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Abstract. Euryuridae Pocock 1909 and Eurymerodesmidae Causey 1951, both endemic to the eastern/central United States (US), are incorporated into Xystodesmidae Cook 1895 and reduced to subfamilies and (sub)tribes **n. stats.** Euryurina and Melaphina Brölemann 1916, **n. stats.,** are sister-taxa that differ primarily in epiproctal configurations and comprise Euryurini; sister-taxa Eurymerodesmina and Nannariina Hoffman 1964, **n. stats.,** the latter transferred from Xystodesminae, comprise Eurymerodesmini**, n. stat.**, in which plesiomorphic forms exhibit sublinear, "stick-like," and subapically curved/bent gonopodal acropodites with moderately-long to long hairs, often with distal tufts, on their "inner" surfaces. Additional transferrals include *Wamokia* Chamberlin from the xystodesmine tribe Xystocheirini to Xystodesmini (= Harpaphini), and *Macellolophus* Attems, from Xystodesmidae to Chelodesmidae. Except for Chonaphini, the term, "prefemoral process," has traditionally been assigned to the secondary and shorter telopodital projection regardless of its position, origin, or configuration. Homology of these different structures has never been demonstrated and requires investigation, but the multitude of differences suggests that they are not such and warrant different names, for example "femoral process," for the similarly positioned branches in *Devillea* Brölemann and *Rhysodesmus* Cook (Xystodesminae: Devilleini, Rhysodesmini). The latter tribe may be polyphyletic, and new tribes may be required for components with acicular "prefemoral processes" (*Boraria* and *Cherokia*, both by Chamberlin, *Gyalostethus* and *Erdelyia*, both by Hoffman, and *Pleuroloma* Rafinesque) and the southeastern US genera with small-bodied species (*Caralinda* Hoffman and *Gonoessa*, *Parvulodesmus*, and *Lourdesia*, all by Shelley). Taxonomic value is accorded the "prefemoral extension/ elongation," which is absent from Eurymerodesmina; complete, encircles the acropodite, and extends for ~1/3 to 1/2 of the latter's lengths in Euryurini; and incomplete and extends for ~1/4 to 1/3 of the "outer" acropodital surfaces in Nannariina and xystodesmine tribes. Other newly recognized taxonomic characters include the "inner" and "outer" acropodital surfaces/margins, the position on the acropodital stem of the "distal curve/bend," and the length of the "distal zone." *Rhysodesmus* and *Sigmoria* (*Rudiloria*) *t. trimaculata* (Wood) (Xystodesminae: Rhysodesmini, Apheloriini) are recorded from, respectively, Chihuahua, Mexico, and Québec, Canada, as are Xystodesmidae/-inae and, provisionally, Chonaphini, *Montaphe* Chamberlin, and *M. elrodi* (Chamberlin), the only plausible taxa for an unidentifiable juvenile from near Yahk and only 2.5 km (1.6 mi) north of the International Border. The southern periphery of interior British Columbia (BC) thus represents the second xystodesmid faunal region in BC and the third in Canada. While incorporation of Euryuridae does not affect the family's overall distribution, that of Eurymerodesmidae fundamentally alters it by joining the formerly separate East-Nearctic and Meso-American regions into a continuous one extending, north-south, from Montréal Island, Québec, to Santa Ana Department, El Salvador, a distance of around 4,944 km (3,090 mi). Xystodesmidae also inhabit two West-Nearctic regions, one in the interior stretching from southernmost BC to northeastern Oregon and the other running along the Pacific Coast from southern Alaska to southern California. The family also occupies two Palearctic regions, each with three subregions, an eastern one spreading from Hokkaido, Japan, and the southern Maritime Province, Russia, to Taiwan; a point locality in northern Vietnam; and southern/eastern China. The

second Palearctic area extends along the Mediterranean and adjoining seas from Morocco, Sardinia, and the southeastern corner of France to Cyprus and southern coastal Turkey. New locality data, references, and maps are provided along with diagnostic accounts of all reconceptualized taxa and new/revived statuses.

A simple, sublinear, "stick-like" acropodite with a curve or bend near midlength or subapically and without a secondary telopodital projection is the hypothesized plesiomorphic gonopodal condition in Xystodesmidae. This form has undergone multitudinous modifications/alterations – twists, curls, variably configured thickened and laminate expansions, reductions, bi-/trifurcations, enlargements, ornamentations, etc. that are manifested in today's xystodesmine tribes. When Avalonia collided with Baltica 450 million years ago, ancestral xystodesmoideans on the former dispersed into the latter, penetrated and occupied vacant niches, and evolved into today's Melaphina (Euryurinae: Euryurini) and Devilleina (Xystodesminae). A similar evolutionary burst leading to today's Nearctic and East-Palearctic faunas occurred 10 million years later when Avalonia + Baltica collided with Laurentia to form Euramerica. Ancestral forms of Euryurinae and Xystodesminae again penetrated vacant niches and evolved; the former maintained the general gonopodal structural pattern of Melaphina but changed the epiproct from triangular to broad and spatulate, thereby creating Euryurina. The earliest xystodesmine taxa to evolve in Laurentia were Rhysodesmini and *Rhysodesmus*, which spread southwestward, penetrated "proto-Mexico, and left relict populations in today's southern Appalachians. Eurymerodesmina and Nannariina arose from ancestral euryurine stock prior to the Cretaceous in western Appalachia in their present area of overlap. The former dispersed to the west and south while the latter expanded to the east and north; consequently, the Western Inland Seaway minimally impacted Nannariina while eradicating Eurymerodesmina from the inundated area. Today's populations in the Plains and south-southeastern states therefore represent secondary dispersion in the past 50-60 million years. The Seaway also eradicated *Rhysodesmus* from these areas, but enough forms survived in high mountain refugia to replenish the fauna when the embayment receded.

Key words. Acropodite, acropodital hairs/surfaces, Apheloriini, Chonaphini, *Devillea*/Devilleini, *Melaphe*/Melaphina, Nannariina, Pachydesmini, prefemoral process/extension, *Rhysodesmus*/Rhysodesmini.

Dedication

We dedicate this contribution to our late American colleague Richard Lawrence Hoffman (1927–2012), whose pioneering mid-20th century descriptions and generic revisions set the stage for meticulous field samplings and additional treatments by RMS, whose resultant observations and in-depth understanding of the taxon enabled this work. Dr. Hoffman (1990, 2005) published monographs of the primarily Afrotropical families Oxydesmidae and Gomphodesmidae, and our treatment of their Northern Hemisphere cohort attempts to supplement these while not repeating redescriptions of taxa that have already received such.

Introduction

Per the latest concept (Golovatch and Enghoff 2015), the milliped superfamily Xystodesmoidea (Polydesmida: Leptodesmidea) comprises five families: Eurymerodesmidae Causey 1951 and Euryuridae Pocock 1909 (Nearctic and endemic to the eastern 1/3–1/2 of the United States [US]), Xystodesmidae Cook 1895 (Holarctic and the northern continental Neotropics), Oxydesmidae Cook 1895 (Afrotropical and Middle Eastern Asia [Lebanon and Israel]), and Gomphodesmidae Cook 1896 (Afrotropical) (Hoffman 1963a, 1969, 1978a, 1980, 1982, 1990, 2005; Shelley 1987; Tabacaru 1995; Golovatch 2007; Golovatch and Enghoff 2015). Previous superfamilial taxonomies (Hoffman 1980; Shelley 2003; Shear 2011) also included the Afrotropical Campodesmidae Cook 1896 that Golovatch and Enghoff (2015) transferred to Sphaeriodesmoidea. We accept these assignments and focus on the Holarctic taxa that inhabit former Laurasian territory. Eurymerodesmidae was revised by Shelley (1990a) and the two valid euryurid genera, *Euryurus* Koch and *Auturus* Chamberlin, were reviewed by Hoffman (1978b, 1999) and Shelley (1982a, b) with another species of the former described by Jorgensen (2009). The present concept of Xystodesmidae is based largely on the continually evolving ones of Hoffman (1969, 1978a, 1980, 1982, 1999), which were summarized by Marek et al. (2014), who placed all genera in their proper tribes. The family's general areas of occurrence were mapped by Hoffman (1969, 1978a), and Shelley (1987) depicted those in the Nearctic, one of which extends southward into Central America and the northern Neotropics (Mexico, Belize and Honduras [projected for both], Guatemala, and El Salvador) (Kraus 1954; Hoffman
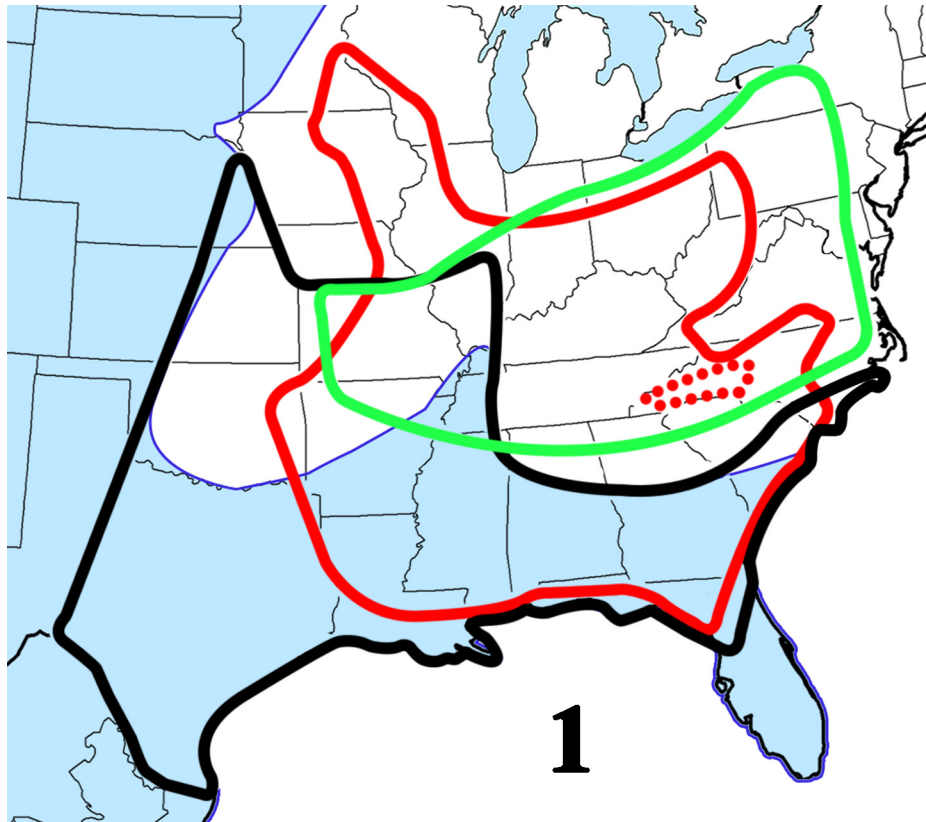
Figure 1. Distribution of Euryurinae plotted against the maximal extent of the Cretaceous Western Inland Sea. Euryurina (Euryurini, red), Eurymerodesmina (Eurymerodesmini, black), Nannariina (Eurymerodesmini, green). The red line, Euryurina, in eastern North Carolina and southcentral Virginia connects disparate peripheral localities; the area of greatest euryurinan concentration is circumscribed by the red dots.

1966, 1970, 1980, 1999; Loomis 1966, 1968; Bueno-Villegas et al. 2004).

In the late Nineteenth Century, Euryuridae included *Euryurus* plus several Neotropical genera. The addition of *Auturus* by Chamberlin (1942) brought the North American components to two, and Hoffman (1998a) confirmed familial status, restricted it to these taxa, and revived Aphelidesmidae for Neotropical forms. Hoffman (1962a) and he and Lohmander (1968) considered the Mediterranean xystodesmoideans, *Melaphe* Cook and *Ochridaphe* Hoffman, to be xystodesmids, and he (Hoffman 1998) documented affinity between Melaphini Brolemann 1916 and Euryuridae anatomically. We concur with these conclusions and since Euryuridae is related to a component of Xystodesmidae it must also be such, but nobody has formalized this logical action. We therefore do so here at the subfamilial level, Xystodesmidae holding priority by 14 years for the familial name. The distribution of Euryurinae **rev. stat**. is depicted in Fig. 1 (red line); relevant gonopod illustrations for Euryurini are provided in Fig. 2–7.

Eurymerodesmidae, established as a full family by Causey (1951), exhibits a host of apomorphies, but without a shared feature with another xystodesmoidean, familial status was the only option for Shelley's (1990a) revision. While examining gonopods for Hennen and Shelley's (2015) study of the xystodesmine tribe Nannariini, RMS observed that their acropodital hairs are longer and stouter than in other tribes, that they extend (dis)continuously for longer distances along the "inner" acropodital surfaces (definitions in next section), and that they tend to cluster at their distal extremities. These features of nannariinine acropodites resemble ones in Eurymerodesmidae (Fig. 8–15), thus constituting a shared feature with not only another xystodesmoidean but also with an indisputable component of Xystodesmidae themselves. Additionally, plesiomorphic forms of each possess nearly identical "stick-like" acropodites (compare Fig. 8–9 and 12–15), although those of Eurymerodesmidae are rotated 180° *in situ*. Shear (1977) suggested that "Euryuridae and Eurymerodesmidae taken together form a 'sister-group' to Xystodesmidae," and

Hoffman (1978a, 1980) regarded Eurymerodesmidae as a "specialized derivative group of Xystodesmidae of recent origin." Shear's statement is accurate at the subfamilial, rather than familial, level, and as shown comparatively in fig. 2–15, both taxa actually are xystodesmids. We therefore propose a "hairy" subfamily with hairs on both the "prefemoral extensions" and/or acropodites that are longer than those in sympatric xystodesmines and extend (dis)continuously along the "inner" margins for 2/3–3/4 of their lengths. These conditions contrast with those in the nominate subfamily, in which hairs are only or primarily on the "outer" margins of the "prefemoral extensions" and acropodital bases, and Pocock's (1909a) familial name based on *Euryurus* Koch 1847 has priority by 43 years over that of Causey (1951) based on *Eurymerodesmus* Brölemann 1900. While most acropodites in Euryurinae exhibit simple, "stick-like" configurations that we interpret as plesiomorphic, the two basic forms differ in the lengths of the "distal zones," longer ones resembling the number "7," so we propose two tribal components with two subtribes each. Reconceptualized Euryurinae are wholly sympatric with Xystodesminae and occupy a large part of the East-Nearctic faunal region (Fig. 1) along with two smaller areas in the Mediterranean region (Fig. 17, 21).

