# A NEW SPECIES OF *POTAMOGETON* (POTAMOGETONACEAE) FROM THE UNIQUE HABITAT: MONTEZUMA WELL, ARIZONA, U.S.A.

Jon M. Ricketson & Glenda M. Ricketson

*Missouri Botanical Garden*
*4344 Shaw Blvd.*
*St. Louis, Missouri 63110, U.S.A.*
*jon.ricketson@mobot.org*

Tina L. Greenawalt

*National Park Service*
*Montezuma Castle National Monument*
*Camp Verde, Arizona 86322, U.S.A.*

ABSTRACT

Montezuma Well is a geothermal limnocrene spring within Montezuma Castle National Monument, Yavapai County, Arizona, U.S.A. The Well's unusual geological qualities, water chemistry, and a history of aquatic plant collecting are discussed. Evidence to support the fact that a unique species of *Potamogeton* has likely grown in this location for thousands of years and is now recognized as the seventh apparent autochthonous endemic species from this small area is presented. Although this new species shares a few superficial characters with *P. illinoensis* Morong, it is easily distinguished by its massive height (7–8 m tall), lack of floating leaves, long acuminate leaf apices of its submerged leaves, and bright translucent green leaf color. A complete description with drawing and photographs is provided.

RESUMEN

Montezuma Well es una fuente geotérmica limnocrena en el Montezuma Castle National Monument, Yavapai County, Arizona, U.S.A. Se discuten las cualidades geológicas inusuales, química del agua, y una historia de la recolección de plantas acuáticas del Well. Se reconoce ahora la prueba que sostiene que una especie única de *Potamogeton* ha crecido probablemente en esta locación durante miles de años, y se presenta como la séptima especie aparentemente autóctona endémica de esta pequeña área. Aunque esta nueva especie comparte unos pocos caracteres superficiales con *P. illinoensis* Morong, se distingue fácilmente por su gran altura (7–8 m), ausencia de hojas flotantes, ápices foliares largamente acuminados en las hojas sumergidas, y hojas de color verde brillante translucido. Se aporta una descripción completa con dibujos y fotografías.

Key Words: Arizona, Yavapai County, Montezuma Castle National Monument, Montezuma Well, Potamogetonaceae, *Potamogeton*, systematics, taxonomy, ecology, geology, Sinagua, endemic, new species

## INTRODUCTION

Montezuma Well is perhaps one of the most unusual, and given its size, one of the most studied areas on the planet, fostering about 150 publications on geology, hydrology, paleontology, archaeology, ecology, and biology. Montezuma Well is a unique ecosystem that supports at least six apparently autochthonous endemic species [a water scorpion, *Ranatra montezuma* (Polhemus 1976); an amphipod, *Hyadella montezuma* (Cole & Watkins 1977); a diatom, *Gomphonema montezumense* (Czarnecki & Blinn 1979); a spring snail, *Pyrgulopsis montezuma* (Hershler & Landye 1988); and two leech species, *Erpobdella montezuma* (Davies et al. 1985 [= *Motobdella montezuma* (Govedich et al. 1998)]; and *Helobdella blinni* (Beresic-Perrins et al. 2017)]. Montezuma Well is also the type locality of the extinct Southwestern River Otter or Arizona River Otter, *Lontra canadensis sonora* (Rhoads 1898), and two diatoms, *Caloneis latiuscula* var. *reimeri* and *Cyclotella pseudostelligera* (Czarnecki & Blinn 1979). In addition, Montezuma Well hosts many first and often only state records including some extreme range extensions of a variety of biological species. However, with all the research that has been conducted, little attention has been turned to the most obvious species present, a new *Potamogeton* proposed here.

The identity of the single *Potamogeton* species in Montezuma Well has been confused for the last century, identified alternately as *P. gramineus* L. var. *maximus* Morong (Kearney et al. 1951, 1960), *P. gramineus* L. (McDougall & Haskell 1960; McDougall 1973), *P. illinoensis* Morong (Cole 1963; Cole & Batchelder 1969; Correll & Correll 1972; Lehr 1978), or perhaps a hybrid between *P. gramineus* L. × *P. illinoensis* Morong (Ogden 1943; Ricketson 1990). However, all of these identifications were made with uncertainty, as this *Potamogeton* species does not conform to any of these entities, although it appears to share certain characteristics with *P. illinoensis*.

**J. Bot. Res. Inst. Texas 12(2): 447 – 459. 2018**

## THE SITE—MONTEZUMA WELL

Montezuma Well is located in Central Arizona, between Phoenix and Flagstaff, north of Camp Verde in the Verde Valley adjacent to Wet Beaver Creek (34°38'57.2"N, 111°45'08.1"W [34.649233, -111.752246]) at an elevation of 1103 m (3618 ft), near present day Interstate Highway 17, in Yavapai County, Arizona. Montezuma Well is a detached portion of Montezuma Castle National Monument and is protected by the National Park Service, an agency of the United States Department of the Interior. Montezuma Castle National Monument is one of the four original United States National Monuments (including Devils Tower, El Morro, and the Petrified Forest) created as part of the 1906 American Antiquities Act, signed by President Theodore Roosevelt. The Monument is an IUCN category V Protected Landscape (IUCN 2017) and was placed on the National Register of Historic Places (No. 66000082) in 1978. The "Castle" portion of the Monument protects a series of well-preserved cliff dwellings built and used by the Sinagua ("seen-aug-wah") people between ca. 1100–1425 CE. The Montezuma Well portion of the Monument (referred to as "the Well"), located several miles north of the Castle, was added in 1947, also protects a series of Sinagua dwellings and structures, in addition to the natural aspects of the Well. The name "Montezuma," applied to both the Castle and Well, is a misnomer. In the 1860s, while establishing a Camp/Fort to protect settlers in the new Arizona Territory, U.S. Army soldiers came across these ruins and cliff dwellings in the Verde Valley. They unknowingly referred to the architecture as Aztec in origin, like those they had encountered in Mexico during the Mexican-American War (1846–1848). However, these structures were likely abandoned in the early 15$^{th}$ century, before the formation of the Aztec Empire and the birth of Emperor Montezuma (Lange 1957; Cole & Watkins 1977; Beckman 1991; Blinn 2012).

