



THE GENUS *MEGALEUCTRA* NEAVE (PLECOPTERA: LEUCTRIDAE) IN NORTH AMERICA

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ABSTRACT

The extant Nearctic *Megaleuctra* are reviewed and five species are recognized: *M. complicata* Claassen, *M. flinti* Baumann, *M. kincaidi* Frison, *M. stigmata* (Banks), and *M. williamsae* Hanson. Diagnostic illustrations and SEM images are provided for the male and female of all species. The females of *M. complicata* and *M. flinti* are described for the first time and *M. sierra* Fields is placed as a synonym of *M. stigmata*.

Keywords: Plecoptera, stonefly, Leuctridae, *Megaleuctra*, North America

INTRODUCTION

The genus *Megaleuctra* Neave was established on the basis of four female specimens collected in the Kootenay Lake area of southeastern British Columbia, Canada by Neave (1934). The genus is considered one of the rarest of stonefly genera (Jewett 1959, Baumann et al. 1977, Scudder 1994, Stagliano and Maxell 2010) and is usually associated with spring seeps and rheocrenes of the Appalachian Mountains, Pacific Northwest, and the northern Rocky Mountains. Two fossil species are known: *M. jewetti* Lewis, from Miocene deposits of the Latah Formation near Juliaetta, Idaho (Lewis 1969), and *M. neavei* Ricker, described from a Prussian Baltic Amber specimen from the Lower Oligocene (Ricker 1935; Illies 1967). Hynes (1988) postulated that Pleistocene ice ages caused the extinction of *Megaleuctra* in the Palearctic realm. However, recently Ham & Bae (2002) described the first Asian species from the Republic of Korea, and Zwick (2010) and Zwick & Baumann (2011) provide additional records.

The position of *Megaleuctra* as a genus within

Leuctridae has not always been secure. Illies (1967), primarily on the basis of internal male reproductive morphology and female ovipositor structure, placed the genus in the subfamily Notonemourinae (at that time considered part of the Capniidae). However, this position was not accepted by Nelson and Hanson (1973), who continued to treat it as a primitive member of Leuctridae, and (Zwick 2000), who stated "Transformations of the paraproct base confirm that the genus *Megaleuctra*...belongs to Leuctridae; it is not a notonemourid..." and he includes it in this family in his paper on family larval characters Zwick (2006). Terry (2003) suggests that the inclusion of *Megaleuctra* in Leuctridae renders the family paraphyletic and advocates recognition of a new family, Megaleuctridae, to accommodate this enigmatic genus.

Adults of *Megaleuctra* can be distinguished from all known Leuctridae by their large size, dark colored stigma in the costal space of the forewing beyond the cord, six longitudinal veins in the hind wing, an elaborate epiproct, which can appear in three

positions on tergum 10: basal, midlength or completely extended, an elongate subanal probe which curves upward over the abdomen and fits in a dorsal groove in the epiproct, and a large ovipositor structure projecting beyond the abdominal apex in the female.

The Nearctic species form two distinct clades. The tips of the subanal probe of the Pacific Northwest and Northern Rocky Mountain species, *M. complicata* Claassen, *M. kincaidi* Frison and *M. stigmata* (Banks) are similar, having an enlarged apically lobed process which bears a subapical notch (Baumann et al. 1977; Claassen 1937; Fields 1977; Frison 1942; Jewett 1959). In contrast, the two Appalachian species, *M. flinti* Baumann and *M. williamsae* Hanson, have cylindrical, apically acute subanal probes (Baumann 1973).

MATERIALS AND METHODS

The following personal and institutional collections were accessed as part of this study.

ABRC	Austin Brady Richards Collection, Chico, CA
BPSC	Bill P. Stark Collection, Mississippi College, Clinton, MS
BYUC	Brigham Young University Collection, Provo, UT
CASC	California Academy of Science Collection, San Francisco, CA
CHNC	Charles H. Nelson Collection, Chattanooga, TN
CNCI	Canadian National Collection of Insects, Ottawa, ON
CSUC	Colorado State University Collection, Fort Collins, CO
CUCC	Clemson University Collection, Clemson, SC
CUIC	Cornell University Collection, Ithaca, NY
DBDC	David B. Donald Collection, Regina, SK
FMNH	Field Museum of Natural History, Chicago, IL
INHS	Illinois Natural History Survey, Champaign, IL
ISUI	Iowa State University Collection, Ames, IA
JJLC	Jonathan J. Lee Collection, Eureka, CA
MCZC	Museum of Comparative Zoology Collection, Cambridge, MA
NCSU	North Carolina State University Collection,

	Raleigh, NC
OSUC	Oregon State University Collection, Corvallis, OR
PMSL	Slovenian Museum of Natural History, Ljubljana, Slovenia
RLBC	Richard L. Bottorff Collection, Placerville, CA
RFSC	Rebecca F. Surdick Collection, White Post, VA
ROMC	Royal Ontario Museum Collection, Toronto, ON
SAGC	Scott A. Grubbs Collection, Western Kentucky University, Bowling Green, KY
SEMC	Snow Entomological Museum Collection, Lawrence, KS
UIIC	University of Idaho Insect Collection, Moscow, ID
UMBS	University of Montana Biological Station, Polson, MT
UNTC	University of North Texas Collection, Denton, TX
USNM	United States National Museum Collection, Washington, D. C.
USUC	Utah State University Collection, Logan, UT
UWVC	University of West Virginia Collection, Morgantown, WV
VPIC	Virginia Polytechnic Institute Collection, Blacksburg, VA
ZCSC	Zach Crete Stonefly Collection, Lolo, MT

Adult genitalia were studied with a WILD M8 or an Olympus SZH 10 stereomicroscope. Scanning electron micrographs (SEM) were taken using a Philips XL30 ESEM FEG microscope at Brigham Young University, Provo, Utah, or an Amray 1810D microscope at Mississippi College, Clinton, Mississippi. The SEM egg images were prepared at VPI&SU in Blacksburg, Virginia. The color photograph of the live male of *M. stigmata* was taken by Bob Newell using a Nikon D 300 camera with a 105mm macro lens, that of the brachypterous male of *M. complicata* by Brady Richards using a Sonyshot DSC-W80 camera and the macropterous female of *M. complicata* by Greg Courtney with a Nikon D7000 DSLR camera with a Mikro-Nikkor 105mm lens and combination SB-800/R1 flash system. The line drawings were constructed using a Wild M-7



Fig. 1. *Megaleuctra stigmata*, Talking Water Creek, Montana. Male, Live, habitus, dorsal, macropterous. (Photo courtesy of R.L. Newell).

stereomicroscope with a camera lucida attachment. Previously published figures of *Megaleuctra* species from Baumann (1973) and Baumann et al. (1977) were used in some of the figure plates and permission was granted by the American Entomological Society.

RESULTS AND DISCUSSION

Key to the Adults of Extant Nearctic *Megaleuctra*

Males

- 1 Tip of subanal probe acute or threadlike (Figs. 21-22, 25, 29, 75, 77, 81); known distribution Appalachian Mountains region of eastern North America 2
- 1' Tip of subanal probe enlarged and bearing a subapical notch (Figs. 3, 10, 16, 36, 64, 68); known distribution northern Rocky Mountains, Sierra Nevada and Cascades of western North America 3
- 2 Tergum 9 bearing a small, darkly sclerotized, median, toothed process between low lateral

- lobes (Figs. 21, 28); subanal probe expanded above base and about mid length, tip thread-like (Figs. 21, 22, 25, 29); known from Maryland, Pennsylvania, West Virginia and Shenandoah National Park, Virginia *M. flinti*
- 2' Tergum 9 without median process or low lateral lobes (Figs. 74, 78); lateral aspect of subanal probe relatively uniform in diameter throughout, tip truncate (Fig. 75, 81); known from North and South Carolina, Tennessee and the Mount Rogers area of southwestern Virginia *M. williamsae*
- 3 Tergum 9 bearing large pair of rounded dorsal processes near posterior margin, anterior margin of process rounded, posterior margin angled abruptly downward, lateral profile forming a broad arc (Figs. 55, 67), cerci short ... *M. stigmata*
- 3' Tergum 9 bearing smaller pair of processes near posterior margin, processes thinner and pointed at apex, cerci long (Figs. 3, 5, 36, 42) 4
- 4 Processes on tergum 9 relatively symmetrical, broad basally, narrowed apically and bluntly pointed or conical at tip (Figs. 6, 13), dorsal lobe of subanal probe long, thin and pointed at tip (Fig. 14), epiproct large, bearing large downward

directed hooks medially when partially expanded (Fig. 9), hooks extending to apex of subanal probe when fully expanded (Fig. 8), ventral portion forming an elongate triangle when viewed dorsally (Fig. 6) *M. complicata*

- 4' Processes on tergum 9 thin, delicate, long and abruptly pointed (Figs. 36, 38), distal portion of subanal probe broad, and diamond shaped, with a small thin tip (Figs. 46-47), epiproct extending to near tip of unexpanded subanal probe (Fig. 42), but reaching far short of expanded probe (Fig. 48), thin tips not very conspicuous when expanded (Figs. 46, 50), hooks less obvious when extended to apex of subanal probe, ventral portion forming a stout triangle when viewed dorsally (Fig. 35) *M. kincaidi*

Females

- 1 Known distribution Appalachian Mountains region of eastern North America 2
 1' Known distribution northern Rocky Mountains, Sierra Nevada and Cascade Mountains of western North America 3
 2 Subgenital plate (ovipositor) almost subequal in width from beyond base to apex (Fig. 83), known distribution North and South Carolina, Tennessee and Mount Rogers area of southwestern Virginia *M. williamsae*
 2' Subgenital plate (ovipositor) narrowed conspicuously from base to apex; known from Maryland, Pennsylvania, West Virginia and Shenandoah National Park, Virginia *M. flinti*
 3 Stigma beyond cord large, darkly pigmented and filling most of costal space; usually more than 3 branches of radial sector vein (Fig. 1) .. *M. stigmata*
 3' Stigma beyond cord small, less darkly pigmented and filling less than half of coastal space; usually 2 or 3 branches of radial sector vein (Fig. 85) *M. complicata*/*M. kincaidi*

Systematic Treatment

Megaleuctra complicata Claassen

(Figs. 2-20, 85, 86)

Megaleuctra complicata Claassen 1937:48. Holotype ♂ (CUIC). Type locality: Corvallis, (Benton Co.) Oregon,

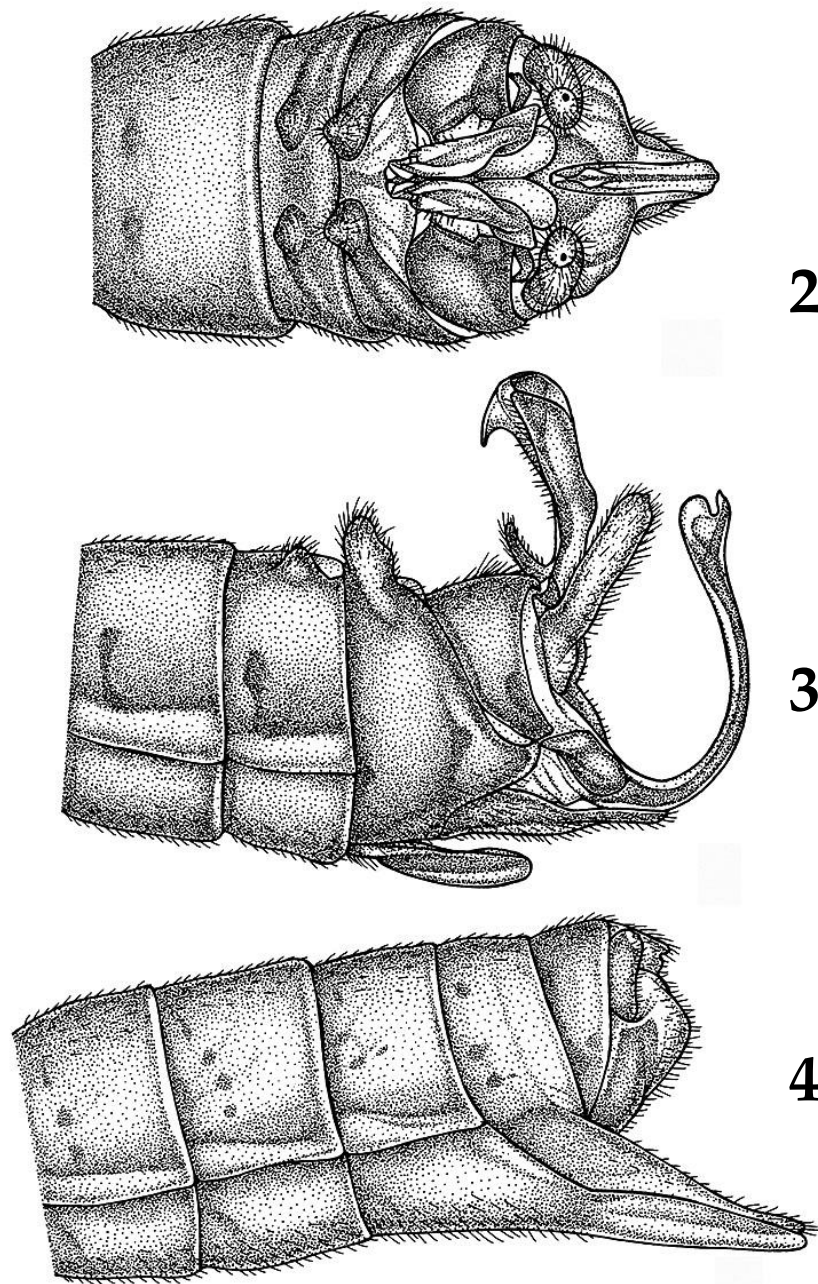
examined

Megaleuctra complicata: Frison, 1942:12. Figures of male

Megaleuctra complicata: Stewart & Sandberg, 2004:126.

