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RESEARCH PAPER

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

Andrey N. Efremov[1], Veronika S. Grishina[2], Dmitry E. Kislov[3], Attila Mesterházy[4] & Cezary Toma[5]

Andrey N. Efremov[1]*
e-mail: stratiotes@yandex.ru

Veronika S. Grishina[2]
e-mail: nika.grishina2011@yandex.ru

Dmitry E. Kislov[3]
e-mail: kislov@easydan.com

Attila Mesterházy[4]
e-mail: amesterhazy@gmail.com

Cezary Toma[5]
e-mail: cezarytoma@poczta.onet.pl

[1] Research Center of Fundamental and Applied Problems of Bioecology and Biotechnology of Ulyanovsk State Pedagogical University, Ulyanovsk, Russia

[2] Omsk State Pedagogical University, Omsk, Russia

[3] Botanical Garden-Institute FEB RAS, Vladivostok, Russia

[4] Directorate of Hortobágy National Park, Hungary

[2] Kazimierz Wielki University, Bydgoszcz, Poland

* corresponding author

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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 subboreal-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

РЕЗЮМЕ

Ефремов А.Н., Гришина В.С., Кислов Д.Е., Местерхази А., Тома Ц. Род *Hydrocharis* L. (Hydrocharitaceae): особенности распространения и статус охраны. Род *Hydrocharis* L. включает три географически изолированных вида. Анализ фактических данных (32 тыс. географических локаций и 1946 гербарных листов), охватывающих период 1765–2019 гг., позволил выяснить характер распространения этих видов и его изменения. *Hydrocharis morsus-ranae* L. имеет дизъюнктивный евразийско-североамериканский умеренный ареал, формирование крупного анклава в Северной Америке началось в 1930–1940-е годы. Ареал *Hydrocharis dubia* (Blume) Backer является дизъюнктивным юговосточноазиатско-австралийским суббореально-тропическим, австралийский анклав начал формироваться в 1850–1870-х годах. *Hydrocharis chevalieri* (De Wild.) Dandy – макротермальный экваториальный эндемик Центральной Африки. Современный охранный статус всех видов можно оценить как не вызывающий опасения. Среднегодовая температура является наиболее контрастной особенностью районов распространения вида, глубина воды, тип донного грунта и гидрохимический состав имеют меньшее значение. Построены прогностические модели потенциального распространения исследуемых видов.

Ключевые слова: *Hydrocharis*, Hydrocharitaceae, ареал, статус охраны, экология, инвазия

The genera *Hydrocharis* L. and *Limnobium* Rich., united in the subfamily Hydrocharitoideae, 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, *H. dubia* (Blume) Backer and *H. morsus-ranae* L. (Cook & Lüönd 1982). *Hydrocharis dubia* and *H. morsus-ranae* have formed extensive secondary ranges, causing significant damage to local ecosystems (Cook & Lüönd 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 & Lüönd 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 (q.v. 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 remperature – min remperature); 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 enclave 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-