The formation of the Well is the result of the collapse of a domed spring mound or limnocrene (Blake 1906; Cole & Batchelder 1969; Nations et al. 1981; Blinn 2012), formed within a Mio-Pliocene limestone deposit that is localized to the Verde Valley along the present-day Verde River and which has been termed the Verde Formation (Jenkins 1923). According to Nations et al. (1981:140), the fossil records of the Verde Formation include "leaves or stems of aquatic herbs [including *Lemna* and *Potamogeton*], sedges (*Scirpus* [=*Schoenplectus*]), cattail (*Typha*), reedgrass (*Phragmites*), and scouring rush (*Equisetum*)," all of which are currently known from the Well area.

Montezuma Well is an unusual area both geologically and hydrologically. The remnants of the mound are clearly visible today (Fig. 1A), rising 25 m (83 ft) above Wet Beaver Creek, along the east edge of the Well, creating a riparian habitat through the surrounding mixed Sonoran Desert-Juniper woodland. Wet Beaver Creek has eroded part of the eastern side of the mound, where the mound wall is only 46–65 m (144–204 ft) thick. The Well has a flat top with a nearly circular opening 112 m (368 ft) across. The inner walls are perpendicular, 6–12 m (20–40 ft) tall, with occasional talus areas leading down to a nearly circular water-filled depression 17–24 m (55–75 ft) below the rim. Along the eastern edge of the Well, the water from the pool exits through a cave or "swallet" where the water is filtered through a series of micro-cracks and subterranean "caves" and is discharged into an ancient manmade irrigation ditch just above Wet Beaver Creek. Fluorescein dye tests have shown that this journey takes ca. 7 minutes (Cole & Batchelder 1969). The Well provides a near constant flow of water into the ditch year-round and is an important habitat for aquatic plants, such as many of the species found in the Well [the aquatic moss *Fissidens fontanus* (John Atwood (MO), pers. comm.), the red alga *Batrachospermum,* and various macrophytes such as *Hypocotyle* sp., and *Zannichellia palustris* L.] The ditch also supports the pondweed, *Potamogeton nodosus* Poir (mistakenly reported as *P. natans* L.) (Cole & Batchelder 1969) but not the common *Potamogeton* species from within the Well.

The pool within the Well is roughly circular and has a gradual ledge, before it makes a nearly shear drop to a false bottom (i.e., essentially funnel-shaped). The surface of the water covers ca. 0.76 ha (Cole & Barry 1973), clearly supporting two distinct limnological features. The pelagic zone is a well-defined area of 0.23–0.33 ha (3280 m$^2$) with a maximum depth of 17–21 m (55–68 ft) (Cole & Barry 1973; Blinn & Sanderson 1989; Runck & Blinn 1992) and a littoral zone of 0.32–0.43 ha on a shelf 3–20 m (9.8–65.6 ft) wide, with a depth of 1–2 m (3.2–6.5 ft) around the perimeter of the Well (Blinn et al. 1982; Runck & Blinn 1990). The littoral zone

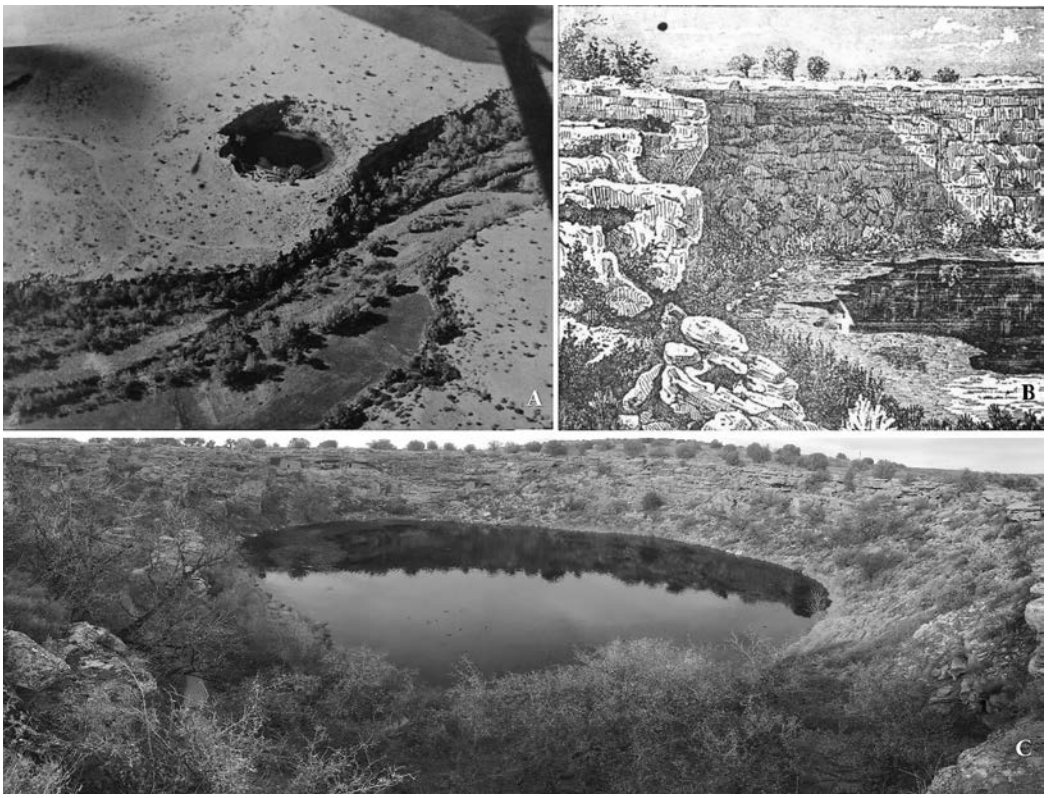


Fig. 1. **A.** Aerial view of Montezuma Well, showing the circular Well on a raised mound which has been cut by Wet Beaver Creek; note the proximity of the creek to the edge of the Wall (Credit: National Park Service 1950). **B.** Montezuma Well (Hinton 1878). **C.** Panoramic view of Montezuma Well (Credit: J. Ricketson 2015).

is made up of a dense mixture of emergent species composed of *Eleocharis rostellata* (Torr.) Torr., *Schoenplectus acutus* (Muhl. ex Bigelow) Löve & Löve var. *occidentalis* (Wats.) S.G. Smith, and *Berula erecta* (Huds.) Coville, and a floating population of mixed algae (Kidd & Wade 1963) and *Lemna minucula* Herter (at least historically), as well as submerged aquatic macrophytes.

The bottom of Montezuma Well has erroneously been reported over the years as "bottomless" according to a story from 1880, related by Beckman (1991:9) or "of unfathomable depth" (Blake 1906:568). However, a number of scuba dives have been conducted which discovered an interesting anomaly of a "false" bottom consisting of a thick layer of "ooze" made of a green gelatinous organic material and fluidized sand (Cole & Barry 1973). The National Park Service produced an informative video during a 2015 underwater survey that is available online (https://vimeo.com/188237709). Because of the nature of this false bottom, the actual pool depth varies from 23–43 m (74–137 ft), the number of thermal vents is uncertain (2 to 6).