As to the ostensibly confamilial European genera *Devillea* Brölemann 1902 and *Macellolophus* Attems 1940, we retain the former in monotypic Devilleini Silvestri 1903 (Xystodesminae). *Macellolophus*, however, is misplaced not just in a monotypic melaphine tribe (Hoffman 1980, Mauriès et al. 2006) but also in Xystodesmidae; its general anatomical features conform to those of Chelodesmidae, so we transfer them there and address them in a future contribution. Consequently, we fundamentally alter the concept of Xystodesmidae by removing *Macellolophus*/Macellolophini, incorporating Euryuridae and Eurymerodesmidae at subfamilial and tribal levels, transferring Nannariini from Xystodesminae to **Eurymerodesmini n. stat.** (Euryurinae) and reducing them to a subtribe, and transferring Melaphini from Melaphinae to Euryurini and reducing them to a subtribe. We also revise the familial taxonomy, provide diagnostic accounts for all new statuses and reconceptualized taxa, remap the family's distribution, detail the occupied areas and new localities, and provide an evolutionary hypothesis. Repository acronyms are **BME**, Bohart Museum of Entomology, University of California, Davis, USA; **BMNH**, Natural History Museum, London, UK; **BYUC**, Monte L. Bean Life Science Museum, Brigham Young University, Provo, Utah, USA; **CAS**, California Academy of Sciences, San Francisco, USA; **CMN**, Canadian Museum of Nature, Ottawa, Ontario; **CNC**, Canadian National Collection, Ottawa, Ontario; **EME,** Essig Museum of Entomology, University of California, Berkeley, USA; **INHS**, Illinois Natural History Survey, Champaign, USA; **LEM,** Lyman Entomological Museum, Macdonald Campus, McGill University, Ste.-Anne-de-Bellevue, Québec, Canada; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; **MSB**, Museum of Southwestern Biology, University of New Mexico, Albuquerque, USA; **NCSM**, North Carolina State Museum of Natural Sciences, Raleigh, USA; **NMNH**, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; **OSU**, Entomology Department, Oregon State University, Corvallis, USA; **RBCM**, Royal British Columbia Museum, Victoria, Canada; **ROM**, Royal Ontario Museum, Toronto, Canada; **SDMNH**, San Diego Museum of Natural History, California, USA; **TBMNH**, Thomas Burke Museum of Natural History, University of Washington, Seattle, USA; **UBC**, Zoology Department, University of British Columbia, Vancouver, Canada; **UMMZ**, University of Michigan Museum of Zoology, Ann Arbor, USA; **UMN,** Entomology Department, University of Minnesota, St. Paul, USA; **UTIC**, University of Texas Insect Collection, Austin, USA; **UVT,** Biology Department, University of Vermont, Burlington, USA; **VMNH**, Virginia Museum of Natural History, Martinsville, USA.

Terminology

The gonopods of male helminthomorph millipeds represent ambulatory appendages on segments 7 or 7 and 8 (8th, 8th–9th, or 9th–10th legs) that are modified and specialized for copulation (Hopkin and Read 1992). In this anatomical position, they can be little other than modified walking legs, but the best direct evidence is the abnormal "mixed" appendage in *Sigmoria* (*Sigmoria*) *l. latior* (Brölemann) (Xystodesminae: Apheloriini) (Shelley 1977) that contains both gonopodal and ambulatory podomeres. In Polydesmida, only the anterior appendages of segment 7 (8th legs) are so modified, and they arise from a metazonal opening/aperture that may traverse the stricture, extend into the prozonum, and reduce the

latter to a narrow, sclerotized strip. Polydesmidan gonopods comprise two articles, a basal coxa with an attached sternal apodeme, a tubular solenite/cannula, and occasionally a short process/apophysis, and a distal "telopodite," that is fully homologous to the ambulatory prefemur in Polydesmida, as Petit (1976) showed in histological studies of the gonopodal primordia in two species of Polydesmidae and Shear et al. (2016) supported. Consequently, the accepted gonotelopodital divisions named for ambulatory podomeres – prefemur, femur, postfemur, tibia, tarsus – are purely conventional, but they nevertheless exhibit a wealth of taxonomic characters so we retain these accepted names. Telopodital terminology, particularly that relevant to the one to three distal projections, is as follows:

Acropodite. The projection arising from the globose, basal prefemur that carries the prostatic groove. It may be a single structure, as in Euryurinae and many xystodesmine genera, or divided into, usually, two branches. It is the dominant projection in taxa with two or three prefemoral branches except for Chonaphini (Xystodesminae), in which the prefemoral process dominates (Shelley 1994).

Distal curve/bend. Most undivided and curved xystodesmid acropodites, exhibit an additional curve or bend distad. In genera like *Apheloria* Chamberlin (Xystodesmini: Apheloriini), the bend is abrupt, approximately 90°, and directs the "distal zone" away from the plane of the rest of the acropodite. Its position varies from subapical to near midlength, whereas in *Boraria* and *Cherokia*, both by Chamberlin, and *Gyalostethus* Hoffman (Xystodesminae: Rhysodesmini), the acropodite is sublinear with no, or at most only a slight, distal curve/bend.

Distal zone. The terminal sector of the acropodite distal to the distal curve/bend. It usually is not coplanar with proximal parts of the stem and is absent from (sub)linear structures.

"Inner"/"Outer" acropodital margins/surfaces. Our study shows that the acropodital hairs hold taxonomic significance, so the surface(s) from which they arise must be distinguished. In curved acropodites, the "inner surface/margin" is the one inside the arc, on the side to which the acropodite curves, and the opposite is the "outer surface/margin."

Solenomere. Not recognized in "single" or undivided acropodites, the solenomere is the branch in divided structures that carries the prostatic groove to its opening. We believe that the third projection in *Pachydesmus* Cook (Xystodesminae: Pachydesmini), the "primary telopodite" according to Hoffman (1958), is homologous to the "solenomere" in contribal genera -- *Thrinaxoria* Chamberlin and Hoffman and *Dicellarius* Chamberlin — where it arises distad/subapically and around midlength, respectively (Shelley 1984a; Shelley and McAllister 2006). The position where the solenomere arises, the "division point," effectively moves proximad in Pachydesmini to become basal and absent from *Pachydesmus*, as the solenomere/"primary telopodite" arises separately from the prefemur itself.

Prefemur and prefemoral elongation/extension. Dr. Hoffman consistently contended that xystodesmid telopodital hairs arise exclusively from the globose, densely hirsute prefemur, but in Euryurini, it narrows and extends distad along, and surrounds, the acropodital stem. This extension is absent from Eurymerodesmina and extends only short distances along the "outer" acropodital surfaces in Nannariina and all tribes of Xystodesminae, so it holds previously unrecognized taxonomic value. We therefore name it the "prefemoral extension/ elongation," which is "complete" and encircles the acropodite in Euryurini and incomplete and covers only the basal part of the "outer" acropodital surface in Nannariina and Xystodesminae. In some xystodesmines, hairs continue beyond the "extensions" for short distances along the acropodital stems, while in Eurymerodesmina, they arise exclusively from the latter as do those on the "inner" surfaces in Nannariina.

Prefemoral process. We follow tradition and, if present, label the second and, except in Chonaphini (Shelley 1994), shorter telopodital projection the "prefemoral process." It does not carry the prostatic groove and, in species with curved acropodites, arises on the side to which the latter curves, its position varying from close to or well separated from the latter or even arising from the proximal 1/3 of the stem. Sublinear acropodites are typically accompanied by shorter, sublinear, and often acicular processes that are closely appressed, and at least partly parallel, to the stems. Despite the different origins, positions, and configurations, all these structures are termed "prefemoral processes," but true homology has never been demonstrated or, to our knowledge, investigated. Those that arise from the acropodite itself, as in

Rhysodesmus Cook and *Stenodesmus* Saussure and *Devillea* (Xystodesminae: Rhysodesmini: Devilleini) (Hoffman 1966, 1970; Hoffman and Lohmander 1968), closely resemble each other and, positionally, seem more like "femoral projections." Perhaps bifurcating from acropodital stems is the plesiomorphic condition, but regardless of polarity, the different positions call into question their homologies, terminologies, and homogeneity of Rhysodesmini, as the structure arises separately from the prefemur itself and is acicular in *Boraria*, *Cherokia*, *Gyalostethus*, *Erdelyia* Hoffman, and *Pleuroloma* Rafinesque (Hoffman 1960, 1962b, 1965, 1980, 1999; Hoffman and Shear 1969; Shelley 1980). If the structures are not homologous, the name, Rhysodesmini, will remain with a generic namesake and perhaps become junior to Devilleini, and the above genera with acicular projections will require a new tribe. We also believe that the small-bodied southeastern US genera (*Caralinda* Hoffman, and *Gonoessa*, *Lourdesia*, and *Parvulodesmus*, all by Shelley) (Hoffman 1978c, 1980, 1999; Shelley 1979, 1983a, b, 1984b, 1991, 2001a) provisionally assigned to Rhysodesmini in Hoffman's three treatments, require from one to three new tribes, as they share few gonopodal features and seemingly cannot share ancestry with *Rhysodesmus*. Consequently, the true nature(s) of the secondary projections, the proper terminologies, and the true affinities among rhysodesmine genera as presently constituted warrant serious analyses. Additionally, potential affinity between *Rhysodesmus* and *Devillea*, which share strongly sclerotized projections of varying lengths arising from, and often closely appressed to, their acropodital stems, should be investigated along with potential contribal status, in which case Devilleini Silvestri 1903 has 13 years of priority for the tribal name. *Devillea* exhibits a curved acropodite with a second projection arising subbasally from, and often closely appressed to, the latter, instead of separately from the prefemur itself. The projection's length varies (Strasser 1960), and its subbasal acropodital origin is shared with *Rhysodesmus* (Xystodesminae: Rhysodesmini) (Hoffman 1966, 1970; Hoffman and Lohmander 1968), which may partly explain why Hoffman (1980) placed Devilleini in the nominate subfamily. However, the broadly curved acropodites distinguish *Devillea*/Devilleini from *Rhysodesmus*/Rhysodesmini. Resolving these issues and the apparent heterogeneity of Rhysodesmini are beyond our scope and require molecular analyses, so we conserve the present statuses (Hoffman 1980, Marek et al. 2014).

Euryuridae, Melaphini, and Devilleini.

The family-group taxon based on *Euryurus* has been repeatedly reconceptualized, and its tangled history is summarized by Hoffman (1954, 1998a) and Jorgensen (2009). Most recently, Hoffman (1998a, 1999) considered it a full family with close affinity to the Mediterranean xystodesmid tribe Melaphini because of somatic and gonopodal similarities between *Euryurus* and *Melaphe*. Obviously, *Euryurus* and *Melaphe*, and hence Euryuridae and Melaphinae, are related. Their paranota possess marginal anteriolateral teeth, and their gonopodal acropodites curve/bend around midlengths and possess complete "prefemoral elongations" that extend for equivalent distances with similar pilosities along their "inner" surfaces (Fig. 2–7). Indeed, the gonopodal configurations of *M. corrupta* Attems, *E. maculatus* (Koch), and *E. l. leachii* (Gray) (Fig. 2–5) are closely similar as are those of *M. vestita* (Koch) and *E. mississippiensis* (Causey) (Fig. 6–7). Thus, since Euryuridae is closely related to Melaphini, a xystodesmid component, it must also be such or together they comprise a separate family. The evolutionary hypothesis of Shelley and Golovatch (2011) provides a basis for interpreting how confamilial statuses developed and a reasonable explanation for the evolution of *Euryurus*, *Melaphe*, and traditional Xystodesminae from common ancestral stock (see Evolution section). Confirmation or disproval with molecular data is desirable, but this is beyond our present scope.

Relevant illustrations of *Melaphe* spp. showing long hairs extending distad along the inner surfaces of the prefemoral elongations and acropodites are available in Hoffman (1962a, 1998a) and Hoffman and Lohmander (1968). Published illustrations of *Devillea* spp. gonopods (Brölemann 1902, 1916; Verhoeff 1931; Attems 1938, 1940; Strasser 1960) differ from those of *Melaphe* and *Ochridaphe* in possessing looped acropodites, "prefemoral processes," and acropodital hairs on the "outer" surfaces. Hoffman (1980) accepted *Devillea* in the monotypic tribe Devilleini (Xystodesminae) and Marek et al (2014) reiterated this assignment. *Melaphe* and *Ochridaphe* are properly contribal, as they share gently curved acropodites, "prefemoral extensions," "distal zones," and moderately long hairs along the "inner" surfaces of the extensions and acropodites to near the "distal bends." This positional marker is sharp and subapical in
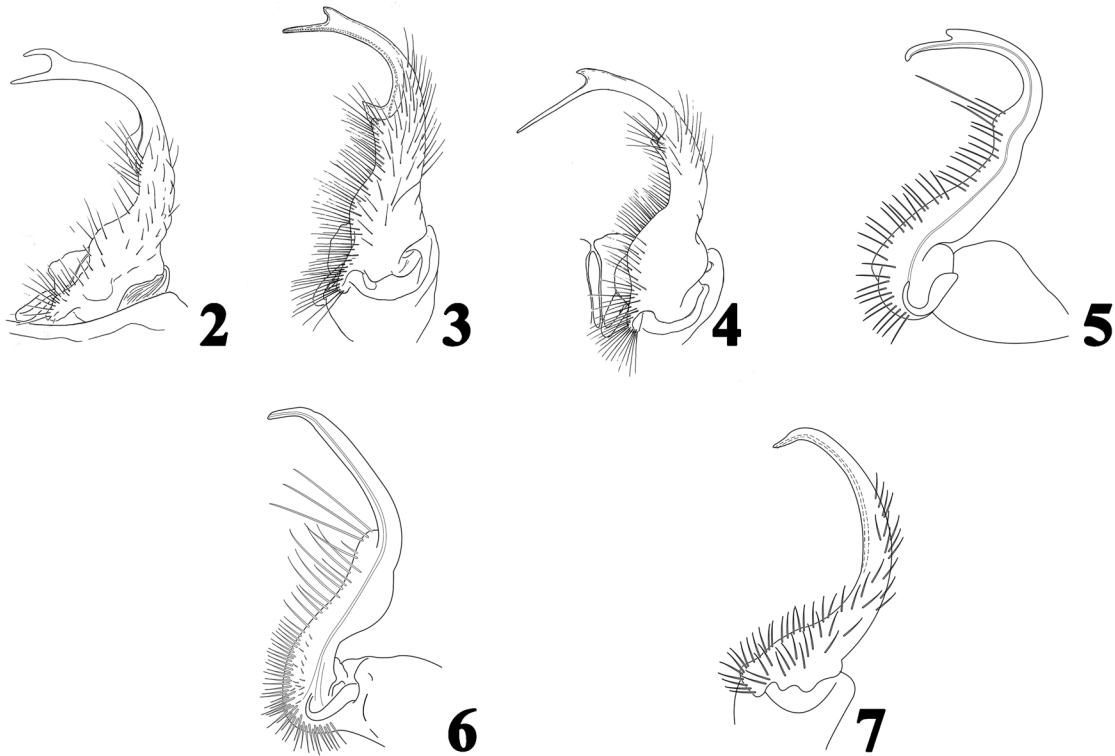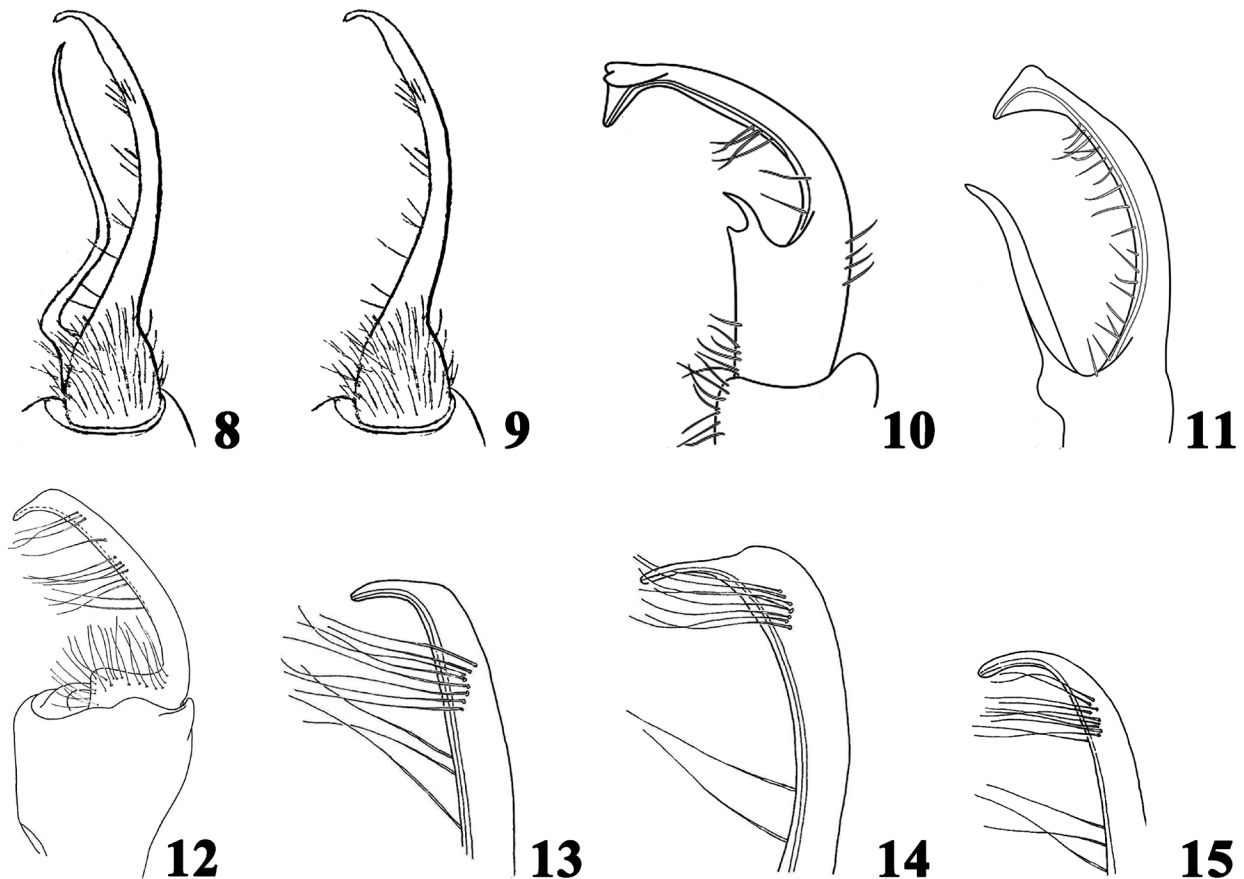
Figures 2–7. Euryurini gonopodal telopodites; **2–4** and **7**, Euryurina, **5–6**, Melaphina. **2)** *Euryurus carolinensis* (Saussure), Orange Co., NC. **3)** *E. l. leachi* (Gray), Hamilton Co., OH. **4)** *E. maculatus* Koch, Wilkinson Co., GA. **5)** *Melaphe corrupta* Attems, locality unknown. **6)** *M. vestita* (Koch), locality unknown. **7)** *E. mississippiensis* (Causey), Jackson Co., MS. Figures 2–4 reprinted from Hoffman (1978b) with permission from the American Entomological Society. Figure 5 reprinted from Hoffman (1962a) with permission from the Bavarian State Collection of Zoology, Munich. Figure 6 reprinted from Hoffman (1998a) with permission from the Virginia Museum of Natural History. Figure 7 adapted from Causey (1955a) with permission from the Biological Society of Washington.

