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Freshwater Isopods (Crustacea: Isopoda: Asellidae) Inhabiting Upland Vernal Pools in Maryland

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Abstract: Three species of surface-dwelling freshwater isopods—*Caecidotea forbesi* (Williams), *C. nodula* (Williams), and *C. scrupulosa* (Williams)—inhabit upland vernal pools in Maryland (temporary waters that are dry a substantial part of each year, and are not connected to permanent surface water). All three also occur in permanent surface waters, but were found in every ecologically uncompromised upland temporary pool examined. Despite comments in the literature to the contrary, these isopods should be considered normal members of the aquatic community of these fragile habitats. They survive the seasonal dry period by moving below the surface of the substrate and lying dormant, a mechanism identified by Kenk (1949), Belk and Cole (1975), and Wiggins et al. (1980) as a specialization exhibited by certain vernal pool inhabitants. These three species show distinctive patterns of distribution within Maryland.

Key Words: freshwater ecology, freshwater isopods, *Caecidotea forbesi* (Williams), *Caecidotea nodula* (Williams), *Caecidotea scrupulosa* (Williams), vernal pools, Maryland

INTRODUCTION

In 1980, Dr. Thomas E. Bowman (Smithsonian Institution) and I initiated a survey of the freshwater isopods of Maryland. Over 400 collections were ultimately made, and we also examined material preserved in the collection of the National Museum of Natural History, Smithsonian Institution (USNM), as well as reviewing the pertinent literature. Effort was made to sample a wide variety of permanent and temporary waters throughout Maryland, including all of its 23 counties and Baltimore (city). Those collections showed that about ten species of pigmented surface-dwelling isopods inhabited Maryland's freshwaters, as many as three of which had not been named. The fieldwork was conducted primarily by me. Dr. Bowman made or confirmed identifications and was to have completed the taxonomic portion of the study. Unfortunately, he passed away in 1995, leaving the new taxa undescribed.

Because the local fauna was found to be unexpectedly rich, we originally intended to jointly publish a single paper describing the new species and recording data on distribution and natural history. I attempted to follow that plan, however, in the absence of a taxonomist to complete the descriptions, it proved to be impractical. In order to make the range extensions and other natural history information available, I decided to publish

the information in several segments, the first being a discussion of the three species—*Caecidotea forbesi* (Williams), *C. nodula* (Williams), and *C. scrupulosa* (Williams)—that inhabit upland vernal pools in Maryland. Vernal pool residents were selected first due to concern over threats to these special aquatic habitats and their fauna (Williams 1997, Zedler 2003, Brown and Jung 2005, Williams 2006). The second installment will consider the remaining pigmented surface dwellers, including *Caecidotea communis* (Say), *C. kenki* (Bowman), *C. racovitzai* (Williams), *Lirceus brachyurus* (Harger), and as many as three undescribed species of *Caecidotea* Packard.

A review of the Maryland subterranean isopods—*Caecidotea alleghenyensis* Lewis and Bowman; *C. franzi* (Holsinger and Steeves); *C. holsingeri* (Steeves); *C. mausi* Lewis and Bowman; *C. nordeni* Lewis and Bowman; *C. pricei* Levi; and *C. vandeli* (Bresson)—was given by Lewis and Bowman (2010) and Lewis et al. (2011).

VERNAL POOL HABITATS

A wide variety of temporary water bodies are found in eastern North America (Williams 1997, 2006). They differ primarily in the timing of their wet and dry cycles, and the length of time during which they remain wet. They are frequently grouped as seasonal pools even though they fall into several distinct types. The pools to be considered here typically fill in fall or early winter and usually remain wet until June, generally giving them a wet period of up to seven months. They are isolated habitats unconnected to permanent surface water and filled exclusively by rain, snowmelt, or groundwater (Brooks 2004). In the eastern United States, these have been termed vernal pools and typically support breeding mole salamanders, *Ambystoma* Tschudi spp. (Amphibia: Caudata: Ambystomatidae), and fairy shrimp, (Crustacea: Branchiopoda: Anostraca), (Brown and Jung 2005). Those species are assumed to utilize vernal pools because they lack effective defenses against predatory fishes, and the yearly summer dry period of vernal pools precludes fish populations. These habitats have often been referred to as woodland pools. (See Zedler [2003] for a more detailed discussion of terminology.)

Although the three species of isopods considered here also occur in permanent freshwater habitats (Figures 1–3), they occurred in vernal pools so regularly that they should be considered a significant part of the normal fauna. All examples of ecologically uncompromised vernal pools examined during this study supported a population of at least one of these three species. Vernal pools that occurred on floodplains receive floodwater and typically lacked these three species. Such pools in Maryland often support populations of *C. communis*, which is a common species occurring in a wide variety of freshwater habitats including streams, rivers, and permanent ponds. Because *C. communis* did not occur in upland vernal pools it is not considered here.