While the geological aspects of the Well area are interesting, it is truly the hydrology and water chemistry that make the Well unique. Blinn (2012) estimated that over 4164 liters (1100 gallons) of water enter the Well through these vents every minute or 5.1 million liters (1.35 million gallons) per day. The exact source of the water is unknown, but it is believed to be ancient water, perhaps over 3000 years old (Damon et al. 1964b; Blinn 2012). The Well has a high concentration of dissolved $CO_2$ (550–864 mg/l), more than 600 times higher than an average fresh water pond (Cole 1963). The concentration levels of $CO_2$ decrease rapidly from when the water enters the Well until it mixes with water from Wet Beaver Creek as it leaves the Monument property

(Cole & Batchelder 1969). The water has high alkalinity of $CaCO_3$ (>600 mg/l); a low concentration of dissolved $O_2$ (<6 mg/l), a nearly constant pH (6.1–6.9), and a moderately high specific conductance (925–1394 µS/cm at 25°C) (Cole 1963; Cole & Barry 1973; Czarnecki & Blinn 1979; Boucher et al. 1984; Blinn & Sanderson 1989; Konieczki & Leake 1997). The water temperature remains constant, between 17–25°C (62.6–77°F) "… in the pelagic zone, but has daytime temperatures of 30°C (86°F) or higher in the littoral vegetation" (Oberlin & Blinn 1997:55), the high constant temperature year-round prevents the water from ever freezing. The average mean air temperature is 10.6°C (51.08°F). Additionally, the water has a high concentration of arsenic, 110 µg/l, the EPA drinking water standard is no more than 10 µg/l (Johnson et al. 2008). Finally, radiocarbon analysis on material within the Well (Damon et al. 1964a; Damon et al. 1964b; Haynes et al. 1966; Cole & Barry 1973), using Carbon 14 methods, has discovered an "anomalous $^{14}C/^{12}C$ ratio in the water and the modern organisms, a phenomenon that has precluded accurate dating by the radiocarbon method" (Cole & Watkins 1977:181).

Avery and Helmke (1991:205) have shown that "Montezuma Well is a dynamic hydrological system rather than a homeostatic one: water levels within the Well fluctuates "slightly" on a daily and annual basis." The Well is a relatively enclosed ecosystem with limited external impact, primarily only airborne, and has likely been a stable environment for thousands of years (Czarnecki 1979). Photographic evidence suggests that the Well has not changed significantly over the past 150 years. Note the similarities between the drawing from Hinton (1878) (Fig. 1B) and a panoramic photograph taken in 2015 (Fig. 1C), the cliff dwellings are visible, the shore line remains nearly the same and the aquatic vegetation remains consistent, with open water in the center of the pool.

**Aquatic Plant Collection History**

Hevly (1974) and Batchelder and Cole (1978) have analyzed *Potamogeton* pollen retrieved from sediment core samples taken from the Well. Their findings indicate that a species of *Potamogeton* has occupied the Well for ca. 27,750 ± 400 years. Data from the surrounding environment "suggest that aquatic macrophytes were abundant throughout the past 11,000 years in Montezuma Well" (Blinn et al. 1994:200). However, while studying the diatom records from these sediment core samples, Blinn et al. (1994:203) determined that "the aquatic pollen record fails to indicate any change during the middle Holocene until 4200 yrs. B.P. when an abrupt and major increase in *Potamogeton* pollen occurs." Because of the $^{14}C/^{12}C$ anomaly of the Well water, we may never be certain when or for that matter which species of *Potamogeton* first appeared in the Well. However, it is certain that *Potamogeton* pollen has been present for thousands of years (Hevly 1974; Davies & Shafer 1992; Blinn et al. 1994).

Beckman (1991) and Protas (2002) give a detailed history of the Well from its early discovery by Spanish explorers in 1583, including the transfer of the region to the United States after the Mexican-American War, to more recent events. The first naturalist to visit the Well site was Dr. Edward Palmer, as a member of the U.S. Army. Palmer was stationed at Camp/Fort Lincoln (later renamed Camp/Fort Verde), near the confluence of the Verde River and Beaver Creek, in the Arizona Territory, between 1865 and 1866. Palmer was able to make plant, animal, and archaeological collections in the area around the Verde Valley, including the Well, that were to be sent to the Smithsonian Institution. The first recorded herbarium specimens from Montezuma Well are from Dr. Palmer in 1865, and were sent to Dr. George Engelmann at the Missouri Botanical Garden; few duplicates have been located. Unfortunately, a large quantity of material Palmer collected was lost after he was hospitalized for malaria and was transferred out of the region (McVaugh 1956; Protas 2002). Although Dr. Palmer visited the Well in 1865 and perhaps in 1866 and 1869, no collections of *Potamogeton* have been found in the herbaria of ARIZ, ASC, ASU, DES, GH, MNA, MO, NY, RSA, TEX, or US.

The first known collections of *Potamogeton* from the Well are two specimens from 1916 by Hartley T. Jackson and Walter P. Taylor during a biological survey of the area (Jackson & Taylor 1916); both herbarium sheets are housed at US. The identities of these collections remained uncertain until Eugen Ogden (1943) monographed the broadleaved species of North America *Potamogeton* and placed these disjunct collections under *P. gramineus* × *illinoensis* without explanation. The next collection of *Potamogeton* at the Well is a

gathering of 3 sterile sheets at ARIZ by Leslie Goodding in 1918; although sterile, this gathering is significant because it reflects the height of this species. No additional herbarium material is available from the Well from 1918–1947, presumably because the Well was privately owned until it came under federal protection in 1947. Kearney et al. (1951:66; 1960:66) in *Arizona Flora* place the Jackson and Taylor collections under *P. illinoensis* Morong, but state "It is doubtful that they are distinguishable from *P. gramineus* var. *maximus*." However, Kearney et al. (1951; 1960) also identify a 1947 Leslie Goodding collection from Montezuma Well as *P. gramineus* var. *maximus*.