Devillea, the distal zone is bifurcate, and short, scattered hairs extend about halfway along the "outer" acropodital surfaces (Brölemann 1902; Attems 1938; Strasser 1960, 1974a). Both *Devillea* and *Melaphe* have highly disparate distributions (Fig. 17, 21) that seem somewhat relictual, and both logically derive from xystodesmoidean radiations onto Baltica after it merged with the Avalonia terrane in the early Silurian Paleogeological Period, some 450 million years ago (mya) (Shelley and Golovatch 2011).

Eurymerodesmidae

An assemblage of derived xystodesmoideans, Eurymerodesmidae is the dominant polydesmidan taxon in prairie ecosystems, and they extend into southeastern forests. They range southward from northeastern Nebraska, eastern Illinois, and southeastern North Carolina to northern peninsular Florida, the Gulf Coast, and the Rio Grande (Fig. 1, black line) (Hoffman 1980, 1982, 1999; Shelley 1990a). The taxon has never been encountered south of this river in Coahuila, Nuevo León, or Tamaulipas states, Mexico, and presently terminates at the International Border. It occurs sympatrically with both Euryuridae and all east-Nearctic xystodesmine tribes except Chonaphini (Hoffman 1978b, 1980, 1999; Shelley 1982a, b, 1990a, 1994).

Eurymerodesmids are reknown for their pilosities. The acropodital hairs so impressed Wood (1864, 1865), that he characterized the structure as "beset with very numerous long hairs" and named the first species *hispidipes*. Venters are littered with moderately long hairs in both sexes, but the gonopods and segment 7 in males are especially hirsute. Aperture adornments like caudolateral pockets/pouches and lobes/projections from the caudal margins are moderately to densely hirsute, and long hairs extend (dis)

Figures 8–15. Eurymerodesmini gonopodal tel-/acropodites; **8–11**, Nannariina. **8)** telopodite of *Nannaria cayugae* Chamberlin, Tompkins Co., NY. **9)** acropodite of the same. **10)** telopodite of *Mimuloria castanea* (McNeill), Monroe Co., IN. **11)** the same of *M. d. dilatata* Hennen and Shelley, Marshall Co., TN. **12–15**, Eurymerodesmina. **12)** *Eurymerodesmus varius louisianae* Chamberlin, Natchitoches Par., LA. **13)** acropodite of a second individual from the same locality. **14)** the same, Columbia Co., AR. **15)** *E. v. varius* (McNeill), Escambia Co., FL. Figures 8–9 reprinted from Chamberlin (1949) with permission from the Biological Society of Washington. Figures 10–11 reprinted from Hennen and Shelley (2015) with permission of the Center for Systematic Entomology. Figures 12–15 reprinted from Shelley (1990a) with permission of the American Entomological Society.

continuously along the "inner" acropodital surfaces as far as the "distal curve/bend," often terminating in a small "tuft" or denser region. "Outer" acropodital margins generally lack hairs, but there may be an isolated tuft proximal to the curve. Brölemann (1900) aptly characterized these hairs as long and silken, and those comprising the tuft(s) may be so long and dense as to overlie and largely obscure the short "distal zones." Despite dissecting hundreds of eurymerodesmid gonopods, RMS has never encountered loose or flimsily attached acropodital hairs nor accidentally dislodged any during handling; all were firmly attached to acropodital stems, and only a few were dislodged and loose in vials after a century of preservation. This fact suggests that conditions in which hairs are discontinuous or extend only short distances along stems are natural, do not reflect accidental losses during the millipeds' lives, and are not artifacts of samplings, dissections, and/or examinations. Contrastingly, acropodites of east-Nearctic xystodesmine tribes (Apheloriini, Pachydesmini, Rhysodesmini) typically exhibit short stretches of comparatively short hairs along the "outer" surfaces of the "prefemoral extensions" that run for only 1/3 of the structures' lengths. These attributes of eurymerodesminans and nannariinans are even evident in published illustrations; for example, Chamberlin (1949, Fig. 1, reproduced here with permission as Fig. 8-9, the latter without the "prefemoral process") shows discontinuous hairs along the "inner" acropodital

surface of *N. cayugae* Chamberlin followed by a gap and a slight apical tuft. We therefore believe that (dis)continuous stretches of moderately long to long hairs on "inne**r**" acropodital surfaces coupled with apical tufts constitute shared features between Eurymerodesmidae and Nannariini, an unquestioned component of Xystodesmidae (Hoffman 1964a, 1980, 1999; Marek 2014; Hennen and Shelley 2015), and since it is related to such, Eurymerodesmidae must also belong to Xystodesmidae and submerged under the older familial name.

Affinity between Eurymerodesmidae and Nannariini is also revealed by a shared acropodital configuration that we interpret as plesiomorphic. Shelley (1990a) characterized the basic eurymerodesmid structure as simple and "stick-like," with stems extending sublinearly from the prefemur and bending/curving subapically. This configuration also exists in plesiomorphic nannariinines, but it is less noticeable because the "prefemoral process" tends to mask the acropodite. Although not rotated 180°, the acropodite of *N. cayugae* (Chamberlin 1949, Fig. 1; Fig. 8–9) matches that of plesiomorphic eurymerodesmids, and, coupled with the similar hair lengths and arrangements (compare Fig. 8–9 and 12–15) has constituted published, but unperceived, evidence of this affinity for 69 years. "Stick-like" acropodites, or ones that conceivably derive from this condition, also occur in representatives of Devilleini, Rhysodesmini, Apheloriini, and Pachydesmini, so we believe that this simple structure constitutes the basic, plesiomorphic configuration that is thickened, expanded, prolonged, shortened, ornamented, curved, coiled, etc., in these and other xystodesmine tribes. We therefore reduce Eurymerodesmidae to tribal status under Euryurinae, the older name, and propose Eurymerodesmini**, n. stat.**, to encompass subtribes Eurymerodesmina and Nannariina Hoffman**, n. stats.**, the latter transferred from Xystodesminae (Hoffman 1964a, 1980, 1999; Marek et al. 2014). Because of the longer acropodital hairs that extend along the "inner" surface to the level of the "distal curve/bend" in at least plesiomorphic forms, Nannariina are grouped with Eurymerodesmina and reduced to subtribal status.

Affinity between Eurymerodesmina and Nannariina is further supported by their comparably small body sizes and their distributions, which overlap in Illinois, Missouri, and Arkansas (Fig. 1, 16), the logical source area for Eurymerodesmini. Nannariina expanded eastward while Eurymerodesmina spread southwestward and then southward and eastward after the Western Inland Seaway receded during the late Cretaceous. While divergence could have occurred post-Cretaceous and hence relatively recently, we believe it came prior to the Seaway and Cretaceous because most of Nannariina's area was land during this geological period enabling the taxon to spread without impediment. Eurymerodesmina would have spread southward then only to be inundated and eradicated from the area of the Seaway, we believe its presence today in the Plains and southern/southeastern states reflects secondary dispersal and reoccupation of a previously inhabited area, and its occurrence in non-inundated southeastern North Carolina reflects northward post-Cretaceous dispersal along the Atlantic Coast. The partial geographic overlap of Eurymerodesmina and Nannariina supports our sister-group hypothesis; they share ancestry, diverged in the present area of overlap, dispersed in opposing directions, and logically comprise a separate tribe, **Eurymerodesmini**, in Euryurinae. The belated detection of this relationship despite over a half-century of clues in published literature emphasizes the need for comprehensive anatomical knowledge of all relevant taxa by specialists addressing nebulous and confused situations.

Revised Taxonomy of Xystodesmidae

Superorder Merocheta Cook 1895
Order Polydesmida Pocock 1887
Suborder Leptodesmidea Brolemann 1916
Superfamily Xystodesmoidea Cook 1895
   Family Xystodesmidae Cook 1895
      Subfamily Euryurinae Pocock 1909. Revived Status from Pocock (1909a) and Hoffman (1954, 1980)
         Tribe Euryurini Pocock 1909. Revived Status from Brolemann (1916) and Hoffman (1980)
            Subtribe Euryurina Pocock 1909. **New Status**
            Subtribe Melaphina Brolemann 1916. **New Status**
         Tribe Eurymerodesmini Causey 1951. **New Status**
            Subtribe Eurymerodesmina Causey 1951. **New Status**
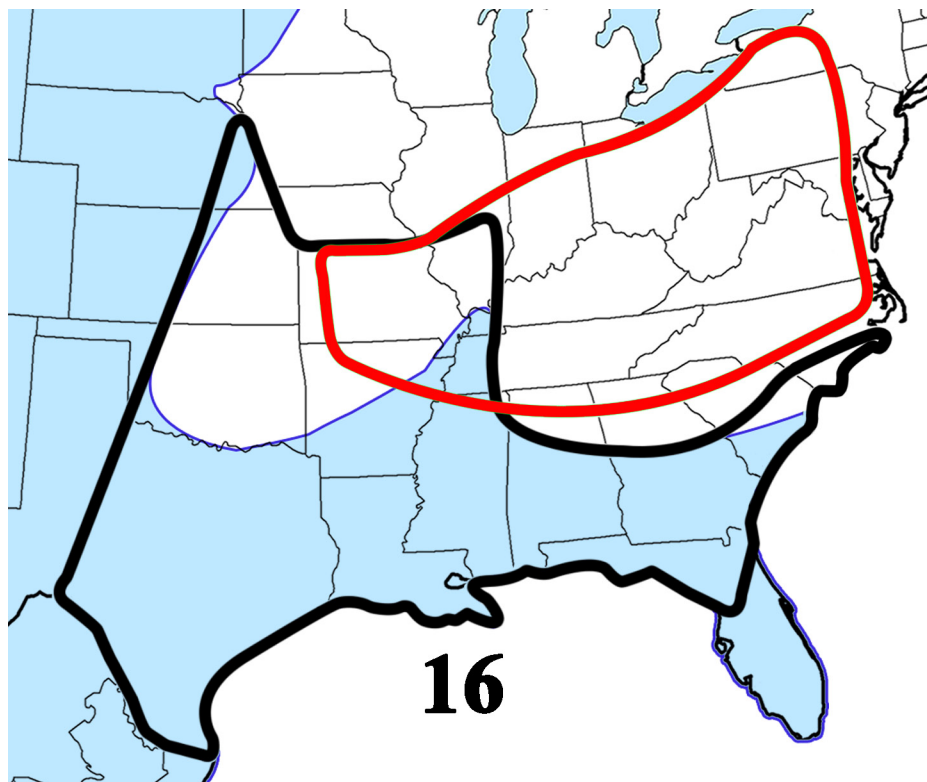
Figure 16. Distribution of Eurymerodesmini plotted against the maximal extend of the Cretaceous Western Inland Sea. Black line, Eurymerodesmina. Red line, Nannariina.

Subtribe Nannariina Hoffman 1964. **New Status**
Subfamily Xystodesminae Cook 1895
Tribe Apheloriini Hoffman 1980
Tribe Chonaphini Verhoeff 1941
Tribe Devilleini Silvestri 1903
Tribe Orophini Hoffman 1964
Tribe Pachydesmini Hoffman 1980
Tribe Rhysodesmini Brolemann 1916
Tribe Sigmocheirini Causey 1955
Tribe Xystocheirini Hoffman 1980
Tribe Xystodesmini Cook 1895 (=Harpaphini Hoffman 1980)
Subfamily Parafontariinae Hoffman 1978

Diagnostic Accounts of New Statuses and Reconceptualized Taxa

Family Xystodesmidae (Adapted from Hoffman (1962a, 1982) and Golovatch and Enghoff (2015))

Diagnosis. Small- to large-bodied (~8–85 mm long), moderately convex, usually glabrous, glossy, and smooth-bodied Xystodesmoidea with 20 segments, dorsums usually smoothly glossy black, occasionally pustulate, often adorned with vivid pigmentations (yellow, orange, red, blue, white, lavender, gray) on caudolateral paranotal corners, as bands along anterior margins of collums and caudal metatergal margins, or as spots in metatergal midlines; bodies usually relatively broad (W/L ratio >18%) and

subparallel-sided from segments 3–16, occasionally long and slender (W/L ratio < 18%); paranota broad, usually declined, occasionally subhorizontal, usually in contact or overlapping when segments compressed, peritremata extending along lateral margins and containing ozopores; antennae moderately long, usually with four but occasionally up to 20 terminal sensory cones, margins of seventh antennomeres not invaginated, cones not grouped into diads; collum usually small, semilunar, and exposing epicranium in dorsal view; epiproct flattened dorsoventrally, usually bluntly subtriangular, broad and spatulate in Euryurina (Euryurinae: Euryurini); vasa deferentia opening apically on cylindrical processes on 2nd legs; ambulatory prefemora with or without sharply acuminate, distoventral spines. Gonopodal aperture primarily on 7th metazonite and usually relatively large, occasionally extending beyond stricture into prozonite and reducing latter to narrow strip, usually smoothly rounded to ovoid, variably expanded, lobed, or with caudolateral corners flared and anterior margin slightly indented in Eurymerodesmina (Euryurinae: Eurymerodesmini). Gonopodal coxae joined by either sclerotized sternum, remnant of latter, or membrane, solenite socket completely separated from distal margin. Telopodites *in situ* usually overlapping, interlocked, or subparallel, extending anteriad and overhanging anterior margin of aperture, subparallel, projecting caudad, and overhanging caudal margin in Eurymerodesmina; comprised of a globular, pilose "prefemur" giving rise to "acropodite" and often one or occasionally two additional and highly variable projections, "prefemur" extending distad for varying lengths along "outer acropodital surfaces," completely encircling latter in Euryurini and absent from Eurymerodesmina; prefemoral hairs sometimes shorter and extending (dis)continuously along "prefemoral extensions." "Acropodite" structurally variable, plesiomorphic condition long, slender, and "stick-like," sublinear or curving/bending distal to midlength, a single projection or divided at varying positions into "solenomere" and one or two variably long additional branches, apomorphically prolonged, shortened, expanded, thickened, twisted, looped, ornamented, cingulate, or varying combinations of these; with at most only a few scattered hairs distal to "prefemoral extension**s**" except in Euryurinae where they extend (dis)continuously for varying distances along "inner" or, occasionally, "inner" and "outer" margins beyond "prefemora" or "prefemoral extensions," hairs varying in lengths and densities, often denser and "tufted" distad.

