



Description of last instar nymph of *Zoraena sarracenia* (Abbott & Hibbitts, 2011) (Odonata: Cordulegastridae) with notes on its life history

JOHN C. ABBOTT^{1*} & KENNETH J. TENNESSEN²

¹UA Museums Research and Collections, The University of Alabama, Tuscaloosa, AL, USA.

²Research Associate, Florida State Collection of Arthropods, Gainesville, FL, USA.

✉ tenkenneth43@gmail.com; <https://orcid.org/0000-0003-4799-026X>

*Corresponding author: ✉ jabbott1@ua.edu; <https://orcid.org/0000-0002-6773-3976>

Abstract

The last instar (F0) nymph of *Zoraena sarracenia* (Abbott & Hibbitts, 2011) (Odonata: Cordulegastridae) is described for the first time based on 34 lab-reared and field-collected specimens from Texas and Louisiana. Diagnostic morphological characters, measurements, and setal counts are provided, and the nymph is compared with other members of the **diastatops species group**. Characters useful for identification include premental structure, labial dentition and setation, and setae along the posterior margin of the compound eyes. Notes on habitat, distribution, and life history are presented based on field observations and laboratory rearings. The species inhabits small, boggy rivulets and seepages, often associated with pitcher plant (*Sarracenia alata*) bogs, but also occurs in shaded seepage habitats. Laboratory rearings suggest a minimum nymphal development time of approximately two years, with some individuals requiring three years. This description completes knowledge of nymphal morphology within the **diastatops species group** and facilitates identification and conservation assessment of this geographically restricted species.

Key words: *Cordulegaster*, Anisoptera, Spiketail, threatened, larva, naiad

Introduction

Zoraena sarracenia (Abbott & Hibbitts, 2011) is the most recently described species in the family Cordulegastridae from the United States. It was originally placed in the genus *Cordulegaster* Leach, 1815, but Schneider *et al.* (2024) recovered *Zoraena* in their analysis and placed all members of the family occurring in the western Hemisphere in the genus, except for *Cordulegaster diadema* Selys, 1868 and *Cordulegaster virginiae* Novelo-Gutiérrez, 2018. Diagnostic characters separating the nymphs of all cordulegastrid species occurring in North America, except for *C. virginiae*, are included in the keys provided by Tennessen (2019).

Zoraena sarracenia is known from few locations in eastern Texas and western Louisiana, generally characterized by shallow, narrow, muddy seeps, often on gently sloping, open hillsides supporting the pale pitcher plant (*Sarracenia alata*), but can also be found in seepages within dense canopy forests. Abbott & Hibbitts (2011) placed it in the **diastatops species group** as defined by Tennessen (2004), which includes *Zoraena talaria* (Tennessen, 2004), *Z. bilineata* (Carle, 1983), *Z. diastatops* (Selys, 1854), and *Z. sayi* (Selys, 1854). Schneider *et al.* (2024) only included *Z. diastatops* amongst these species in their analysis and found it to be sister to *Zoraena obliqua* (Say, 1840).

The final instar, F0, nymph of *Z. sarracenia* has not been formally described; we do so here and compare it to other *Zoraena* species. We also provide insights into its life history based on rearing and observational field data.

Material and Methods

Examined Material

Some of the following sites were collected on multiple dates and number of individuals represented in this study are shown in brackets: Louisiana, Natchitoches Parish, Middle Branch Bog, Kisatchie Ranger District of

Kisatchie National Forest, 31.48324, -93.07553, 8.Apr.2011 [2], 13.Apr.2011 [1], 14.Mar.2012 [2], 6.Apr.2012 [2], 28.Mar.2017 [4], John C. Abbott & Kendra K. Abbott; Louisiana, Rapides Parish, Brown Creek at Brown Creek Rd., Evangeline Unit of Kisatchie National Forest, (31.28651, -92.70346), 7.Apr.2017 [1], John C. Abbott & Kendra K. Abbott; Louisiana, Rapides Parish, Clear Creek off FR 240 in Evangeline Unit of Kisatchie National Forest, (31.19422, -92.62267), 30.Mar.2017 [1], John C. Abbott & Kendra K. Abbott; Louisiana, Rapides Parish, small tributaries of creek at Wild Azalea Trail, Kincaid Recreation Area, (31.23656, -92.61539), 3.Apr.2016 [1], 30.Mar.2017 [5], 9.Apr.2017 [1], John C. Abbott & Kendra K. Abbott; Louisiana, Rapides Parish, seepages off of Loving Creek, Evangeline Unit of Kisatchie National Forest, (31.17908, -92.5641) 7.Apr.2017 [2], John C. Abbott & Kendra K. Abbott; Texas, Anderson Co., Gus Engeling Wildlife Management Area, Tennessee Colony, Pitcher Plant Bog and small stream, (31.98358, -95.88629), 14.Apr.2017 [6], John C. Abbott & Kendra K. Abbott; Texas, Jasper Co., Boykin Springs Recreation Area, Angelina National Forest, (31.06285, -94.28025), 16.Mar.2011 [1], 11.Mar.2012 [2], 29.Mar.2017 [2], John C. Abbott & Kendra K. Abbott; Texas, Walker Co., small stream at FS Rd. 216, Sam Houston National Forest, west of Stubblefield Recreation Area, (30.55851, -95.64661), 19.Jul.2015 [1], John C. Abbott & Kendra K. Abbott. Some nymphs were reared to F0 stage in the laboratory (see below for details about rearing). All specimens above are deposited in the University of Alabama Museums Research and Collections (Tuscaloosa, Alabama).

