3cd; (Chepurno et al. 2008); AD; probably neophyte in Eastern Siberia; WESTERN ASIA: Iran, Iraq – probably neophyte (Assadi &amp; Wendelbo 1977), Israel – EW (Sapir 2003); NORTH AFRICA: EN (García et al. 2010), probably neophyte.</td>
</tr>
</tbody>
</table>

Western Asia) the number of populations and their area is reduced due to degradation of the typical habitats (Table 3). It is probably extinct in the wild in Azerbaijan (since late XX) and Israel (since 2006s). In the Asian part of the range (most of the regions of Russia and Kazakhstan) the population status does not cause concern. In regions with intensive agricultural activity (e.g. Ciscaucasia, some regions of Kazakhstan) population numbers are somewhat reduced, however, in such areas H. morsus-ranae often populates technogenic waterbodies.

Hydrocharis dubia is widespread only in subtropical and tropical regions, its global threat status is given as LC (IUCN 2019). In some territories, there is a destruction of habitats due to agricultural and industrial activities (South-Eastern Asia, Indian subcontinent); at northern borders the populations are quite small as well (Russian Far East) (Table 3). The global threat status of H. chevalieri according to IUCN is given as LC (IUCN 2019), in savanna regions status probably is NT. Although this species is scattered in its distribution area, due to the big extent of occurrence and common
habitats we consider that the IUCN assessment is appropriate. Probably *H. chevallieri* is simply undercollected. Probable causes of the decline and extinction of *Hydrocharis* populations include degradation of habitats (agricultural and industrial activities), and changes of hydrochemical characteristics and the hydrological regime of waterbodies. *Hydrocharis morsus-ranae* and *H. dubia* respond well to moderate eutrophication, thought excessive concentrations of some components can detrimentally affect the plants. Poor seed reproduction and sexual segregation are limiting the possibilities of seed regeneration.

There are some abiotic factors limiting the spreading along with the geographical ranges of *Hydrocharis* species. The mean annual temperature is the most contrasting feature of the distribution areas of the species (Table 4, q.v. material and methods, indicators BIO3, BIO2). Such features of the habitats as water depth, bottom soil type and hydrochemical composition are also significant factors. Comparative analysis of the tolerance boundaries of *Hydrocharis* species in the global range is given in the Table 4. The spread along the northern boundary is limited not only by mean annual temperatures, but also by ultra-fresh water and oligotrophic water bodies, that are unsuitable for *H. morsus-ranae*. *Hydrocharis dubia* and *H. chevallieri* are more thermophilic, and their suitable biotops (shallow mesotrophic waterbodies with very weak or absent current and muddy bottom sediments) are transformed or destroyed during agriculture and mining activities. *Hydrocharis morsus-ranae* and *H. dubia* are used as ornamental, fodder, fishery and water protection plant; *H. chevallieri* also as medicinal plant (Den Hartog 1957, Dubina et al. 1993, Sosef 2017). *Hydrocharis chevallieri* is used for the production of salt from ash (Sosef 2017), in Gabon leaves are used for preparing tea (Mesterházy ined.). In the 20th century water transport and ornamental gardening also became a significant factor of invasion. It is possible that waterfowl migration could transport viable vegetative disperses across water basins at relatively short distances. In such a way recently *H. morsus-ranae* broke down of the historical biogeographic barrier, invasion sites were discovered in Kashmir Himalaya, on the border of *H. dubia* range (Granie 2016). The performed modeling (Fig. 2) allows assessing the possible potential of invasion of the studied species. Despite quite abundant flowering and fruiting of *H. morsus-ranae* and *H. dubia* (apart from northern borders), vegetative reproduction plays a great part in maintaining population sizes. Specialized turions (hibernacula) allow *H. morsus-ranae* and *H. dubia* to tolerate a brief period of freezing conditions (Catling et al. 2003), which helps expanding northern distribution borders. In some regions, the ability of *H. morsus-ranae* (e.g. the US, Canada) and *H. dubia* (e.g. Australia) to spread rapidly by vegetative organs causes significant economic and environmental damage. Dense clones limit the growth of other aquatic species, change hydrochemical composition of the water, affect the development of phytoplankton, and can interfere with navigation and irrigation systems.

**CONCLUSIONS**

The modern *Hydrocharis morsus-ranae* range is disjunctive Eurasian – North American temperate, limited by annual isotherms at 9.9°C. The species expanded its secondary range significantly, primarily in North America since 1930–1940s. New invasion localities also have appeared in some regions of the Western Asia, the Middle and the Eastern Siberia, the Indian subcontinent and probably in the North Africa due to high economic activities since 1970–1980s. Currently, there is an expansion of the nor-

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**Table 4.** Limits of ecological tolerance of *Hydrocharis* species according to some indicators

<table>
<thead>
<tr>
<th>Environmental factors</th>
<th>The range of variation of the factor (optimum) within global habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Hydrocharis chevallieri</strong></td>
<td><strong>Hydrocharis dubia</strong></td>
</tr>
<tr>
<td>Annual precipitation, mm (Appendix 1: WorldClim2019)</td>
<td>1400−2600 (≈1800−2400)</td>
</tr>
<tr>
<td>Mean annual temperature, °C (Appendix 1: WorldClim2019)</td>
<td>20.1−25.0 (≈20.1−25.0)</td>
</tr>
<tr>
<td>Altitude, m above sea level (Cook &amp; Lüönd 1982, Appendix 1: WorldClim2019)</td>
<td>0−1000 (≈100−500) (WAG, YA)</td>
</tr>
<tr>
<td>Type of water body (Cook &amp; Lüönd 1982)</td>
<td>Flooded swamps, aquatic meadows, streams in forest (still waters), bare mud, thalweg with periodical floods, small swampy hollows, small waterbodies (Lubini 1983)</td>
</tr>
<tr>
<td>Depth, m</td>
<td>0.0−0.6 (≈0.3) (Lubini 1983)</td>
</tr>
<tr>
<td>Type of bottom deposit</td>
<td>Silty, silty-detrital (Lubini 1983)</td>
</tr>
<tr>
<td>pH, pH units</td>
<td>6.7 (≈6.5) (Lubini 1983)</td>
</tr>
<tr>
<td>Trophicity</td>
<td>≈ meso-eutrophic (AD)</td>
</tr>
</tbody>
</table>
Figure 2 The model showing the potential distribution range of Hydrocharis chevalieri (De Wild.) Dandy (A); H. dubia (Blume) Backer (B) and H. morsus-ranae L. (C).

tern and eastern distribution borders. Meanwhile in the Western and the Southern Europe, the Western Asia area occupied by populations is reduced. On the other hand anthropogenic activities (the building of reservoirs, agriculture, etc.) and increasing eutrophication contribute to the distribution in secondary habitats (e.g. Central Europe, Caucasus). Hydrocharis dubia has a disjunctive Southeast Asian – Australian subboreal-tropical range. Extensive enclave in Aust-
ralia probably formed in 1850–1870s. Distribution of this thermophilic species is limited by mean annual temperature 1.0–30.0°C. In the South-Eastern Asia, Japan, the Indian subcontinent there is a decrease in the number of known habitats and population sizes of *H. dubia*. *Hydrocharis chevalieri* is a macrothermal Central African (Guineo-Congolean) equatorial species. The current world threat status of all species of genus *Hydrocharis* may be estimated as LC.

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**LITERATURE CITED**


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**The genus Hydrocharis: distribution and conservation status**

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The genus *Hydrocharis*: distribution and conservation status


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**References**


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