Male drumming signal and larval description

Material examined. CALIFORNIA: Butte Co., Seep, along Butte Creek, Cherry Hill Campground, 40.10194° N, 121.49861° W, 10 November 2003, A.B. Richards, 1♂, 2♀ (ABRC, BYUC). Same site, 3 February 2007, A.B. Richards, J.B. Sandberg, 3 larvae (ABRC, BYUC). Same site, 10 November 2007, A.B. Richards, D.A. Richards, 1♀ (BYUC). Same site, 26 April 2010, A.B. Richards, 1♀, 1 larva (ABRC). Unnamed stream, S Butte Creek bridge, Doe Mill Road, 39.90845° N 121. 61804° W, 21 January 2010, A.B. Richards, 1♂ (ABRC). Humboldt Co., Spring, East Fork Willow Creek Campground, 2-5 May 2008, J.J. Lee, 1♂, 12♀ (BYUC, CSUC, JJLC). Tehama Co., Unnamed spring, tributary Big Chico Creek, along Hwy 32, 40.07841° N 121.59568° W, 10 November 2007, A.B. Richards, 3♀ (JJLC, ABRC). Same site, 25 November 2007, A.B. Richards, 3♂, 1♀ (ABRC). Same site, 30 November 2007, J.J. Lee, A.B. Richards, 1♂ (JJLC). Same site, 9 March 2008, A.B. Richards, D.A. Richards, 1♂, 3♀ (ABRC, BYUC). Same site, 22 March 2008, A.B. Richards, D.A. Richards, 1♂, 2♀ (ABRC). Same site, 13 April 2008, A.B. Richards, D.A. Richards, 2♀ (ABRC). Same site, 21 February 2009, A.B. Richards, 2♂, 1♀ (ABRC). Same site, 28 February 2009, A.R. Richards, 1♀ (ABRC). Same site, 28 March 2009, A.B. Richards, D.A. Richards, B.C. Richards, 1♂, 2♀ (ABRC). Same site, 26 April 2010, R.W. Baumann, B.C. Kondratieff, A.B. Richards, 2♀ (BYUC, CSUC). Same site, 16 January 2011, A.B. Richards, 1♀ (ABRC). Same site, 9 March 2013, A.B. Richards, 1♂, 2♀ (ABRC). **OREGON:** Benton Co., Stream near, North Fork Alsea River, 3.5 mi. NE Alsea, 13 April 1961, J.D. Lattin, 1♂, 1♀ (OSUC). Rest area 12 mi. E Alsea, 12 April 1962, S.G. Jewett, Jr., 2♂ (BYUC). Spring, 8 mi. E Alsea, 27 September 1962, J.D. Lattin, 2♀ (OSUC). Corvallis, 28 March 1930, R.J. Norberg, 1♂, Holotype (CUIC). Chintimini Creek, Marys Peak, 14 April 1964, Wiggins, Scott, 1 larva (ROMC). Oak Creek, 12 May 1938, S.G. Jewett, Jr., 1♀ (BYUC). Marys Peak, Marys Peak Road, 3 April, 1970, J.F.G. Clark, 1♂ (USNM). Parker Creek, Marys Peak Campground, 14 June 1968, Wiggins,



Figs. 2-4. *Megaleuctra complicata*, Still Creek, Oregon. Terminalia: 2. Male, dorsal. 3. Male, lateral. 4. Female, lateral.

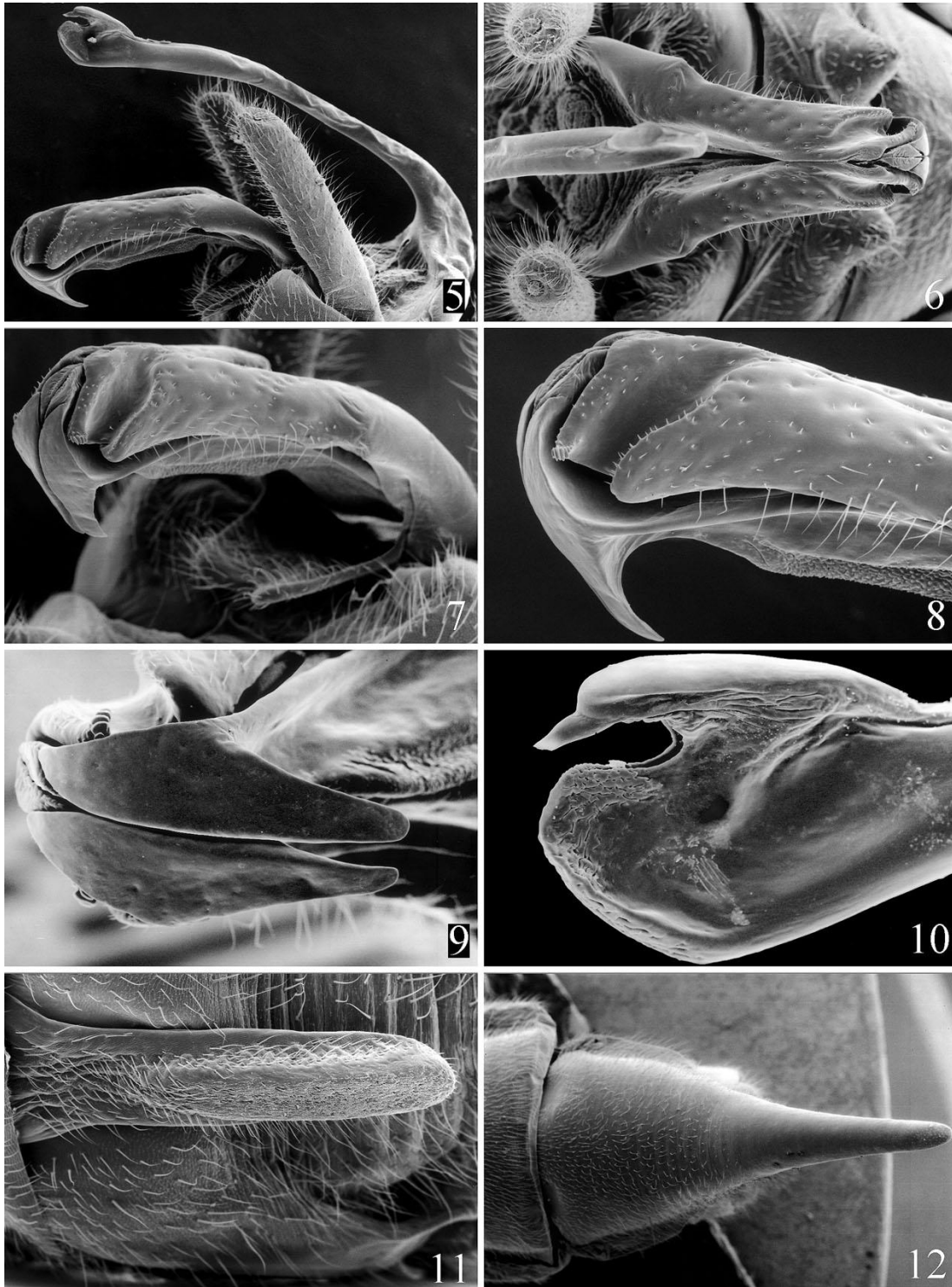
Yamamoto, Smith, 1♀ (ROMC); Parker Creek, Marys Peak, 15 June 1968, N.H. Anderson, 1♀ (OSUC). Marys Peak, upper Parker Creek, 44° 30.51'

N 123° 33.49' W, 1115m, 30 May 1982, G.W. Courtney, 1♂, 2♀ (ISUI). Same site, 19 June 1996, G.W. Courtney, 4♀ (ISUI). Same site, 26 April 1997,

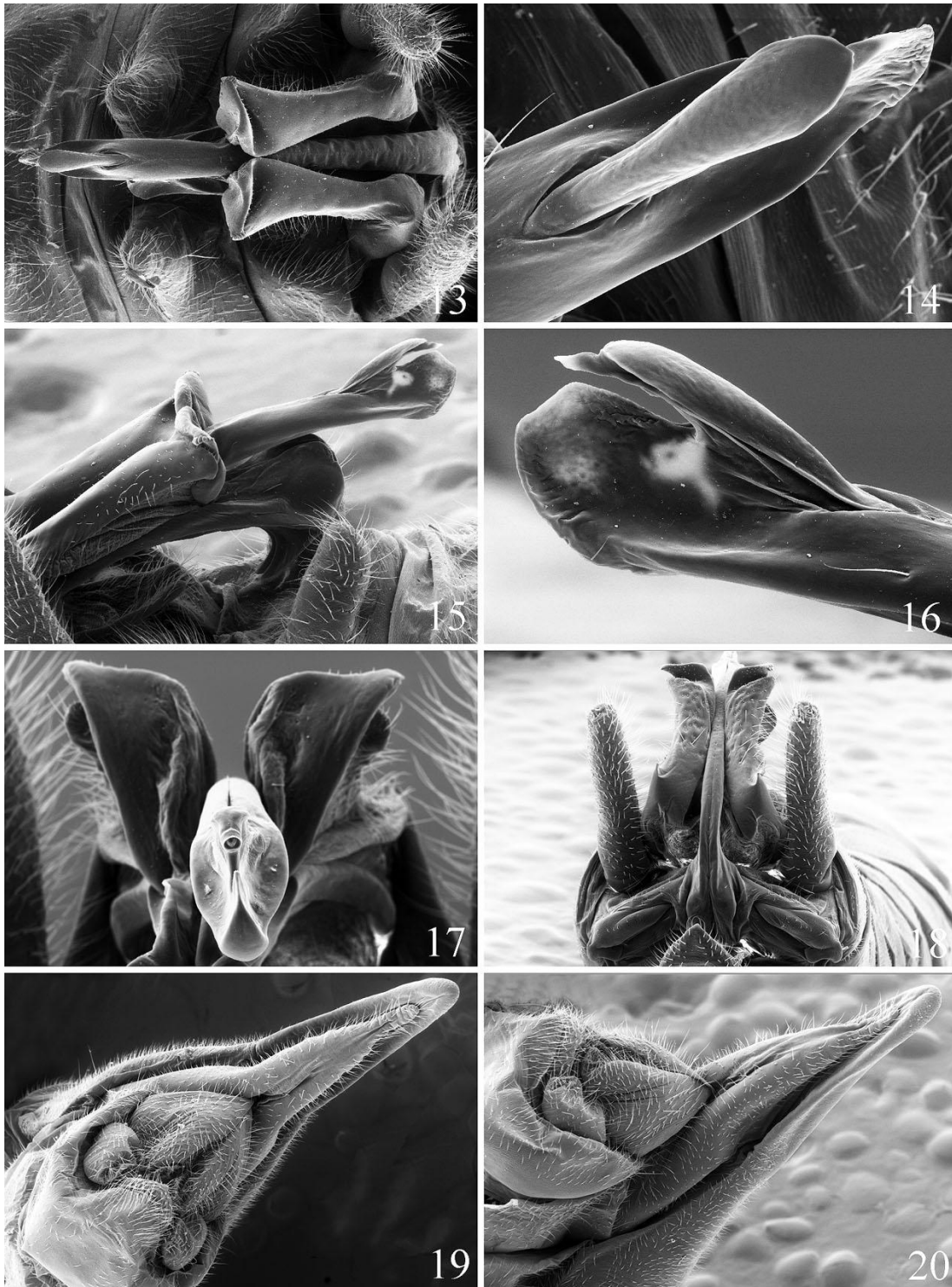
R.W. Wisseman, 1 larva, (BYUC). Same site, 23 May 2007, G.W. Courtney, 1 ♀ (ISUI). Same site, 28 May-4 June 2009, G.W. Courtney, 2 ♀ (ISUI). Same site, 1 June 2013, G. Courtney, S. Fitzgerald, 9 ♀ (ISUI, CSUC). Marys Peak, 1 mi. from Hwy 34 turnoff, 14 miles W Corvallis, 17 March 1963, N.H. Anderson, 2 larvae (OSUC). Same site, 17 March 1969, N.H. Anderson, 5 larvae, (BYUC). Clackamas Co., Austin Hot Springs, Clackamas River, 16 June 1957, S.G. Jewett, Jr., 1 ♀ (BYUC). Camp Creek, Camp Creek Campground, 26 May 1983, G.R. Fiala, 2 ♂, 2 ♀ (BYUC). Same site, 2 April 1994, G.R. Fiala, 2 ♀ (BYUC). Eagle Fern Park, 22 April 1962, S.G. Jewett, Jr., 2 ♀ (BYUC). Seep, 3 miles E Rhododendron, 28 June 1959, G.W. Byers, 1 ♀ (SEMC). Run, entering Salmon River, Salmon River Campground, Mount Hood National Forest, 10 June 1967, T. Yamamoto, 1 larva (ROMC). Seep, Still Creek, Still Creek Campground, Hwy 26, Mount Hood National Forest, 23 July 1955, S.G. Jewett, Jr., 1 ♂, 1 ♀ (BYUC). Same site, 8 July 1965, S.G. Jewett, Jr., 1 ♀ (CASC). Same site, 17 June 1967, S.G. Jewett, Jr., 3 ♀ (CASC). Same site, 5 July 1982, S.G. Jewett, Jr., 1 ♂, 1 ♀ (CASC). Same site, 28 May 1983, G.R. Fiala, 10 ♂, 18 ♀ (BYUC, CSUC). Clatsop Co., Osweg Creek, 2 mi. E Elsie, 9 May 1965, S.G. Jewett, Jr., 1 ♀ (BYUC). Tributary, Necanicum River, Saddle Mountain State Park, 1 April 1967, S.G. Jewett, Jr., 1 ♂, 1 ♀ (BYUC, FMNH). Columbia Co., Beaver Creek, 10 April 1940, S.G. Jewett, Jr., 1 ♀ (CASC). Coos Co., Little Rock Creek, 2 mi. from Hwy 42 up Rock Creek Road, 29 March 1982, G.W. Courtney, 1 larva (ISUI). Douglas Co., Big Camas Ranger Station, Umpqua National Forest, 30 April 1958, S.G. Jewett, Jr., 4 ♂, 18 ♀ (BYUC, CASC, CSUC). Headwaters, Bulldog Creek, Umpqua National Forest, 5000', 19 June 1998, R.W. Wisseman, 2 larvae (BYUC). Tributary, Smith River, 22.5 mi. from Hwy 101 on Smith River Road, 29 March 1982, G.W. Courtney, 1 larva (ISUI). Hood River Co., Hood River Meadows, 21 June 1958, W.M. Kulash, 3 ♀ (BYUC, NCSU). Oxbow Springs, 18 April 1940, S.G. Jewett, Jr., 1 ♀ (BYUC). Jackson Co., Whiskey Springs, Whiskey Springs Campground, 9 June 2004, B.P. Stark, R.W. Baumann, 5 ♀ (BPSC, BYUC). Lane Co., Quartz Creek, 10 March 1983, N.H. Anderson, 1 ♀ (OSUC). Linn Co., Seeps, Willis Creek, 1.3 mi N Hwy 22,