McDougall and Haskell (1960) report three species of *Potamogeton* from the Monument (*P. gramineus* L., *P. nodosus* Poir, and *P. pectinatus* L. [= *Stuckenia pectinata* (L.) Börner]). *Potamogeton gramineus* is presumably the identity of the most common species in the Well, but without the varietal name *maximus* attached to the report (apparently based on older material since no vouchers appear to have been collected to support this identification). *Potamogeton nodosus* is based on an E.R. Blakley collection on 8 Aug 1953 from the irrigation ditch and a collection by Horace S. Haskell on 3 Jul 1958 reported from "Montezuma Well." If we assume that the Haskell collection was actually collected from within the Well, it is the first and only time this species has been documented; although certainly possible, it is more likely that this collection is from the irrigation ditch associated with the "Montezuma Well" portion of the Monument. In fact, Cole & Batchelder (1969:272) report "*Potamogeton natans* L. [= *P. nodosus* Poir] occurs in the ditch beside the picnic ground." Coincidentally, on the same day Haskell collected *P. nodosus*, Richard H. Hevly collected a juvenile specimen of *P. pectinatus* L. [= *Stuckenia pectinata* (L.) Börner], apparently also from "Montezuma Well." If correct, this is the first and until 2016 the only collection or mention of this species from the Well. It is interesting to note that on 3 Jul 1958 when both H.S. Haskell & R.H. Hevly collected at or near the Well, neither made a collection of the most common species of *Potamogeton* (i.e., *P. gramineus*) within the Well. It should also be noted on the day E.R. Blakley collected *P. nodosus* from the irrigation ditch (as mentioned above), he also collected the common *Potamogeton* species from within the Well. Finally, none of these collectors re-collected the other known Potamogetonaceae ally, *Zannichellia palustris* L., which was first collected by Chester F. Deaver in 1948 reportedly from within the Well.

While working on the dynamics of the Well and irrigation canal, Cole and Batchelder (1969:278) became concerned with the identity of the common *Potamogeton* in the Well and noted "We are indebted to Dr. Eugene C. Ogden for identifying this pondweed (Ogden, in lit.). The population in the Well is not typical of *P. illinoensis* elsewhere, and is puzzling to the non-specialist." By 1975, the common *Potamogeton* in the Well was referred to as either *P. gramineus, P. illinoensis, P. gramineus* var. *maximus*, or *P. gramineus* × *illinoensis*.

During the course of preparing a treatment of the genus *Potamogeton* for the "Vascular Plants of Arizona" Project, it has been determined that *P. illinoensis* is not found within the boundaries of the state of Arizona. Between 1983 and 1990, Ricketson (1990) conducted an extensive survey (including literature, herbaria and field work) of the aquatic plants of Coconino National Forest including Montezuma Castle National Monument. Attempts to identify the *Potamogeton* species in Montezuma Well were unsuccessful because the plant did not conform to any known species. The current study shows that this species is unique and deserves species status.

**Potamogeton montezumawellensis** Ricketson, G. Ricketson, & Greenawalt, **sp. nov.** (**Fig. 2**). TYPE. U.S.A. ARIZONA. Yavapai Co.: Montezuma Well, Montezuma Castle National Monument, 0.4 mi E of the junction of U.S.F.S. Road 119 (Beaver Creek Road), at the end of the Well Entrance Road, E of the towns of Lake Montezuma, Rimrock and McGuireville, next to Beaver Creek, 8 air miles N of Camp Verde at the Verde River and about 40 air miles S of Flagstaff, Lake Montezuma Quad, R6E, T15N, Sect 31, (34°38'57.2"N 111°45'08.1"W [34.649233, -111.752246]), 1146 m (3760 ft), 11 Oct 1985 (fl.), *Jon Ricketson 4185A* (HOLOTYPE: MO; ISOTYPES: ARIZ, ASC, ASU, BRIT, DES, MNA, MO, NY, TEX, UC, US).

Quoad folia demergia oblonga vel elliptica secus margines minute denticulata vel crispa ad P. illinoensi valde arcte affinis sed ab ea caulibus 7–8 (non 0.28–1.28) m longibus, foliis demergibus mono- (non di-) morphibus longio-attenuatis 10–22 mm longibus (nec caudato-acuminatibus mucronisque 2.5–17 mm longibus statim distiguitur.

Roots fibrous at the nodes. Stems with rhizomes present, turions absent, cauline portion terete to 8 m tall (making this one of the tallest aquatic plants in the world), stout, 3–6 mm in diam., simple below, few branches


Fig. 2. *Potamogeton montezumawellensis* Ricketson, G. Ricketson, & Greenawalt habit, flowering branch (drawn from holotype: *J. Ricketson 4185A* (MO)). (Credit: J. Ricketson)

above, 1–5 near apex; nodal glands absent. Leaves all submerged, no true floating leaves present; submerged leaf blades bright translucent green to dark green, narrow-lanceolate to narrowly elliptic, 2.5–18 × 0.4–1.9 cm, basally acute to decurrent on the petiole, apically long acuminate, the acumen 10–22 mm long, the margins entire, but appearing crispate or denticulate with age, lacunae of 2–5 rows along the midvein or often absent, lateral veins 11–13; petioles 0.3–1.8 cm long. Stipules green, persistent, conspicuous, convolute, free from the blade, 1.1–4 cm long, not ligulate, fibrous or shredding at the tip, apically acute, margins entire. Inflorescences unbranched emergent, axillary and terminal, erect to ascending, 6–17.5 cm long; spikes cylindrical, 2.5–3.7 cm long, multi-flowered, 15–30-whorled; peduncles terete, 2.3–15 cm long. Flowers sessile or on short pedicles to 0.5 mm long, perianth lobes green to reddish with age, claw-like to orbicular, 3-lobed, 2.7–3 × 1.8–2 mm, the lobes rounded, margins entire; stamens sessile, adnate to the perianth, 1.5–1.7 × 1.2–1.8 mm, anthers yellowish-green, ovate, 1.3–1.5 × 0.3–0.6 mm; pistil sessile, laterally compressed, 1.5–2 × 0.8–1 mm, with hump on dorsal ridge, stigma and style sessile, lateral. Fruits (fully formed, but appearing sterile) sessile or on short pedicels, obovoid, 4–4.2 × 2.8–3 mm, laterally compressed. 2–2.2 mm wide, dorsal keel obscure with few projecting knobs, the two lateral keels absent to obscure, beak erect to slightly recurved, 0.2–0.3 mm; embryo ½ to ¾ coil.

*Distribution.*—*Potamogeton montezumawellensis* is endemic to Montezuma Well: Montezuma Castle National Monument in Yavapai County, Arizona., 34°38'57.2"N 111°45'08.1"W (34.649233, -111.752246) at 1103 m (3618 ft) in elevation; growing in a sheltered collapsed travertine limnocrene.