Sampling

Nymphs were collected across a total of eight sites distributed in Texas and Louisiana. They were collected using a small hand scoop while searching narrow mucky rivulets, seining out the muck to reveal nymphs. F0 nymphs were par-boiled and then preserved in 80% ethanol. Earlier instar nymphs were brought back to the lab and reared to F0 in a temperature controlled Frigid Unit living stream. They were provided a near constant food source of black worms (*Lumbriculus variegatus* Müller, 1774).

Measurements. All nymphs of *Z. sarracenia* were measured with an ocular micrometer on an Olympus SZX10 stereo microscope in the laboratory. The following characters, based on the measurements, were quantified and analyzed: total length, head capsule width, maximum width of prementum, antennal total length, maximum thoracic width, hindwing sheath length, hind femur length, abdominal length, maximum abdominal width, epiproct length, epiproct width (measured laterally), number of palpal setae, number of primary premental setae, and number of secondary prementum setae (Table 1).

TABLE 1. Measurements (mm) for *Zoraena sarracenia* F0 nymphs. Number of individuals given in parentheses of first row. Data presented as range with mean in parentheses except for setal counts, where it is given as the range with the mode and frequency of most prevalent setal number. Setal counts are for left and right sides separately. Primary is abbreviated as 1° and secondary as 2°.

| Feature | ♂ (17) | ♀ (17) | Total (34) |
|------------------------------|------------------|------------------|------------------|
| Total length | 30.0–37.0 (32.6) | 31.5–35.5 (33.2) | 30.0–37.0 (32.9) |
| Head capsule width | 6.3–7.2 (6.7) | 6.6–7.4 (6.9) | 6.3–7.4 (6.8) |
| Prementum max width | 5.1–6.0 (5.6) | 5.3–6.0 (5.7) | 5.1–6.0 (5.7) |
| Antennae total length | 2.9–3.5 (3.1) | 3.0–3.5 (3.2) | 2.9–3.5 (3.2) |
| Thorax max width | 6.0–7.4 (6.9) | 6.7–8.6 (7.0) | 6.0–8.6 (7.0) |
| HW sheath length | 7.1–8.1 (7.5) | 6.9–8.6 (7.9) | 6.9–8.6 (7.7) |
| Hind femur length | 5.1–6.7 (6.0) | 5.2–6.4 (5.9) | 5.1–6.7 (6.0) |
| Abdominal length | 19–26.5 (21.8) | 20.0–24.0 (21.8) | 19–26.5 (21.8) |
| Abdominal width | 6.9–8.0 (7.5) | 6.8–8.3 (7.7) | 6.8–8.3 (7.6) |
| Epiproct length | 2.6–3.1 (2.8) | 2.5–3.1 (2.9) | 2.5–3.1 (2.9) |
| Epiproct width | 1.2–1.6 (1.4) | 1.1–1.6 (1.4) | 1.1–1.6 (1.4) |
| Paraproct length | 2.6–3.0 (2.8) | 2.4–3.0 (2.8) | 2.4–3.0 (2.8) |
| # Palpal setae | 4–6 (5, 85.3%) | 5–7 (5, 73.5%) | 4–7 (5, 79.4%) |
| # 1° Premental setae | 2–7 (5, 67.6%) | 3–6 (5, 47.1%) | 2–7 (5, 60.9%) |
| # 2° Premental setae | 2–4 (3, 58.8%) | 2–4 (3, 52.9%) | 2–4 (3, 59.4%) |

Results

Description of the last instar (F0) nymph of *Zoraena sarracenia*

Total length of nymph 30.0–37.0 mm (Table 1), head width 6.3–7.4 mm, length of hind femur 5.1–6.7 mm.