METHODS

Starting in the spring of 1980, freshwater habitats throughout Maryland were surveyed for asellid isopods. They were searched for in beds of aquatic vegetation, accumulations of detritus, and beneath rocks, logs and other places of concealment. Freshwater isopods in vernal pools were occasionally observed at night with the aid of a light. Whenever

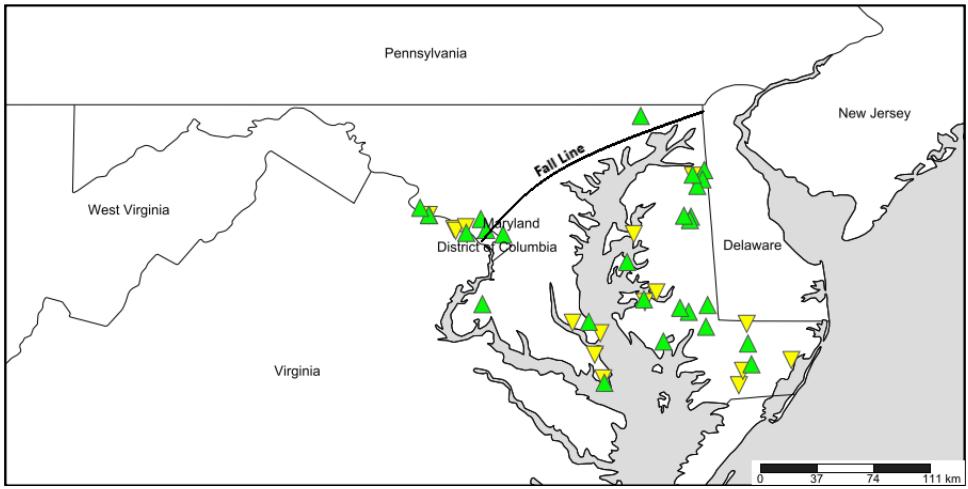

Figure 1. Map of Maryland showing locations for 48 collections of *Caecidotea forbesi* (Williams). Green triangles (▲) represent vernal pool habitats. Other habitats are indicated by yellow inverted triangles (▼). The transverse line shows the approximate location of the Fall Line, which separates the Atlantic Coastal Plain and the Piedmont Plateau physiographic provinces (after Vokes 1957). Some symbols encompass more than one collection site. The map was created using SimpleMappr (Shorthouse 2010).

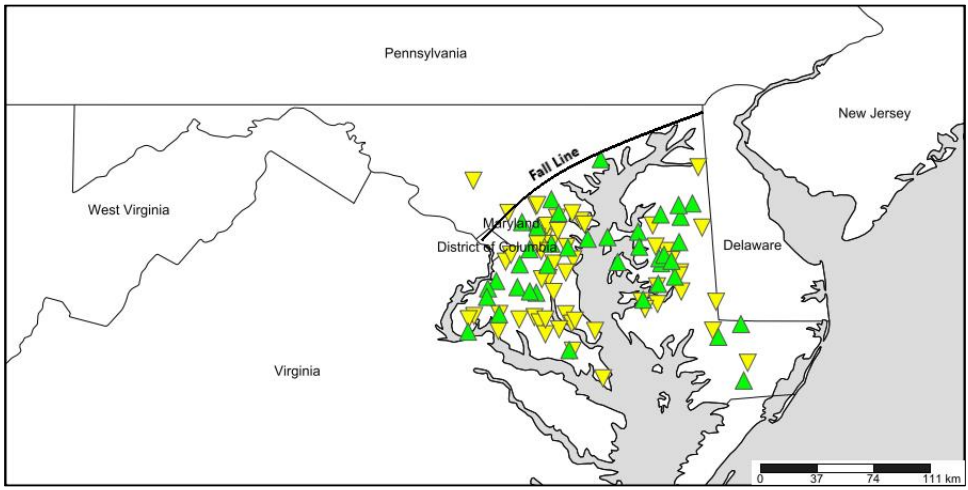

Figure 2. Map of Maryland showing locations for 112 collections of *Caecidotea nodula* (Williams). Green triangles (▲) represent vernal pool habitats. Other habitats are indicated by yellow inverted triangles (▼). The transverse line shows the approximate location of the Fall Line, which separates the Atlantic Coastal Plain and the Piedmont Plateau physiographic provinces (after Vokes 1957). Some symbols encompass more than one collection site. The map was created using SimpleMappr (Shorthouse 2010).

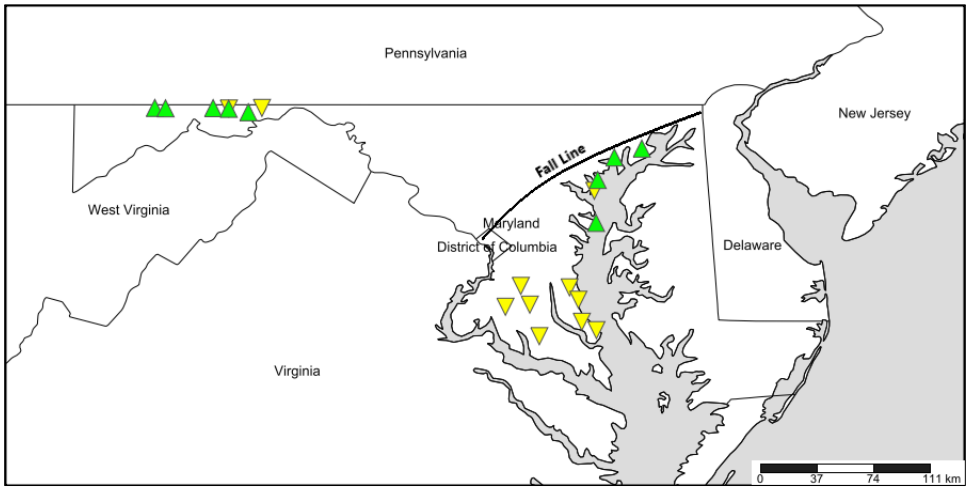

Figure 3. Map of Maryland showing locations for 20 collections of *Caecidotea scrupulosa* (Williams). Green triangles (▲) represent vernal pool habitats. Other habitats are indicated by yellow inverted triangles (▼). The transverse line shows the approximate location of the Fall Line, which separates the Atlantic Coastal Plain and the Piedmont Plateau physiographic provinces (after Vokes 1957). The map was created using SimpleMappr (Shorthouse 2010).

encountered, series of specimens were preserved in 70% ethyl alcohol and deposited in the USNM invertebrate collection. Maryland freshwater isopods already in the USNM collection were also examined and have been included in this study. Distributional data for Maryland asellids are given under the heading Material Examined in each of the following species accounts. Habitat data is taken from the literature, or the USNM catalogue entry. Records from the literature are discussed under the heading Range. Catalog numbers are given for all specimens in the USNM collection. Complete label data for USNM material is available at the Invertebrate Zoology Division's online collections database (https://collections.nmnh.si.edu/search/iz/). In the Material Examined sections, the collector "AN" refers to me.