Components. Three subfamilies, one monobasic and two divided into two or nine tribes.

Distribution (Fig. 17–21). Five major Holarctic regions, one extending into the northernmost continental Neotropics. Xystodesmidae is the dominant and virtually only Holarctic leptodesmidean family, and it is particularly so in the three regions of the New World detailed in the Distribution section. In the Palearctic, it occurs in three areas/subregions of far eastern continental and insular Asia as well as three along the Mediterranean and adjoining seas and in two large and several small islands in southern Europe, northern Africa, and the Middle East. The family is absent from the vast intervening area of Central Asia and overall is known from 22 countries and projected for two others as follows: North and Central America, five countries – Canada, United States, Mexico, Guatemala, El Salvador (projected for Belize and Honduras); Africa, two countries – Morocco, Algeria; Europe, six countries – France, Italy ("mainland" and Sardinia), Albania, Macedonia, Greece, Turkey; Mediterranean Islands, one country—Cyprus; Asia Middle East, one country—Turkey, Asia Far East, seven countries—Russia, North Korea, South Korea, Japan, Taiwan, China, Vietnam.

Remarks. With the incorporation of Euryuridae and Eurymerodesmidae, Xystodesmidae essentially becomes a "catch-all" taxon and the Holarctic leptodesmidean counterpart to the primarily Neo- and Afrotropical Chelodesmidae (Chelodesmoidea). The ventrodistal spine on the ambulatory prefemora that has been considered diagnostic only occurs in four east-Nearctic taxa: Nannariina (Euryurinae) and Apheloriini, Pachydesmini, and Rhysodesmini (Xystodesminae). Practically every character has an exception, particularly in Euryurinae. The primary unifying feature is its Holarctic distribution, but even this has an exception, the northern continental Neotropics. These additions overwhelmingly render Xystodesmidae the dominant leptodesmidean taxon in the Northern Hemisphere or land masses deriving from the supercontinent Laurasia. Only three other leptodesmidean families inhabit continental regions of this enormous area: Sphaeriodesmidae (Sphaeriodesmoidea), a Neotropical immigrant represented by the two species of *Desmonus* Cook in the southern/southeastern US (Cook 1898; Causey 1958; Chamberlin and Hoffman 1958; Hoffman 1980, 1999; Shelley 2000a); Chelodesmidae (Chelodesmoidea), represented by *Cantabrodesmus lorioli* Mauriès, in caves in northern Spain (Mauriès 1971, 1974; Luque and Labrada

2017) and, with our action, *Macellolophus excavatus* Verhoeff, in southeastern Spain (Verhoeff 1931; Attems 1940; Mauriès 1978; Mauriès and Vicente 1978; Vicente 1988; Ceuca 1988; Mauriès et al. 2006); and Oxydesmidae (Xystodesmoidea), represented by the two species of *Libanaphe* Hoffman in the coastal Middle East (Lebanon and Israel) (Hoffman 1963; Tabacaru 1995; Golovatch 2007).

Subfamily Euryurinae Pocock 1909, Revived Status from Pocock (1909a) and Hoffman (1954, 1980))

Diagnosis. Small to moderately long (~12–40 mm) and relatively slender Xystodesmidae, anteriolateral paranotal corners with or without a small tooth; ambulatory prefemora without ventrodistal spines, epiproct bluntly subtriangular (Melaphina) or broad and spatulate (Euryurina). Gonopodal aperture rounded or with slight anterior indentation and flared caudolateral corners, margins smooth and glabrous or lobed and hirsute; gonopodal telopodites with or without prefemoral processes, prefemora with (in)complete extensions; acropodites arising from either prefemora or their extensions and with three configurations: long, slender, "stick-like," and bent subapically; long, slender, gently curved around midlength and resembling the number "7"; or sublinear and terminating in apical calyx.

Components. Two tribes, Euryurini and Eurymerodesmini.

Distribution (Fig. 1). East-Nearctic/eastern, southcentral, and southeastern US and Palearctic of northwestern Mediterranean Africa, southern Balkan Peninsula, western Turkey, and Aegean and Mediterranean Islands including Cyprus. In the Nearctic, Euryurinae extends, north/south, from Lake Ontario New York, northern Ohio and Indiana, central Illinois, eastern Minnesota, and northeastern Nebraska, to central peninsular Florida, the Gulf Coast, and the Rio Grande. East/west, it extends from western New York, eastern Pennsylvania, Maryland and Virginia west of Chesapeake Bay, and the Atlantic Coast of southeastern North Carolina through northeastern Florida to southeastern Minnesota, central Iowa, northeastern Nebraska, and central Kansas to west of the Pecos River at its confluence with the Rio Grande. The area includes two gaps, a narrow one in eastcentral North Carolina and a wider one in western Iowa and adjoining northern Missouri. In the Palearctic, Euryurinae cover the familial areas in Africa, the Middle East, Balkans, and Aegean and eastern Mediterranean Islands.

Remarks. In accordance with the transferral of *Macellolophus* to Chelodesmidea, we delete the area of Spain ascribed to Melaphina, formerly Melaphinae, by Hoffman (1962a, 1980) and him and Lohmander (1968). Neither Xystodesmidae nor Melaphina per our concept inhabit the Iberian Peninsula.

Tribe Euryurini Pocock 1909, Revived Status from Brolemann (1916) and Hoffman (1980)

Diagnosis. Moderately long, relatively slender, pliable and flexible Euryurinae with reddish-orange or yellow middorsal spots and paranotal markings, anteriolateral paranotal corners with small but distinct teeth, postgonopodal sterna in males and all sterna in females glabrous or nearly so. Gonopodal apertures rounded and glabrous. Gonopodal coxae connected by sclerotized sternum; telopodites with complete "prefemoral elongations" extending for around 1/3-½ of acropodital lengths and completely encircling latter, acropodites usually gently or moderately curved/bent around midlengths, usually bifurcated distad into subacuminate, longer, dorsal solenomere and shorter ventral branch, undivided in two species, terminating in short apical calyx in one genus.

Components. Two subtribes, Euryurina and Melaphina.

Distribution (Fig. 1, red line). East-Nearctic/eastern US and Mediterranean Palearctic. In the former, Euryurini range, north/south, from western Pennsylvania, the northern half to 2/3 of Ohio and Indiana, central Illinois, southwestern Wisconsin, and southeastern Minnesota to northern peninsular Florida, the Gulf Coast of the Panhandle and Alabama/Mississippi, and southern Louisiana. East/west, it extends from western Pennsylvania, southcentral Virginia, southeastern North Carolina, and the Atlantic Coast of South Carolina and Georgia to southeastern Minnesota, central Iowa, southwestern Missouri, and eastern Oklahoma. The boundary through eastcentral North Carolina connects the state's disparate

easternmost localities with those in Virginia and South Carolina, but euryurinines are concentrated in the dotted western/westcentral area.

Subtribe Euryurina Pocock 1909, New Status

Diagnosis. Euryurini/-inae with apically broad, spatulate epiprocts.

Components. *Euryurus* Koch, *Auturus* Chamberlin. (Hoffman 1954, 1978b, 1980, 1999; Shelley 1982a, b; Jorgensen 2009).

Distribution. Same as that of Euryurini (Fig. 1, red line).

Subtribe Melaphina Brolemann 1916, New Status

Diagnosis. Euryurini/-inae with apically narrow, subtriangular epiprocts.

Components. *Melaphe* Cook, *Ochridaphe* Hoffman (Hoffman 1962a, 1978a, 1980; Hoffman and Lohmander 1968).

Distribution. Same as those of Euryurinae/Euryurini in the Mediterranean Region (Fig. 21).

Tribe Eurymerodesmini Causey 1951, New Status

Diagnosis. Small to moderately long and broad, stiff and inflexible or flexible Euryurinae with apically narrow, subtriangular epiprocts, anteriolateral paranotal corners smoothly rounded, without teeth; postgonopodal sterna in males and all sterna in females nearly glabrous or variably hirsute; ambulatory prefemora with or without spines. Gonopodal aperture glabrous and rounded/ovoid or large, hirsute, and elaborately modified with anterior indentations, and triangular or clavate lobes on caudal margins or flared caudolateral corners. Gonopodal coxae connected by membrane only, without sclerotized sterna or remnant of same; telopodites with or without variably long prefemoral processes and partial prefemoral extensions; plesiomorphic acropodites long, slender, and "stick-like," extending sublinearly from prefemur and curving/bending abruptly (90°) subapically, "distal zones" short, apically (sub)acuminate; "inner" surfaces of acropodital stems adorned (dis)continuously up to "distal bends" with moderately long to long, stiff or wavy and flexible hairs, with or without apical clusters/tufts and equivalent tufts on "outer" margins. Cyphopod valves normal for family or enlarged with modified, dactyliform distal corners.

Components. Two subtribes, Eurymerodesmina and Nannariina, **new statuses**.

Distribution. East-Nearctic/eastern, central, southcentral, and southeastern US. The combined ranges of the two components encompass much of the eastern 1/2–2/3 of the US and extend, north/south, from western New York, northern Ohio and Indiana, central Illinois, Missouri south of the Missouri River, and northeastern Nebraska to northern peninsular Florida, the Gulf Coasts of Florida through Texas, and the Rio Grande. East/west, Eurymerodesmini extends from westcentral New York, eastcentral Pennsylvania, Maryland and Virginia west of Chesapeake Bay, and the Atlantic Coast of southeastern North Carolina through northeastern Florida to northeastern Nebraska and central Kansas, then angling progressively southwestward to the Rio Grande in Texas west of the confluence with the Pecos River (Fig. 1, 7). A curious, slit-like hiatus curves from eastern North Carolina through central South Carolina and northcentral Georgia to northern Alabama. RMS has sampled intensively in this lacuna from North Carolina to Georgia without encountering either component, so students should be alert to potentially filling it in the future.

Subtribe Eurymerodesmina Causey 1951, New Status

Diagnosis. Stiff and inflexible Eurymerodesmini, mandibular stipes with basal ridges extending into variable projections, postgonopodal sterna of males and all sterna of females hairy and without spines,

caudal margins sublinear or gently curved, ambulatory prefemora without ventral spines, pregonopodal tarsal claws in males acuminate, gently curved or bisinuate. Gonopodal aperture usually heavily pilose, often enlarged or ornamented with variable configurations, anterior margin usually slightly indented, lateral margins simple or divided near midlengths into flared inner and outer margins forming hirsute pouches at caudolateral corners, caudal margins with or without densely hirsute subtriangular or clavate lobes, latter usually extending below level of adjacent ambulatory coxae. Gonopods laterally oriented, each rotated 180° *in situ* with cannulae laterad and telopodites extending caudad and overhanging caudal aperture margins; telopodites without prefemoral processes and extensions; acropodites arising directly from prefemora, hairs long and thickened, extending (dis)continuously varying distances along stems to "distal bends" or ~7/8ths of acropodital lengths, usually with variably dense tufts apically on "inner" or "inner" and "outer" margins, former overhanging and partly obscuring bends and much of "distal zones"; cyphopodal valves large and hirsute, distal corners often modified into ridges and variable projections, occasionally long, dactyliform, and protruding through cyphopodal aperture.

Component. *Eurymerodesmus* Brölemann (syns. *Kewanius* and *Paresmus*, both by Chamberlin) (Shelley 1990a, Hoffman 1999).

Distribution (Fig. 1, black line, 16). East-Nearctic, endemic to the central, southcentral, and southeastern US. Eurymerodesmina occur, north/south, from northeastern Nebraska, the Missouri River in Missouri, central Illinois, the Fall Zone region of the southeast, and the Atlantic Coast of southeastern North Carolina to northern peninsular Florida and the Gulf Coasts of the Panhandle through Texas to the Rio Grande. East/west, they extends from the Atlantic Coasts of southeastern North Carolina through northeastern Florida to eastern Nebraska, the plains of central Kansas and southwestern Oklahoma, the Edwards Plateau of central Texas, and west of the Pecos River near its confluence with the Rio Grande.

Remarks. While Shelley (1990a) addressed virtually every aspect of *Eurymerodesmus*, a few bear repeating here. In addition to each gonopod's being rotated 180° in the aperture such that the cannula is lateral instead of medial and the acropodites extend caudad *in situ* overhanging the caudal, rather than the anterior, aperture margins, the genus and its higher taxa reverse the overall gonopodal condition in both Xystodesmoidea and Leptodesmidea. To our knowledge, the apertures are simple and unmodified while the gonopods are elaborate and ornate in most representatives of these taxa. Likewise, while the lengths of the acropodital hairs vary, the long ones that usually extend well down the stems are the most conspicuous and contrast markedly with the short hairs in xystodesmines that are primarily basal and restricted to the "prefemoral extensions." The hairs actually comprise two or three rows, and the apical tufts have from 4–18 hairs that substantially overhang the "distal zones", with the higher numbers of hairs obscuring the latter.

Previously, the cumulative weight of the host of autapomorphies left no alternative to according separate familial status to *Eurymerodesmus*, and even now, its ties to the rest of Xystodesmidae seem weak compared to the magnitude of unique features. However, anatomical connections undeniably exist through Nannariini, and as *Eurymerodesmus* shares ancestry with an unquestioned xystodesmid component, it must also belong to the family. Like Chelodesmidae in the Neo- and Afrotropics, Xystodesmidae is thus a "catch-all," heterogeneous assemblage with no single unifying anatomical feature. The ventrodistal spines on the ambulatory prefemora are shared only by Nannariina and the endemic east-Nearctic xystodesmine tribes—Apheloriini, Pachydesmini, and Rhysodesmini—as now constituted. No west-Nearctic tribe possesses the spine including Chonaphini, represented in the east by only *Semionellus* Chamberlin. Additionally, while *Eurymerodesmus* spp. tend to be smaller than sympatric xystodesmines, the convex dorsums and general facies are so similar that adults can be mistaken for juveniles of the latter, and juveniles of these taxa are virtually indistinguishable. Consequently, we submerge Eurymerodesmidae under Euryurinae, which holds 42 years of priority for the family-group name, the shared "hairiness" alone constitutes evidence of common ancestry and a sufficiently close relationship to justify this action.

Subtribe Nannariina Hoffman 1964, New Status

Diagnosis. Flexible and pliable Eurymerodesmini; mandibular stipes smooth, without ridges or projections; postgonopodal sterna of males and all sterna of females essentially glabrous, caudal margins with acuminate, subtriangular spines subtending leg coxae; ambulatory prefemora with ventrodistal spines; pregonopodal tarsal claws of males twisted, broad, and spatulate. Gonopodal aperture glabrous, rounded or ovoid, margins not modified. Gonopods *in situ* medially oriented, cannulae mediad and telopodites extending anteriad over anterior margins of apertures; telopodites usually with variable prefemoral processes, acropodital hairs moderately long, usually discontinuous with light apical tufts on "inner" margins not obscuring "distal zones." Cyphopodal valves of normal sizes and proportions for family, completely hidden in apertures, distal corners without extensions and projections.