Large nymphs, generally tan to brown, head and prothorax lacking any distinctive coloring. Dorsally, the abdomen has paired dark brown ovoid spots centrally and laterally. Body surface covered in fine hairs, longer along edge (Fig. 1), that can trap sediment over the body (Fig. 2).

Head. Clypeus rectangular and paler in color than labrum with thin dark longitudinal dark stripe laterally. Anterior margin of frons with row of long, stout setae that are longest at middle (no more than 2/3 length of labrum) (Fig. 3). Lateral margin of compound eyes protrude above height of head. Antennae filiform, 7-segmented, sparsely setose with antennomere 3 the longest; total length 2.9–3.5 mm and average ratio of antennal segments S1/total length is 0.1. Prementum maximum width 5.1–6.0 mm for both sexes, averaging 5.7 mm. Median lobe of prementum (anterior margin of ligula) with large, laterally curved tooth along with smaller lateral tooth on each side (Fig. 4). Distal margin of palpus with larger, irregular teeth and usually bearing 5 (ranging from 4–7) large setae (Fig. 4). Movable hook noticeably longer than large irregular palpal teeth. Mandibular formula L 1 2 3 4 0 a (m^{1,2,3,4}) b R 1 2 3 4 y a (m^{1,2,3,4}) b. Interior margins of palpal lobes with irregular dentation: 3 large teeth on both left and right lobe and every tooth with additional 1–5 smaller teeth. Apex of all teeth dark brown. Movable hooks long and stout with dark brown apex. Typically, 5 setae on each palp (61% of individuals) but variable ranging from 4–7 and sometimes asymmetrical in number (12.5% of individuals) (Fig. 4). Primary premental setae 2–7 (mean 5), smaller secondary premental setae 2–4 (mean 3) (Fig. 4).

Thorax. Prothorax slightly narrower than width of head, with broadly rounded edges. Pterothorax essentially same width as head; ratio of head/thorax max width is 0.86–1.05 (see Table 1). Wing sheaths divergent reaching to posterior edge of S4. Lateral margin of thorax with fine pale setae.



FIGURE 1. Dorsal habitus of last instar nymph of *Zoraena sarracenia*.

Abdomen. Pale brown or tan with pale middorsal longitudinal stripe and paired dark ovoid spots that project laterally at anterior, especially on S5–7 (Fig. 1). Additional, paler, ovoid dark spot laterally along length of abdomen. Posterior margin of S1–9 with row of pale setae becoming longer laterally. Middorsal hooks or spines absent. Row of pale longitudinal stripes present on intersegmental membrane, most noticeable on S3–9 (Fig. 1). Short posterolateral spines present on S8 and S9, less than 0.5 mm long. Epiproct as long as paraprocts; both slightly curved ventrally at tips (Fig. 5). Ratio of length to basal width of anal pyramid is 1.2–1.8, averaging 1.4. Ovipositor reaches to $\sim 2/3$ length of S9 (Figs. 5 & 6).



FIGURE 2. Dorsal habitus of last instar nymph of *Zoraena sarracenia* covered with sediment.



FIGURE 3. Anterodorsal portion of head of last instar nymph of *Zoraena sarracenia* showing frons with setae along anterior margin.



FIGURE 4. Labium of last instar nymph of *Zoraena sarracenia*.



FIGURE 5. Lateral view of a female last instar nymph of *Zoraena sarracenia* showing terminal abdominal segments, including anal pyramid (epiproct and paraprocts).



FIGURE 6. Ovipositor on ventral side of S9 on a female last instar nymph of *Zoraena sarracenia*.

Comparative Analysis

Zoraena sarracenia falls within a closely related group of species referred to as the **diastatops species group** that includes *Z. bilineata*, *Z. diastatops*, *Z. sarracenia*, *Z. sayi*, and *Z. talaria* (Abbott & Hibbitts 2011; Tennesen 2004). Of these, *Z. sarracenia* is thought to be most closely related to *Z. sayi* (Abbott & Hibbitts 2011). Tennesen (2019) identified characters to separate the species within this group from other Cordulegastridae in North America, namely that the base of the prementum is transverse in the **diastatops species group** and V-shaped in the remaining species (Fig. 7). The ratio of the basal width of the prementum to its length also differs with the group, ranging from 0.40–0.47 compared to the remaining species with a ratio of less than 0.4 (Tennesen 2019). In the **diastatops species group**, the ovipositor does not extend to the posterior margin of S9 (except in *Z. talaria*) whereas it extends beyond the margin of S9 in the other species, except in some *Z. obliqua* (Tennesen 2019).