The three isopods discussed here were described in detail, and features having taxonomic significance illustrated, by Williams (1970, 1976).

SPECIES ACCOUNTS

Caecidotea forbesi (Williams)

Material Examined: Maryland: Calvert Co.: Vernal pool at Flag Ponds, AN, 19 Apr 1985 (241813). Webster Pond at Cove Point, J. McKnight, 2 Mar 1987 (241841). Caroline Co.: Vernal pool 4 miles WNW of Goldsboro, AN & M. Dircks, 25 Apr 1985 (241811). Vernal pool at Bridgetown, J. Hill, 6 Feb 1986 (264537). Cecil Co.: Vernal pool along Rt 222 SE of Octoraro Creek, AN, 7 Mar 1987 (241848). Charles Co.: Vernal pools at Myrtle Grove WMA, AN, 30 Jan 1991 (258534). Dorchester Co.: Swamp W of

Cambridge, R. Jackson, 21 Mar 1943 (264533). Vernal pools at Nanticoke Boy Scout Reservation, AN & B. Norden, 2 Feb 1980 (264531). Vernal pools along Rt 50 E of Big Millpond, AN, 5 May 1986 (264536). Vernal pools along Lovers Lane S of Horn Point Rd, AN, 9 Mar 1993 (264539). Vernal pool along Johnson Rd N of Vienna, AN, 18 Apr 1984 (264536). Kent Co.: Vernal pool along Peacock Corner/No. 10 School Rd, AN, 18 Mar 1987. Vernal pool S of Walnut Tree Rd, AN, 18 Mar 1987 (241845). Vernal pool at Golts, AN, 14 Apr 1989 (250160). Swamp along Rt 301 S of Rt 313, AN, 30 Jan 1990 (250428). Montgomery Co.: Great Falls, C. Shoemaker & W. Appel, no date (45599). Ice pond, J. Benedict, 28 Feb 1926 (60283). Shore ponds near Plummers Island, W. Appel, 12 January 1935 (135762). Temporary pond on shore near Plummers Island, W. Appel, 5 May 1935 (122653). Temporary pond near Plummers Island, W. Appel, 19 May 1935 (135762). Pond at McKee Beshers WMA, J. Norvell, 4 Apr 1983 (250925). Vernal pool along Rock Creek in Kensington, AN, 22 Apr 1985 (241814). Pothole on Plummers Island, AN, 10 Jul 1986 (241903). Vernal pools along Meadowbrook Rd near entrance to Rock Creek Park, AN, 29 Apr 1993 (264551). Pothole at S end of Bear Island, D. Mehlman, 21 Apr 1984 (264560). Vernal pool at McKee Beshers WMA, AN, 1 May 1984 (264561). Small stream at McKee Beshers WMA, AN, 12 May 1984 (264562). Seepage area along Seneca Creek N of River Rd, AN, 1 May 1984 (264564). Prince George's Co.: Hyattsville, R. Greenfield, 18 Feb 1928 (61739). Hyattsville, R. Greenfield, 10 Feb 1929 (62659). Vernal pool along Oxon Hill Rd E of Henson Creek, AN & B. Norden, 17 May 1981 (264535). Queen Anne's Co.: Pond at Hess Rd and Rt 50, M. Dircks, 18 Mar 1985 (250921). Vernal pool along Rt 301 S of Rt 290, AN, 18 Mar 1987 (241844). Vernal pools along Roe Ingleside Rd N of Roe, AN, 30 Jan 1990 (250427). Somerset Co.: Ditch along Rt 24 N of Rt 675, AN, 17 Mar 1987 (241855). St. Mary's Co.: Rain water in ditch at Ridge, W. Ball, 26 Apr 1930 (67620). Vernal pool at Point No Point, W. Ball, 27 Apr 1930 (67619). Swamp SE corner of Patuxent Naval Air Station, AN, 20 May 1985 (241818). Vernal pools along Rt 5 S of Harry James Rd, AN, 27 Apr 1993 (254554). Talbot Co.: Vernal pool along Rt 33 W of St. Michaels, AN, 16 Mar 1987 (241850). Stream crossing Rt 50 N of Choptank River, AN, 29 Mar 1990 (250429). Wicomico Co.: Mayer Creek at Gordy Mill Rd, AN, 23 May 1984 (264558). Vernal pool along Rt 50 W of Maiden Forest Rd, AN, 17 Mar 1987 (241852). Vernal pool along Rt 347 NE of Athel Rd, AN, 29 Mar 1990 (250430). Worcester Co.: Permanent pond inland of Chincoteague Bay at Saint Lawrence Neck, D. Boone & F. Hirst, 10 Apr 1984 (264559). Vernal pool along Old Furnace Rd E of Dividing Creek, AN, 17 Mar 1987 (241858). Swamp along Dividing Creek at Rt 364, AN, 22 May 1988 (241945). Swamp along Dividing Creek at Five Bridges Rd, AN, 12 Apr 1990 (250431). Swamp along Dividing Creek at Fleming Millpond Rd, AN, 12 April 1990 (250432). Vernal pool along Fleming Millpond Rd N of Rt 364, AN, 12 Apr 1990 (250443).