Components. *Nannaria* and *Mimuloria*, both by Chamberlin; *Oenomaea* Hoffman (Hoffman 1964a, 1980, 1999; Hennen and Shelley 2015).

Distribution (Fig. 1, green; Fig. 16, red). East-Nearctic; endemic to the central and eastcentral US. The distribution extends, north/south, from Lake Ontario New York, northern Ohio, central Illinois, and Missouri south of the Missouri River to northeastern/eastcentral North Carolina, northernmost South Carolina, northern Georgia and Alabama, and northeastern Arkansas; east/west, it ranges from Virginia and Maryland west of Chesapeake Bay, eastcentral Pennsylvania, and adjacent New York to western Missouri and adjacent northern Arkansas.

Remarks. Because of their clearly shared ancestry, we transfer this taxon from Xystodesminae to Eurymerodesmini, which holds priority by 13 years for the tribal name. Nannariinan acropodital hairs are longer than in any xystodesmine taxon, and they extend (dis)continuously along primarily the "inner" surface rather than the "outer," as shown by Chamberlin (1949, Fig 1) and Hoffman (1964a, Fig. 11) in the *in situ* gonopods of *Nannaria minor* Chamberlin. Additionally, eurymerodesminans and nannariinans are similar in overall body sizes and convexities of the dorsums. Divergence entailed development of a prefemoral process by Nannariina, which retained plain, ovoid apertures and traditional cyphopods, while Eurymerodesmina developed extreme elaborations of both, and their overlapping ranges in Arkansas and Missouri, west of the Mississippi River, and Illinois, Kentucky and Tennessee to the east, support our shared ancestry hypothesis. Molecular investigations are also in order.

Geography

Xystodesmidae were previously thought to occupy four areas in the Nearctic biogeographic realm, one extending southward into the northern continental Neotropics, and two in the Palearctic, but the latter encompasses three separate areas of both the Mediterranean regions of Africa, Europe, and the Middle East and eastern Asia including both the continent and eastern islands (Hoffman 1962a, 1969, 1978a, 1980, 1999; Hoffman and Lohmander 1968; Shelley 1987). However, the taxonomic changes herein result in combining the east-Nearctic and Meso-American areas of Shelley (1987) such that the family now inhabits three parts of the New World/Nearctic. Hoffman's sketchy world distribution maps (1969, 1978a) are outdated, so we provide a new one (Fig. 17) and closer and more detailed one of the four general regions (Fig. 18–21). Distances between the closest points of these general regions are as follows:

East-Nearctic to West-Nearctic/Western Interior: Cass Co., North Dakota – northwestern Montana: 1,192 km (745 mi). Meso-American subregion to West-Nearctic/Pacific Coastal: Grant Co., New Mexico – to disjunct area in southern California and southern tip of eastern branch: 954 km (596 mi).

West-Nearctic/Pacific Coastal to East-Asian: Central-coastal Oregon to Hokkaido, Japan: 7,229 km (4,518 mi).

East-Asian/China Interior to Mediterranean: Sichuan Prov., China to southern coastal Turkey: 6,613 km (4,518 mi).

Mediterranean to East-Nearctic: Morocco to northern New Jersey: 5,928 km (3,705 mi).
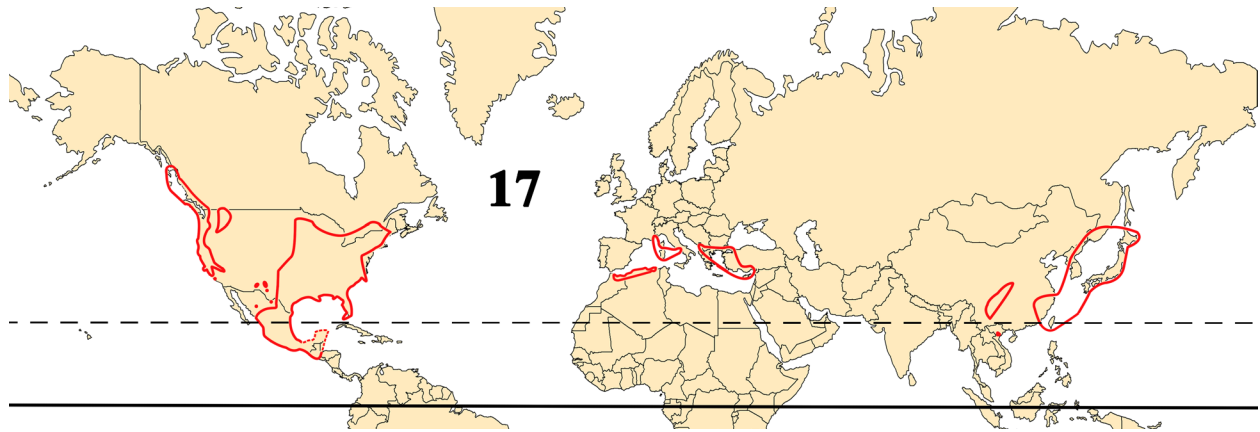
Figure 17. Global distribution of Xystodesmidae.

Figure 18. The East-Nearctic Region of Xystodesmidae. The eastern- and northernmost dots denote localities of the two Appalachian species of *Rhysodesmus*; the dot in Texas within the black line signifies the northernmost locality of *R. texicolens* (Chamberlin), San Diego, Duval Co. The arrow indicates Bald Head Island, NC, occupied by *Apheloria* (Xystodesminae: Apheloriini).

New World Areas (Fig. 17–19)

Eastern/Southern Nearctic and Northern Continental Neotropics (Fig. 18)

While Euryurini occur entirely within this subregion as previously mapped (Hoffman 1978a, b; Shelley 1982a, b, 1987), incorporation of Eurymerodesmidae fills the hiatus between the east-Nearctic and Meso-American areas depicted by Shelley (1987). This action yields an enormous area extending continuously from Montréal Island, Québec, Canada, to the south Florida Keys, the entire Gulf Coast of the US, "mainland" Mexico to at least Tabasco (projected for the Yucatan states) that terminates in western El Salvador. The eastern Mexican border coincides with the Gulf Coast through part of Tabasco, and we show a dashed line around the Yucatan Peninsula where *Rhysodesmus mayanus* Chamberlin was described from an unknown site. We arbitrarily continue this projected border around Belize and a corner of Honduras to the known site in El Salvador, which therefore encompasses nearly all of Guatemala. The maximal north/south distance of this continuous area, extending from Montréal Island to El Salvador, is around 4,944 km (3,090 mi); for convenience, we recognize two subregions and address them separately.

East-Nearctic subregion (Fig. 18). Formerly, this area terminated in eastern Texas (Jasper to Nacogdoches Cos.), leaving a lacuna of some 968 km (605 mi) to the Rio Grande Valley at Edinburg, Hidalgo Co., where the "Mesoamerican" region arose. Although this void is shortened with the discovery of *Rhysodesmus texicolens* (Chamberlin) at San Diego, Duval Co., around 161 km (101 mi) north of Edinburgh, it is still fully occupied by Eurymerodesmina, which angles through eastern Nebraska, central Kansas, western Oklahoma, and central Texas to west of the Pecos River near its confluence with the Rio Grande (Shelley 1990a). The borders of Eurymerodesmina and East-Nearctic Xystodesminae coincide from Nebraska to Ellsworth Co., Kansas, where the latter curves southeastward to northeastern Texas. The northernmost records, of Xystodesminae, are from Montréal Island, Québec, and to the east, the boundary angles southeastward to St. Johnsbury, Caledonia Co., Vermont, and then eastward to Norway, Oxford Co., Maine (Shelley and Whitehead 1986). To the west, it slants southwestward through Simcoe Co., Ontario, and along southern Lake Huron before crossing the St. Claire River into Michigan, curving through Clinton and Ottawa/Muskegon Cos., and crossing Lake Michigan to Washington Co., Wisconsin. The northern border then heads sharply northwestward to Polk Co., Minnesota, and Cass Co., North Dakota, around 141 km (88 mi) south of the Canadian border. Thus, in addition to Québec and Ontario in eastern Canada, Xystodesmidae/-inae may also occur around Gretna and Tolstoi, Manitoba.

The western border, still of Xystodesminae, arises at Fargo and heads southward through eastern South Dakota (Shelley and Snyder 2012) before crossing the Missouri River and intersecting Eurymerodesmina in Cuming Co., Nebraska. They align and run southwestward to Ellsworth Co., Kansas, where Eurymerodesmina continues this slope through western Oklahoma and central Texas while Xystodesminae angles southeastward through central Oklahoma and northeastern Texas. The boundary from Ellsworth Co. to the Rio Grande is as shown by Shelley (1990a), and the southern margin follows the River downstream until it intersects the Meso-American subregion between Webb Co., Texas, and Coahuila, Mexico.

Lacking records from Maine and New Hampshire, the eastern margin logically runs southward from Oxford Co., Maine, to Norfolk Co., Massachusetts, in western metropolitan Boston. It then slants southwestward through northwestern Rhode Island (projected occurrence), New Haven and the Thistle Islands, Connecticut, crosses Long Island Sound, the Island itself through Queens/Brooklyn, and the "neck" of New Jersey to the Delaware River thus enclosing all of Pennsylvania. It then angles across northern Delaware and northeastern Maryland before heading southward along the western shore of Chesapeake Bay and crossing Virginia west of Portsmouth. In North Carolina, the border, still of Xystodesminae, touches the western corners of Albemarle and Pamlico Sounds and the Neuse River Estuary before intersecting Eurymerodesmina, which spreads eastward through Carteret Co to the Atlantic Coast. They run together along the coast of southeastern North Carolina, with Xystodesminae diverging to encircle Bald Head Island (Fig. 18, arrow), reconnect in Horry Co., South Carolina, and continue along the Atlantic Coast to Amelia Island, Florida, where they diverge again. Eurymerodesmina angle across the Peninsula to Pasco Co. and then run northwestward to the Gulf Coast while Xystodesminae continue

along the Atlantic Coast, encircle the Keys (*Pleuroloma cala* (Chamberlin) inhabit Big Pine Key (Shelley 1980)), run northward along the Gulf Coast, and rejoin Eurymerodesmina at Hernando Co., north of Tampa Bay. They continue along the southern Gulf Coast to Louisiana, where Xystodesminae head inland north of the bayous while Eurymerodesmina follow the coast to the Rio Grande Delta between Cameron Co., Texas, and Tamaulipas, Mexico.

Dimensions of the East Nearctic subregion are, north–south, 2,386 km (1,491 mi), from both Montréal Island to Big Pine Key and Polk Co., Minnesota, to the mouth of the Rio Grande. East-west, the area extends for 2,086 km (1,304 mi) from both Norfolk Co., Massachusetts, to eastern South Dakota and Amelia Island, Florida, to across the Pecos River in Terrell Co., Texas. The area encompasses parts of two Canadian provinces, Ontario and Québec, and every US state east of those with the Rocky Mountains except Rhode Island, where occurrence is projected. This includes parts of 37 states and all or essentially all of 20: Alabama, Arkansas, Connecticut, Florida, Georgia, Illinois, Indiana, Iowa, Kentucky, Louisiana, Mississippi, Missouri, New Hampshire, New York, Ohio, Pennsylvania, South Carolina, Tennessee, Vermont, and West Virginia. The poorly sampled Delmarva Peninsula conspicuously lacks records, the only Delaware locality (see below) being northwest of Wilmington and a mere 5.6 km (3.5 mi) from Pennsylvania. The same holds for southern New Jersey and the moderately sampled Outer Coastal Plain of northern/central North Carolina, where Xystodesmidae/-inae may truly be absent because swamps, pocosins, and pine forests are undesirable habitats. Xystodesmines are even known from coastal islands: the Thistles, Connecticut; Long Island, New York; Bald Head Island, North Carolina; coastal islands of South Carolina and Georgia; and Amelia Island, Big Pine Key, and other Floridian isles and keys. Although incorporation of Eurymerodesmidae expands the area westward in Oklahoma and Texas, by around 154 to 776 km (96 to 485 mi), it does not add any states, all of which were included in Shelley's (1987) mapping.

Taxa represented. Euryurinae: Euryurini: Euryurina; Eurymerodesmini: Eurymerodesmina, Nannariina. Xystodesminae: Apheloriini, Chonaphini, Pachydesmini, Rhysodesmini.

New peripheral records. *Sigmoria* (*Rudiloria*) *trimaculata trimaculata* **(Wood 1864). CANADA: Québec**: Carillon Island (Ottawa River), 6M, 2*F*, 19 September 1964, W. Hoek, D. Johnstone (LEM); and Ile de Montréal, Ste.-Anne-de-Bellevue, Morgan's Woods, 1M, 17 May 1952, A. C. Sheppard, and 1M, 1*F*, July 1965, A. Vlasek (LEM). **New Provincial Record for the (sub)family, genus, and species.**

USA: New York: *Kings Co.*, Brooklyn, 1M, 1885 (NMNH). **Vermont**. *Addison Co.*, Memorial State Park, 1M, 23 April 1976, R. Davidson (UVT). *Bennington Co.*, Beartown, 1M, 19 June 1954, F. and P. Rindge (AMNH). *Caledonia Co.*, St. Johnsbury, 2M, 4*F*, July 1913 (MCZ). *Chittenden Co.*, Burlington, 1M, 1868, J. B. Perry (MCZ). *Orange Co.*, Chelsea, 1M, F (MCZ). *Rutland Co.*, Tweed R., 1M, 10 September 1934 (UMN). *Windsor Co.*, Ascutney, Mt. Escutenary, 1M (MCZ). **New State Record for the (sub)family, genus, and species.**

Apheloria virginiensis corrugata **(C. L. Koch 1847). USA: Delaware**: *Newcastle Co.*, White Clay Creek State Park, 2M, 3*F*, 9 May 2007, R. M. Shelley (NCSM) **New State Record for the (sub)family, genus, and species. Virginia:** *York Co.*, Yorktown, Cheatham Station Naval Supply Center, 8M, 4*F*, 19 June 1989–30 May 1990, K. A. Buhlman (VMNH), Cheatham Pond, 3M, 3*F*, juv., 6 July 1989–2 November 1989, K. A. Buhlman (VMNH), and Jones Millpond, 2M, 6 July 1989, and 1M, 16 April 1990, K. A. Buhlman (VMNH).

Apheloria **sp. USA: North Carolina:** *Pitt Co.*, Greenville, 2*F*, juvs., 26 February 1913, A. T. Anderson (NMNH).

References. Wood (1864, 1865), Pocock (1909a, b), Gunthorp (1913), Williams and Hefner (1928), Attems (1938), Chamberlin (1949), Hoffman (1954, 1956a, 1958, 1960, 1961, 1962b, 1963b, 1964a, 1965, 1967, 1969, 1978a, b, c, d, 1998a, b, 1999), Causey (1955a), Chamberlin and Hoffman (1958), Keeton (1959), Stewart (1969), Hoffman and Shear (1969), Shelley (1975, 1976, 1978, 1979, 1980, 1981a, b, 1982a, b, 1983a, b, 1984a, b, c, 1988, 1990a, b, c, 1991, 1994, 1999, 2000b, c, 2001a, b, c, 2002a, b), Shelley and Filka (1979), Filka and Shelley (1980), Kevan (1983), Shelley and Whitehead (1986), Snider (1991), Watermolen (1995), Shelley et al. (2004, 2011, 2012, 2017), Shelley and McAllister (2006, 2007), Snyder (2008), Jorgensen (2009), Marek (2010), Marek et al. (2014), Hennen and Shelley (2015).