*Ecology and conservation status.*—*Potamogeton montezumawellensis* is an important element to the daily life of Montezuma Well, just as the trees in a forest provide an important function in the lifecycle of that forest, *P. montezumawellensis* performs a similar function within the Well (and at 8 m is taller than some trees). *P. montezumawellensis* is a main link in the daily ecosystem that has evolved within Montezuma Well which is home now to seven endemic species. Both epiphytic and planktonic diatoms like the endemic *Gomphonema montezumense*, and other algae as well as *P. montezumawellensis*, use nutrients that enter the Well and convert it, by photosynthesis, into useful food and oxygen. This is also an interesting case of plants utilizing fossil $CO_2$ and artesian water for photosynthesis (Damon et al. 1964a; 1964b; Cole & Barry 1973; Davies et al. 1988). *P. montezumawellensis* provides the only protection and nursery for the keystone endemic amphipod, *Hyalella montezuma* (Cole & Watkins 1977; Blinn et al. 1988; Wagner & Blinn 1987). *P. montezumawellensis* provides cocoon attachment points that are deep and out of the reach of predators for the endemic leech, *Motobdella montezuma* (Davies et al. (1988: 608). It is directly involved in the lifecycle of most of the aquatic insects, providing egg attachment (on its large diameter stems) and nymph and larval habitat. Its leaves and floating debris provide perches for the endemic water scorpion, *Ranatra montezuma* and other insect predators in the Well (Runck & Blinn 1993; Runck & Blinn 1994; Blinn 2012). Although, the endemic spring snail, *Pyrgulopsis montezuma* does not feed on *P. montezumawellensis*, other snail species like *Physa virgate* and *Ferrisia fragilis* have been reported utilizing this pondweed (O'Brien & Blinn 1999). Without *Potamogeton montezumawellensis* these endemic could lose the protection it provides and become extinct. Finally, *P. montezumawellensis* helps stabilize the ooze covered steep walls within the Well.

It grows in a federally protected National Monument, so the only conservation concerns would come from a catastrophic environmental event (i.e., the rate of flow from the underground springs increasing or decreasing) or a dramatic change in management policy employed by the National Park Service (at one time NPS policy was to "rake" the old floating debris from the surface of the water, because it impeded water flow to the "swallet"). This species is a narrow point endemic that is very well protected but may be subject to population decline if the recent discovery of the aggressive Sago-pondweed, *Stuckenia pectinata,* is not controlled or removed. Therefore, it is here classified as a vulnerable species.

*Etymology.*—The specific epithet refers to the name of the type location, Montezuma Well, which is a part of Montezuma Castle National Monument. As mentioned above, the name "Montezuma" is a misnomer.

*Common name.*—Montezuma Well pondweed.

*Paratypes*. **U.S.A. ARIZONA. Yavapai Co.:** Montezuma Well, Montezuma Castle National Monument, 1146 m (3760 ft), 1 Aug 1916 (fl.), *W.P. Taylor 78* (US); *ibid*., 2 Aug 1916 (fl.) *H.T. Jackson 52* (US); *ibid*., 20 Apr 1918 (ster.), *L.N. Goodding 29* (ARIZ [3 sheets]); *ibid*., 17 Jul 1947 (fl.), *L.N. Goodding 91-47* (ARIZ); *ibid*., 8 Aug 1953 (fl. bud), *E.R. Blakley B-1805* (ARIZ, ASU [2 sheets]); *ibid*., Sep 1960 (ster.), *A. Schultz s.n.* (ASU [2 sheets]); *ibid*., 28 Jul 1964 (fl.), *J.W. Stockert 2348/B16,541* (MNA); *ibid*., 18 Oct 1975 (ster.) *T. Reeves 4579* (ASU); *ibid*., 24 Oct 1975 (fl.), *B. Warzak s.n.* (ASC); *ibid*., Jun 1981 (fl.), *G. Griffith s.n.* (ASC, MO); *ibid*., 13 Aug 1981 (fl.), *G. Griffith s.n.* (ASC, F, MNA, MO, NY, TEX); *ibid*., 3 Jun 1984 (fl.), *C.A. Pinney s.n.* (ASC); *ibid*., 26 Jul 1988 (fl. bud), *J.M. Porter 5562* (RSA, UCR); *ibid*., 7 Aug. 2017 (fl.), *J. Ricketson & R. Meara 5000* (MNA, MO).

Within the genus *Potamogeton*, *P. montezumawellensis* clearly shares some similarities with *P. illinoensis* (Fig. 3A–B); i.e., submerged leaves are oblong to elliptic and the margins at least appear minutely denticulate or crisped. However, on closer inspection, a number of striking features become evident. First and most obvious are that individuals *in situ* (vs. herbarium specimens) are as much as 7–8 m tall (vs. 0.28–1.28 m tall), making this one of the tallest vascular aquatic plants in the world, although Hutchinson (1975) reports specimens of *P. pectinatus* [=*Stuckenia pectinatus*] growing as much as 11.5 m (38 ft) tall from Lake Titicaca. The leaves of *P. montezumawellensis* are all submerged and of similar form (vs. usually dimorphic, of submerged and floating leaves, although certain collections are found of only submerged leaves). The floating leaves of *P. illinoensis* are broadly ovate. The submerged leaves are 2.5–18 × 0.4–1.9 cm (vs. 5–22 × 0.4–5.3 cm). The apex of the leaves is generally very long-acuminate, the acumen 10–22 mm long (vs. acute or rounded with a short acute-mucronate tip, the acumen 2.5–10 mm long, the acute-mucronate tip of the floating leaves is prominent, the acumen of the floating leaves is 1.7–2.5 mm long). The lateral veins of the submerged leaves are 11 to 13-veined (vs. 15 to 17-veined). The leaves are a bright translucent green to dark green (vs. generally a dull green to brownish red color). The petioles are 0.3–1.8 cm long (vs. 0.5–4 cm long). The stipules are 1.1–4 cm long (vs. 1–8 cm long). The inflorescence spikes are 2.5–3.7 cm long (vs. 2–7 cm long). The peduncles are 3–15.5 cm long (vs. 3.5–31 cm long). The fruits of *P. montezumawellensis* are 4–4.2 mm long (vs. 2.5–3.6 mm long) and the dorsal keel and lateral keels are obscure with few projecting knobs (vs. dorsal and lateral keels prominent). However, the fruits that have been collected may in fact be sterile. When opened the embryo does not appear to be fully formed, thus true fruit comparisons may be misleading.