Range: Williams (1970) recorded *C. forbesi* from the District of Columbia, Indiana, Kentucky, Maryland, Michigan, Missouri, North Carolina, Ohio, South Carolina, Virginia, West Virginia, and Ontario, Canada. Lewis (2009) gave records for Virginia and, citing Williams (1970), noted that it had a preference for vernal pools. It was also reported from northwestern Pennsylvania by Wissinger and Gallagher (1999) and from Wisconsin by Watermolen (2017). In addition, there are specimens at the USNM from Arkansas (171445), Georgia (123799), Illinois (128900), Iowa (108835), and Tennessee (1230345). This shows *C. forbesi* to be a very wide-ranging species. However, records

are absent for the area north of Maryland into New England, east of the Great Lakes and Saint Lawrence River.

In Maryland, *C. forbesi* is an inhabitant of the Atlantic Coastal Plain, with encroachment onto the Piedmont Plateau along the Potomac River and Susquehanna River valleys (Figure 1). Figure 1 shows several gaps in the Maryland distribution of this species. For instance, on the Western Shore of the Chesapeake Bay it was not found in a large area drained by the Patuxent River, and on the Eastern Shore it appears to be absent from the entire middle portion of the drainage of the Choptank River. However, Figure 2 shows that both areas had numerous vernal pools that supported *C. nodula*, indicating that habitat for *C. forbesi* was present.

Habitat: Williams (1970) noted that this isopod had been recorded from a variety of microhabitats. He reported it from "temporary pools, flood pools, and sloughs. However, the species has also been collected from marshes, small creeks, and at least on a few occasions from lakes. One of the lakes from which it has been collected was Lake Huron where the species was obtained from a depth of 15 m [49 ft]."

Analysis of the 48 Maryland records that include specific habitat data shows that 29 (60%) were from vernal pools, six were from swamps, five were from permanent ponds, four were from small streams, two were from potholes along the Potomac River, one was from a ditch, and one was from a large river.

Life History Notes: *Caecidotea forbesi* was found from January through May, and once in July. It was absent from collections made in June, and August through December. Most collections occurred during March and April. Sexually mature males were found in every collection and clasping pairs were noted on 7 and 16 March. Females carrying eggs or young in their brood pouches were found on 30 January, 7 March, 16 March, 18 March, 12 April, and 14 April. Some of those earlier dates were for specimens found active beneath a layer of ice.

Caecidotea nodula (Williams)

Material Examined: Maryland: Anne Arundel Co.: Seepage area along Rt 3 S of Crofton, AN, 14 Apr 1979 (230173). Pond at N end of Crofton Industrial Park, AN, 10 June 1979 (230183). Seepage area along Rt 295 S of Rt 175, AN, 25 Mar 1980 (230116). Muddy Creek at Rt 468, P. Dresler, 10 Mar 1981 (250929). Spring along Mill Swamp Rd E of Rt 2, AN, 23 Mar 1981 (230125). Seepage area along Rt 450 W of Rutland Rd, AN, 5 Apr 1984 (230987). Vernal pool along Severn Run N of Dicus Mill Rd, AN & D. Mehlman, 25 Apr 1984 (230997). Vernal pools along Sandpiper Ln, AN & D. Mehlman, 3 May 1984 (230998). Spring above Rucker's Pond, C. Rucker, 1 Jun 1985 (241827). Seepage area along Rt 2 N of Towneck Rd, C. Rucker, 15 Jan 1986 (241910). Vernal pools at west end of BWI Airport runway, AN, 10 Apr 1986 (230154). Spring at Rucker's Pond, AN, 20 Jun 1986 (241904). Vernal pools at Jug Bay Nature Center, AN, 24 Mar 1988 (241935). Seepage area along Rt 50 E of Rt 2, AN, 4 Apr 1990 (250421). Seepage area in woods along Rt 2 N of Rt 261, AN, 27 Apr 1993 (264552). Jug Bay Wetlands Sanctuary, springs in woods, AWN, 18 Mar 1994 (268794). Seepage area along