Meso-American subregion (Fig. 18). The Meso-American subregion comprises a large, continuous southern area and five detached smaller ones that add New Mexico and Chihuahua to the rosters of US and Mexican states harboring Xystodesmidae. To encompass the record of *Rhysodesmus mayanus* from "Yucatan" without further specification (Chamberlin 1925, Loomis 1968, Hoffman 1999, Bueno-Villegas et al. 2004) and allow for undiscovered forms, we project occurrence (dashed line) around that peninsula, all of Belize and Guatemala, and the southwestern corner of Honduras. The continuous area extends, north-south, approximately 1,824 km (1,140 mi) in the east, from the Rio Grande to the El Salvador site, and the overall subregion extends around 3,040 and 1,800 km (1,900 and 1,125 mi) from Lincoln Co., New Mexico, and Duval Co., Texas, to the same. The greatest east-west distance, from the Gulf of Mexico in northern Tamaulipas to the Gulf of California in central Sinaloa, is around 799 km (726 mi) long. Xystodesmidae/-inae are known from parts or all of 25 Mexican states plus Distrito Federal, projected for three – Campeche, Yucatan, and Quintana Roo—with *R. mayanus* Chamberlin occurring in an unstated one, unknown and probably absent from two—Baja California and Baja California Sur, and unknown but potentially present in Sonora. While the projected eastern border encompasses all of Guatemala, the known one angles through the country and encompasses parts or all of 20 of the 22 departments, all but Petén and Izabal. Xystodesmidae/-inae extend only 66 km (41 mi) into El Salvador and are projected for the four northernmost departments—Ahuachapán, Santa Ana, Sonsonate, and La Libertad, the last also containing the southernmost locality of Parajulidae (Shelley 2008, Shelley and Golovatch 2011). The subregion traverses the Rio Grande and the southern boundary of Eurymerodesmina into the "Valley" of southernmost Texas and continues some 253 km (158 mi) north to San Diego, Duval Co. In Mexico, the northern border of the continuous area undulates southwestward through central Coahuila, northern Durango, and central Sinaloa to the Gulf of California northwest of Mazatlan. The western boundary then follows the Pacific Coasts of "mainland" Mexico and Guatemala before angling inland to Santa Ana Dept., about 1/4 of the distance into El Salvador (Kraus 1954, Loomis 1968, Hoffman 1999, Bueno-Villegas et al. 2004). The family also occupies five disjunct areas that include point localities in southwestern Chihuahua, Mexico; the Chisos Mountains, Big Bend National Park, Brewster Co., Texas, USA; and the Guadalupe Mountains, Guadalupe Mountains National Park, Culberson/Hudspeth Cos., Texas, USA. The non-point localities are two small areas in New Mexico – the Sacramento and Capitan mountains of Lincoln and Otero Cos. in the east, and west of the Rio Grande in the Black Mountains of Grant and Sierra Cos. in the west.

Taxa represented. Xystodesminae: Rhysodesmini.

New peripheral records. EL SALVADOR: Santa Ana: Matapan, Los Planes, 3M, 14 May 1973, V. J. Hellebuyck (VMNH) and F, 28 May 1977, V. J. Hellebuyck, E. E. Guardado (ROM).

MEXICO: Chiapas: Palenque, 1M, 18 June 1982, F. A. Coyle (VMNH). **Chihuahua:** Santo Nino, 1M, 2*F*, 26 July 1968, T. A. Sears, R. C. Gardner, C. L. Glaser (BME) **New State Record**. **Durango:** Arroyo Hondo nr. La Flor, 2 juvs., 9 August 1966, G. E. Ball, D. R. Whitehead (VMNH). **Jalisco:** Chamela Biological Sta., 2M, 2F, 20–21 July 1984, J. T. Doyen (EME) and 4M, 2*F*, juv., 16 July 1985, S. C. Williams (CAS). **Sinaloa:** El Palmito, 1M, 2 July 1964, J. E. H. Martin (CNC); 3.2 km (2.0 mi) SE Elota, 4M, 4F, 2 August 1966, J. S. Buckett, M. R. Gardner (BME); and unnamed waterfall on hwy. 40, 6.9 km (4.3 mi) S of Durango State Line, (23.567°N, 105.84517°W), elev. 6,487′, 2M, 13 July 2008. M. F. Medrano et al. (MSB). **Tamaulipas:** 4.8 km (3.0 mi) S Matamoros, 1F, 28 June 1959, W. T. Keeton, B. D. Valentine, Lund (VMNH); 8.0 km (5.0 mi) NE Llera, 1M, 23 June 1966, J. S. Buckett, M. R. Gardner (BME); 9.8 km (6.1 mi) E Nuevo Morelos, 1M, 12 October 1965, G. E. Ball, D. R. Whitehead (VMNH); 6.4 km (4.0 mi) N Juamave, 1M, 1F, 20 September 1979. J. C. and J. E. Cokendolpher (FSCA); and Altas Cumbres, Ciudad Victoria, 2M, 11 May 1987, P. W. Kovarik, R. Jones (FSCA). **Veracruz:** 4.0 km (2.5 mi) W Sontecomapan, San Andros Mts., 1M, 20 September 1965, G. E. Ball, D. R. Whitehead (VMNH).

USA: Texas: *Duval Co.*, San Diego, 1M, 3M, 22 May 1889 (BMNH). *Webb Co.*, 56.0 km (35.0 mi) NW Laredo, 1M, 22 September 1972 (UTIC). *Zapata Co.*, 8.0 km (5.0 mi) N Zapata, 1F, J. F. Karges (NCSM).

References. Chamberlin (1922, 1925, 1941, 1943), Attems (1938), Kraus (1954), Chamberlin and Hoffman (1958), Causey (1964), Loomis (1966, 1968), Hoffman (1966, 1970, 1999), Shelley (1987, 1989, 1992), Bueno-Villegas and Fernandez (1999), Bueno-Villegas et al. (2004), Marek et al. (2014).

Figure 19. The West-Nearctic Region of Xystodesmidae. Left, Pacific Coastal Subregion. Right, Western Interior Subregion. The detached, cluster of dots to the south show the area of *Motyxia monica* Chamberlin in the Santa Monica Mountains and northern metropolitan Los Angeles.

West-Nearctic areas

Pacific coastal region (Fig. 19). The Pacific Coastal Region stretches from the southernmost islands in the Alexander Archipelago, Alaska, to the northern San Joaquin Valley, California, where it forks into western and eastern branches. The former runs along the Pacific to central San Luis Obispo Co. (SLO), with an isolated area some 248 km (155 mi) to the south in the Santa Monica Mountains and northern metropolitan Los Angeles, while the eastern branch continues along the western slope of the Sierra Nevada and associated foothills to Kern Co. Arising on Forrester Island, Alaska, the outer/western border follows the Pacific coasts of the Queen Charlotte (Haida Gwai) and Vancouver islands, British Columbia (BC), and along the subcontinuous coastline in the US, except for swinging offshore at San Francisco Bay to encompass the Farallon Islands. The inner/eastern border extends southward along the eastern side of Prince of Wales (POW) Island, Alaska, enters continental BC around Prince Rupert, runs slightly inland along the western slope of the Coast Range for around 736 km (460 mi), angles eastward around Squamish, in southern BC, and continues southeastward to the summit of the northernmost Cascade Mountains in Manning Provincial Park, thus encircling metropolitan Vancouver. In the lower 48 US states, the eastern boundary passes along the eastern slope of the Cascades in northern Washington and the western slope from southern Washington to Mt. Lassen, California, thereafter continuing along the western slope of the Sierra Nevada to Kern Co. and elevating to >7,000′ in Sequoia National Park. The western border of the eastern branch runs through the Sierra foothills, while the eastern border of the western branch passes through those of the Coast Range before curving to the coast in SLO. Collectively, the region covers islands and continental areas of one Canadian Province and all four Pacific Coastal US states. In addition to Vancouver and the Queen Charlottes, Canadian islands include Dundas, the Scotts, and all those between Vancouver Island and "mainland" BC; major US islands include Forrester, Dall, Kosciusko, and POW, Alaska; the San Juans and Pacific Coastal islands of Washington and Oregon, and the Farallons and islands in San Francisco and San Pablo Bays, California, including Alcatraz. However, xystodesmids/-ines have never been taken on southern California islands like the

Channels and Santa Catalina. Lengthwise, the continuous north-south dimension is some 3,875 km (2,422 mi) in the east and 3,720 km (2,325 mi) along the coast. The detached California area lies south of the southernmost latitude in Kern Co., so the maximal overall length of the Pacific Coastal region is approximately 3,968 km (2,480 mi). Widths range from around 336 km (210 mi) at the International Border to across Vancouver Island, 216 km (135 mi) along that between Oregon and California; selected additional breadths are 192 km (120 mi) from the Pacific Coasts of the Queen Charlotte Islands to the inner border in continental BC and 198 km (180 mi) at the widest point in northern California. Maximal widths of both the western and eastern branches are roughly 26 km (16 mi).

Diversity in the Pacific Coastal region increases markedly from north to south. The only inhabitant of the northern- and westernmost 1,064 km (665 mi), or almost the complete north/south distance in Canada, is *Harpaphe h. haydeniana* (Wood) (Xystodesmini), and the only other Canadian species is *Tubaphe levii* Causey (Chonaphini), in the southwestern corner of Vancouver Island (Cook 1904; Causey 1954; Chamberlin and Hoffman 1958; Buckett and Gardner 1968a; Shelley 1990b, 1994, 2002a, c; Hoffman 1999). Both cross the Strait of Juan de Fuca into Washington's Olympic Peninsula, but *T. levii* is restricted to rainforests in Bogachiel, Hoh, Queets, and Quinalt Valleys, Olympic National Park/Forest (Causey 1954, Chamberlin and Hoffman 1958, Shelley 1994, Hoffman 1999). In addition to *H. h. haydeniana*, three species, all in Chonaphini, occur east of Puget Sound around the latitude of Seattle– *Chonaphe remissa* (Chamberlin), ranging southward to around 80.0 km (50.0 mi) north of the Columbia River; *C. armata* (Harger), in the heart of the Cascades; and *Montaphe paraphoena* Shelley, on their border with the Columbia Plateau (Shelley 1994, Hoffman 1999). *Thrinaphe hargeri* Shelley (Xystodesmini) occurs sympatrically with *C. remissa* in the south and traverses the Columbia River into northern Oregon (Shelley 1993a), and two additional chonaphinines—*C. evexa* and *Selenocheir directa*, both by Shelley (1994), inhabit southwestern Oregon.

Diversity increases dramatically in California, where Xystocheirini and Sigmocheirini are endemic. The former comprises four genera and ~25 species, arises on the Pacific Coast in Humboldt Co., spreads southward to northern Monterey Co. with *Motyxia bistipita* (Shelley) being disjunct in SLO, expands eastward at San Pablo Bay, and extends from El Dorado to Kern Cos. in the Sierras (Shelley 1995a, 1996, 1997; Shelley et al. 2014). Sigmocheirini, by contrast, is endemic to the foothills and lower elevations in the Sierras from Placer to Kern Co. and comprises only four species in two genera (Shelley 1995b). Additionally, two species of *Selenocheir* Shelley occur north of the "Bay Area" in the Coast, Cascade, and Sierra ranges, and *Harpaphe* Cook diversifies, primarily along the Coast, into two additional species and five subspecies of *H. haydeniana* (Buckett 1964, Buckett and Gardner 1968a) The southernmost, *H. h. scotia* Chamberlin, terminates around Big Sur, Monterey Co.

The Pacific Coastal fauna is dominated by three species: *Chonaphe armata* (Harger) (Chonaphini), in Washington and northern Oregon (Shelley 1994, Hoffman 1999); *Xystocheir dissecta* (Wood) (Xystocheirini), in coastal California from Humboldt to Monterey Cos. and also terminating around Big Sur (Shelley 1996, 2002c; Hoffman 1999), and *H. haydeniana* (Xystodesmini) throughout most of the region's length, particularly along the coast (Buckett 1964, Buckett and Gardner 1968a, Hoffman 1999, Shelley 2002c). It occurs from the northern extremity of POW Island to Big Sur, a distance of some 2,376 km (1,485 mi) or ~64% of the continuous coastal length. While we report a potential new record, the only definite one from the Sierras is the type locality of *H. h. maurogona* Buckett and Gardner in Nevada Co., California.

Taxa represented. Xystodesminae: Chonaphini, Sigmocheirini, Xystocheirini, Xystodesmini.

New and newly detailed peripheral records. *Harpaphe h. haydeniana* **(Wood): CANADA: British Columbia: Haida Gwaii (Queen Charlotte Islands): Graham I.,** Massett, F. W. E. Clark (MCZ); and 19.0 km (11.9 mi) E Massett, Tow Hill Rd., 1M, 13 July 1983, D. H. and M. D. Kavanaugh (CAS). **Kunghit I.,** Rose Harbor, 1F, 16 August 1960, J. B. Foster (RBCM); and nr. Bowles Pt., 1M, 28 June 1981, G. G. E. Scudder (UBC). **Moresby I.,** Mosquito L., Alliford Bay, and Paliant Cr. at Camp Moresby, 7M, 10*F*, 24 July 1981 and 16–21 July 1982, D. H. Kavanaugh (CAS); and W side of Louscoore, 1M, 29 June 1981, G. G. E. Scudder (UBC). **Vancouver Island:** *Kyuquot*, mouth of Amai Inlet, 1F, juv., 15 September 1958 (NMNH). *Tofino*, 1M, 21 June 1969 (RBCM). *Ucluelet*, 1M, 1980, R. A. Cannings (RBCM). **Islands Associated with Continental BC:** *Banks I.*, Rawlinson Anchorage (54°34′34″N, 130°32′34″W), 1F, 21 June 2005, C. Copley (RBCM). *Cortes I.*, Protection I. in Squirrel Cove (50°08′N, 124°55′W), 1M, 25 July 1986, D. H. and J. L. Kavanaugh (CAS). *Pitt I.*, Principe Channel, NE arm of

Patterson Inlet, 1M, 11 August 1986, D. H. and J. L. Kavanaugh (CAS); and Petrel Channel, Captain Cove, 1M, 12 August 1986, D. H. and J. L. Kavanaugh (CAS). *Porcher I.*, Chismore Passage, Spiller Cr. (54°01′N, 130°18′W), 1M, 1F, 13 August 1980, D. H. and J. L. Kavanaugh (CAS); Serpentine Bay (53°57′02″N, 130°42′43″W), 1M, 20 June 2005, C. Copley (RBCM); and W side of Refuge Bay, 1M, 9 June 1965, F. W. Grimm (CMN). *Sonora I.*, Owen Bay (50°19′N, 125°13′W), 1M, 1F, 26 July 1986, D. H. and J. L. Kavanaugh (CAS). *West Redonda I.*, Tealerme Arm, SE shore of Cresel Lake (50°12′N, 124°51′W), 1M, 26 July 1986, D. H. Kavanaugh (CAS). **Continental BC:** *Hope*, 2M, 2F, 10 August 1950, H. H. Ross (INHS); nr. Lake of the Woods, 2F, 6 October 1962, C. L. Reid (MCZ); Hidden Canyon Falls, 1M (TBMNH); Silver Cr., 1M, 2F, 12 June 1952, C. P. Holland (CNC); and 4.8 km (3.0 mi) SE Hope, along Silver Skagit Rd., juv., 30 June 1988, S. and J. Peck (NCSM). *Manning Prov. Pk.*, Whitworth Ranch, 39 May 1947, 1M (RBCM) and 3.2 km (2.0 mi) W Allison Pass, 1M, 30 July 1945, G. C. Carl (RBCM). *9.6 km (6.0 mi) N Hell's Gate*, cove along hwy. 1, 1M, juv., 26 July 1989, R. M. Shelley (NCSM). *16.0 km (10.0 mi) S Squamish*, along hwy. 99 at Furry Cr., 2M, 1F, 22 July 1980, D. H. Kavanaugh (CAS).