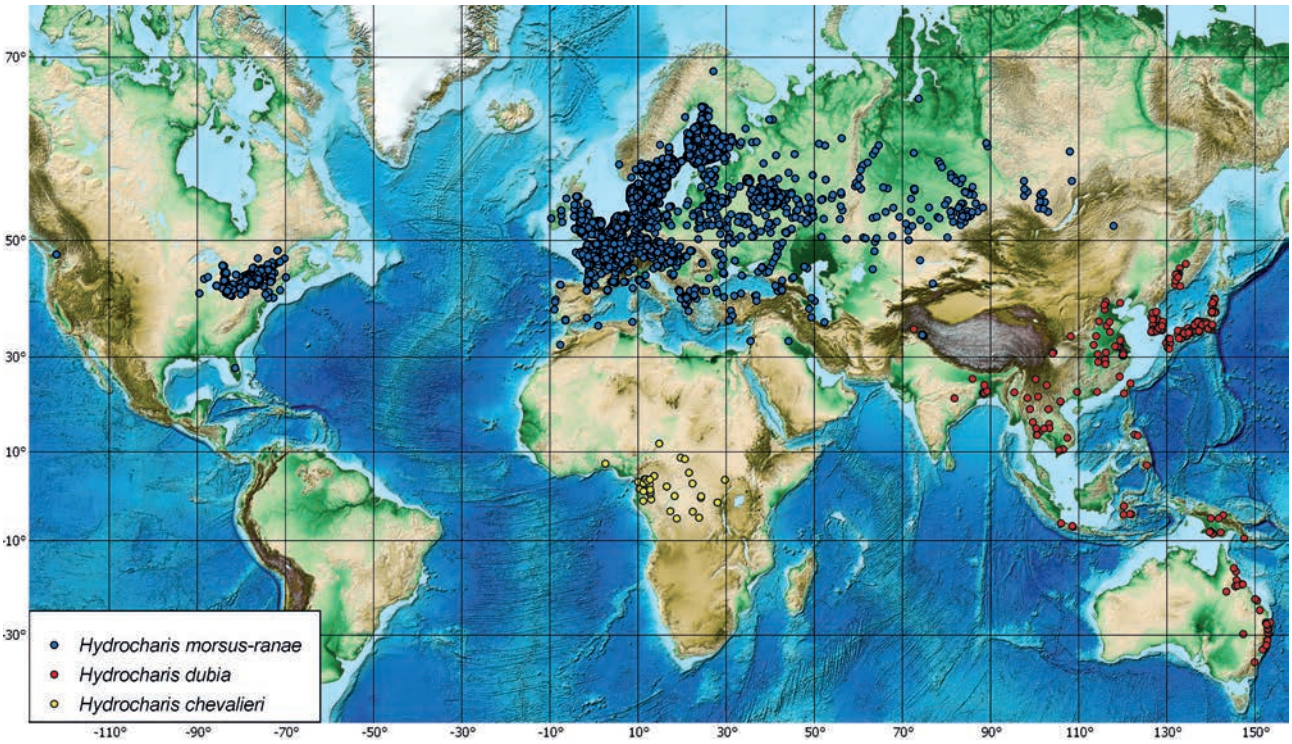

Figure 1 World distribution of the species of *Hydrocharis* L.

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 (Danihelka 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 (Schill & Krautkrämer 2019, Appendix 1: GBIF 2019). In Austria it occurs in all regions except Tirol and Vorarlberg, however, it is highly endangered (Schill & 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 (Borská 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, BC, VAL). It is sporadically distributed in the North and Central Italy, in the south it is rare or extinct (Conti 2005, Acta 2007, Appendix 1: GBIF 2019, Invasive 2019, Z+ZT, FI). In Croatia and Serbia it is limited only by the Pannonian Plain (Jankovich 1975, Vukov et al. 2003, Dÿigurski et al. 2010, Nikolić 2015). *H. morsus-ranae* is rare in Bosnia and Herzegovina (Beck von Mannagetta 1904) and Albania (Shkodra, Ohrid, Prespa Lakes, the Runa River, the Roskovec Swamp) (Barina 2017, W). The species is very rare in North Macedonia (Ohridsko Ezero, Prespansko Ezero, Dojran Ezero, Strumica) (Beck von Mannagetta 1904, Micevski 1969, W) and Montenegro (Skadar Lake) (Pulević 2005). It is rarely found in the continental Greece (North Central Greece, North and South Pindos, North-East Greece, Sterea Ellas) (Dimopoulos 2013; Appendix 1: Vascular 2019) and has not been reported from Crete.

In general, *H. morsus-ranae* is quite common only in the southern parts of the Northern Europe. The plants sometimes flower abundantly and bear fruit; at the northern border vegetative reproduction prevails. The species is often found across Denmark (Hartvig 2005, Appendix 1: GBIF 2019, BP, PR, LE). *Hydrocharis* has become commoner in Finland in recent times due to eutrophication, the most distribution sites are found in the southern and central parts of the country, it is spread up to Lapland with the northern border at 68.9 °N 27.1 °E (Uotila 2002, Appendix 1: Lampinen & Lahti 2017, LE, BP, W, Z+ZT). In Sweden it is currently distributed mainly in the south and less so in the central regions (Appendix 1: LifeWatch 2018, W, Z+ZT).