Rt 295 N of Rt 32, AN, 21 Mar 1994 (268789). Baltimore Co.: Vernal pools at Days Cove in Gunpowder Falls SP, AN, 15 Nov 1989 (250165). Calvert Co.: Boggy ground in Gray's Cypress Swamp, C.R. Shoemaker, 17 Apr 1938 (122058, 122059). Seepage area along Patuxent River S of Ferry Landing Rd, AN, 7 Mar 1987 (241843). Seepage area along Battle Creek Cypress Swamp, AN, 20 Apr 1984 (230993). Seep along Bromes Island Rd, AN, 20 Apr 1984 (230994). Spring-seep along Ross Rd, AN, 20 Apr 1984 (230995). Seepage area along Grays Creek in Calvert Cliffs State Park, AN, 14 Jan 1990 (250405). Seepage areas at Kings Landing Park, AN, 27 May 1987 (241862). Caroline Co.: Spring along Choptank River N of Red Bridges, AN, 15 Jun 1980 (230364). Seepage area along Tanyard Rd S of Rt 331, AN, 10 May 1984 (230999). Vernal pool along Alternate Rt 404 E of Hillsboro, AN, 20 Feb 1990 (250414). Vernal pool along Skeleton Creek Rd W of Poplar Neck Rd, AN, 10 Apr 1990 (250875). Spring seep along Marsh Creek S of Marsh Creek Rd, AN, 10 Apr 1990 (250876). Charles Co.: Rill 2.7 miles S of La Plata, L. Hubricht, 29 Feb 1959 (230193). Stream crossing Rt 301 S of La Plata, AN, 19 Apr 1982 (229827). Seepage area at head of Gilbert Swamp Run, AN, 7 Mar 1987 (241842). Seepage area along Popes Creek, AN, 25 Apr 1989 (250161). Vernal pools along lake at Cedarville State Forest, AN, 25 Apr 1989 (250404). Vernal pools along Pomfret Rd SW of Mattawomen Creek, AN, 19 Feb 1990 (250410). Spring-fed stream along Rt 6 E of Wards Run, AN, 19 Feb 1990 (250411). Swamp along Rt 425 E of Friendship Landing Rd, AN, 19 Feb 1990 (250412). Vernal pools along Rt 224 W of Rt 6, AN, 19 Feb 1990 (250413). Vernal pool along Rt 301 N of Cherry Ln, AN, 25 Mar 1994 (268790). Dorchester Co.: Ditch SW of Cambridge, R. Jackson, 21 Mar 1943 (241886). Swamp 3.3 miles W of Cambridge, R. Jackson, 21 Mar 1943 (230191). Ditch 3 miles SW of Cambridge, R. Jackson, 21 Mar 1943 (230192). Seepage area along Reliance-Delaware Rd in Galestown, AN, 30 Mar 1980 (230119). Spring seep along Rt 16 NE of Rt 50, AN, 29 Mar 1990 (250417). Swamp along Dividing Creek at Fleming Millpond Rd, AN, 12 Apr 1990 (250422). Vernal pools along Lovers Ln S of Horn Point Rd, AN, 9 Mar 1993 (264540). Seepage area along stream crossing Rt 16, AN, 25 Mar 1993 (264545). Swamp along Rt 16 N of Rt 50, AN, 22 Apr 1993 (268787). Howard Co.: Seepage area along Patuxent River W of Rt 94 in Patuxent River State Park, AN, 23 Mar 1990 (1250441). Seepage swamp along Rt 94 in Patuxent River State Park, AN, 23 Mar 1990 (250415). Kent Co.: Swamp between Sassafras River and Rt 299, AN, 30 Jan 1990 (250408). Swamp along Rt 301 S of Rt 313, AN, 30 Jan 1990 (250409). Prince George's Co.: Drinking water of home in Bowie, D. Glover, 23 Dec 1952 (95719). Seepage area along Suitland Road S of Suitland, J. Holsinger, 4 Feb 1973 (144062). Vernal pools along Rt 30 at Missouri Av, AN, 14 Apr 1979 (230176). Vernal pool along Rt 301 S of Rt 5, AN, 14 Apr 1979 (230174). Seepage area along Rt 32 SE of Rt 3, AN, 24 Apr 1979 (230175). Seepage area along Brinkley Rd E of Henson Creek, AN, 7 Feb 1982 (230123). Vernal pool along Indian Head Hwy SW of Accokeek Rd, AN, 19 Apr 1982 (229882). Spring along Rt 382 E of Charles Co. line, AN, 1 May 1982 (229823). Vernal pool along Central Av W of Patuxent River, AN, 20 Apr 1984 (230992). Seepage area along Rt 301 S of Rt 50, AN, 20 Apr 1984 (241547). Seepage area along Greencastle Rd near County line, AN, 17 Mar 1985 (241805). Vernal pool along Rt 197 at Horsepen Branch, AN, 22 Mar 1985 (241806). Seepage area along Church Rd N of Rt 214, AN, 9 Nov 1985 (230170). Vernal pools along Powder Mill Rd E of Rt 295, AN, 9 Apr 1986 (230153). Vernal pools, Accokeek, AN, 18 Mar 1987 (241847). Seepage area along Rt 50 E of Church Rd, AN, 8 Mar 1987 (241849). Seepage-fed stream along Croom Rd N of