Marion Forks Road, 3 June 2000, B.P. Stark, I. Sivec, M.C. Zúñiga, 8 ♂, 20 ♀ (BPSC, BYUC, CSUC, PMSL). Same site, 17 May 2001, B.P. Stark, K.W. Stewart, J. Sandberg, 10 ♂, 1 ♀, 5 larvae (BYUC, UNTC). Marion Co., Elk Lake, 4 July 1958, H. Hacker, 1 ♀ (INHS). Tributaries, French Creek, Willamette National Forest, Detroit Ranger District, Rd. 2225, 19 March 1998, R.W. Wisseman, 1 ♂, 1 ♀ (BYUC). Little North Santiam River, T9S, R3E, section 9, 28 April 1960, unknown collector, 1 ♂ (BYUC). Silver Creek Falls, Silver Falls State Park, 2 May 1949, J.E. Davis, 1 ♀ (CASC). Multnomah Co., Seep, Bridal Veil Falls Trail, Columbia River Gorge, 3 May 1989, R.W. Wisseman, 1 ♀ (BYUC). WASHINGTON: Cowlitz Co., Tributary, Kalama River, 10 April 1967, R. Thut, 1 ♂, 1 ♀ (BYUC). King Co., Raging River, Fall City, 30 April 1932, G. Hoppe, 1 ♀ (INHS). Lewis Co., Stream, 12.1 mi. E Longmire, Hwy 706, Mount Rainier National Park, 4 July 1969, ROM Field Party, 1 larva (ROMC); Ohanapeosh Campground, Mount Rainier National Park, 9 May 1996, R.A. Lechleitner, 1 ♀ (CSUC). Seeps, Paradise River above Narada Falls, Mount Rainier National Park, 20 June 2003, B.C. Kondratieff, J. Schmidt, R.E. Zuellig, 9 ♂, 5 ♀ (BYUC, CSUC). Same site, 17 June 2004, B.C. Kondratieff, J. Schmidt, 1 ♀ (CSUC). Same site, 14 July 2004, B.C. Kondratieff, 1 ♀ (CSUC). Pierce Co., Seeps, Fryingpan Creek, Sunrise Road, Mount Rainier National Park, 6 July 1999, B.C. Kondratieff, 3 ♂, 1 ♀ (CSUC). Same site, 17 June 2004, B.C. Kondratieff, J. Schmidt, 1 ♂ (CSUC). White River Campground, Mount Rainier National Park, 22 July 1984, B. Malkin, 1 ♀ (CASC). Boggy stream, Westside Road, 2 miles N Paradise Road, Mount Rainier National Park, 7 May 2001, R. Lechleitner, 1 ♂ (CSUC). Skamania Co., East Canyon Creek, 23 mi. S Randle, Rt. 23, 2 July 1985, C.M. Flint, O.S. Flint, Jr., 1 ♂ (USNM). Rock Creek, tributary, Little Salmon River, Millard, 15 May 2003, B.C. Kondratieff, R.W. Baumann, 1 ♀ (CSUC).

Stewart and Sandberg (2004) described the larva of *M. complicata*, with associated males, from Willis Creek seeps, Oregon and these records are included in the material listed above. Stewart & Stark (2002) described the supposed larva of *M. kincaidi* from Benton County, Oregon but we are unable to confirm the species determination without associated male adults from this locality. In our study, all



Figs. 5-12. *Megaleuctra complicata*, Willis Creek, Oregon. Male: 5. Genitalia, lateral, open. 6. Genitalia, dorsal, open. 7. Genitalia, lateral, epiproct, extended. 8. Genitalia, apex, lateral, closed. 9. Subanal probe, apex, ventral. 10. Subanal probe, apex, lateral. 11. Vesicle, ventral. Female, 12. Genitalia, ventral.



Figs. 13-20. *Megaleuctra complicata*, Still Creek, Oregon. Male: 13. Genitalia, dorsal, epiproct, midlength. 14. Subanal probe, apex, dorsal. 15. Genitalia, lateral, epiproct, midlength. 16. Subanal probe, apex, lateral. 17. Genitalia, anterior, epiproct, midlength. 18. Genitalia, ventral. Female: 19. Genitalia, ventral. 20. Genitalia, lateral.

unassociated females and larvae collected in the Coast and Cascade Ranges in Oregon and Washington have been listed as *M. complicata*, because it is presently impossible to separate them from *M. kincaidi*, and the two species often occur at the same locality.

Male. Macropterous, but some populations in northern California exhibit brachyptery (Fig. 85). Length of forewing 12-13 mm; body length 11-12 mm. General color brown. Wings hyaline, with dark pigment occupying about half the costal space beyond the cord. Radial sector of forewing with three branches. Tergum 8 sometimes with a pair of small lobes (Fig. 3). Tergum 9 with a pair of widely separated conical lobes, without a basal forked structure (Figs. 2-3, 6, 13, 15); subgenital plate tongue-like, apex rounded (Fig. 18); epiproct variable in shape, depending on expansion position. In midlength position, the upper portion is narrower at the base and expanded near the apex in dorsal view and is subparallel tapering along the middorsal groove (Fig. 13), the anterior portion is expanded into blunt lateral processes, bearing a loose fringe of small stout spines, the lower portion is broader at the base, the apex wedge-shaped laterally and directed downward as two large stout hooks, extending beyond the apex of the upper process (Figs 13, 15, 17). In expanded position, the upper portion is broader at the base and narrow at the apex, fitting into grooves on each side of the expanded lower process (Figs. 2, 5-8), the large wedge-shaped hooks of the lower process are visible on each side of the apex (Fig. 8, 9), the expanded epiproct has a dorsal groove that can cover the apex of the subanal probe (Fig. 6). Subanal probe can be free from the epiproct (Figs. 3, 5) or it can fit into the middorsal groove of the epiproct (Figs. 5-6), tip greatly expanded in lateral view, exhibiting a deep notch, between the narrow elongate upper lobe and a broadly rounded lower lobe, which bears a distinct tube (Figs. 3, 10, 14, 16, 17); cerci consisting of an elongate single segment (Figs. 3, 5, 18); Vesicle long and thin and covered with sparse long hairs (Fig. 11).

Female. Macropterous, but some populations in northern California are slightly brachypterous. Length of forewing 14-15 mm; body length 13-14 mm. Coloration similar to male. Radial sector of forewing with three branches. Sternum 8 with

subgenital plate extending past tip of abdomen 1.5-2.0 mm (Figs. 19, 20), narrowed gradually to tip, round in cross section (Fig. 4). Sternum 9 formed into a long, narrow ovipositor; cerci inconspicuous (Figs. 4, 20).

Larva. Described by Stewart & Sandberg (2004).

Egg. Undescribed.

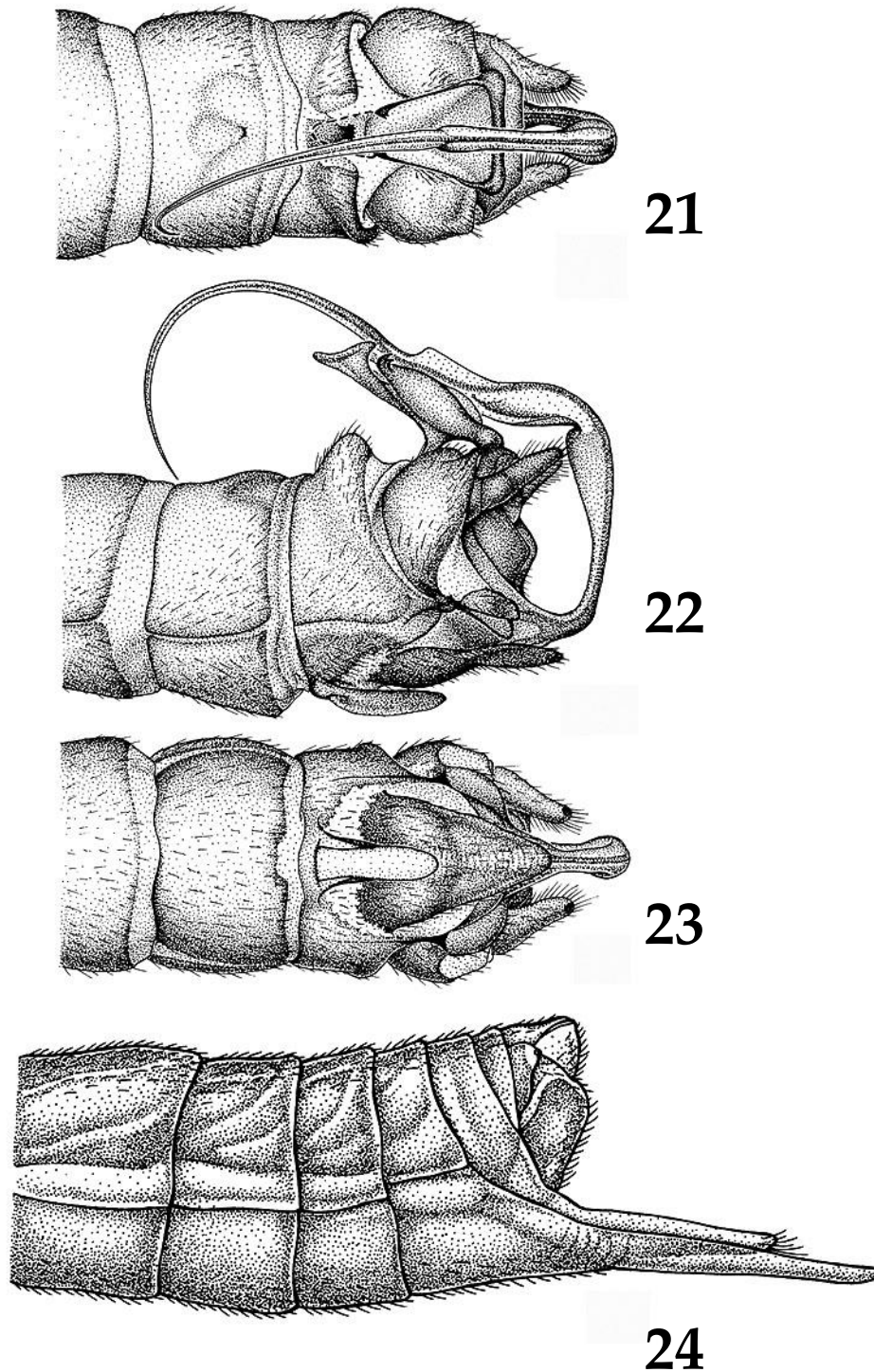
Diagnosis. The combination of paired, conical, widely-separated lobes, on tergum 9 and the absence of a basal forked structure (Figs. 2-3, 6), the distinctive apex of the subanal probe (Figs. 3, 5, 10, 14, 16), and large angular epiproct (Figs. 3, 5, 7, 13, 15, 17) separate the male of *M. complicata* from all other western North American species. The radial sector of the female forewing usually has three branches which may, with caution, be used to distinguish it from females of other western North American *Megaleuctra*.

Megaleuctra flinti Baumann

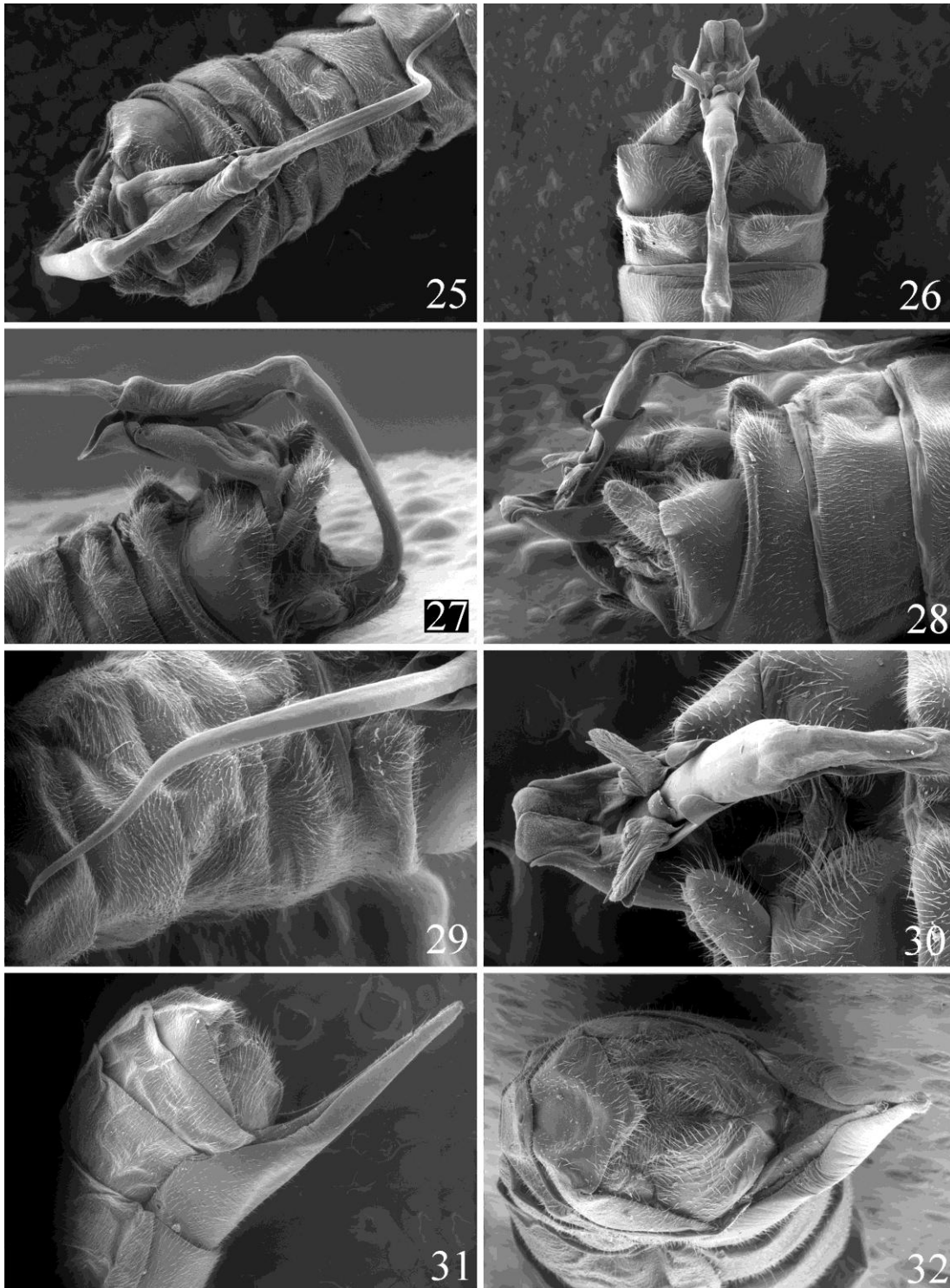
(Figs. 21-34)