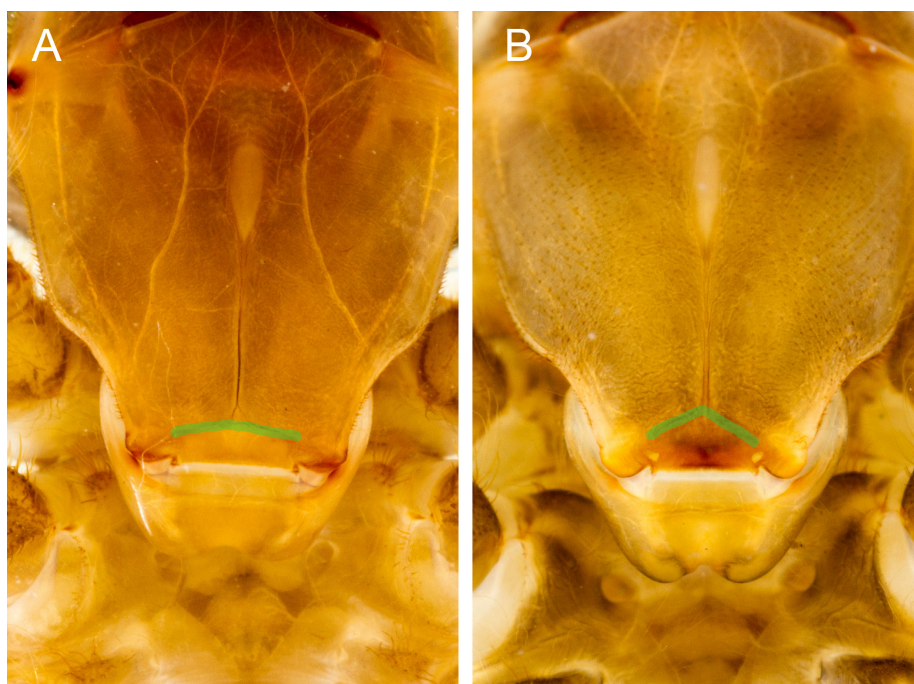


FIGURE 7. Prementum in ventral view showing basal transverse suture indicated by green line. (A) generally straight in *Zoraena sarracenia*, and (B) V-shaped in *Zoraena maculata*.

Zoraena sayi can be differentiated from *Z. sarracenia*, its closest congener, by a staggered row of slender, pointed setae along the posterior margin of the compound eyes, as opposed to a more regular row of flat, blunt setae in *Z. sarracenia* (Fig. 8). *Zoraena bilineata*, *Z. diastatops*, and *Z. talaria* all have numerous short, dark spatulate setae on the pale mesopleura, while *Z. sarracenia* and *Z. sayi* have only slender dark acuminate setae present. For a full key to the nymphs of North American Cordulegastridae, see Tennesen (2019).

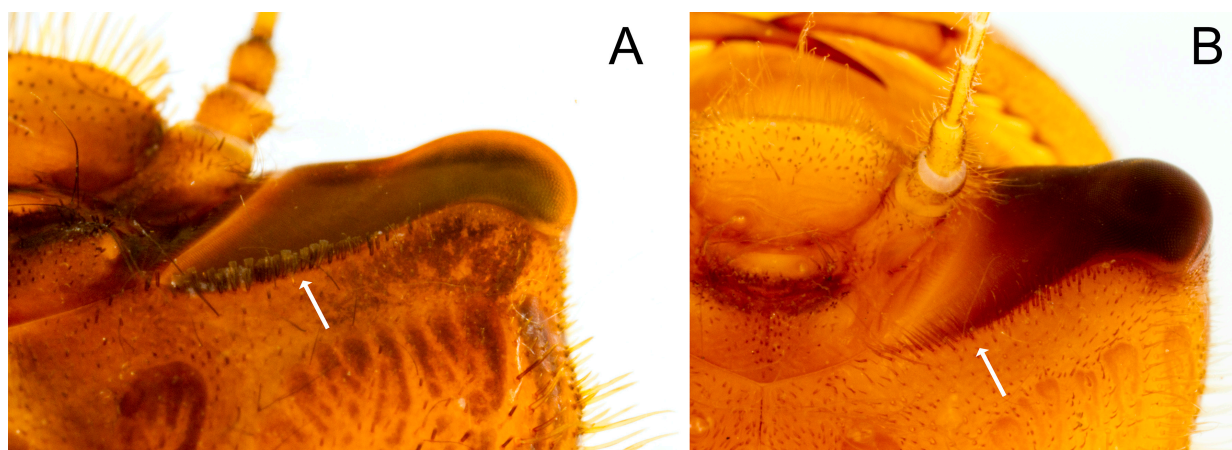


FIGURE 8. Posterior margin of eye showing setae. (A) *Zoraena sarracenia*, (B) *Zoraena sayi*.