   USA: Alaska. *Dall I.,* Rose Inlet, 2M, 2F, 1 July 1947, G. D. Hanna (CAS). *Kosciusko I.*, Shipley Bay, SW slope of "The Nipples," 1M, 1F, 19 August 1991, D. H. Kavanaugh (CAS) **New Island Record**. *Prince of Wales I.*, Tongass National Forest, Daveyville Trail (57°14.7′N, 133°14′W), 1M, 5M, 14 August 2007, R. M. Shelley, M. F. Medrano, K. Ovaska (NCSM). **Washington:** *Jefferson Co.*, Bogachiel State Park, 3M, 25 March 1966, E. Thorn (RBCM). *Pacific Co.*, 2.2 km (1.4 mi) W Iliwaco, 1M, and Bay Center, 1M (TBMNH). **Oregon:** *Curry Co.*, 3.2 km (2.0 mi) E Gold Beach, 2M, 3 June 1991, R. M. Shelley (NCSM). *Deschutes Co.*, Lower Alder Springs Forest Camp along hwy. 242 W of Sisters, 1M, 11 June 1968, T. Yamamoto, I. M. Smith (ROM). *Douglas Co.*, S of Drew, Umpqua National Forest, jct. USFS rd. 1633 and OR hwy. 27, 6.4 km (4.0 mi) S of Tison Rd., 1M, 31 March 2015, C. H. Richart, J. Starret, S. Derkarabetian, A. Cabrero (VMNH). *Lincoln Co.*, nr. Toledo, 1M (TBMNH). *Linn* Co., House Rock Camp along US hwy. 20, Cascade Mtns., 10M, 26 June 1981, A. L. Braswell (NCSM). *Tillamook Co.*, 8.0 km (5.0 mi) W Dolph, juvs., 6 April 1962, D. R. Smith (OSU) and spring on hwy. 22, 1M, 11 July 1963 (ROM). **California**: *Del Norte Co.*, Del Norte Coast Redwoods State Park, 2M, 2F, 12 June 1991, R. M. Shelley (NCSM).

   Harpaphe haydeniana ?maurogona **Buckett and Gardner: USA: California:** *Sierra Co.*, along CA hwy. 49, 3.2 km (2.0 mi) E Yuba Pass, Tahoe National Forest, 1F, 29 May 1991, R. W. Baumann, Stark (BYUC).

   Harpaphe haydeniana scotia **(Chamberlin): USA: California:** *Monterey Co.*, Big Sur, 1F, 18 January 1966, J. Powell (EME) and 2M. 22 December 1968, J. S. Buckett, M. R. Gardner (BME); Pfeiffer Big Sur State Park, 1M, 1F, 3 May 1964, P. R. Craig, and M, 10 May 1970, S. C. Williams (CAS).

   References. Cook (1904), Attems (1938), Causey (1954, 1955b), Chamberlin and Hoffman (1958), Buckett (1964), Buckett and Gardner (1968a, b, 1969 a, b), Causey and Tiemann (1969), Kevan (1983), Shelley (1990d, 1993a, 1994, 1995a, b, 1996, 1997, 2002a, c), Hoffman (1999), Marek et al (2014), Shelley et al. (2014).

Western interior region (Fig. 19). Centered in the Idaho panhandle, the Western Interior Region, the smallest in the Nearctic, encompasses northeastern Oregon, eastern Washington, the northwestern periphery of Montana, and the southern fringe of BC bordering Idaho. Connection between the two western regions cannot now be documented but plausibly exists along the International Border, where they are around 168 km (105 mi) apart, and/or along that between Washington and Oregon, where they are separated by some 296 km (185 mi). Connection through the Columbia Plateau in central Washington is unlikely because its grassy, prairie environments are unfavorable for xystodesmines. Maximal dimensions of the Western Interior Region are 448 km (280 mi), north-south, and 314 km (196 mi), east-west.

   Although small, the Western Interior contains eight species, two chonaphinines—*C. armata* and *Montaphe elrodi* (Chamberlin)—being dominant. The former inhabits three detached areas in addition to the two along the Pacific Coast (Shelley 1994), and these five areas, representing fragments of a formerly continuous range, render *C. armata* the second most abundant xystodesmid in the northwestern US after *H. haydeniana*. The only xystodesmine inhabiting both the Pacific Coastal and Western Interior regions, *C. armata* is also the only inhabitant of all US states of the latter and the only xystodesmid/-ine in northeastern Oregon, where it primarily occupies the Blue and Wallowa Mountains. It also occupies a broad area in the southern Idaho Panhandle that extends into the eastern periphery of Washington

and the western of Montana. By contrast, *M. elrodi* inhabits a continuous area that covers the northern and southeastern Idaho Panhandle, northeastern Washington, and the entire (sub)familial range in Montana. It is also the only species believed to cross the International Border into southcentral BC, a distribution comparable to that of *Ergodesmus compactus* Chamberlin (Polydesmida: Macrosternodesmidae) (Whitney and Shelley 1995). Consequently, this sliver of BC near Yahk constitutes a new and third faunal area for Xystodesmidae/-inae in Canada, a second for BC, and contains a new genus and species for both the country and province. Its discovery just 2.5 km (1.6 mi) north of the International Border confirms the predictions of Shelley (1994, 2002b) for both the genus and species, and its occurrences 12.8 and 32.0 km (8.0 and 20.0 mi) south of the boundary in Pend Oreille and Stevens Cos., Washington (Shelley 1994), respectively, also suggest occurrence near Walneta and Nelway, BC. While our record is based on an unidentifiable juvenile, *M. elrodi* is the only proximate and plausible xystodesmid/-ine for this part of BC. We therefore provisionally record both taxa from the BC interior some 328 km (205 mi) east of the Pacific Coastal region.

Orophe Chamberlin, characterized by long, twisted gonopodal acropodites with short, subequal distal elements and short, spiniform prefemoral processes (Shelley 1993b), is of particular interest. The extreme lengths of the acropodites, which cross *in situ*, overlie the 6th and 7th legs (on segment 6), and extend beyond the lateral protergal margins make males readily recognizable in the field. While presently in Xystodesminae, *Orophe's* affinities lie not with a Nearctic taxon but with the Chinese genera *Pamelaphe* and *Kiulinga*, both authored by Hoffman (1956b, 1964b, 1980, 1999). He proposed a separate subfamily, Orophinae, in the second work but later (Hoffman 1980) demoted it to a tribe. We concur with contribal status for these three genera and employ the Asiamerica concept (Shelley and Floyd 2014) to explain such trans-Pacific disjunctions; the unanswered question, however, is where do Orophini's affinities lie. Based primarily on female characters, Hoffman (1978e) erected Parafontariinae for the Japanese genus *Parafontaria* Verhoeff, but we believe that such is unwarranted and tribal status suffices. However, if *Parafontaria* truly warrants a separate, monotypic subfamily, then surely *Orophe*, *Pamelaphe*, and *Kiulinga*, three genera with distinct male features and unknown affinities, do too. As *Harpaphe* (Xystodesmini) is super-abundant along the Pacific Coast of North America today, we envision ancestral xystodesminines crossing to the adjacent Asiamerica land mass and being transported to eastern Asia (Shelley and Floyd 2014). However, *Orophe* is in the Western Interior, not the Pacific Coast, so we hypothesize wider prior distribution that allowed forms to disperse into Asiamerica with subsequent reduction and extinction along the Pacific Coast. Consequently, today's *Orophe* (Shelley 1993b) may be a mere remnant of a formerly larger distribution, and *Harpaphe* seems the logical culprit both because of its abundance along the Pacific and its absence in the Western Interior. Perhaps it is no accident that *Orophe* and *Harpaphe* occur where the other is absent, and indeed, *Harpaphe's* tribe, Xystodesmini, has only one representative in the Western Interior, *Isaphe* Cook (Shelley 1993c), whose range does not overlap that of *Orophe*.

Taxa represented. Xysyodesminae: Chonaphini, Orophini, Xystodesmini.

New peripheral records. *Montaphe elrodi* **(Chamberlin). CANADA: British Columbia**, 7.0 km (4.4 mi) SW Yahk, along Shorty Cr. Rd. 1.5 km (0.9 mi) W hwy. 95, 2.5 km (1.6 mi) N US/Idaho border, juv., 24 April 2007, R. M. Shelley, M. F. Medrano (RBCM). **New Country and Provincial Records for both the genus and species; New Xystodesmid Faunal Area for both Canada and BC.**

USA: Washington: *Pend Oreille Co.*, 6.4 km (4.0 mi) N Metaline Falls [~12.8 km (8.0 mi) S Canadian/ BC border on WA hwy 6], 1M, 31 May 1993, R. M. Shelley (NCSM).

References. Cook (1904), Attems (1938), Hoffman (1956b, 1964b, 1999), Chamberlin and Hoffman (1958), Buckett and Gardner (1969c), Loomis and Schmitt (1971), Kevan (1983), Shelley (1987, 1990d, 1993b, c, 1994, 2002a), Marek et al. (2014).

Palearctic areas (Fig. 20–21)

East Asia (Fig. 20). Until three years ago, the east-Asian faunal region contained only the large sinusoidal subregion that stretches from Hokkaido, Japan, and the southern Maritime Province, Russia, to Taiwan and central eastern China. Its westernmost record, *Kiulinga jeekeli* Hoffman (Xystodesminae: Orophini), from Jiujiang, just south of the Yangtze River in northern Jiangxi Prov., some 608 km (380
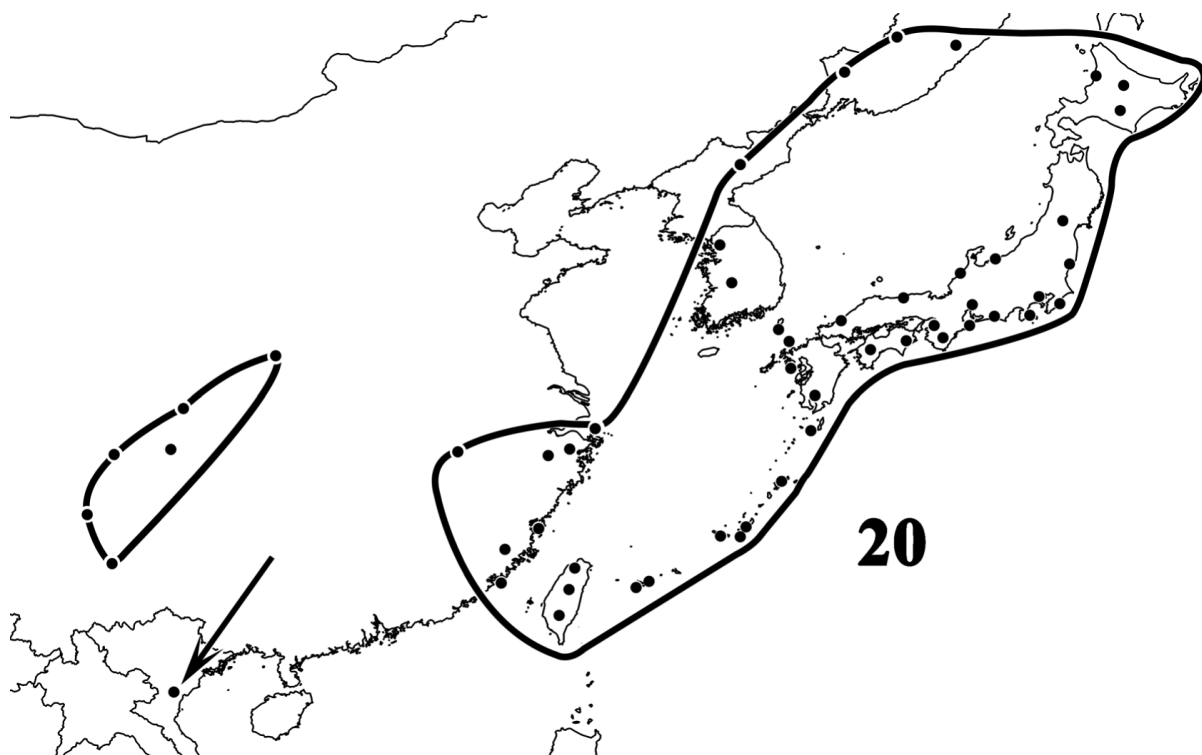
Figure 20. The East-Palearctic/East-Asian Region of Xystodesmidae. The arrow points to the site at Cuc Phuong National Park, Vietnam.

mi) southwest of Shanghai and about 570 km (356 mi) west of the East China Sea (Hoffman 1956b; D. Wang and Mauriès 1996; Marek et al. 2014), was also the westernmost East Asian locality for the (sub)family until Golovatch (2014, 2015) described *Riukiaria martensi* from Houzhenzi, Shaanxi Prov., around 989 km (618 mi) west-northwest of Jiujiang, and proposed five additional species from Sichuan Prov., which borders Shaanxi to the south-southwest. These records circumscribe a new, vertically subtriangular area in eastcentral China that is approximately 800 km (500 mi) in the long, northeast/southwest, dimension. Most recently, Nguyen (2016) described a new genus and species from Cuc Phuong National Park, Ninh Binh Prov., Vietnam, approximately 152 km (95 mi) from the Gulf of Tonkin and 1,368 and 912 km (855 and 570 mi), respectively, from the coastal and interior Chinese subregions. We think that the two Chinese subregions will eventually be connected, but whether one or both also link with the lone Vietnam locality cannot now be projected. This part of eastern continental Asia has received only a modicum of sampling (Hoffman 1969, D. Wang and Mauriès 1996) and surely harbors a large, diverse fauna.

The sinusoidal, coastal/insular subregion enters eastern China south of Shanghai and the Yangtze River and extends around 533 and 1,064 km (333 and 665 mi) westward and southward. The maximal north/south length of the entire region is 4,256 km (2,660 mi); east/west, it is 989 km (618 mi) across Hokkaido and Russia, 1,216 km (760 mi) from easternmost Honshu to northeastern North Korea, 1,141 km (713 mi) from the Ryukyu Islands to Jiujiang, China, and 760 km (475 mi) from southern Taiwan to the longitude of Jiujiang. The subregion covers parts of six countries including all or essentially all of Japan (including the Ryukyu Islands), South Korea, and Taiwan while excluding Sakhalin and the Kurile Islands, Russia (Mikhaljova and Basarukin 1995; Mikhaljova 2010), ones east of Taiwan, the Ryukyus, and "mainland" Japan, and Botel Tobago and minute islets between Taiwan and Luzon, Philippines (Y. Wang 1951, 1955, 1957, 1961, 1963, 1964). A smooth curve drawn through peripheral localities nips the eastern fringes of Heilongjiang and Jilin (formerly Manchuria), China, angles through northeastern and southwestern North Korea, crosses the Yellow and East China Seas, and re-enters China south of the Yangtze River. A faunal boundary exists between Taiwan and Luzon because just as Xystodesmidae
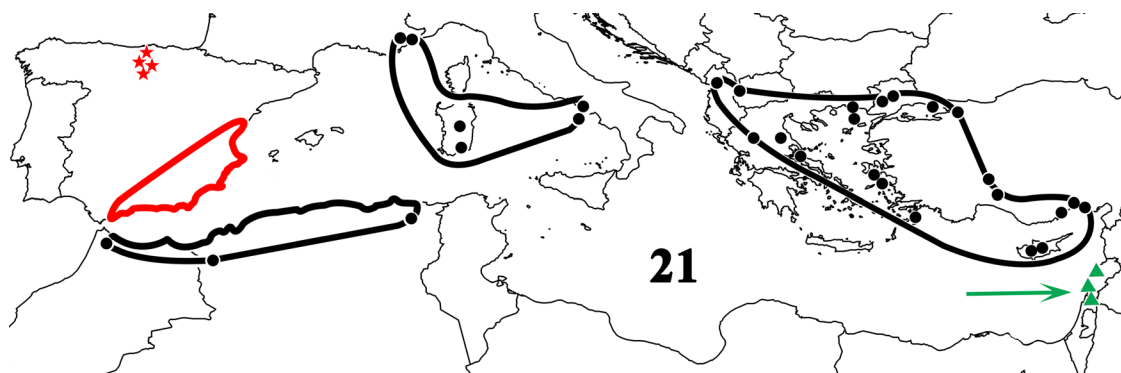
Figure 21. Distribution of the polydesmidan suborder Leptodesmidea in the Mediterranean Region of Europe, Africa, and Middle Eastern Asia. Black lines and dots, West-Palearctic Region of Xystodesmidae. Red line, area of Spain/Iberian Peninsula occupied by *Macellolophus excavatus* (Chelodesmidae). Red stars, localities in the same of *Cantabrodesmus lorioli* (Chelodesmidae). Green triangles, denoted by green arrow in eastern Mediterranean Sea, localities of *Libanaphe* spp. (Oxydesmidae) in Lebanon and Israel.

occur in the former but not latter, Platyrhacidae (Leptodesmidea: Platyrhacoidea) do the opposite, being abundant in Luzon and absent from Taiwan (Y. Wang 1961; Hoffman 1978a; Jeekel 2007).