Megaleuctra flinti Baumann 1973:248. Holotype ♂ (USNM). Type locality: Virginia (Madison Co.), Hogcamp Brook, Shenandoah National Park, examined

Material examined. MARYLAND: Garrett Co., Seep, north slope Black Lick Run, Savage River State Forest, 5 June 1994, S.A. Grubbs, R.E. Jacobson, 1♂, 3♀ (reared), (SAGC). Seep, opposite Elk Lick Run, 1.7 mi. above junction Savage River, Savage River State Forest, 19 May 1995, S.A. Grubbs, 1♂, 1♀ (reared), (SAGC). 3 km. S Sang Run, 23-25 June 1989, W.E. Steiner, J.M. Swearlingen, A. Landvoigt, L. Landvoigt, 1♀ (USNM). **PENNSYLVANIA:** Somerset Co., Spring, north side of Pennsylvania Turnpike, mile 85, 20 April 1974, R.A. Haick, 7 larvae (BYUC, USNM). Westmoreland Co., Maul Spring, Rector, Powder Mill Nature Reserve, 15 May 1976, J.S. Weaver, 1♂, 3♀ (RFSC). Same site, 21 May 1977, J.S. Weaver, 3♀ (BYUC, RFSC). **VIRGINIA:** Madison Co., Hogcamp Brook, Shenandoah National Park, 23 May 1970, O.S. Flint, Jr., 1♂, Holotype (USNM). Hogcamp Brook, Dark Hollow Falls, Shenandoah National Park, 3 June 1983, B.C. Kondratieff, 1♂, 4♀ (CSUC, BYUC). Page Co., Lewis Spring, 3300', Shenandoah National Park, G.L. Daussin, 6 June 1979, 1♀ (CSUC). **WEST VIRGINIA:** Greenbrier



Figs. 21-24. *Megaleuctra flinti*, Hogcamp Brook, Shenandoah National Park, Virginia. Terminalia: 21. Male, dorsal. 22. Male, lateral. 23. Male, ventral. 24. Female, lateral.

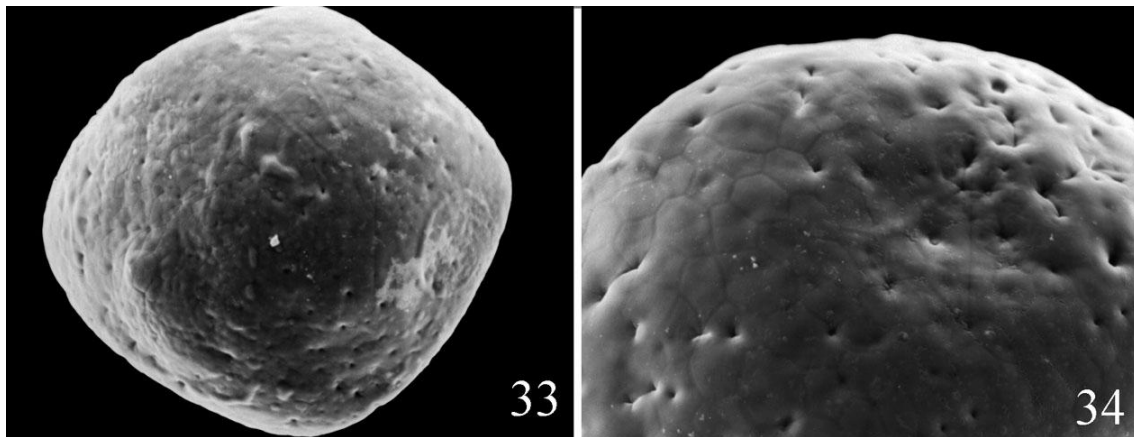


Figs. 25-32. *Megaleuctra flinti*, Dogway Run, West Virginia. Male: 25. Genitalia, dorsal, epiproct, extended. 26. Genitalia, dorsal, epiproct, midlength. 27. Genitalia, lateral, epiproct, extended. 28. Genitalia, lateral, epiproct, midlength. 29. Epiproct, apical half, dorsal. 30. Genitalia, dorsolateral, epiproct, midlength. Female: Pheasant Hollow, West Virginia. 31. Genitalia, lateral. 32. Genitalia, ventral.

Co., Coats Run, small spring above Summit Lake, Monongahela National Forest, Rt. 39, 5 mi. E Richwood, R.F. Kirchner, B.C. Kondratieff, 15 May 1986, 1♂, 1♀ (CSUC). Dogway Run, 14 May 1990, B.C. Kondratieff, J.L. Welch, R.F. Kirchner, 4♂, 2♀ (CSUC, BYUC). Springs, Pheasant Hollow, Forest Rd. 77, Monongahela National Forest, near Summit Lake, R.W. Baumann, R.F. Kirchner, B.C. Kondratieff, 14 May 1990, 3♂, 4♀ (BYUC, CSUC). Same site, 2 June 1992, B.C. Kondratieff, R.F. Kirchner, 2♂, 4♀ (BYUC, CSUC). Same site, 24 May 1994, B.C. Kondratieff, R.F. Kirchner, 2♂, 3♀ (BYUC, CSUC). Same site, 21 May 1999, B.P. Stark, R.F. Kirchner, 2♂, 1♀ (BPSC). Pendleton Co., Spruce Knob, 27 June 1958, W.L. Peters, 1 larva (BYUC). Pocahontas Co., Hwy 150, near Cranberry Glades, S.M. Clark, 13 June 1992, 1♀ (BYUC). Spring fed stream into Charles Creek, Cranberry Glades, B.C. Kondratieff, R.F. Kirchner, 24 May 1994, 1♂ (CSUC). Tributary, Hills Creek, Hills Creek Falls Scenic Area, 2 June 1992, B.C. Kondratieff, R.F. Kirchner, 1♀ (CSUC). Same site, 19 May 1995, S.A. Grubbs, 1♀ (reared), 1 larva

(SAGC). Tucker Co., South Fork Red Run, 6.1 km. S Backwater Falls State Park, M.B. Griffith, 15 May 1991, 1♂ (UWVC).

Male. Macropterous. Length of forewing 9-13 mm; body length 10-12 mm. General color brown. Wings hyaline, with dark pigment occupying about half the costal space beyond the cord. Radial sector of forewing usually with two branches. Tergum 9 divided by two large lateral lobes, located near posterior margin (Fig. 22, 26, 28). Subgenital plate large, narrowed to rounded apex (Figs. 21, 23, 28), vesicle at base of sternum 9 long, thin and of equal width, with apex rounded (Fig. 23). Epiproct sclerotized, broad at base, narrow and triangle-shaped towards apex when expanded (Figs. 25, 29), apex with paired, rounded lobes and larger wing-shaped projections apically when in midlength position (Fig. 30); subanal probe long and narrow, broader at base, abruptly thinner towards apex, extending beyond tip of epiproct, often recurved over abdomen, thread-like at tip (Figs. 21-22, 25-29); cerci consist of an elongate single segment (Figs. 21-22, 28, 30).



Figs. 33-34. *Megaleuctra flinti*, Hogcamp Brook, Shenandoah National Park, Virginia. Egg: 33. Entire, dorsal. 34. Chorionic detail, dorsal. (Photo courtesy of B.C. Kondratieff).

Female. Macropterous. Length of forewing 16-18 mm; body length 19-20 mm. Coloration similar to male. Radial sector of forewing with two branches. Sternum 8 with subgenital plate extending past tip of abdomen 1.5-2.0 mm, narrowing conspicuously

beyond base to apex, round in cross section (Figs. 24, 31-32). Sternum 9 a long, narrow ovipositor; cerci inconspicuous (Figs. 24, 31).

Larva. Undescribed.

Egg. Outline globose with faint hexagonal follicle cell

impressions covering the surface (Fig. 33). Collar and anchor absent. Chorion with scattered, irregularly spaced pits which may be micropyles (Fig. 34).

Diagnosis. The male of this species can be distinguished from *M. williamsae*, the only other eastern North American species, by the presence of a medial toothed process between the lateral lobes of tergum 9, and by differences in epiproct shape, elongate and triangular shaped in *M. flinti* and short and angular in *M. williamsae* (compare Figs. 22, 29 with Figs. 75, 82). Additionally, the subanal probe of *M. flinti* is expanded medially (Figs. 21, 22, 25, 27), and ends in a pointed tip (Fig. 25), whereas in *M. williamsae*, it is essentially cylindrical throughout its length (Figs. 75, 77), and has a tiny truncate tip (Fig. 81). The female subgenital plate of *M. flinti* narrows conspicuously from beyond the base to the apex (Figs. 24, 31), whereas the female subgenital plate of *M. williamsae* is subequal in width beyond the base (Figs. 76, 84).

Megaleuctra kincaidi Frison

(Figs. 35-53)

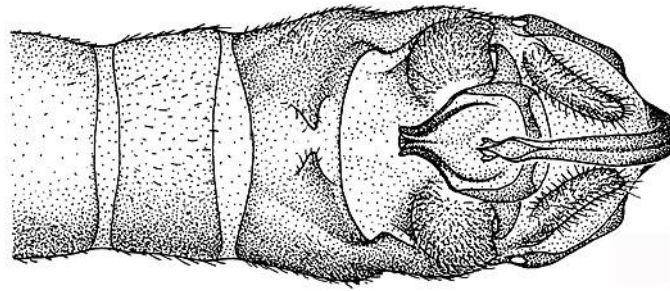
Megaleuctra kincaidi Frison 1942:15. Holotype ♂ (INHS). Type locality: Fryingpan Creek, Mount Rainier National Park (Pierce Co.), Washington, examined

Material examined. IDAHO: Clearwater Co. Lolo Pass, 30 June 1964, W.F. Barr, 1♂, 1♀ (BYUC). Idaho Co., Cow Creek, New Elk Summit Road, 27 May 1972, D.S. Potter, R.A. Haick, L. Lockwood, 1♀ (BYUC). Latah Co., Big Sand Creek, Saint Joe National Forest, 2880', 21 May 1975, J.H. Baker, 1♂, 1♀ (USNM). **MONTANA:** Missoula Co., Seep, Granite Creek, tributary Lolo Creek, 46.74° N 114.59° W, 25 June 2013, Z.J. Crete, 1♀ (ZCSC). Ravalli Co., Inlet to Bryan Lake, 6800', 17 July 1995, A.L. Sheldon, 1♀ (BYUC). Left intermittent tributary Lick Creek, 4760', 25 May 1996, A.L. Sheldon, 1♂ (BYUC). Intermittent right fork, left tributary Lick Creek, 4800', 25 May 1996, A.L. Sheldon, 2♂, 2♀ (BYUC). Roaring Lion Creek, at road head, 18 March 1996, A.L. Sheldon, 2♂, 2♀ (BYUC). **OREGON:** Clackamas Co., Seep, Still Creek, Still Creek Campground, Mount Hood National Forest, 5 June 1991, R.W. Baumann, B.P. Stark, C. Henderson, 7♂, 2♀, 3 larvae (BPSC, BYUC). Same site, 2 June 2000, B.P.

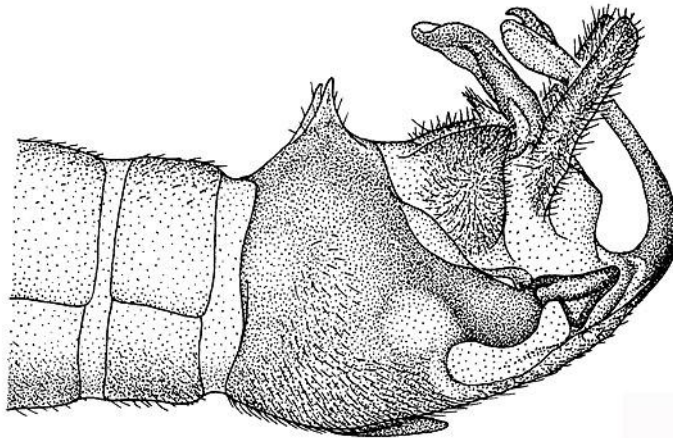
Stark, I. Sivec, M.C. Zúñiga, 3♂, 1♀ (BPSC, BYUC). Clatsop Co., East Fork Humbug Creek, 3 May 1964, S.G. Jewett, Jr., 1♂ (CASC). **WASHINGTON:** Kittatis Co., Bell Creek, Cle Elum Lake, 22 May 1946, S.G. Jewett, Jr., 1♂ (OSUC). Pierce Co., Fryingpan Creek, Mount Rainier National Park, 5000', 23 July 1937, W.E. Ricker, 1♂, Holotype (CUIC). Ghost Lake, 1 km. N jct. Hwys 123 & 410, 46°52'25" N 121°32'23" W, 6 July 2004, M. Grove, 1♂ (CSUC).