The density of a portion of the population of *Potamogeton montezumawellensis* can be seen in Figure 4A, note the flowering inflorescences above the water surface and in Figure 4B, the underwater protection it provides. Freshly gathered material (Fig. 4C) highlights the unbranched, thick stems with similar bright translucent green, narrow-lanceolate submerged leaves, with long acuminate apices, and the crispate or denticulate appearing leaf margins. The dense, multi-flowered, cylindrical spiked inflorescences with sessile flowers in Figure 4D, appear complete and perfect, with stamens and ovaries. It is unclear at this time if fertile pollen and/or fruits are present in this species.

Why hasn't this species spread and what are the factors keeping this entity within the Well? The Well is a thermal spring, with a constant temperature and input of water year-round. Sources of permanent water can be found in the local area (i.e , the drainage ditch, Wet Beaver Creek, Lake Montezuma and the Verde River), yet no records indicate that *Potamogeton montezumawellensis* has spread to any of these locations. Because plant material is unable to exit the Well through the "swallet," the only mode of distribution in and out of the system relies on physical transport. Distribution of fruits and rhizomes/turions by waterfowl is a well-known mode of dispersal for aquatic plants. The Well is a favorite stopping location for transient waterfowl (i.e., Wigeons, Cinnamon Teal, Pied-billed Grebe, Lesser Scaup, and Ring-necked Duck), which have been observed visiting the Well from early September through March and feeding on the plants (Schroeder 1948; Blinn 2012; pers. obs. by authors). "The waterfowl feed on *Potamogeton* foliage and cause a drastic reduction in plant biomass to a depth of 50 cm …" (Runck & Blinn 1990:268). Thomas et al. (1994:100), although working with amphipods, suggests that the "unusual chemical properties of Montezuma Well have … promoted evolution of endemic species" and "discrete aquatic ecosystems, isolated by a xeric landscape, provide an unusual template for genetic differentiation …" (Thomas et al 1994:107). It is possible that this species is sexually sterile and is essentially a single colonial individual that is unable to survive outside the unique conditions of the Well.

Based on the literature and herbarium collections, it would be easy to get the impression that the Well


Fig. 3. **Left.** *Potamogeton montezumawellensis* **habit, flowering branch (holotype:** *J. Ricketson 4185A* **(MO); Tropicos.org. Missouri Botanical Garden. 16 Feb 2018). Right.** *P. illinoensis* **Morong habit, flowering branch (lectotype:** *H. Patterson s.n.* **(NY); C.V. Starr Virtual Herbarium, The New York Botanical Garden, 20 Feb 2018).**

supports an almost pure stand of *Potamogeton montezumawellensis* with only scattered reports of *Zannichellia palustris*. However, during the 2016 NPS summer monitoring boat trip of the Well, it came to our attention that *Stuckenia pectinata* has become well-established. The 2017 NPS summer inspection revealed that the aquatic population has developed an assemblage of *P. montezumawellensis*, *Z. palustris,* and *S. pectinata* in almost equal proportions. Historically, based on pollen from sediment core samples (Blinn et al. 1994), *Z. palustris* has been a member of the Well for thousands of years. However, the presence of *S. pectinata* is concerning because, except for a single unspecific collection of by Richard Hevly in 1958 (as noted above), this species has not been reported within the Well until recently. Since the NPS does not keep records of this data, we reached out to several biologists who have spent countless hours working at the Well. Although not specifically trained to identify aquatic macrophytes (these three [*Potamogeton, Stuckenia* and *Zannichellia*] species are easily identifiable), all of these researchers only recall the *Potamogeton* sp. [= *P. montezumawellensis*] and occasionally *Z. palustris* from within the Well (Dr. Dean Blinn, pers. comm.; Dr. Ron Davies, pers. comm.; Dr. Fredric Govedich, pers. comm ; Dr. Clay Runck, pers. comm.; and Dr. Perry Thomas, pers. comm.). Unfortunately, there is no way of determining the previous population dynamics regarding the aquatic macrophytes within the Well, thus the 2016–2017 data must be used as a baseline to monitor the population in the future.

The population size of *P. montezumawellensis* could be imperiled by the apparent increase of the potentially aggressive species like *S. pectinata* [Sago-pondweed] and *Z. palustris* [horned pondweed], the ecological implications can only be speculated on at this time. The native species *S. pectinata* is aggressive and is known to tolerate a wide variety of conditions. The USDA notes that "Sago Pondweed is considered a nuisance weed or noxious weed in some waters …" although "Waterfowl extensively use and rely on sago pondweed as a food


Fig. 4. **A.** Montezuma Well, habitat from water level, showing mixed aquatic macrophytes assemblage. Erect flowering heads above water are of *P. montezumawellensis*. **B.** Underwater image of *P. montezumawellensis*. **C.** Image of specimen of *P. montezumawellensis*. **D.** Inflorescences of *P. montezumawellensis*. [Credits: National Park Service 2006 (B.), 2016 (A., C., D.)].

source" (Casey 2010), which has likely increased this species' presence within the Well. *P. montezumawellensis* clearly provides a shelter, a nursery, oxygen, food and a slew of other benefits that are irreplaceable to this unique ecosystem. Further ecological studies should be conducted to monitor and assess the impact of these species on the dynamics of the endemic populations that inhabit the Well.

ACKNOWLEDGEMENTS

A portion of this work was supported by the Missouri Botanical Garden and the National Park Service and Supervisor Bill Cummins, Scientific Research for providing Collecting Permit, Study # MOCA-00051, Permit # MOCA-2017-SC1-0003. We would like to thank the following NPS personnel: Fraser Watson, Hannah Siroky, Dan Batha, John Cannon, Tom McLaren, Beth Welling, Richard Lory, and Karen Gravely for their assistance with weekly monitoring and photographic documentation of the Well. A thank you to the U.S.G.S. for the use of their boat to inspect the Well. The authors wish to thank Rachael Meara, a 2017 NPS summer intern at the Well, for her support of this project. We also wish to thank John Atwood, Ron Davies, Fredric Govedich, Clay Runck, and Perry Thomas for their personal communications, expert knowledge, and valuable input into our understanding of this ecosystem. A special thanks to John J. Pipoly, III for his invaluable input, Spanish resumen, Latin text and for his and Dale Benham's insightful review of this manuscript. With sincere appreciation to the late James M. Rominger, the lead author's major professor at Northern Arizona University, and his wife Redonda Rominger, we give thanks for their guidance and encouragement. A special note of thanks is extended to the late Prof. Richard G. Walter, who taught generations of students the art of plant identification. In addition, we thank Dean Blinn and the late Richard H. Hevly, who both served on the lead author's thesis

committee, for providing invaluable information regarding the Well. Finally, a special thanks to all the NPS personnel, past and present, under whose guardianship is entrusted the preservation of this national wonder.