Life History, Habitat & Distribution

The overall distribution of *Z. sarracenia* has not been expanded significantly since its original discovery (Abbott & Hibbitts 2011), although a number of new populations have been discovered in western Louisiana (Fig. 9). It is generally found in boggy areas with small rivulets of running water, typically no wider than 30 cm, and often, but not always, in open canopy areas associated with the pale pitcher plant (*Sarracenia alata*) (Fig. 10). Nymphs are also found in more close-canopied bogs lacking pitcher plants and more diffuse water conditions.

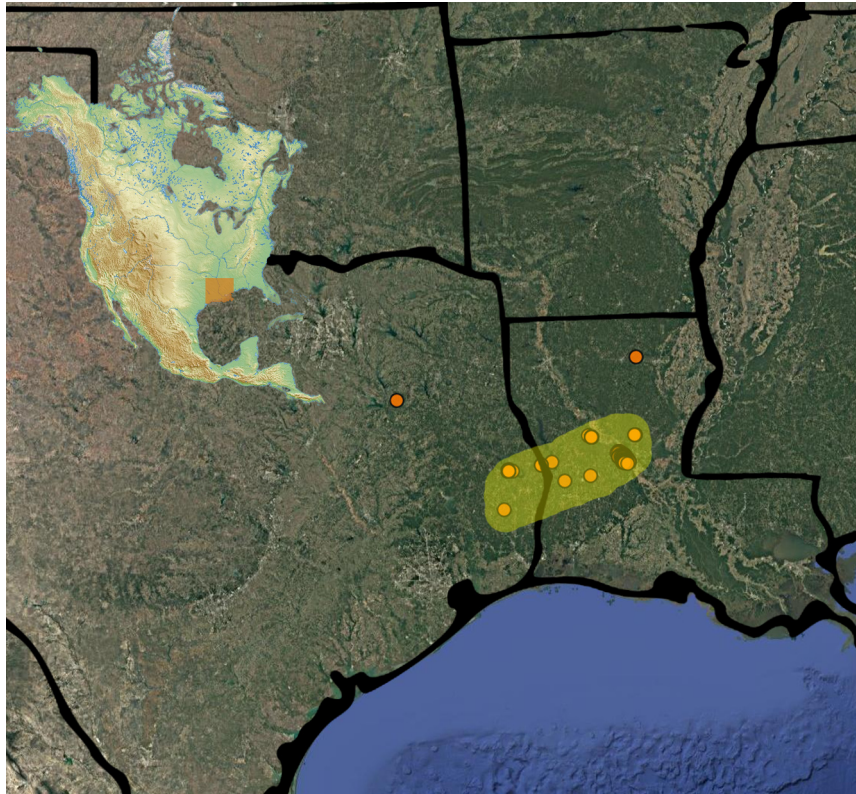


FIGURE 9. Distribution map *Zoraena sarracenia*.

Adults have an early, short flight period, 6 March through 29 April, with ~80% of observations occurring between March 19 and April 15. This flight season can often be cut short by severe spring weather. Laboratory rearing in Frigid Units Living Streams with water temperature regulated to closely match the environment suggests a minimum of 339 days to go from F8 to emergence with a max of 365 days and an average of 357 days (Table 2). Rearing temperatures ranged between 10°C and 21°C.

TABLE 2. Life history data for *Zoraena sarracenia* nymphs reared in the laboratory. N is the number of individuals for each instar. Range is across the different rearing temperatures (10°C to 21°C).

| Instar | N | # Days in instar (Range) | Average (# days) |
|--------|----|--------------------------|------------------|
| F0 | 14 | 69–166 | 99 |
| F1 | 14 | 21–93 | 58 |
| F2 | 14 | 20–87 | 39 |
| F3 | 14 | 15–94 | 53 |
| F4 | 14 | 19–84 | 36 |
| F5 | 12 | 17–47 | 30 |
| F6 | 10 | 14–29 | 23 |
| F7 | 7 | 13–35 | 22 |
| F8 | 7 | 11–21 | 15 |



FIGURE 10. Examples of habitats of *Zoraena sarracenia* nymphs. (A) Middle Branch Bog in Kisatchie National Forest (Louisiana: Natchitoches Parish), (B) Boykin Springs Recreation Area, in Angelina National Forest (Texas: Jasper Co), (C) Brown Creek in Kisatchie National Forest (Louisiana: Rapides Parish), (D) *Z. sarracenia* ovipositing in small rivulet at Middle Branch Bog, (E) small tributary off of Wild Azalea Trail at Kincaid Recreation Area (Louisiana: Rapides Parish).