In addition, Frison (1942) lists two male paratypes from the following localities that were not examined by us: Oregon, between St. Helens and Veronia, 17 April 1937, Gray and Schuh, 1♂, and Washington, Seattle, 14 April 1932, unknown collector, listed by Hoppe (1938) as *M. stigmata*.

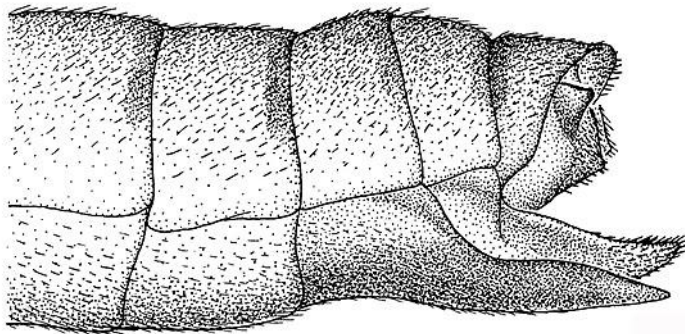
Male. Macropterous. Length of forewing 12-15 mm; body length 12-14 mm. General color brown. Wings hyaline, with dark pigment occupying less than half the costal space beyond the cord. Radial sector of forewing usually with two or three branches. Tergum 9 with a pair of long thin lobes, narrowing to a pointed tip, without basal forked process (Figs. 35, 36, 38, 42, 48); subgenital plate tongue-like, apex narrowly rounded (Fig. 44); ventral lobe at base sternum 9 in lateral view subparallel, apex rounded. Tergum 10 with ventrobasal expansion short, sclerotized, bearing paired narrowly pointed processes (Figs. 36, 40, 51). Epiproct broadly triangular dorsally when expanded, formed into two sclerotized plates lateral of middorsal groove (Figs. 35, 38, 39), when basal, divided into two plates, each ending in pointed apical processes (Figs. 46, 50). Subanal probe directed upward fitting in middorsal groove of epiproct, tip expanded with subapical notch in lateral view, forming two lobes: upper lobe broader at base and narrowing to apex, bearing tube, lower lobe terminating in broad, rounded groove, which surrounds the tube (Figs. 38-43, 47-49), cerci formed into an elongate single segment (Figs. 36, 42). **Female.** Macropterous. Length of forewing 16-18 mm; body length 19-20 mm. Coloration similar to male. Radial sector of forewing with two branches. Sternum 8 with subgenital plate extending past tip of abdomen 1.5-2.0 mm, narrowing gradually to tip, round in cross section (Fig. 37). Sternum 9 a developed ovipositor (Fig. 52); cerci inconspicuous (Fig. 37).



35



36



37

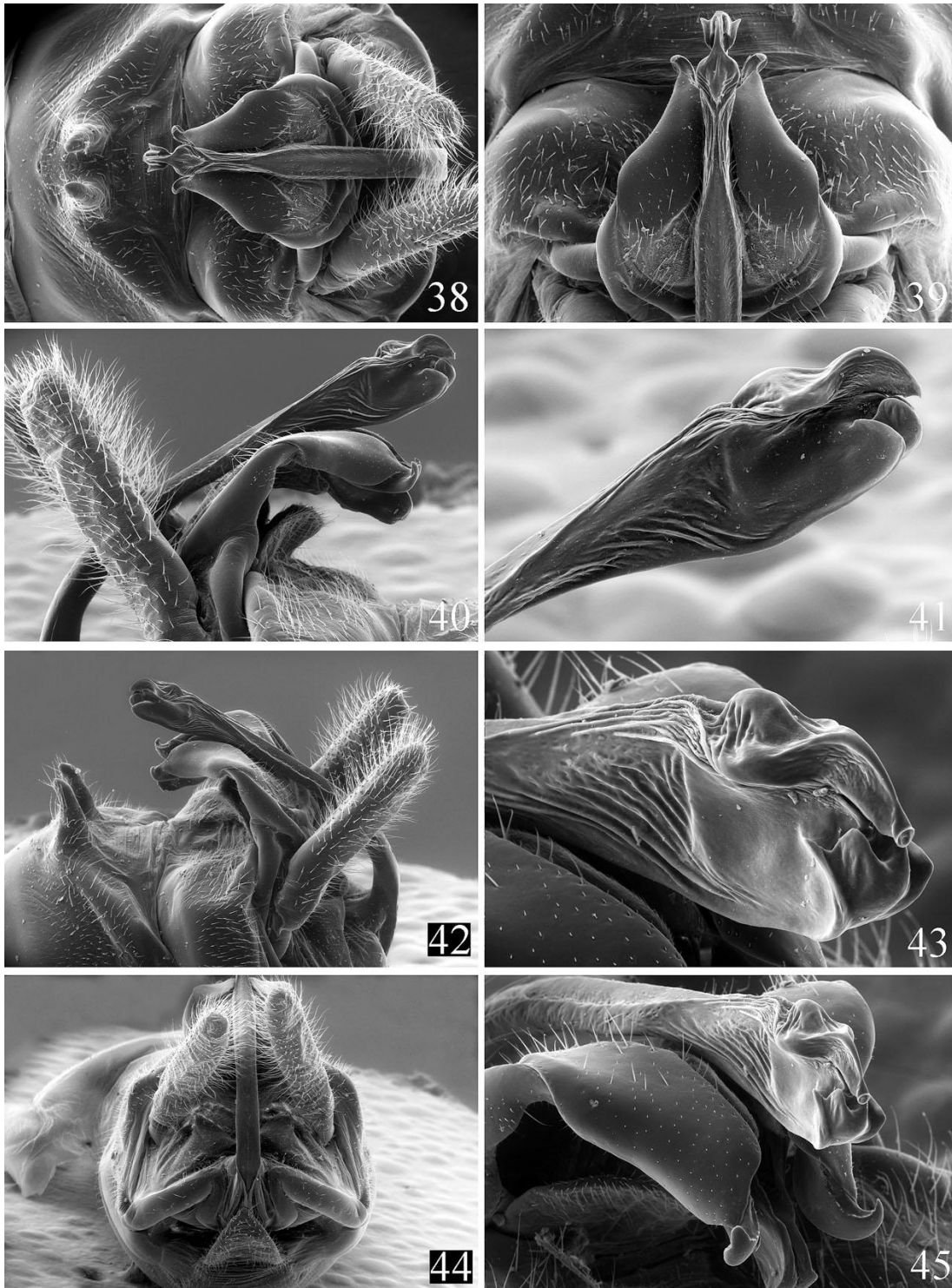
Figs. 35-37. *Megaleuctra kincaidi*, Lolo Pass, Idaho. Terminalia: 35. Male, dorsal. 36. Male, lateral. 37. Female, lateral.

Larva. Described by Stewart and Stark (2002) from unassociated material.

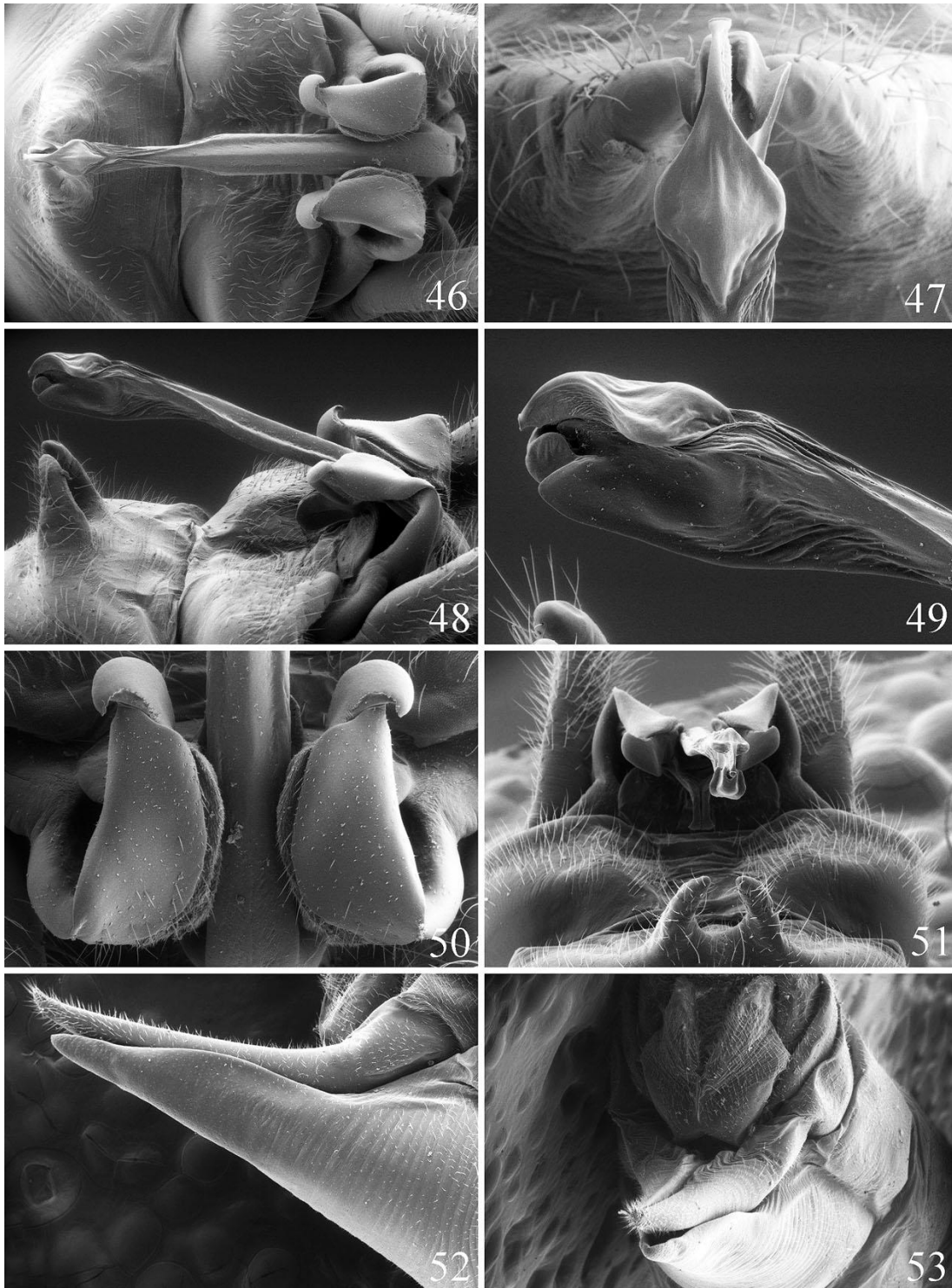
Egg. Undescribed.

Diagnosis. Males of *M. kincaidi* can be distinguished from *M. complicata* and *M. stigmata* by the shape of the paired processes on tergum 9. They are narrow and very thin, ending in a pointed tip in *M. kincaidi* (Figs. 42, 48) while in *M. complicata* (Figs. 3, 6, 13) and

M. stigmata (Figs. 54, 55, 61, 67, 69) they are broader basally and terminate in a rounded or slanted tip. In addition, the epiproct is triangular dorsally and bears small pointed processes on each side in *M. kincaidi* (Figs. 36, 38, 40, 46), while it is elongate and broad with large paired backward directed hooks apically in *M. complicata* (Figs. 3, 6-9, 13, 15, 17) and in *M. stigmata* it is parallel and even more elongate, bearing



Figs. 38-45. *Megaleuctra kincaidi*, Still Creek, Oregon. Male: 38. Genitalia, dorsal, showing 10th tergal lobes. 39. Genitalia, dorsal, epiproct, extended. 40. Genitalia, lateral, epiproct, extended. 41. Subanal probe, apex, lateral. 42. Genitalia, lateral. 43. Subanal probe, apex, dorsolateral, showing sperm tube. 44. Genitalia, ventral. 45. Subanal probe, seated on epiproct.



Figs. 46-53. *Megaleuctra kincaidi*. Still Creek, Oregon. Male: 46. Genitalia, dorsal, epiproct, midlength. 47. Subanal probe apex, dorsal. 48. Genitalia, lateral, epiproct, midlength. 49. Subanal probe, apex, lateral. 50. Epiproct, midlength, dorsal, close up. 51. Genitalia, anterior. Female: 52. Genitalia, lateral. 53. Genitalia, terminal.

ornamented lateral fringes terminally, and sharp, angular, backward directed prongs apically (Figs. 57, 58, 61, 62, 65, 67). The female of *M. kincaidi* may be provisionally distinguished from *M. complicata* by the presence in the forewing of usually only 2 radial sector branches (typically 3 in *M. complicata* and 5 in *M. stigmata*, however, all three species are variable in this character). Associated males should be examined to confirm identifications.