## REFERENCES

American Antiquities Act. 1906. 1906 American Antiquities Act. Prepared for Legislative and Congressional Affairs. www.nps.gov/subjects/legal/american-antiquities-act-of-1906.htm. Accessed 7 Dec 2017.

Avery, C.C. & M. Helmke. 1991 [1993]. Montezuma Well: A dynamic hydrologic system. In: P.G. Rowlands, C. van Riper, III, & M.K. Sogge, eds. Proceedings of the first biennial conference on research in Colorado Plateau National Parks. U.S. Department of the Interior, National Park Service Transactions & Proceedings Series NPS/NRNAU/NRTP-93/10. Pp. 200–207.

Batchelder, G.L. & G.A. Cole. 1978. Evidence of post-pluvial water level fluctuation at Montezuma Well, Coconino County, Arizona, U.S.A. Report to National Park Service. U.S. Department of Interior.

Beckman, J.E. 1991. A history of Montezuma Well. Report to the National Park Service. Archived at the headquarters of Montezuma Castle National Monument. McGuireville, Arizona, U.S.A. www.beavercreekaz.org/jack%20beckman's%20history%20of%20montezumz%20well.pdf. Accessed 7 Dec 2017.

Beresic-Perrins, R.K., F.R. Govedich, K. Banister, B.A. Bain, D. Rose, & S.M. Shuster. 2017. *Helobdella blinni* sp. n. (Hirudinida, Glossiphoniidae) a new species inhabiting Montezuma Well, Arizona, USA. ZooKeys 661:137–155. doi:10.3897/zookeys.661.9728

Blake, W.P. 1906. Origin of the depression known as Montezuma's Well, Arizona. Science, N.S. 24(618):568.

Blinn, D.W. 2012. Life beneath the water surface in Montezuma Well, Arizona: A large thermally constant spring. Maple Creek Media, Hampstead, Maryland, U.S.A.

Blinn, D.W. & M.W. Sanderson. 1989. Aquatic insects in Montezuma Well, Arizona, USA: A travertine spring mound with high alkalinity and dissolved carbon dioxide. Great Basin Naturalist 49(1):85–88.

Blinn, D.W., R.H. Hevly, & O.K. Davis. 1994. Continuous Holocene record of diatom stratigraphy, Paleohydrology, and Anthropogenic activity in a spring-mound in Southwestern United States. Quaternary Res. 42:197–205.

Blinn, D.W., C. Pinney, & M.W. Sanderson. 1982. Nocturnal planktonic behavior of *Ranatra montezuma* Polhemus (Nepidae: Hemiptera) in Montezuma Well, Arizona. J. Kansas Entomol. Soc. 55(3):481–484.

Blinn, D.W., C. Pinney, & V.T. Wagner. 1988. Intraspecific discrimination of amphipod prey by a freshwater leech through mechanoreception. Canad. J. Zool. 66:427–430.

Boucher, P., D.W. Blinn, & D.B. Johnson. 1984. Phytoplankton ecology in an unusually stable environment (Montezuma Well, Arizona, U.S.A.). Hydrobiologia 119:149–160.

Casey, P.A. 2010. Plant fact sheet for sago pondweed (*Stuckenia pectinata* (L.) Börner). USDA-Natural Resources Conservation Service, Kansas Plant Materials Center, Manhattan, Kansas, U.S.A. https://plants.usda.gov. Accessed 7 Dec 2017.

Cole, G.A. 1963. The American Southwest and middle America. In: D.G. Frey, ed. Limnology of North America. Univ. Wisconsin Press, Madison, Wisconsin, U.S.A. Pp. 393–434.

Cole, G.A. & W.T. Barry. 1973. Montezuma Well, Arizona, as a habitat. J. Arizona Acad. Sci. 8:7–13.

Cole, G.A. & G.L. Batchelder. 1969. Dynamics of an Arizona travertine-forming stream. J. Arizona Acad. Sci. 5:271–283.

Cole, G.A. & R.L. Watkins. 1977. *Hyalella montezuma*, a new species (Crustacea: Amphipoda) from Montezuma Well, Arizona. Hydrobiologia 52 (2–3):175–184.

Correll, D.S. & H.B. Correll. 1972. Aquatic and wetland plants of Southwestern United States. Environmental Protection Agency, Washington, D.C., U.S.A.

Czarnecki, D.B. 1979. Epipelic and epilithic diatom assemblages in Montezuma Well National Monument, Arizona. J. Phycol. 15:346–352.

Czarnecki, D.B. & D.W. Blinn. 1979. Observations on southwestern diatoms. II. *Caloneis latiuscula* var. *reimeri* n. var., *Cyclotella pseudostelligera* f. *parva* n.f., and *Gomphonema montezumense* n. sp., new taxa from Montezuma Well National Monument. Trans. Amer. Micros. Soc. 98(1):110–114.

Damon, P.E., C.V. Haynes, & G.A. Cole. 1964a. Carbon 14 content of aquatic plants, Montezuma Well, Arizona. Trans. Amer. Geophys. Union. 45:117.

Damon, P.E., C.V. Haynes, & A. Long. 1964b. Arizona Radiocarbon dates V. Radiocarbon 6:91–107.

Davies, R.W., D.W. Blinn, B. Dehdashti, & R.N. Singhal. 1988. The comparative ecology of three species of Erpobdellidae (Annelida = Hirudinoidea). Arch. Hydrobiol. 111(4):601—614.

Davies, R.W., R.N. Singhal, & D.W. Blinn. 1985. *Erpobdella montezuma* (Hirudinoidea: Erpobdellidae), a new species of freshwater leech from North America. Canad. J. Zool. 63:965–969.

Davis, O.K. & D.S. Shafer. 1992. A Holocene climatic record for the Sonoran Desert from pollen analysis of Montezuma Well, Arizona, USA. Palaeogeog. Palaeoclim. Palaeoecol. 92(1992):107–119.

Govedich, F.R., D.W. Blinn, P. Keim, & R.W. Davies. 1998. Phylogenetic relationships of three genera of Erpobdellidae (Hirudinoidea), with a description of a new genus, *Motobdella*, and species, *Motobdella sedonensis*. Canad. J. Zool. 76:2164–2171.

Haynes, Jr., C.V., P.E. Damon, & D.C. Grey. 1966. Arizona radiocarbon dates VI. Radiocarbon 8:1–21.