Tanyard Rd, AN, 21 Jul 1987 (241870). Vernal pool along Brown Station Rd N of Old Marlboro Pike, AN, 27 Nov 1989 (250167). Seepage swamp along Collington Branch at Leeland Rd, AN, 26 Mar 1993 (264546). Vernal pools along White House Rd NW of Rt 202, AN, 26 Mar 1993 (264547). Vernal pools at Andrews Air Force Base, D. Feller and D. Davis, 7 Jul 1993 (264594). Mill Swamp at Marshall Rd, AN & N. Robbins, 30 Jun 1998 (250878). Queen Anne's Co.: Vernal pools along Rt 50 W of Rt 301, AN, 23 Feb 1980 (230105). Vernal pool along Rt 8 S of Matapeake, AN, 6 Mar 1984 (230982). Vernal pool along Rt 301 S of Rt 302, AN, 6 Mar 1984 (230984). Vernal pools along Wye Island Rd, AN & D. Richerson, 11 Apr 1985 (241807). Vernal pools on Wye Island, AN, 23 Nov 1989 (250164). Vernal pool along Roe Ingleside Rd N of Roe, AN, 30 Jan 1990 (250406). Vernal pools along Rt 302 E of Barkley, AN, 30 Jan 1990 (250407). Spring along Rt 50 N of Rt 404, AN, 29 Mar 1990 (250416). Saint Mary's Co.: Rain water in ditch at Ridge, W.H. Ball, 26 Apr. 1930 (122655). Stream at Mechanicsville, W.H. Ball, 11 May 1937 (122656). Spring at Bristol, A. Pizzini, 31 Oct. 1937 (122657). Ye Coole Spring in Charlotte Hall, S. Fuller, 30 Jun 1969 (230592). Seepage area along Indian Bridge Rd S of St. Andrews Church Rd, AN, 25 Aug 1986 (241907). Seepage area along Rt 301 W of Rt 213, AN, 26 Mar 1988 (241936). Vernal pool along Rt 213 at Schelhouse Rd, AN, 26 Mar 1988 (241938). Spring along Rt 6 W of Flora Corner Rd, AN, 10 Jun 1988 (229811). Seepage area along Rt 5 S of Rt 238, AN, 2 May 1989 (250162).). Vernal pools along St. Andrews Church Rd W of Indian Bridge Rd, AN, 27 Apr 1993 (264555). Vernal pools along stream crossing Rt 235 N of Rt 489, AN, 27 Apr 1993 (264553). Somerset Co.: Vernal pool along Rt 13 N of Rt 675, AN, 17 Mar 1987 (241854). Seepage swamp along Dividing Creek at Old Furnace Road, AN, 17 Mar 1987 (241856). Talbot Co.: Vernal pool along Beaverdam Branch S of Rt 328, AN, 10 May 1984 (230101). Seepage area along Mill Creek N of Rt 662, AN, 10 May 1984 (230102). Spring-seep along Rt 328 W of Kittys Corner Rd, AN, 10 May 1984 (230100). Seepage area in Trappe, AN, 17 Mar 1987 (241851). Vernal pools along Rt 50 S of Rabbit Hill Rd, AN, 3 Feb 1989 (250157). Vernal pools along Rt 50 S of Tarbutton Rd, AN, 9 Mar 1993 (264541). Vernal pools along Rt 309 SW of Klondike Rd, AN, 25 Mar 1993 (264542). Vernal pools along Beaverdam Branch at Rt 328, AN, 25 Mar 1993 (264543). Seepage swamp along Rt 309 SW of Cordova, AN, 25 Mar 1993 (264544). Vernal pools in mixed woods at Wittman, Steiner & Swearingen, 29 Mar. 1993 (268792). Vernal pools in woods at Wittman, Steiner & Swearingen, 10 Apr. 1994 (268801). Wicomico Co.: Seepage swamp along Rt 50 W of Salisbury, AN, 17 Mar 1987 (241853). Vernal pool along Rt 513 S of Rt 13, AN, 22 May 1988 (241943). Swamp along Rt 50 E of RT 50 bridge, AN, 29 Mar 1990 (250418). Vernal pool along Rt 349 E of Rt 347, AN, 29 Mar 1990 (250419). Seep-fed ditch along Athel Rd N Rt 347, AN, 29 Mar 1990 (250420). Spring along Camp Road E of Rt 3, AN & J Norden, 8 May 1994 (268800). Worcester Co.: Vernal pools along Fleming Mill Rd N of Rt 364, AN, 12 Apr 1990 (250423).

Range: Williams (1970) reported *C. nodula* from a "small peninsula southeast of Washington, D.C., bordered by the Potomac River and Chesapeake Bay." The records he cited were all from three counties (Anne Arundel, Calvert, and St. Mary's) in southern Maryland. Lewis (2009) subsequently reported it from Virginia. As Figure 2 shows, *C. nodula* occurs throughout the Maryland portion of the Atlantic Coastal Plain on both sides of the Chesapeake Bay. There is also encroachment onto the Piedmont Plateau along the Patuxent River valley. The only specimens at the USNM from outside of

Maryland are two series (1436190, 1436191) from Virginia reported by Lewis (2009), and a specimen lot from the District of Columbia (241986).

The type locality for *C. nodula* is "boggy ground in Gray's Cypress Swamp, below Prince Frederick, Calvert County, Maryland" (Williams 1970). Gray's Cypress Swamp is now known as Battle Creek Cypress Swamp, most of which is a nature preserve owned by The Nature Conservancy and leased to Calvert County.

Habitat: Williams (1970) examined four series of *C. nodula* and noted that they came from "a variety of habitats: boggy ground in a swamp, rainwater in a roadside ditch, a woodland stream, and the outlet of a spring." Among the 112 Maryland collections that we examined, label data specifically mentions vernal pools 44 times (39%), seepage areas 33 times, springs 14 times, swamps 11 times, streams/creeks six times, ditches twice, ponds once, and drinking water brought to a home once. If the groundwater-fed habitats (springs, seeps, drinking water) are grouped they account for 48 (43%) of the *C. nodula* collections, while vernal pools account for 44 (39%). The remaining 20 (18%) collections (ditches, swamps, ponds, streams/creeks) could have been groundwater influenced.

Life History Notes: *Caecidotea nodula* was found during every month of the year except September and December, although most collections were made in March and April. Sexually mature males were present in all collections. Ovigerous females were present in collections made on 14 January, 30 January, 3 February, 19 February, 20 February, 23 March, 29 March, 4 April, 25 April, and 2 May.

Caecidotea scrupulosa (Williams)

Material Examined: Maryland: Allegany Co.: Vernal pool in gorge below dam, Rocky Gap State Park, AN, 28 Apr 1988 (229814). Vernal pool N I-70 (I-68), 0.2 mi E of (Frank) Davis (Road), AN, 1 Apr 1986 (230156). Vernal pool along Town Creek, 0.3 mi S of Rt 40, E. Thompson, 17 Apr 1985 (241826). Stream along Rt 40, 5.8 mi E Flintstone, AN, 30 May 1985 (241823). Spring along Flintstone Creek just S Black Valley Road, AN, 10 Jan 1990 (250424). Anne Arundel Co.: Vernal pools, Corcoran Environmental Study Area, AN, 14 Apr 1981 (230124). Baltimore Co.: Vernal pools along Hollyneck Rd, 4 mi E Essex, AN, 24 Mar 1986 (230155). Swamp, Black Marsh, AN, 5 May 1987 (241860). Calvert Co.: Swamp, Camp Kaufmann, AN, 24 Apr 1982 (229833). Swamp along Parran Rd W of Route 4, AN, 20 Apr 1984 (230996). Swamp along Fishing Creek at Dalrymple Rd, AN, 20 Apr 1984 (230991). Swamp, Calvert Cliffs State Park, AN, 11 May 1987 (241861). Charles Co.: Pond, Myrtle Grove Wildlife Management Area, AN, 19 Apr 1982 (229828). Swamp along Rt 488, 3 mi E La Plata, AN, 1 May 1982 (229822). Garrett Co.: Spring pools along reservoir 3 mi E Frostburg, AN, 28 Apr 1988 (229815). Vernal pools along Swamp Rd, AN, 13 May 1986 (230157). Harford Co.: Vernal pools along Beach Rd, Edgewood, AN, 15 Mar 1990 (250425). Vernal pools, Aberdeen Proving Ground, AN, 15 Mar 1990 (250426). Prince George's Co.: Stream at Cedarville Rd 1 mi E of Rt 301, AN, 1 May 1982 (229826). Saint Mary's Co.: Tributary of St. Clements Creek SW of Helen, AN, 27 Apr 1993 (264556).