Megaleuctra stigmata (Banks)

(Figs. 1, 54-72)

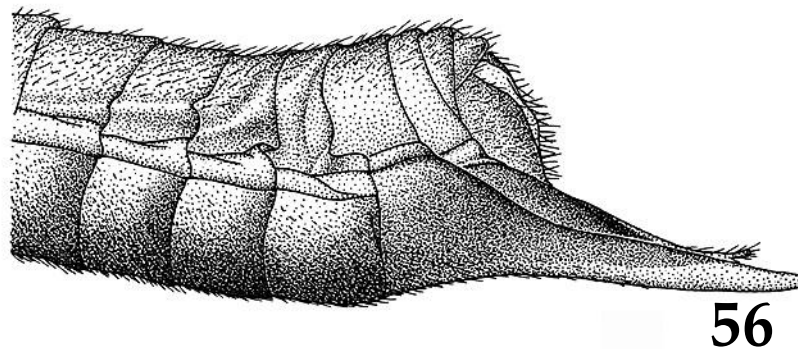
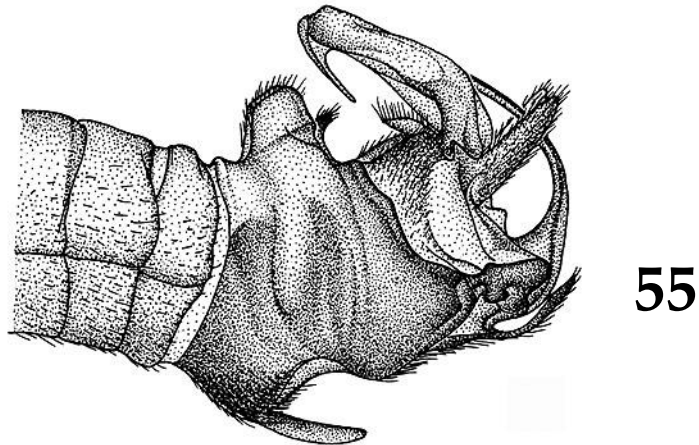
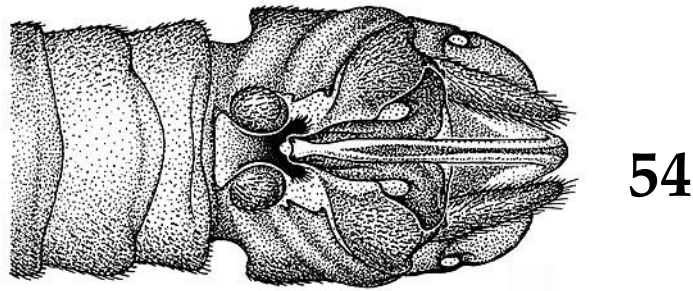
Nemoura stigmata Banks 1900:244. Holotype ♂ (MCZC). Type locality: Winnipeg, British America, (British Columbia or Manitoba), examined, slide of wings and leg

Megaleuctra spectabilis Neave 1934:4. Holotype female (CNIC). Type locality: Campbell Creek, Purcell Range, British Columbia, examined, synonymy Claassen 1937:47

Megaleuctra sierra Fields 1977:211. Holotype female (CASC). Type locality: Shirttail Creek, Tahoe National Forest, (Placer County), California, examined, new synonymy

Material examined. CANADA: Province Uncertain: Winnipeg, J.B. Smith, 17 June, unknown year, 1♂, *M. stigmata* Holotype (MCZC). **ALBERTA:** Lower Caribou Lake, Jasper National Park, 20 June 1979, D.B. Donald, 1♀ (DBDC). Lineham Brook, 7200' Waterton Lakes National Park, 9 July 1975, D.B. Donald, 1♀ (DBDC). High River, 1 June 1927, O. Bryant, 1♀ (CUIC). **BRITISH COLUMBIA:** Campbell Creek, Purcell Mountains, 29 May 1933, R. Neave, 2♀, includes *M. spectabilis* Holotype (CNIC). Same site, 11 June 1933, R. Neave, 1♀ (CNIC). Seeps, Duhamel Creek, above West Arm Kootenay Lake, 49° 38' N 117° 16' W, 27-30 May 2010, R.W. Baumann, B.P. Stark, 1♂, 4♀ (BYUC, BPSC). Tributary, Fry Creek, Purcell Mountains, 18 June 1933, R. Neave, 1♀ (CNIC). Seep, South Fork Gray Creek, Oliver Lake Road, Purcell Mountains, 49°37' N 116°42' W, 1 June 2010, R.W. Baumann, B.P. Stark, 1♂, 1♀ (BYUC). **UNITED STATES: CALIFORNIA:** El Dorado Co., Tributary, North Cosumnes River, E Grizzly Flats, near Meiss Ranch, R.L. Bottorff, 6 June 1986, 1♀ (RLBC). Bendorf Spring, near Grizzly Flat, R.L.

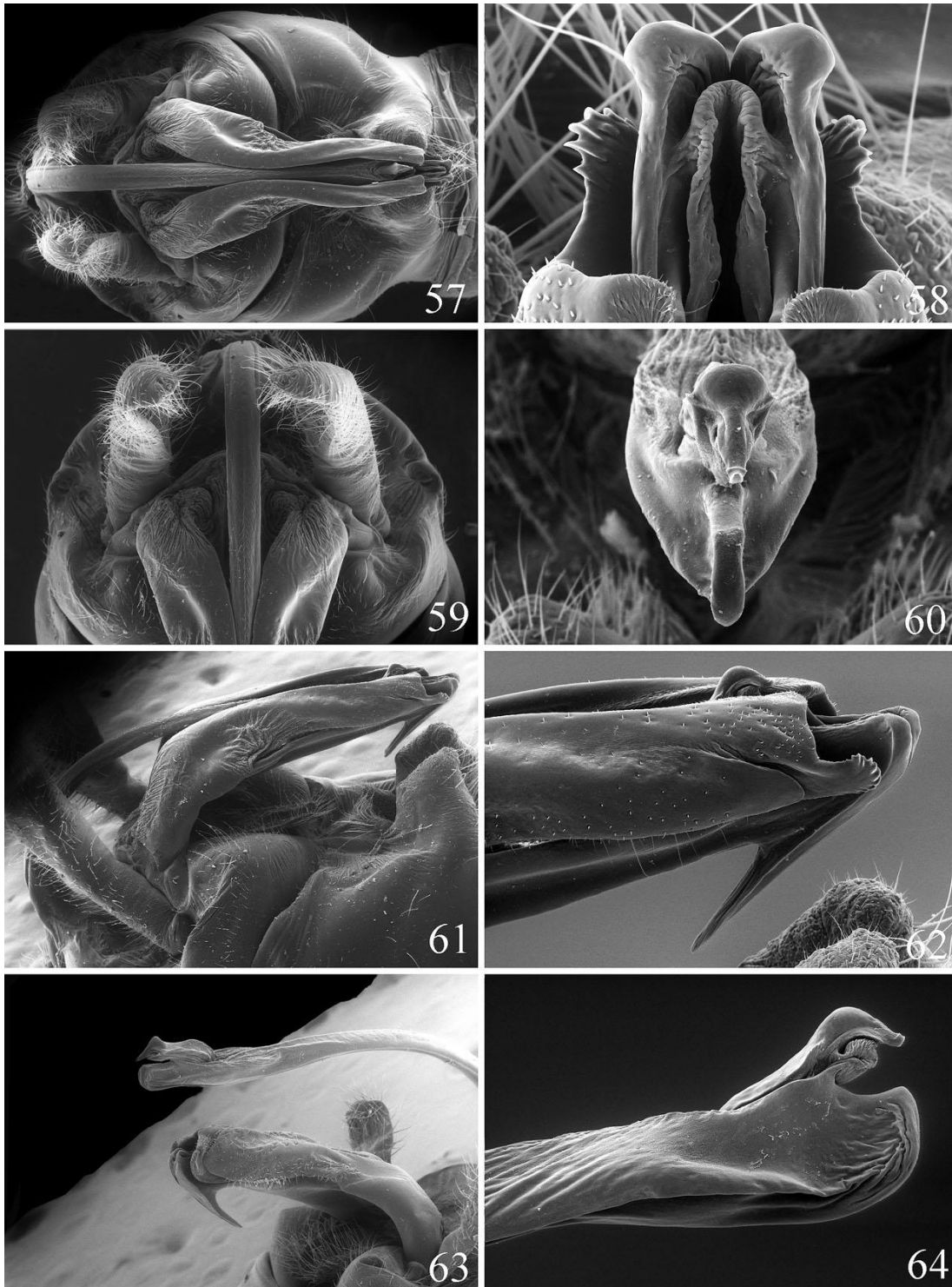
Bottorff, 4 December 1986, 2 larvae (RLBC). Same site, 9-26 March 1987, R.L. Bottorff, 1♂ (RLBC). Same site, 14-27 April 1987, R.L. Bottorff, 10♂, 4♀ (BYUC, CSUC, RLBC). Same site, 4 May 1987, R.L. Bottorff, 3♂, 7♀ (BYUC, CSUC, RLBC, USNM). Same site, 16 May 1998, B.P. Stark, C.R. Nelson, R.L. Bottorff, S.W. Szczytko, I. Sivec, 1♀ (BYUC). 1 mi. E Pacific House, Hwy 50, near El Dorado Canal, W.D. Shepard, C. Barr, 4 April 1992, 2♂, 3♀ (CASC). Same site, 28 April 1992, F. Andrews, T. Eichlin, 1♂, 1♀ (BYUC). Placer Co., Shirttail Creek, Tahoe National Forest, W.C. Fields, Jr., 9 June 1974, 1♀, *M. sierra* Holotype (CASC). Sierra Co., Mossy falls, Hwy 49, near Indian Creek, 18 May 1983, R.W. Baumann, R.C. Mower, M.F. Whiting, 1♂ (BYUC). Seep along unnamed stream, Hwy 49, mile marker 1.02, 39.49845° N 121.01535° W, 21 March 2010, A.B. Richards, 1♂ (ABRC). **IDAHO:** Idaho Co., Low Creek, New Elk Summit Road, Powell District, 27 May 1972, R.A. Haick, L. Lockwood, D.S. Potter, 1♂, 5♀ (BYUC, USNM). Seep, below 'Isoperla' Springs, Powell District, 27 May 1972, R.A. Haick, 1♂ (BYUC). Seep, Savage Pass, 27 May 1972, R.A. Haick, 3 larvae (BYUC). Winis Spring, Grave Peak, Selway Bitterroot Wilderness Area, 11 Sept. 1971, D.S. Potter, R.A. Haick, 2 larvae (BYUC). Latah Co., Moscow Mountain, 25 April 1953, W.F. Barr, 1 larva (UIC). **MONTANA:** Flathead Co., Bear Creek, Hwy 2, Morias Pass, 17 July 1969, R.A. Haick, 1♀ (BYUC); Bear Creek, E Echo Lake, 24 April 2006, B. Reid, 1♀ (UMBS). Spring, south end of Johns Lake, 10 August 1966, G.W. Swenson, 1 larva (BYUC); Mac Donald Creek, Marve Cascade, Glacier National Park, 13 May 1993, J. Giersch, 1♀ (UMBS). Seep, Red Meadow Lake Road, 13 July 1972, R.A. Haick, L.A. Fisher, 1 larva (BYUC). Glacier Co., Grinnell Glacier Trail, Glacier National Park, 5 August 1972, D.S. Potter, R.A. Haick, 1 larva (BYUC). Lake Co., Boulder Creek, Flathead Lake, 8 May 1971, D.S. Potter, 2♀ (BYUC). Crane Creek, Hwy 35, east shore, Flathead Lake, 25 April 1970, D.S. Potter, R.A. Haick, 1♂, 2♀ (BYUC). Same site, 3 May 1970, D.S. Potter, 1♀ (BYUC). Same site, 15 May 1970, R.L. Newell, 1♂ (BYUC). Same site, 10 April 1973, R.A. Haick, C. Daugherty, 1 larva (BYUC). Spring, Hundred Road, Flathead Indian Reservation, near Saint Ignatius, 7 April 2007, R. Durfee, 1♀ (CSUC).



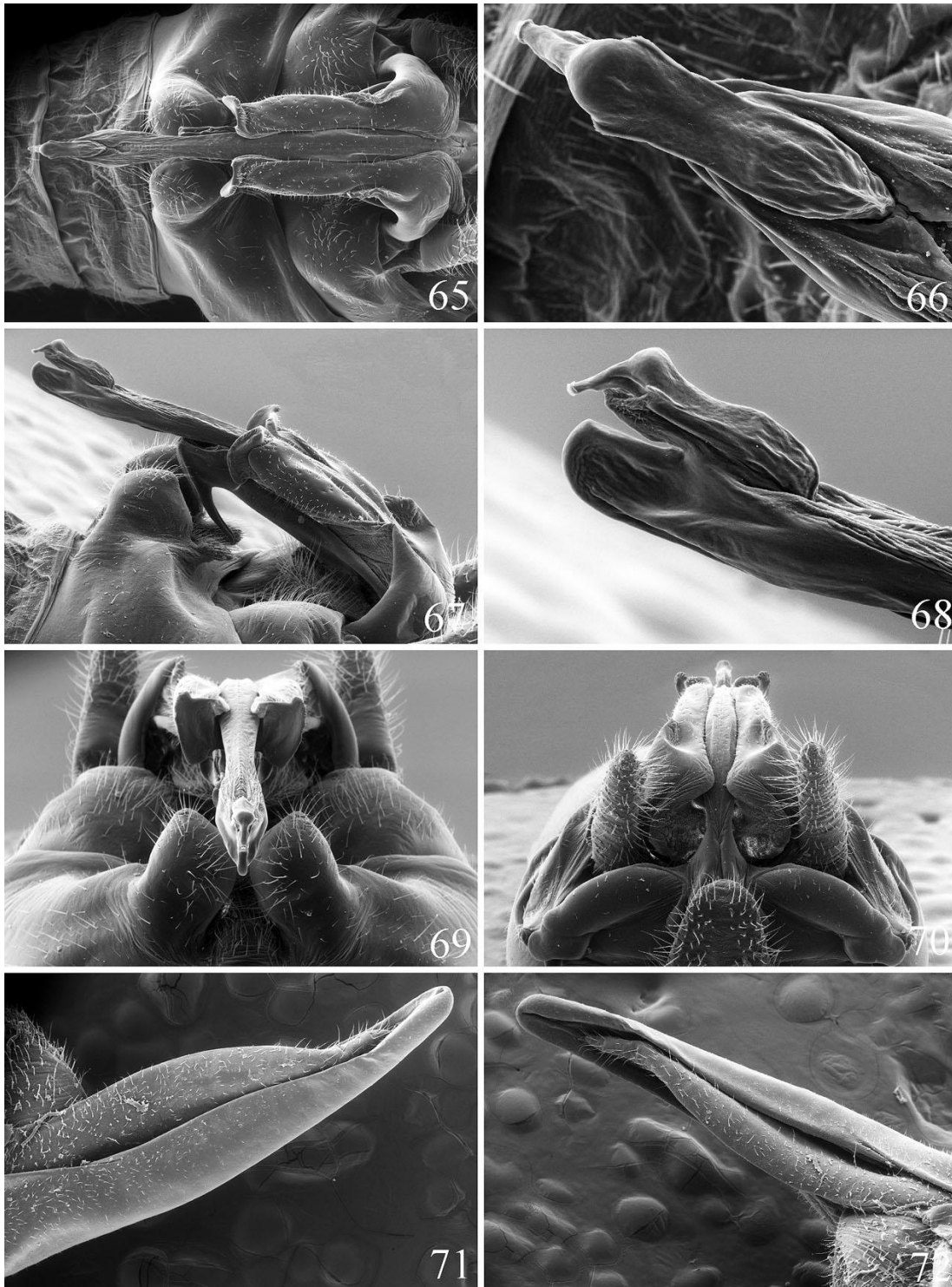
Figs. 54-56. *Megaleuctra stigmata*. Butler Creek, Montana. Terminalia: 54. Male, dorsal. 55. Male, lateral. 56. Female, lateral.