Hydrocharis morsus-ranae is a widespread in the Eastern Europe. It is often found in Belarus (Dubovik 2013, LE, MW), common in all regions of Latvia (mainly in the South and South-East) (Birkmane 1953, Appendix 1: GBIF 2019, LE, RIG), Estonia (Lellep 1984, Appendix 1: GBIF 2019, LE, TLM), Lithuania (Pipnys 1963, Appendix 1: GBIF 2019, LE) and Kaliningrad region of Russia (LE). In Ukraine it is distributed unevenly: it is common in Polesye (forest) and forest and steppe zone, in the Ciscarpathian Plain and steppe it occurs sporadically (Dobrochaeva 1987, Dubina 1993, Appendix 1: GBIF 2019, LE, MW). In Romania it is occasionally found across the territory with the exception of the Carpathians (Topa 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 (Minyaev 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 (Kamyshev 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 (Skvortsov 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 Imereti) and Ab-

khazia (Gagnidze 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 (Garielyan & Oganisyan 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 Crimea Peninsula *H. morsus-ranae* is an introduced species which was found in the 2011 in the vicinity of Sevastopol (Appendix A: All flowers 2019).

Hydrochsris 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 (Ovesnov 1997, Ryabinina & Knyazev 2009, Kulikov 2010, Appendix 1: GBIF 2019, LE, MW, IBIW). The northern border of its distribution lies in the south of the Komi Republic, and thus in the taiga zone (Martynenko & 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) (Dobrokhotova 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 Cisyenissey 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 (Dobrokhotova 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, E, W, 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 & Jamous 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 (Jacono & 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 (QBG), 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 occurencies 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-

land of Borneo). There are known locations in Indonesia (Northen Java, Eastern ana Southern New Guinea, South and South-East Sulawesi, Philippines (Luzon)) and Oceania (Papua New Guinea (main island group)) (Den Hartog 1957, Ito & Barfod 2014, Appendix 1: IUCN 2019, Pelser 2017, GBIF 2019, WAG, Z+ZT). The distribution pattern in the Republic of Singapore is not defined.

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 Chhattisgarh) (Cook 1998, Guha & Maondal 2005, Appendix 1: Barooah & Iftikher 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.

Hydrocharis dubia is common in China, Korea and Japan. It is found in the southern and eastern provinces of China (Anhui, Fujian, Guangdong, Guangxi, Northeast Hainan, Hebei, Heilongjiang, Henan, Hubei, Hunan, Jiangsu, Jiangxi, Jilin, Liaoning, Shaanxi, Shandong, Sichuan, Yunnan, Zhejiang), Hong Kong, Taiwan. It is also ubiquitous in Japan (Honshu, Shikoku, Kyushu, Okinawa, Ryukyu Islands) and Korean Peninsula (Cook & Lüönd 1982, Wu 1986, Choi 2000, Chen et al. 2012b, Wang et al. 2010, Appendix 1: Chang et al. 2014, Japanese 2019, Global 2019, GBIF 2019, IBSC, LE, W, Z+ZT, SNU).

In the Russian Far East the species is found at 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 & Lüönd 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 & Lüönd 1982, Symoens 1984, Akoegninou et al. 2006, Symoens 2015, Sosef 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, Carrión & 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 Kholmech 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*

Species	Fossil status	Stratigraphy	Location
Hydrocharis batrachodigma A. Massal.	leaves	Oligocene	Schiavon (Chiavon), Vicenza, Veneto, Italy
Hydrocharis langsdorfii R. Ludw.	leaves	Miocene	Salzhausen, near Nidda, Wetterau, Hessen, Germany
Hydrocharis lusatica Mai in Mai, H. Walther	seeds	Miocene	Oberoderwitz borehole, Saxony, Germany
Hydrocharis magna Mai in Mai, H. Walther	seeds	Oligocene	Haselbach, Landkreis Altenburg, Thuringia, Germany
Hydrocharis morsus-ranae L.	seeds, pollen	Eocene – Holocene	Navarrés, eastern Spain; Poland; Belarus; Lithuania; Ukraine; Voronezh region, Lower Kama, Upper Volga, Western Siberia (common in the south, the northern border is the mouth of the Ob, Russia)
Hydrocharis orbiculata Heer	leaves	Miocene (Tortonian)	Öhningen, Landkreis Konstanz, Baden-Württemberg, Germany
Hydrocharis ovata R. Ludw.	leaves and flowers	Miocene	Salzhausen, Münzenberg, Wetterau, Hessen, Germany
Hydrocharis rottensis Weyl.	not available	Oligocene (Chattian, Rott Formation)	Rott near Bonn, North Rhine-Westphalia, Germany
Hydrocharis tertiaria Hartz	seeds	Miocene	Sønderskov near Silkeborg, Jutland, Denmark
Hydrocharis cf. dubia (Blume) Backer	leaves	Late Senon – Paleocene	Amur region, South of Russia Far East
Hydrocharis sp.	not available	Miocene	South China
Hydrocharis sp.	seeds	Oligocene, Miocene, Neopleistocene	South of Western Siberia
Hydrocharis sp.	pollen	Upper Pliocene – Middle Pleistocene	Caspian Lowland (Baku)