Ferreras-Romero & Corbet (1999) suggested egg hatching time of 17 to 43 days for *Cordulegaster boltonii* (Donovan, 1807) and Schütte (1997) found a hatching time of 24–43 days, while Pfuhl (1994) reports a hatching time for *C. boltonii* at 57 days if at 15°C and at 120 days if at 10°C. In the field, Pfuhl found hatching in the same

year as oviposition, with most nymphs overwintering as the second larval instar. Nymphs of *Z. sarracenia* likely hatch the same year as oviposition and do most of their growing in year 2, but depending on winter temperatures and food availability, may require a third year to fully develop. Glotzhober (2006) reared *Z. erronea* (Selys, 1878) in the laboratory and found an estimated total development time of 3–4 years, based on laboratory rearings. He estimated 13 to 14 instars for *Z. erronea*, which is likely the same for *Z. sarracenia*.

Females oviposit in March and April; designated as Year 1 (Fig. 11). Their eggs begin to hatch in June and continue through July. The newly hatched nymphs begin development that spring, continuing to molt and grow until late fall; a portion of the cohort reaches F7 or F8 by late fall, the instars in which they overwinter. From laboratory rearing, little growth or molting occurs overwinter. Depending upon late winter and early spring temperatures, development ensues in February of Year 2. Late in Year 2, a percentage of the cohort reaches either F0 or F1; the short southern winter is passed in various instars, from F7 to F0. It is probable that most F1s molt to F0 in the early spring and complete development along with the overwintering F0s. These individuals emerge in March and April of Year 3 to reproduce resulting in the next generation. This scenario represents the fastest life cycle of *Z. sarracenia* (two years). Note that not all individuals in this cohort complete development and reach adulthood at the end of two years; if they don't reach F1 by the end of Year 2, they don't emerge to adult stage until the next year, which equates to a 3-year life cycle.

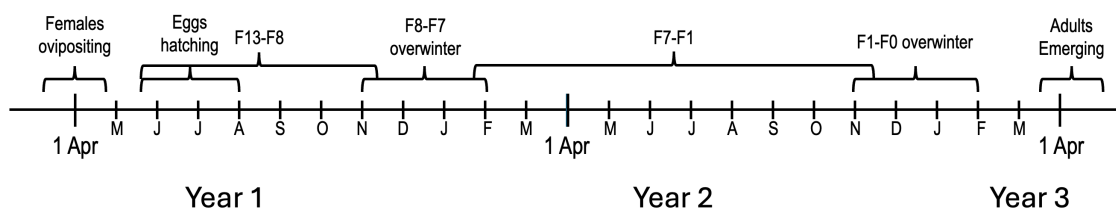


FIGURE 11. Predicted phenology of *Zoraena sarracenia*. Letters indicate months of year.

Discussion and Conclusion

Within the *diastatops* species group, all nymphs are known and keys were provided by Tennessen (2019). All five species occur in the eastern United States and two, *Z. bilineata* and *Z. diastatops* are widely distributed (*Z. bilineata* from southern Mississippi to Michigan, and *Z. diastatops* from West Virginia north into southern Canada). The other three species have much more limited ranges and are all found in the south (*Z. talaria* in Ouachita Mountains of Oklahoma and Arkansas; *Z. sayi* in northern Florida and southern Georgia; *Z. sarracenia* east Texas and west Louisiana).

Taxonomy

There are 11 species of Cordulegastridae known from North America. Historically, they have all been included in the genus *Cordulegaster*. Lohman (1992) advocated for six genera for these species, two of which had previously been described. One of these, *Zoraena* Kirby, 1890, was resurrected to contain *Z. bilineata* and *Z. diastatops*. Lohman (1992) described several new genera in his treatment of the North American Cordulegastridae, including *Archegaster*, in which he placed a single species, *Z. sayi*; *Archegaster* and the other genera proposed by Lohman have not been generally accepted by the Odonata community, and molecular studies in the decades since his reclassification have supported nonacceptance (Carter *et al.*, in review; Schneider *et al.*, 2024). Tennessen (2004), when describing *Z. talaria*, recognized similarities between his new species and *Z. bilineata*, *Z. diastatops*, and *Z. sayi* and referred to the species cluster as the *diastatops*-group. When *sarracenia* was described, Abbott & Hibbitts (2011) recognized that it was also a member of this group. Tennessen (2019) later identified several nymphal characters that united these five species and recognized the genus *Zoraena*. Most recently Schneider *et al.* (2024) following a molecular study, expanded the genus *Zoraena* to include all North American species except for *C. diadema* and *C. virginiae*.