Range: The specimens described by Williams (1970) were all from vernal pools (including "woodland pools"). Subsequently, Fleming (1972) recorded this species from caves in Virginia and West Virginia, small streams in Virginia, and three localities in Georgia. A fourth Georgia occurrence was given by Nickol and Heard (1973) and one of Heard's Georgia specimens is at the USNM (238970). Additional occurrences of *C. scrupulosa* from caves and springs in Virginia and West Virginia were given by Steeves (1969), Holsinger et al. (1976), and Holsinger and Culver (1988).

Habitat: During this survey *C. scrupulosa* was collected at 20 locations in Maryland. Nine of these were vernal pools (45%), seven were freshwater swamps, two were low order streams, one was a spring, and one was the edge of a permanent pond. Thirteen of these Maryland localities were located in the east-central portion of the state on the Atlantic Coastal Plain (Figure 3). The other seven were in the western two counties, within the Allegheny Plateau and the Valley and Ridge portions of the Appalachian Plateau physiographic province (Vokes 1957). This species was not found east of the Chesapeake Bay, and the eastern and western populations are disjunct. These Maryland records represent the first reports of this species from the state, the northernmost localities for the species, and its first recorded occurrence on the Atlantic Coastal Plain.

Life History Notes: This species was the least frequently encountered of the isopods inhabiting upland vernal pools in Maryland. Collections were made during January, March, April, and May, with most in the latter two months. Sexually mature males were present in all collections, and clasping pairs were noted at two different sites on 20 April 1984. One collection made on 15 March 1990 included ovigerous females.

Remarks: Vernal pool and swamp habitats are abundant throughout the Maryland Atlantic Coastal Plain, where they are frequently occupied by *Caecidotea forbesi* and *C. nodula* (Figures 1 and 2). However, *C. scrupulosa* replaces those species on the northern extension of the Atlantic Coastal Plain along the western side of the Chesapeake Bay north of Baltimore.

Although *C. scrupulosa* inhabits caves in Virginia and West Virginia, it has not been found in any Maryland cave. Holsinger et al. (1976) and Steeves (1969) reported that cave populations of *C. forbesi* show varying adaptation to subterranean waters and range from normally pigmented individuals to lightly pigmented isopods with no apparent eyes. Steeves further stated that some cave populations in Virginia are more attenuate with longer appendages than non-cave populations in the same drainage. This degree of morphological variation is notable, and those cave-inhabiting populations deserve close study. Specimens from apparently eyeless cave-inhabiting populations in the USNM collection were found to have very small eyes (Thomas E. Bowman, personal communication).

DISCUSSION

Dry Period Survival

Since upland vernal pools are typically dry for as much as five months each year, aquatic species inhabiting them must have some way of surviving the dry period. Kenk (1949) suggested that the life history of vernal pool inhabitants must allow for at least one of the following: 1) must not be exclusively aquatic and move to and from the pool each year; 2) must produce a dormant egg or cyst; 3) must become a drought-resistant dormant adult; or 4) must follow groundwater down into the soil column. Belk and Cole (1975), Wiggins et al. (1980), and Williams (1997) discussed these adaptations in greater detail. Subsequent authors have treated aquatic isopods as having no such adaptations for dry season survival. For instance Colburn (2004) believed that aquatic isopods have no adaptations for dry season survival so should not be considered typical vernal pool residents, and Kenny and Burne (2000) stated that they "have no specialized adaptations, such as drought-resistant eggs or a diapause phase to survive the dry periods characteristic of vernal pools." Batzer and Sion (1999) studied temporary pools in western New York and noted that the occurrence of abundant isopods was surprising because they were thought to lack "desiccation-resistant stages and are poorly adapted to disperse into newly created habitat." This determination made despite the fact that isopods (*Caecidotea racovitzai*) were present in 25 temporary pools examined by them.

Kenk (1949) discussed isopods from vernal pools in Michigan—as *Asellus militaris* Hay, a junior synonym of *Caecidotea intermedia* (Forbes)—and suggested that they followed the retreating water table into the soil column and lived a subterranean existence until the pools filled again. He based this on the observation that isopods in the pools he studied appeared as small but adult individuals just after the pools filled. He thought that they could move directly down into the substrate, or occupy the water-filled chambers at the bottom of crayfish burrows as observed by Creaser (1931).