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

Characteristic	***Hydrocharis chevalieri***	***Hydrocharis dubia***	***Hydrocharis morsus-ranae***
Extent of occurrence, Mkm^2	3.134	6.820	16.030
Area of occupancy, Mkm^2	0.074	0.199	0.785
Extreme latitudes	11.9°N – 5.0°S	46.5°N – 35.2°S	68.9°N – 33.1°N
Extreme longitudes	2.6°E – 29.8°E	72.6°E – 153.0°E	90°W – 122.0°E

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

Species	Category for the World	Category for macroregions
Hydrocharis chevalieri	LC	Benin and Cameroon (savana regions): probably NT (A4c,e) (AD)
Hydrocharis dubia	LC	South-East Asia: probably NT (AD); Japan: NT (Appendix 1: Global 2020); Indian subcontinent: probably NT/VU (AD); Russian Far East: NT (AD)
Hydrocharis morsus-ranae	LC	Western Europe: United Kingdom and Ireland − VU (A2c) (Cheffings & 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 & Krautkrämer 2019, AD); Switzerland − EN (B2ab(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, Dyigurski et al. 2010, Dimopoulos 2013, Nikolić 2015, Barina 2017); **Caucasus**: Georgia, Azerbaijan – probably EW (AD); Middle and Eastern Siberia: NT – (Chepinoga et al. 2008; AD); probably neophyte in Eastern Siberia; Western Asia: Iran, Iraq − probably neophyte (Assadi & Wendelbo 1977), Israel − EW (Sapir 2003); North Africa: EN (García et al. 2010), probably neophyte.

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 2000s). 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 savana 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. chevalieri* 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. chevalieri* 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. morsus-ranae* and *H. chevalieri* also as medicinal plant (Den Hartog 1957, Dubina et al. 1993, Sosef 2017). *Hydrocharis chevalieri* 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 diaspores 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 (Ganie 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-

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

Environmental factors	The range of variation of the factor (optimum) within global habitat		
	Hydrocharis chevalieri	***Hydrocharis dubia***	***Hydrocharis morsus-ranae***
Annual precipitation, mm (Appendix 1: WorldClim2019)	1400−2600 (≈1800−2400)	800−3200 (≈1200−2000)	400−2000 (≈600−1000)
Mean annual temperature,° C (Appendix 1: WorldClim2019)	20.1−25.0 (≈20.1−25.0)	1.0−30.0 (≈10.1−25.0)	-9.9−20.0 ((≈1.0−15.0)
Altitude, m above see level (Cook & Lüönd 1982, Appendix 1: WorldClim 2019)	0−1000 (≈100−500) (WAG, YA)	0−2600 (≈0−1000) (Den Hartog 1957, Haynes 2001, IBSC, LE, Z+ZT, W)	0−1600 (≈0−500) (BP, E)
Type of water body (Cook & Lüönd 1982)	Flooded swamps, aquatic meadows, streams in forest (still waters), bare mud, thalweg with periodical floods, small swampy hollows, small waterbodies (Lubini 1983)	Shallow water bodies or slow moving streams, marshes, locally swamp forest, ditches, ponds, reservoirs, habitats that dry out each year (Den Hartog 1957; AD)	Small waterbodies, sheltered bays or inlets of larger lakes and rivers; oxbow lakes, canals, ditches, reservoirs, flooded swamps, habitats that dry out each year (Dubina et al. 1993, Sviridenko 2000, AD)
Depth, m	0.0−0.6 (≈0.3) (Lubini 1983)	0.1−3.0 (≈0.5−1.5) (AD)	0.1-2.0 (≈0.5−1.5)(Cook & Lüönd 1982, Sviridenko 2000, Dubina et al. 1993, AD)
Type of bottom deposit	Silty, silty-detrital (Lubini 1983)	Silty, silty-peaty, wet mud (Cook & Lüönd 1982, AD)	Silty, silty-peaty, sandy (Cook & Lüönd 1982, Sviridenko 2000, AD)
pH, pH units	6-7 (≈6.5) (Lubini 1983)	≈7.0 (AD)	6.4-8.8 (≈7.0) (Sviridenko 2000, AD)
Trophicity	≈ mesoeutrophic (AD)	mesoeutrophic – eutrophic (≈mesoeutrophic) (AD)	oligotrophic − eutrophic (≈mesoeutrophic) (Cook & Lüönd 1982, Sviridenko 2000, Dubina et al. 1993, AD)