Conservation

The last assessment for the IUCN Red List for the *diastatops* species group was 2014 (Paulson 2017, 2018) (Table 3). We have learned more over the last 10 plus years about each of these species, especially through observations from community science initiatives like iNaturalist.com and OdonataCentral.com. Considerable effort

has been invested by the senior author and others to locate suitable habitat for *Z. sarracenia* across its range. While new populations have been discovered, suitable habitat remains a limiting factor. Likewise, targeted surveys in the Ouachita Mountains of Arkansas and Oklahoma reveal limited habitat and populations for *Z. talaria* (Smith & Patten 2021). We suggest a reassessment may be appropriate for at least *Z. sarracenia* and *Z. talaria*. Both species inhabit restricted habitats within exceptionally small geographic ranges. While the number of locations for *Z. sarracenia* have increased, the population structure suggests very little genetic variation (Abbott *et al.* 2018). *Zoraena talaria* is listed as Least Concern by the IUCN Red List (Paulson 2018) and G1 (Critically Imperiled) by NatureServe (2026), two different rankings, suggesting a reassessment by one or both entities is needed.

TABLE 3. The five species belonging to the *diastatops* species group of *Zoraena* with their IUCN Red List and NatureServe rankings, along with a description of the typical habitat each are found in.

| Species | IUCN Red List ¹ | G-rank (NatureServe) ² | Habitat |
|----------------------|----------------------------|-----------------------------------|--|
| <i>Z. talaria</i> | LC | G1 | tiny streams with overhanging woodland vegetation |
| <i>Z. bilineata</i> | LC | G5 | small woodland streams |
| <i>Z. diastatops</i> | LC | G5 | spring-fed seeps and small streams (wooded or open) |
| <i>Z. sayi</i> | LC | G3 | small, mucky woodland seeps; bay swamps in sandhills or ravines in hardwood bluffs |
| <i>Z. sarracenia</i> | EN | G3 | rivulets associated with pitcher plant bogs; hillside seeps and associated water |

¹LC: Least Concern, EN: Endangered; G1: Critically Imperiled, G3: Vulnerable, G5: Secure.

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References

- Abbott, K.K., Abbott, J.C., Lozier, J.D., Beasley, R.R. & Lance, S.L. (2018) Development of polymorphic microsatellite markers for a rare dragonfly, *Cordulegaster sarracenia* (Odonata: Cordulegastridae), with notes on population structure and genetic diversity. *International Journal of Odonatology*, 21, 1–7.
<https://doi.org/10.1080/13887890.2018.1498398>
- Abbott, J.C. & Hibbitts, T.D. (2011) *Cordulegaster sarracenia*, n. sp. (Odonata: Cordulegastridae) from east Texas and western Louisiana, with a key to adult Cordulegastridae of the New World. *Zootaxa*, 2899 (1), 60–68.
<https://doi.org/10.11646/zootaxa.2899.1.3>
- Carle, F.L. (1983) A new *Zoraena* (Odonata: Cordulegastridae) from eastern North America, with a key to the adult Cordulegastridae of America. *Annals of the Entomological Society of America*, 76 (1), 61–68.
<https://doi.org/10.1093/aesa/76.1.61>
- Carter, P., Goodman, A., Abbott, J., Bota-Sierra, C., Bybee, S.M., Kijkstra, K.-D.B., Dow, R.A., Fomekong Lontchi, J., Frandsen, P., Gonzalez Moso, L., Guralnick, R., Hämäläinen, Joshi, S., Kohli, M.K., Lupiyaningdyah, P., Montana, K., Newton, L., Onsongo, V., Orr, A.G., Parise Pinto, A., Sanchez-Herrera, M., Sutherland, L., Theischinger, G., Ware, J.L., Zhang, H & Kalkman, V.J. (2026) The classification and diversity of dragonflies and damselflies (Odonata). *International Journal of Odonatology*. [in press]
- Donovan, E. (1807) *The natural history of British Insects explaining them in their several states, with the periods of their transformations, their food, economy, etc. together with the history of such minute Insects as require investigation by the microscope. 16 Vols.* Rivington, London, 1630 pp.
- Ferreras-Romero, M. & Corbet, P.S. (1999) The life cycle of *Cordulegaster boltonii* (Donovan, 1807) (Odonata: Cordulegastridae) in the Sierra Morena Mountains (southern Spain). *Hydrobiologia*, 405, 39–48.
<https://doi.org/10.1023/A:1003763819991>
- Glotzhofer, B. (2006) Life history studies of *Cordulegaster erronea* Hagen (Odonata: Cordulegastridae) in the laboratory and the field. *Bulletin of American Odonatology*, 10 (1), 1–18.
- Kirby, W.F. (1890) *A synonymic catalogue of Neuroptera Odonata, or dragonflies, with an appendix of fossil species.* Gurney