Hershler, R. & J.J. Landye. 1988. Arizona Hydrobiidae (Prosobranchia: Rissoacea). Smithsonian Contr. Zool. 459:1–63.

Hevly, R.H. 1974. Recent paleoenvironments and geological history at Montezuma Well. J. Arizona Acad. Sci. 9:66–75.

Hinton, R.J. 1878. The hand-book to Arizona: Its resources, history, towns, mines, ruins and scenery. Payot, Upham & Co., San Francisco, California, and American News Co., New York, New York, U.S.A.

Hutchinson, G.E. 1975. A treatise on Limnology, Vol. III. Limnological Botany. John Wiley & Sons, New York, New York, U.S.A.

IUCN. 2017. IUCN Protected Areas. Prepared for the 2008 Guidelines for Applying Protected Area Management Categories. IUCN, Gland Switzerland, and Cambridge, United Kingdom. www.iucn.org. Accessed 7 Dec 2017.

Jackson, H.T. & W.P. Taylor. 1916. Biological survey reports, Verde Valley, 1916. U.S. Department of the Interior. Washington, D.C., U.S.A.

Jenkins, O.P. 1923. Verde River lake beds near Clarkdale, Arizona. Amer. J. Sci. 5(25):65–81.

Johnson, R.H., E. DeWitt, & R. Arnold. 2008. Arsenic in and around Montezuma Well, a natural spring in Central Arizona: Evaluating regional ground water flow and resulting arsenic transport. 2008 Ground Water Summit. National Ground Water Association web site. https://ngwa.confex.com/ngwa/2008gws/techprogram/P4872.HTM. Accessed 6 Jun 2018.

Kearney, T.H., R.H. Peebles, & collaborators. 1951. Arizona Flora. Univ. Calif. Press, Berkeley & Los Angeles, California, U.S.A.

Kearney, T.H., R.H. Peebles, & collaborators. 1960. Arizona Flora. 2nd ed. with supplement. J.T. Howell, E. McClintock, & collaborators. Univ. Calif. Press, Berkeley & Los Angeles, California, U.S.A.

Kidd, D.E. & W.E. Wade. 1963. Algae of Montezuma Well, Arizona and vicinity. Plateau. 36:63–71.

Konieczki, A.D. & S.A. Leake. 1997. Hydrogeology and water chemistry of Montezuma Well in Montezuma Castle National Monument and surrounding area, Arizona. U.S. Geological Survey, Water-Resources Investigations Report 97-4156. Tucson, Arizona, U.S.A.

Lange, A. 1957. Studies on the origin of Montezuma Well and cave, Arizona. Cave Studies 1(9):39–53, pl. 1.

Lehr, J.H. 1978. A catalogue of the flora of Arizona. Desert Botanical Garden, Phoenix, Arizona, U.S.A.

McDougall, W.B. 1973. Seed plants of northern Arizona. Museum of Northern Arizona, Flagstaff, Arizona, U.S.A.

McDougall, W.B. & H.S. Haskell. 1960. Seed plants of Montezuma Castle National Monument: With keys for the identification of species. Mus. Northern Arizona Bull. 35.

McVaugh, R. 1956. Edward Palmer: Plant explorer of the American West. University of Oklahoma Press, Norman, Oklahoma, U.S.A.

National Register of Historic Places. 1978. National register of historic places (No. 66000082). Prepared by the National Park Service. https://npgallery.nps.gov/NRHP. Accessed 7 Dec 2017.

Nations, J.D., R.H. Hevly, D.W. Blinn, & J.J. Landye. 1981. Paleontology, paleoecology, and depositional history of the Miocene-Pliocene Verde Formation, Yavapai County, Arizona. Arizona Geol. Soc. Dig. 13:133–149.

Oberlin, G.E. & D.W. Blinn. 1997. The affect of temperature on the metabolism and behavior of an endemic amphipod, *Hyalella montezuma*, from Montezuma Well, Arizona, U.S.A. Freshwater Biol. 37:55–59.

O'Brien, C. & D.W. Blinn. 1999. The endemic spring snail *Pyrgulopsis montezumensis* in a high $CO_2$ environment: Importance of extreme chemical habitats as refugia. Freshwater Biol. 42:225–234.

Ogden, E.C. 1943. The broad-leaved species of *Potamogeton* of North America, North of Mexico. Rhodora 45:57–105, 119–163, 171–214.

Polhemus, J.T. 1976. Notes on North American Nepidae (Hemiptera: Heteroptera). Pan-Pacific Entomol. 52:204–208.

Protas, J. 2002. A past preserved in stone: A history of Montezuma Castle National Monument. Western National Parks Association. Tucson, Arizona, U.S.A. www.nps.gov/moca/learn/historyculture/upload/moca_hist.pdf. Accessed 7 Dec 2017.

Rhoads, S.N. 1898. Contributions to a revision of the North American beavers, otters and fishes. Trans. Amer. Phil. Soc., N.S. 19:417–439.

Ricketson, J.M. 1990. Aquatic and wetland vascular plants of Coconino National Forest, Arizona. Masters thesis, Northern Arizona University, Flagstaff, Arizona, U.S.A.

Runck, C. & D.W. Blinn. 1990. Population dynamics and secondary production by *Ranatra montezuma* (Heteroptera: Nepidae). J. N. Amer. Benthol. Soc. 9(3):262–270.

Runck, C. & D.W. Blinn. 1992. The foraging ecology of *Ranatra montezuma* (Heteroptera): An optimal forager in Montezuma Well, Arizona. J. Arizona-Nevada Acad. Sci. 26(2):119–130.

Runck, C. & D.W. Blinn. 1993. Secondary production by *Telebasis salva* (Odonata) in a thermally constant aquatic ecosystem. J. N. Amer. Benthol. Soc. 12(2):136–147.

Runck, C. & D.W. Blinn. 1994. Role of *Belostoma bakeri* (Heteroptera) in the trophic ecology of a fishless desert spring. Limnol. Oceanogr. 39(8):1800–1812.

Schroeder, A.H. 1948. Montezuma Well. Plateau 20(3):37–40.

Thomas, P.E., D.W. Blinn, & P. Keim. 1994. A test of an allopatric speciation model for congeneric amphipods in an isolated aquatic ecosystem. J. N. Amer. Benthol. Soc. 13(1):100–109.

Wagner, V.T. & D.W. Blinn. 1987. A comparative study of the maxillary setae for two coexisting species of *Hyalella* (Amphipoda), a filter feeder and a detritus feeder. Arch. Hydrobiol. 109(3):409—419.