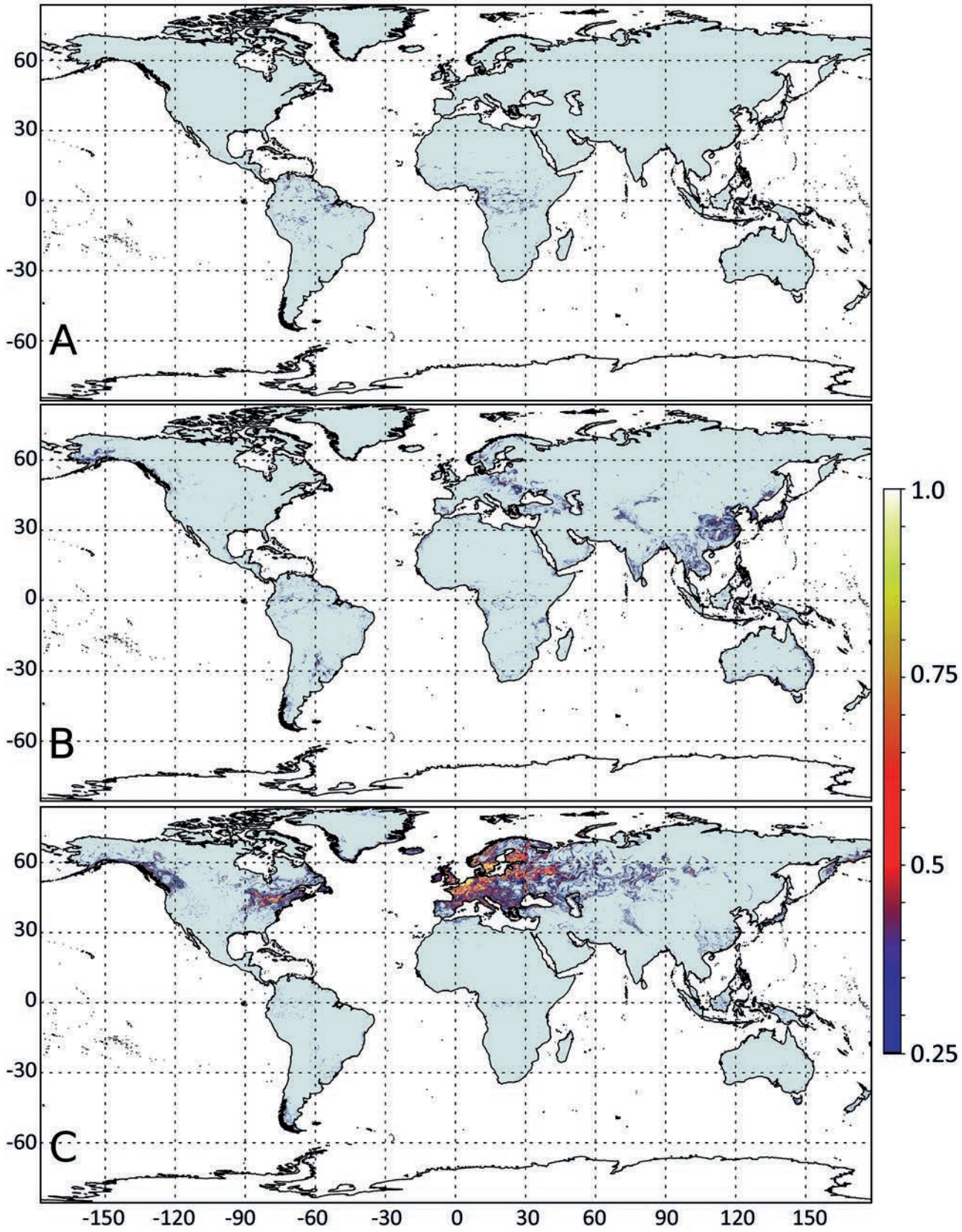

Figure 2 The model showing the potential distribution range of *Hydrocharis chevalieri* (De Wild.) Dandy (A); *H. dubia* (Blume) Backer (B) and *H. morsus-ranae* L. (C)

thern 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, Caucasia). *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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