Spring, Thorne Creek, Hundred Road, Flathead Indian Reservation, 20 April 2007, R. Durfee, 1 ♀ (CSUC). Talking Water Creek, Hwy 35, Flathead Lake, 15 April 2003, R.L. Newell, 1 ♂, 2 ♀ (BYUC). Same site, 19 April 2003, R. L. Newell, 1 ♂, 2 ♀ (UMBS). Same site, 9 May 2005, R.L. Newell, 1 ♀ (UMBS). Rotten log in groundwater seep, Yellow Bay State Recreation Area, Flathead Lake, 28 June

1987, unknown collector, 5 larvae (UMBS). Missoula Co., Seep, Butler Creek, Snow Bowl Ski Area, 4 May 1972, R.A. Haick, 2 ♂, 7 ♀, 6 larvae (BYUC, CSUC). Same site, 10 May 1972, R.A. Haick, 6 ♂, 1 ♀ (BYUC, CSUC). Same site, 26 May 1972, D.S. Potter, 1 ♂ (BYUC). Same site, 25 August 1972, R.A. Haick, 12 larvae (BYUC). Same site, 19 May 1973, R.A. Haick, 3 ♂, 6 ♀ (BYUC). Same site, 17-18



Figs. 57-64. *Megaleuctra stigmata*. Bendorf Spring, California. Male: 57. Genitalia, dorsal, epiproct, extended. 58. Epiproct, apex, dorsal. 59. Genitalia, dorsal, base. 60. Subanal probe, apex, anterior. 61. Genitalia, lateral, epiproct, extended. 62. Epiproct, expanded, enclosing subanal probe. 63. Subanal probe and epiproct, lateral, separated. 64. Subanal probe, apex, lateral.



Figs. 65-72. *Megaleuctra stigmata*. Gray Creek, British Columbia. Male: 65. Genitalia, dorsal, epiproct, midlength. 66. Subanal probe, apex, dorsal. 67. Genitalia, lateral, epiproct, midlength. 68. Subanal probe, apex, lateral. 69. Genitalia, anterior. 70. Genitalia, ventral. Female: Bendorf Spring, California. 71. Genitalia, lateral. 72. Genitalia, ventrolateral.

August 1973, G.B. Wiggins, 1 larva (ROMC). Seep, Glacier Lake Trail, Mission Mountains Wild Area, 24 June 1971, D.S. Potter, R.H. Haick, 18 exuviae (BYUC); Seep, Grant Creek, E Missoula, 11 April 1972, R.A. Haick, 4 larvae (BYUC). Same site, 23 May 1972, R.A. Haick, 2♀ (BYUC). Powell Co., Keno Creek Spring, Lubrecht Experimental Forest, R.A. Haick, 1 July 1971, 12 exuviae (BYUC). Ravalli Co., Left tributary, Middle Fork Bear Creek, 6180', Bitterroot Valley, 1 July 1996, A.L. Sheldon, 1♂ (BYUC). Headwater spring, FR 5623, 1 mi N Como Lake, Bitterroot National Forest, 24 April 2007, R.L. Durfee, 1♂ (CSUC). Same site, 2 May 2008, R.L. Durfee, 1♂, 2♀ (CSUC). Tributary, Gash Creek, 6200', Bitterroot Valley, 21 June 1995, A.L. Sheldon, 1♂ (BYUC).

Male. Macropterous. Length of forewing 14-15 mm; body length 12-13 mm. General color brown. Wings hyaline, with dark stigma in costal space occupying more than half the costal space beyond the cord. Radial sector of forewing with 2-5 branches. Tergum 9 with a pair of large narrowly separated lobes, apically blunt, slanted posteriorly; darkly sclerotized forked structure at base, with long setae (Figs. 54, 55, 61); subgenital plate tongue-like, apex rounded, sometimes upturned (Figs. 55, 70); vesicle at base of sternum 9 long, and narrow. Tergum 10 with ventrobasal expansion darkly sclerotized, elongate, tip emarginate (Figs. 55, 61); epiproct broad at base dorsally, with large middorsal groove (Figs. 57, 65), forming rounded fork at apex, bearing small rounded processes laterally, ornamented with narrow leaf-like lobes, when expanded (Figs. 58, 62); epiproct stout and broad, rectangular dorsally, with large, paired, downward forked apical processes when in midlength position (Figs. 65, 67), when expanded, broader at base, terminating in narrow apex, which surrounds apex of subanal probe (Figs. 54, 55, 57, 61). Subanal probe directed upward, fitting in middorsal groove of epiproct (Figs. 54, 57, 61, 62), tip expanded, with subapical notch in lateral view (Figs. 64, 68), upper lobe small, arched dorsally, with a pointed tube bearing apex, lower lobe large and broadly rounded (Figs. 60, 64, 66, 68). Cerci single segmented, elongate (Figs. 54, 55, 59, 70).

Female. Macropterous. Length of forewing 16-18 mm; body length 19-20 mm. Coloration similar to male. Radial sector of forewing with 2-5 branches, crossveins in intercubital space 15-20. Sternum 8 with subgenital

plate extending past tip of abdomen 1.5-2.0 mm, narrowing gradually to tip, round in cross section (Fig. 56). Sternum 9 forming a long, narrow ovipositor (Figs. 71, 72).

Larva. Undescribed.

Egg. Undescribed.

Diagnosis. The epiproct of *M. stigmata* males is more similar to that of *M. complicata* than to *M. kincaidi*, the other western species. In *M. complicata* this structure bears prominent, ventrally directed apical hooks (Figs. 3, 5, 8, 9) which gives the lateral aspect of the structure a meat hook-like appearance not found in *M. kincaidi* (Figs. 36, 40), whereas in *M. stigmata* the ventrally directed hooks are thinner and pointed downward at a sharper angle (Figs. 55, 61-63, 67). Males of *M. stigmata* have a pair of stout dorsal lobes on tergum 9, which are broadly rounded and slant posteriorly (Figs. 54, 55, 61, 65, 67, 69), whereas in *M. complicata* (Figs. 2, 3, 13, 15) and *M. kincaidi* (Figs. 36, 38, 42, 48, 51), the paired lobes are thinner and terminate in pointed tips.

Remarks. The exact type locality of *M. stigmata* is unknown, but Frison (1942) indicated the probability "...that the type was collected at or near Winnipeg, Manitoba", however, Burton (1984) indicated "...its occurrence in Manitoba is questionable." Ricker and Scudder (1975) listed the Purcell Mountains, British Columbia *Megaleuctra* records by Neave (1934), as *M. spectabilis*, but Baumann & Stark (2010) recently collected males and females, indistinguishable from those of *M. stigmata*, from near the type locality of *M. spectabilis*, consequently we treat *M. spectabilis* as a junior synonym in agreement with Claassen (1937). *Megaleuctra sierra* Fields (1977) has been recognized as a different species since its description. However, comparison of the holotype and males collected from nearby localities in the Sierra Nevada Mountains, with specimens of *M. stigmata* from the northern Rocky Mountains, indicates that *M. sierra* is also a synonym of *M. stigmata*.

Megaleuctra williamsae Hanson

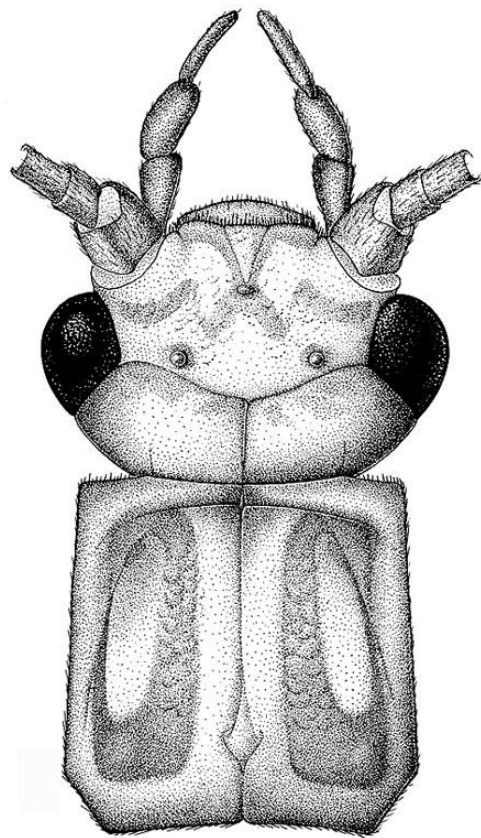
(Figs. 73-84)

Megaleuctra williamsae Hanson 1941:64. Holotype ♂ (USNM). Type locality: Greenbriar Cove, Great Smoky Mountains, (Sevier Co.) Tennessee, examined

Megaleuctra williamsae: Baumann, 1973:248. Description of ♀

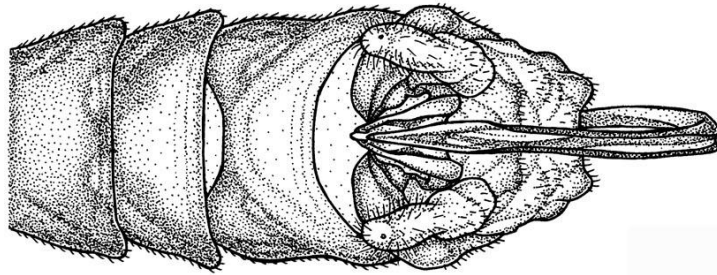
Material examined. NORTH CAROLINA: Graham Co., Robinsville, 9 June 1976 G.E. Bohart, 1♀ (USUC). Haywood Co., unknown locality, 16 June 1956, H.V. Weems, Jr., 1♂ (CUIC). Tributary, Cove Creek, near Great Smoky Mountains National Park, 19 May 1994, R.W. Baumann, R.F. Kirchner, B.C. Kondratieff, 1♂, 1♀ (BYUC). Jackson Co., Mull Creek, Nantahala National Forest, 23 May 1993, B.C. Kondratieff, R.F. Kirchner, 1♂, 1♀ (CSUC). Same site, 26 May 1993, B.P. Stark, 1♀ (BPSC). Same site, 19 May 1994, R.W. Baumann, R.F. Kirchner, B.C. Kondratieff, 1♂, 1♀ (CSUC). Macon Co., Robin Branch, Wayah Bald, 11 March 1990, B.P. Stark, 4 larvae (BPSC, ROMC). Same site, 21 May 1990, B.P. Stark, J. Parham, D. Tanner, 2♂ (BPSC). Same site, 9 June 1998, B.P. Stark, 1♀ (BPSC). Seep, Wayah Creek, Wayah Bald, 35° 09.523'N, 83° 33.916'W, 17 May 2011, B.P. Stark, 1♀ (BPSC). Mitchell Co., Tributary, Little Rock Creek, Hwy 261, E Roan Mountain, 38.10112N, 82.09245W, 14 May 2010, B.C. Kondratieff, R.E. Zuellig, D.R. Lenat, R.F. Kirchner, 1♂ (CSUC). Swain Co., Trickle to, Oconaluftee River, 26 April 1976, H.B.N. Hynes, 1 larva (USNM). Yancey Co., Tributary seep, Cane Creek, Mount Mitchell, 18 May 1994, R.W. Baumann, R.F. Kirchner, B.C. Kondratieff, 1♂ (BYUC). Crabtree Meadows, 11 June, 1967, G.W. Byers, 1♂ (SEMC); Tributary, Rock Creek, Hwy 80. S Hamrick, 35.7527N 82.20085W, 14 May 2010, B.C. Kondratieff, R.E. Zuellig, D.R. Lenat, R.F. Kirchner, 1♂ (CSUC). **SOUTH CAROLINA:** Oconee Co., Townes Creek, Bartram Trail, 26-27 May 1980, T.R White, J.S. Weaver, 1♀ (BPSC). Pickens Co., Sassafras Mountain, 18 May 1937, O.L. Cartwright, 1♀ (CUCC). **TENNESSEE:** Sevier Co., Greenbriar Cove, Great Smoky Mountains, 15 May 1938, I. W. Williams, 1♂, Holotype (USNM). 10.2 mi. E Gatlinburg, Great Smoky Mountains National Park, 20 May 1970, O.S. Flint, Jr., 1♂, 1♀ (USNM). Le Conte Trail, first stream, Great Smoky Mountains National Park, 25 May 1946, J.F. Hanson, 1♂, 2♀ (USNM). Le Conte Lodge, Mount Le Conte, Great Smoky Mountains National Park, 9 August 1946, P. Hoff, 1♀ (USNM). West Prong Little Pigeon River, Chimney Top Picnic Area, Great Smoky Mountains National Park, 29 April 1977, C.H. & E.S. Nelson, 1♂ (CHNC). Ramsay

Prong, Little Pigeon River, Great Smoky Mountains National Park, 20-21 May 1978, C.H. Nelson, 1♀ (CHNC). West Prong Little Pigeon River, Hwy 441, Great Smoky Mountains National Park, 26 May 1984, R.W. Baumann, C.R. Nelson, 1♀ (BYUC). **VIRGINIA:** Grayson Co., Headwaters, Lewis Fork, Rt. 603, Lewis Fork Trail, Mount Rogers, 29 May 1982, B.C. Kondratieff, 1♂, 1♀ (BYUC). Same site, 7 May 1983, B.C. Kondratieff, 2♀ (VPIC). Same site, 12 May 1983, B.C. Kondratieff, 1 larva (CSUC). Washington Co., Seeps along Whitetop Road, SW Elk Garden, 36.63939N 81.59625W, 1 June 2006, B.C. Kondratieff, R.F. Kirchner, R.E. Zuellig, 2♂, 4♀ (CSUC).