Batzer and Sion (1999) discussed the transportation of isopods into temporary pools through groundwater, by surface flooding or on the feathers or feet of water birds, but determined these mechanisms to be improbable for the pools that they studied in western New York. Although their sites were identified as "autumnal" pools, they would fall into the category of vernal pools as defined here. The isopods present at their sites were *Caecidotea racovitzai*, a species also occurring in Maryland but not found in vernal pools during this study. They believed that the isopods survived in pockets of permanent water or in "damp organic detritus in dry basins." This conclusion was based on the assumption that they had no resistant dry-season stages and did appear soon after rains began to fill the pool's basin. They were able to find small numbers of isopods in the dry substrate of a pond bed, and showed in laboratory studies that their aquatic isopods were able to survive at least three weeks in damp detritus.

Among the adaptations exhibited by vernal pool obligate macroinvertebrates in the mid-Atlantic region, dormancy in dry soil by adults is least common. The only other animals that I am aware of relying on it are mollusks, particularly some pisidiid clams (Mollusca: Pisidiidae) (Herrington 1962, McKee and Mackie 1980). Pisidiid clams are of regular occurrence in mid-Atlantic vernal pools (Brown and Jung 2005, personal observation),

and several species are restricted to temporary waters (Herrington 1962). McKee and Mackie (1980) studied desiccation resistance in one of these, *Sphaerium occidentale* (J. Lewis), and found that it burrowed into the substrate when the pool dried, and lay dormant until the pool again filled. Gladden and Smock (1990) found that *Pisidium* L. Pfeiffer sp. on floodplains also survived dry periods by simply closing their valves and lying dormant in the substrate until water returned.

Williams (2006) gives an interesting summary of the occurrence of crustaceans in temporary waters in relation to hydroperiod in Ontario, Canada. *Caecidotea* was listed as occurring only in habitats that are wet for a minimum of 70 days. Since there is evidence that adults appear soon after pools fill (Kenk 1949, Batzer and Sion 1999), I suggest that this is the minimum time required for a generation to reproduce, allowing for multiple generations in a single wet cycle.

Seasonal Occurrence

Although isopod collections were made in Maryland during every month of the year, field effort was least during the coldest months (December, January and February) and collecting effort was greater from March through November. Collecting effort during those months was relatively even. Data collected for this study shows that all three species appeared in winter, reached peak numbers (estimated) in March–April–May then dwindled in June. That periodicity coincides with the times that vernal pools in Maryland fill (fall–winter) and then experience their dry period (late June–July through November).

It is interesting that populations of these same three species inhabiting non-vernal pool habitats (i.e., springs, seepage areas, swamps, etc.) persist slightly longer, but also decline and disappear during those months when vernal pools are dry. As noted previously, observation of a population of *Caecidotea scrupulosa* in Anne Arundel County showed them to be present and active throughout the winter, even when the pool was covered by a layer of ice. Observations made during this study showed that populations of all three species in Maryland vernal pools reached their highest density in May, then decreased in number and disappeared several weeks before the pools actually dried in June or July. Although the disappearance of the isopods was probably due to some biotic/abiotic seasonal change in the aquatic habitat, available data does not suggest what that change might be.

Co-occurrence of Species

Among the collections made or examined during this study, *Caecidotea scrupulosa* did not occur with either of the other two species while *C. nodula* and *C. forbesi* occurred together seven times. Since *C. scrupulosa* was found relatively few times, it is possible that had it been encountered more frequently it might have been found with another species. The substrate of vernal pools in Maryland is characteristically fallen deciduous leaves over soil. The leaves are intact at the top, but lower down the leaf material becomes more finely divided. On a number of occasions, I had the opportunity to observe isopods undisturbed atop the leaf layer. Typically, the species observed was *C. nodula*. In addition, *C. nodula* were “clean” when captured while other species frequently carried bits of detritus or other material. Based on these observations, I believe that where *C.*

nodula and *C. forbesi* occur together in vernal pools, they occupy different levels in the leaf/detritus layer, *C. nodula* near the top where the leaves are intact, and *C. forbesi* lower down, in the more finely divided detritus near the soil surface. Such a distribution would serve to partition the habitat as well as food resources.

Maryland Distribution

As Figures 1–3 show, these three isopods have distinctive distributions within Maryland. *Caecidotea forbesi* and *C. nodula* were both found on the Atlantic Coastal Plain along both sides of the Chesapeake Bay, and both were found to have gaps in their apparent distribution in the interior of the Coastal Plain. *Caecidotea forbesi*, in particular, was not found in large areas of the Western Shore.

Caecidotea scrupulosa inhabits Maryland's Atlantic Coastal Plain wetlands but only on the western side of the Bay. It also shows a cluster of occurrences in the western part of the State (Figure 3). This is interesting because the freshwater habitats are profoundly different. The Atlantic Coastal Plain sediments are deep unconsolidated clays, sands, and gravels, while surface and near-surface substrates in Western Maryland are typically hard, consolidated shale, sandstones, and limestone (Vokes 1957). However, as discussed above, *C. scrupulosa* occurs in Virginia and West Virginia, including solution caves in the hard rocks of the Appalachian Mountains. It is possible that when we understand the wider distribution of this isopod, it may be found to occur along the Appalachian Front, linking the Western Maryland population with *C. scrupulosa* farther south. The eastern population and the western population are clearly disjunct in Maryland.

Since the freshwater habitats available are generally similar on both sides of the Bay, the absence of *C. scrupulosa* on the Delmarva Peninsula is likely a result of the timing of recolonization of freshwater habitats in eastern Maryland at the end of the Wisconsin Glaciation when melting ice sheets restored the Chesapeake Bay, limiting habitat and restricting the movement of non-flying invertebrates.

Although vernal pool habitats are more abundant on Maryland's Atlantic Coastal Plain, they are present west of the Fall Line (separating the Atlantic Coastal Plain and the Piedmont Plateau), making the general absence of these three species from the Piedmont Plateau physiographic province surprising.

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