- & Jackson, London, 202 pp.
<https://doi.org/10.5962/bhl.title.5534>
- Leach, W.E. (1815) Entomology. In: Brewster, D. (Ed.), *The Edinburgh Encyclopedia*, 9, 57–172.
- Lohman, H. (1992) Revision der Cordulegastridae. 1. Entwurf einer neuen Klassifizierung der Familie (Odonata: Anisoptera). *Opuscula Zoologica Fluminensia*, 96, 1–18.
- Müller, O.F. (1774) *Vermivm terrestrium et fluviatilium, seu Animalium infusoriorum, helminthicorum et testaceorum, non marinorum, succincta historia. Vols. 2*. Heineck et Faber, Havniæ [Copenhagen] et Lipsiæ [Leipzig], 135 pp. & 214 pp.
<https://doi.org/10.5962/bhl.title.46299>
- NatureServe (2026) NatureServe Explorer [web application]. NatureServe, Arlington, Virginia. Available from: <https://explorer.natureserve.org/pro/> (accessed 26 March 2026)
- Novelo-Gutiérrez, R. (2018) *Cordulegaster virginiae* sp. nov. from Mexico, including a comparison with *C. diadema* Selys, 1868, and a redescription of its larva (Odonata: Cordulegastridae). *Zootaxa*, 4394 (3), 371–382.
<https://doi.org/10.11646/zootaxa.4394.3.3>
- Paulson, D.R. (2017) *Cordulegaster diastatops*. *The IUCN Red List of Threatened Species*, 2017, e.T50967776A65836209. Available from: <https://doi.org/10.2305/IUCN.UK.2017-3.RLTS.T50967776A65836209.en> (accessed 26 March 2026)
- Paulson, D.R. (2018) *Cordulegaster talaria*. *The IUCN Red List of Threatened Species*, 2018, e.T165047A80689957. Available from: <https://doi.org/10.2305/IUCN.UK.2018-1.RLTS.T165047A80689957.en> (accessed 26 March 2026)
- Pfuhl, D. (1994) *Autökologische Untersuchungen an Cordulegaster boltoni* (Donovan, 1807) (Insecta, Odonata). Unpublished thesis, Georg-August-Universität Göttingen, Göttingen, 112 pp.
- Say, T. (1840) Description of new North American neuropterous insects, and observations on some already described. *Journal of the Academy of Natural Sciences of Philadelphia*, 8, 2–46.
- Schneider, T., Vierstraete, A., Kosterin, O.E., Ikemeyer, D., Hu, F.S., Novelo-Gutiérrez, R., Kompier, T., Everett, L., Jr. & Dumont, H.J. (2024) Molecular phylogeny of the family Cordulegastridae (Odonata) worldwide. *Insects*, 15 (8), 1–33.
<https://doi.org/10.3390/insects15080622>
- Schütte, C. (1997) Egg development and early instars in *Cordulegaster boltonii immaculifrons* Selys: a field study (Anisoptera: Cordulegastridae). *Odonatologica*, 26 (1), 83–87.
- Selys, E. de (1854) Synopsis des Gomphines. *Bulletin de l'Académie royale de Belgique*, 21 (2), 23–112.
- Selys, E. de (1868) Communication sur quelques Odonates nouveaux du Mexique. *Annales de la Société entomologique de Belgique*, 11, 1–6.
- Selys, E. de (1878) Quatrièmes additions au synopsis des Gomphines. *Bulletin de l'Académie royale de Belgique*, 46, 408–471 + 658–698.
- Smith, B.D. & Patten, M.A. (2021) *Dragonflies at a Biogeographical Crossroads: The Odonata of Oklahoma and Complexities Beyond its Borders*. CRC Press, Taylor & Francis Group, Boca Raton, Florida, 738 pp.
<https://doi.org/10.1201/9781003007562>
- Tennessee, K.J. (2004) *Cordulegaster talaria*, n. sp. (Odonata: Cordulegastridae) from west-central Arkansas. *Proceedings of the Entomological Society of Washington*, 106 (4), 830–839.
- Tennessee, K.J. (2019) *Dragonfly nymphs of North America*. Springer Nature, Cham, 620 pp.
<https://doi.org/10.1007/978-3-319-97776-8>