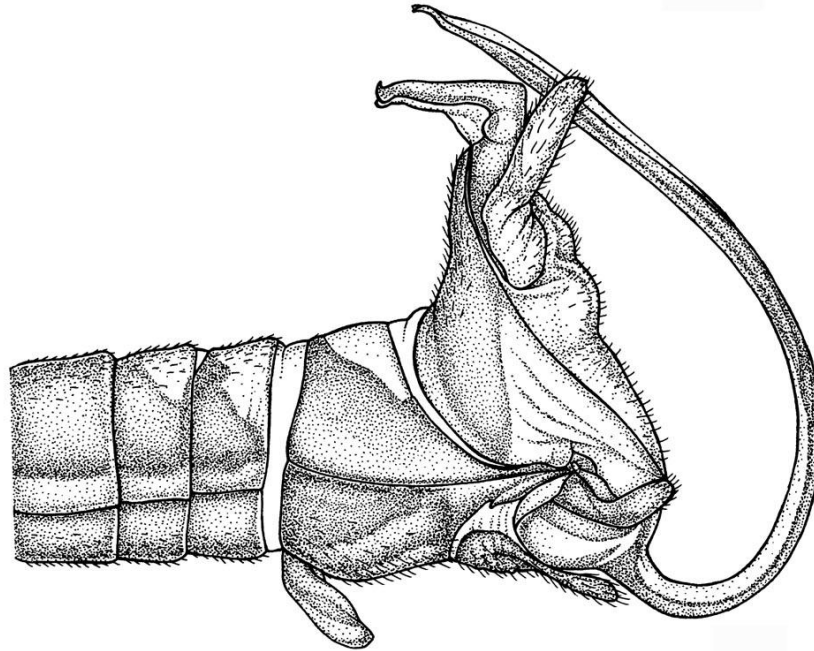


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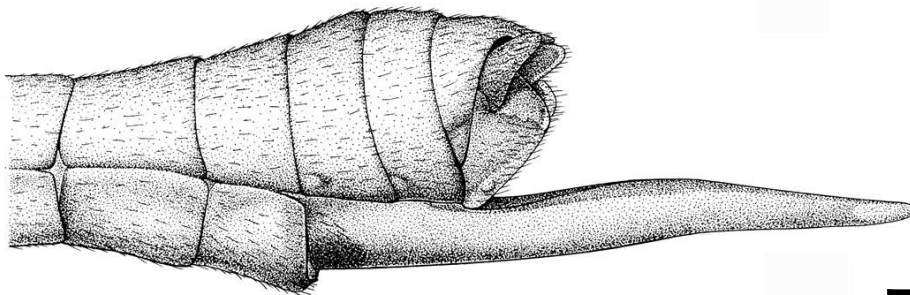
Fig. 73. *Megaleuctra williamsae*. 10 miles east of Gatlinburg, Tennessee, Great Smoky Mountains National Park. Female, head and pronotum.



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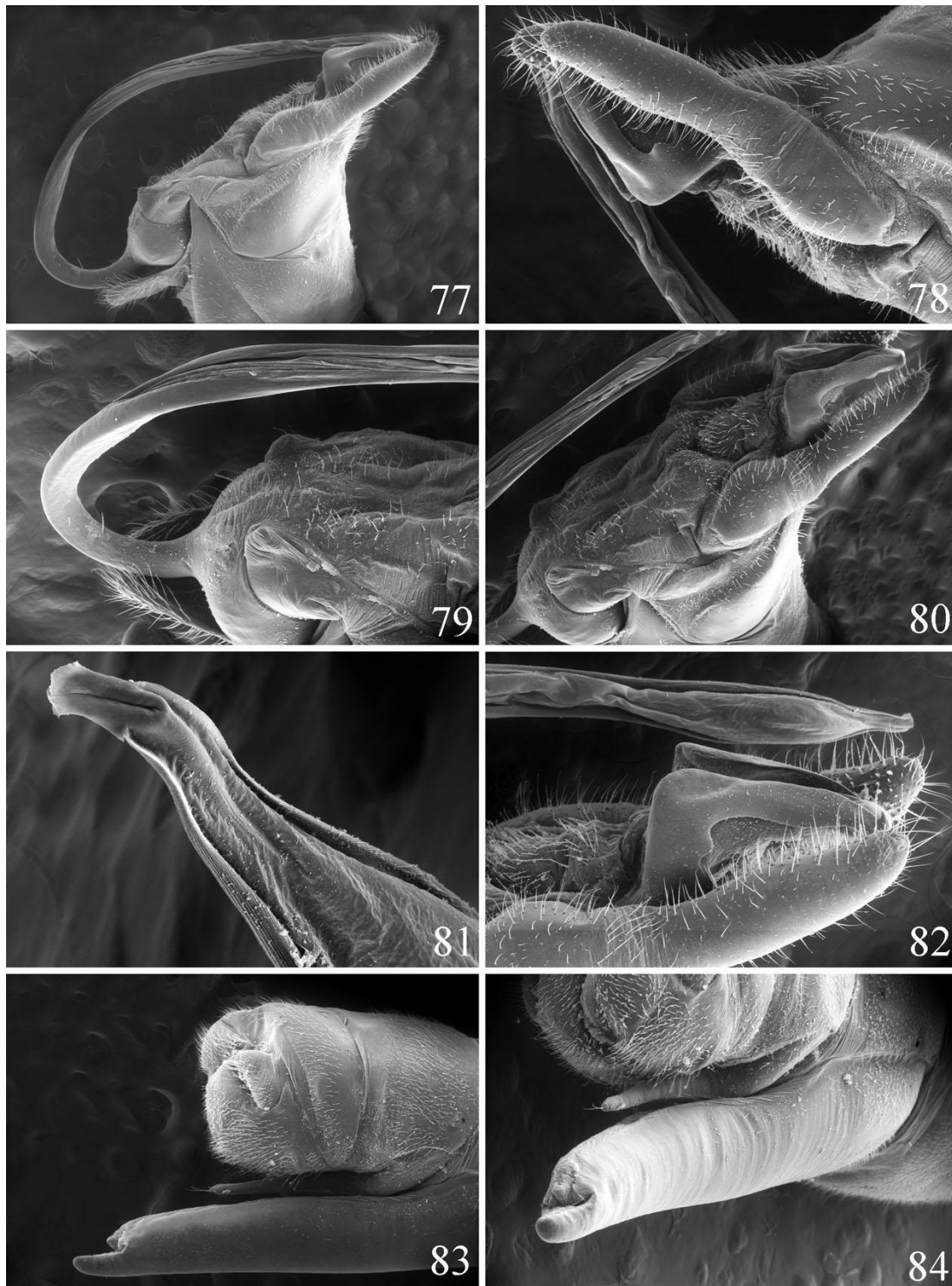


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Figs. 74-76. *Megaleuctra williamsae*. 10 miles east of Gatlinburg, Tennessee. Terminalia: 74. Male, dorsal. 75. Male, lateral. 76. Female, lateral.

Male. Macropterous. Length of forewing 14-15 mm; body length 11-13 mm. General color light brown. Wings hyaline, with dark stigma occupying more than half the costal space beyond the cord. Radial sector of forewing with two branches. Tergum 9 without large lobe-like processes (Figs. 75, 78);

subgenital plate tongue-like, apex slightly emarginated (Figs. 75, 79); vesicle at base sternum 9 short, and narrow (Fig. 75). Tergum10 without ventrobasal expansion (Fig. 79). Epiproct short, forming a right angle at base in lateral aspect (Figs. 75, 78, 80, 82), broad at base, with middorsal groove



Figs. 77-84. *Megaleuctra williamsae*. White Top Road, southwest of Elk Garden, Virginia. Male: 77. Genitalia, lateral, epiproct, terminal on subanal probe. 78. Genitalia, lateral, epiproct enclosing subanal probe at apex. 79. Subanal probe, base, dorsolateral. 80. Genitalia, dorsolateral, separated. 81. Subanal probe, apex, dorsal, close up. 82. Subanal probe and epiproct separated, dorsolateral. Female: 83. Genitalia, lateral. 84. Genitalia, terminal, lateral.

and upturned hooks at apex (Figs. 75, 82). Subanal probe very long, cylindrical, directed upward and forward, usually fitting in middorsal groove of epiproct (Figs. 74, 77, 82), apex tapered, slightly truncate at tip (Figs. 75, 81, 82); cerci consist of a greatly elongate single segment (Figs. 75, 77, 78).

Female. Macropterous. Length of forewing 12-16 mm; body length 12-15 mm. Coloration similar to male. Head oval and somewhat flattened. Pronotum elongate, anterior corners squared off, posterior angles with large inward directed bevels (Fig. 73). Radial sector of forewing with two branches. Sternum 8 formed to an ovipositor-like structure, with subgenital plate extending past tip of abdomen (Figs. 76, 83, 84), broadly rounded from beyond the base to almost the apex (Figs. 76, 83, 84); narrowing to short tip (Fig. 84). Sternum 9 long and very thin (Fig. 84). Cerci inconspicuous (Figs. 76, 83).

Larva. Undescribed.

Egg. Undescribed.

Diagnosis. The male of this species is distinguished

from *M. flinti*, the only other eastern North American species, by its differently shaped epiproct. In *M. williamsae* the epiproct is short and consists of a pair of angled processes, which form a groove that encloses the tip of the subanal probe (Figs. 74, 77, 78, 82), while in *M. flinti* it consists of a stout triangular structure that supports the midlength portion of the subanal probe when it is fully extended (Figs. 22, 25, 27) but forms a short wing-like structure when it is located at the base (Figs. 26, 28, 30). Additionally, the subanal probe of *M. williamsae* lacks a median expansion (Figs. 74, 75, 77) whereas in *M. flinti*, it is expanded at midlength (Figs. 22, 25-28, 30). The subgenital plate of the female of *M. williamsae* is subequal in width from beyond the base to almost to the apex (Figs. 83-84); whereas in *M. flinti* this structure narrows conspicuously from the base to the apex (Figs. 31, 32). Additionally, the species are allopatric, with *M. williamsae* reaching its most northern range extension in southwestern Virginia, and *M. flinti* reaching its southernmost range extension in northern Virginia.



Fig. 85. *Megaleuctra complicata*, Spring, Big Chico Creek, California. Male, Live, habitus, dorsal, brachypterous. (Photo courtesy of A.B. Richards).

DISCUSSION

The genus *Megaleuctra* is rheophilic in that it inhabits exclusively spring habitats, ranging from small seeps to large flowing springs. Even when it occurs in large rheochrenes, it is usually found along the edges instead of out in the area of flow. Water quality must be consistently good and the temperature cold. The nymphs are often found in small seepage areas some distance from nearest the creek, river or lake habitat. The important requirement seems to be that the area must always remain wet. Thus, even though most of the collecting localities given in this paper are listed as major water sources, the critical habitat for the nymphs is springs or seeps that might not even be visibly flowing.

The extant North American species can be divided as noted into two definite regional populations. The two eastern species seem to be limited to areas in the Appalachian Mountains that range from Maryland and Pennsylvania in the north to the Carolinas in the south. Although their presence has not been confirmed from Alabama,

Georgia and Kentucky, this is probably simply a result of limited collecting efforts at the correct habitat and time of year. Ideal habitats seem to be present further north but the genus has not been collected. Comparatively, the western species have been found as far north as Jasper National Park in Alberta, with the most southern records occurring in the Sierra Nevada Mountains in California. The species *M. complicata* and *M. kincaidi* are found mostly in the Cascade and Coast Range Mountains from Washington to northern California. The reality that *M. kincaidi* appears in the Rocky Mountains in northern Idaho and Montana can be explained by the fact that this area is a known refugium for Pacific Coast species as noted in Stark and Gustafson (2004). However, *M. stigmata* exhibits a peculiar distribution pattern. It occurs furthest north in the Canadian Rocky Mountains and furthest south in the Sierra Nevada Mountains in central California, but drops out in the central part of this region, and seems to be absent from the Cascade Mountains and northern California.



Fig. 86. *Megaleuctra complicata*, Headwaters, Parker Creek, Marys Peak, Oregon, Female, Live, habitus, lateral, macropterous. (Photo courtesy of G.W. Courtney).

Megaleuctra species are sometimes found together in the same habitat. It is not uncommon to find *M. complicata* and *M. kincaidi* in the same spring in the

Cascade Mountains. In the border refugia mentioned above, in Idaho and Montana, *M. kincaidi* and *M. stigmata* can also occur at the same location. There

may be some division of microhabitat, and possibly they grow and mature at slightly different times of the year but too little is known about their life cycles to do more than speculate.

The adult genitalia of this genus are quite different when compared to the other stonefly species that inhabit the Nearctic realm. Males have an extremely elongate subanal probe that can reach forward several segments anteriorly on the tergal segments. The apex of the probe in the western species is highly modified with upper and lower portions that are separated with a deep lateral groove. Apically the upper portion bears a large hose-like tube that may be the sperm conveyer in mating. The probe in the eastern species has a long, thin apex which is very delicate and is able to fit in a groove in the epiproct. The epiproct, in all species is able to extend from the base of tergum 10 to the tip of the elongate subanal probe. It can occur at the base of the probe, half way along its length, or enclose the apex of the probe in a potentially protective position. Females have an extremely well developed subgenital plate complex that forms an elongate ovipositor-like structure reminiscent of some Orthoptera species.

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