    Taxa represented. Parafontariinae; Xystodesminae: Orophini, Xystodesmini.

    New peripheral records. *Riukiaria hoffmani* **Jeekel: Japan: Ryukyu Is.** *Amami-O-Shima*, Tsunaku, 1M, 28 August 1928, K. Kiba (UMMZ).

    References. Verhoeff (1931, 1936a, b, 1939), Attems (1938), Takakuwa and Takashima (1940), Gressitt (1941), Jeekel (1952), Chamberlin and Y. Wang (1953), Y. Wang (1955, 1957, 1963), Hoffman (1956, 1964b), Paik (1958), Murakami (1972), Shinohara (1973, 1986, 1989), Lokšina and Golovatch (1977), Golovatch (1981, 2014, 2015), Mikhaljova (1981, 1990, 1993, 1998, 2004), Zhang and Mao (1984), Tanabe (1988, 1990, 1994, 2002), Mikhaljova and Kim (1993), D. Wang and Zhang (1993), Tanabe and Shinohara (1996), Tanabe et al. (1996, 2001), D. Wang and Mauriès (1996), Mikhaljova and Lin (2000), Mikhaljova et al. (2000), Mikhaljova and Korsós (2003), Korsós (2004), Sota and Tanabe (2010), Korsós et al. (2011), Nakamura and Tanabe (2011), Golovatch et al. (2011), Marek et al. (2014), Nguyen (2016).

The Mediterranean/West-Palearctic region (Fig. 21)

    Transferral of *Macellolophus* from Xystodesmidae to Chelodesmidae removes the former from Spain and the Iberian Peninsula, as all supposed xystodesmid records from there are actually of *Macellolophus* (Fig. 21, red line). The Mediterranean Region therefore involves three disparate subregions that cover almost the entire length of the Mediterranean Sea, extending from near the Strait of Gibraltar in the west to Cyprus and southern coastal Turkey in the east, a distance of 3,496 km (2,185 mi), and it also includes southeastern coastal France, Sardinia, and coastal Campania in peninsular Italy. The West-Palearctic area includes the three sides of the Mediterranean, and it is the only region that involves more than one continent, in this case three – Africa, Europe, and Middle-Eastern Asia. Xystodesmidae are represented in every continental or insular European nation bordering or in the Sea except Spain and Malta (Enghoff and Schembri 1989). It occupies six European nations—France, Italy, Albania, Macedonia, Greece, and Cyprus—two in Africa, Morocco and Algeria, and only Turkey in Middle-Eastern Asia. Cyprus, occupied by Melaphina (Euryurinae: Euryurini), is the only country entirely within both the eastern subregion and the overall area (Turk 1952), and it is also one of only two sizeable islands in the latter, the other being Sardinia (Italy), occupied by Devilleini (Xystodesminae) (Strasser 1974a). Xystodesmidae are absent from such dependent islands/island groups as the Balearics (Mauriès and Vicente 1976, Enghoff and Vicente 2000), Corsica (Verhoeff 1943, Mauriès 1969), Sicily (Silvestri 1898), and Crete (Curčič et al. 2001). As with eastern Asia, we recognize three West-Palearctic subregions— western, central, and eastern—but here they clearly do not connect, and, based on the evolutionary hypothesis of Shelley and Golovatch (2011), this is the oldest xystodesmid region. Below, we discuss

its subregions from east to west, excluding Ethiopia, which is implausible and a likely labeling error (Hoffman and Lohmander 1968), and Syria, which, though plausible, was cited by Hoffman (1962a) without a specific locality. Confirmation with fresh material is necessary before either, and particularly Ethiopia, can truly be considered for Xystodesmidae.

Eastern subregion. The largest subregion stretches southeastward from near the Adriatic Sea in northwestern Albania to Cyprus, a lengthwise distance of around 1,406 km (879 mi). Its easternmost continental locality, Silifke, west of Mersin (city) along the Mediterranean Coast of Mersin Prov., Turkey (Hoffman and Lohmander 1968, Enghoff 2006) is only 246 km (141 mi) west of Hatay, Prov., which extends southward along the eastern Mediterranean to coastal Syria, where xystodesmids have not been documented. In addition to Cyprus, the subregion includes numerous Aegean Islands, both Greek and Turkish, but not Crete (Curčič et al. 2001) or other Greek Mediterranean Islands. Both European and Asian Turkey are included, so the (sub)region traverses the Bosporus, heads northwestward through northern/northeastern Greece, curves northward through Macedonia, and terminates in northwestern Albania near the Adriatic. It includes five countries—Albania, Cyprus, Greece, Macedonia, and Turkey—but excludes Peloponnesia and the Greek Ionian Islands, as well as Bulgaria, where xystodesmids have never been encountered (Verhoeff 1928; Ceuca 1973, 1992; Golovatch and Kondeva 1999; Beron et al. 2004; Stoev 2004; Golovatch 2017, pers. comm. to RMS).

    Taxa represented. Euryurinae: Euryurini: Melaphina.
    New peripheral records. None.
    References. Attems (1938), Turk (1952), Verhoeff (1940), Strasser (1960, 1974a, b), Hoffman (1962a, 1978a, 1980), Hoffman and Lohmander (1968), Ceuca (1992), Mauriès et al. (1997), Stoev (2004), Curčič et al. (2002), Enghoff (2006), Shelley and Golovatch (2011), Marek et al. (2014).

Central subregion. The central subregion encompasses the small-bodied xystodesmids of *Devillea* (Xystodesminae: Devilleini) that inhabit disparate localities in France (Maritime Alps in the southeastern corner of Provence/Cote d'Azur), Sardinia, and coastal Campania on the Italian mainland. The result is a curious, elbowed area, approximately 848 km (530 mi) in length, with the French and Campania areas distinguished by their minuteness in comparison to Sardinia.

    Taxa represented. Xystodesminae: Devilleini.
    New peripheral records. None.
    References. Brölemann (1902), Attems (1938), Manfredi (1956), Ceuca (1964), Strasser (1974a), Hoffman (1978a, 1980), Strasser and Minelli (1984), Minelli (1985), Foddai et al. (1995), Marek et al. (2014).

Western subregion. The Western subregion encompasses the three northwest African localities of Melaphina, which spread along a 1,104 km (690 mi) stretch of coastal Morocco and Algeria, the easternmost, an unknown cave in Constantine Prov., Algeria (Attems 1938), being only 94 km (59 mi) from the Tunisian border. This stretch of the Mediterranean Coast is the only part of Africa where Xystodesmidae and Melaphina are authentically known, and the localities seem relictual.

    Taxa represented. Euryurinae: Euryurini: Melaphina.
    New peripheral records. None.
    References. Attems (1938), Hoffman (1962a, 1969, 1978a, 1980), Hoffman and Lohmander (1968), Marek et al. (2014).

Evolution

    In a molecular study of Pancrustacea, Pisani (2009) documented that Diplopoda originated 524 million years ago (mya) in the mid-Cambrian Period, Paleozoic Era. Considering it plausible, Shelley and Golovatch (2011) accepted this dating because it allowed a realistic 44 million years (m.y.) for the basic body plan and four modern orders — Polyxenida, Polyzoniida, Chordeumatida, and Polydesmida — to evolve and become established on both the existing Gondwana (derived from breakup of the supercontinent Pannotia) and "proto-Avalonia" on the north coast of the proto-Africa/South America sector of Gondwana, before Avalonia rifted in the early Ordovician Period, 480 mya, and drifted northward. Being present on both land areas, partitioned by the rifting, and passively transported by Avalonia is the only timely manner that Diplopoda could have reached the present Northern Hemisphere after originating on or very

close to "proto-Avalonia." As Leptodesmidea and Xystodesmoidea occur today in both former Laurasian and Gondwanan territories, these taxa also had to have diverged, be fully evolved, and be present on both land areas in order to be partitioned and ferried northward when Avalonia rifted. Consequently, these polydesmidan taxa also had to arise before rifting and between 524–480 mya.

After rifting, Avalonia drifted northward for 30 m.y. before colliding in the early Silurian, 450 mya, with the microcontinent Baltica in the Iapetus Ocean. Xystodesmoidean stock remaining on Gondwana, specifically the "proto-Africa" sector, evolved into the modern families Gomphodesmidae and Oxydesmidae while that trapped on Avalonia dispersed onto Baltica after merger and evolved into Xystodesmidae. Ten m.y. later (440 mya), Baltica + Avalonia collided with another northern microcontinent, Laurentia, and forms on the former dispersed onto the latter. Bursts of evolution occurred after both mergers as dispersing xystodesmoideans penetrated, occupied, and adapted to the vacant and newly encountered niches in these larger land masses. Those that dispersed from Avalonia onto Baltica became ancestral to today's Mediterranean xystodesmids, both Melaphina (Euryurinae/-ini), and Devilleini (Xystodesminae); those that dispersed onto Laurentia 10 m.y. later became ancestral to today's Nearctic, northern continental Neotropical, and eastern Palearctic taxa.

As shown by Melaphina, we believe that ancestral xystodesmid stock possessed simple, sublinear, and somewhat "stick-like" acropodites with complete "prefemoral extensions." The initial modification was distal bifurcation exhibited by both Melaphina and Devilleini, which then diverged, the former lacking secondary projections but possessing complete "prefemoral extensions" and relatively long hairs on their "inner" surfaces that extend onto the gently curved acropodites. Devilleini, however, possesses partial "prefemoral extensions," curled/looped acropodites, secondary projections from their "inner" surfaces, and comparatively short hairs on their "outer" surfaces. During the subsequent evolutionary burst on Laurentia/Euramerica, Melaphina developed broad, spatulate epiprocts while retaining their basic acropodital structure, and Eurymerodesmini arose without a "prefemoral extension" but with a linear, upright acropodite, an abrupt subapical "curve/bend," and "inner" surface hairs arising from the acropodite itself. This lineage yielded both Nannariina, the first clade with ventrodistal spines on the ambulatory prefemora, and Eurymerodesmina. In addition to Nannariina itself, ancestral stock further split into a lineage with simple "prefemoral processes" and highly and variously modified acropodites that diverged into present Nearctic/East-Asian tribes and one with the conditions reversed, represented today by Chonaphini only. The lineage with simple "prefemoral processes" has been more successful, and Chonaphini and Xystodesmini link through *Selenocheir* (Shelley 1994).

We believe that ancestral xystodesmine stock dispersed westward on Euramerica and became Xystodesmini of today while splitting off Xystocheirini and Sigmocheirini in proto-California and, through anatomically transitional *Selenocheir* (Shelley 1994), Chonaphini in its area of greatest present diversity. The one east-Nearctic chonaphinine, *Semionellus placidus* (Wood), logically reflects eastward dispersion prior to the Cretaceous, when the Western Inland Seaway segregated it from the rest of the tribe, which proliferated into five genera and 11 species (Chamberlin and Hoffman 1958, Shelley 1994, Hoffman 1999). Orophini, however, is a mystery taxon represented by *Orophe*, in the Western Interior, and *Kiulinga* and *Pamelaphe*, in the east-Palearctic subregion/China, with a lacuna of around 10,400 km (6,500 mi). The tribe and genera seem somewhat relictual, and the overriding question is where their affinities lie, which seems to require molecular analyses. We follow Shelley and Floyd (2014) and employ the "Asiamerica" concept as defined on (http://palaeos.com/earth/paleogeography/asiamerica.htm) to explain this vast allopatry, as it seems more plausible than a lengthy trans-Beringian journey that raises more questions than it answers (see Shelley and Floyd 2014). "Asiamerica" existed from the late-Cretaceous to the Eocene (Cenozoic), ca. 94–50 mya, and contained present-day Taiwan and parts of China, Mongolia, and western North America; it harbored dinosaurs, archaic mammals, and, we think, spirobolid and xystodesmid millipeds.

This is as far as we can develop the story of xystodesmid evolution with any degree of confidence, but we add miscellaneous commentaries in the following paragraphs.

Auturus is a derived Euryurinan whose terminal calyces probably arose from a form like *Euryurus l. leachii* (Gray) with short apical branches that curled/coiled in a plane with the apices then fusing. Over time, the sides of these branches disappeared leaving an apical calyx.

Plesiomorphic forms of Nannariina, an unquestioned xystodesmid, possess simple, stick-like acropodites (Fig. 8–9) with long, narrow "prefemoral processes," all of which became elaborate and derived in species like *Nannaria scutellaria* Causey and *N. ericacea* Hoffman. While the origins of the endemic East-Nearctic tribes, Apheloriini and Rhysodesmini, as presently conceived, cannot now be inferred, we interpret the former's acropodites as modifications of the simplistic, sublinear, original configuration, that became curved, coiled, doubly curved, and sigmoidal with multitudinous adornments including expansions, impressions, indentations, cingula, and developments of flanges, spurs, and short, secondary projections. We envision Pachydesmini, now in Xystodesminae, deriving from nannariinan dichotomies because their sublinear solenomeres/"primary telopodites," while modified and broadened, clearly display the "stick-like" pattern shown by plesiomorphic eurymerodesminans (Hoffman 1958; Shelley and Filka 1979; Filka and Shelley 1980; Shelley 1990a; Shelley and McAllister 2006).

Eurymerodesmina constitute a lineage that went "evolutionarily berserk." The acropodites remained simple and "stick-like" in plesiomorphic forms, but the entire gonopods rotated 180° in the apertures, whose margins developed ornate modifications. We cannot infer how such bizarre structures proffer selective advantages, but the taxon has been successful. If, as seems likely, it spread to the west and south to the extent that Nannariina spread eastward, and hence beyond the boundaries of Appalachia, the Western Inland Seaway eradicated it from these areas (Fig. 16), and the forms we see there today reflect reoccupation by a second dispersion after the Seaway receded. As lowlands constitute most of Eurymerodesmina's present range, the Seaway markedly impacted its evolution but not that of sister-group Nannariina, which expanded, proliferated, and diverged while Eurymerodesmina stagnated.

Three times in their history, Xystodesmidae underwent evolutionary "about-faces," adopting obverse body patterns, and those in Eurymerodesmina are downright bizarre. In the dominant conditions, apertures are ovoid with lightly hirsute margins, and tel-/acropodites lie either directly below or in the apertures and overhang the anterior margins. However, in Eurymerodesmina, plesiomorphic tel-/acropodites are simple and "stick-like" while the apertures are hairy, enlarged, and elaborately adorned. In addition to anterior indentations, the apertures primarily exhibit one of two marginal specializations—expansions of the caudolateral corners into pockets/pouches that emit tufts of long hairs and elevations of the lateral and caudal margins with the latter extending into subpyramidal or long, clavate, and densely pilose lobes. As noted by Shelley (1990a), the "baseball bat-like" lobes of *E. mundus* Chamberlin are so long and prominent that they surpass the coxae of the adjacent 9th legs, thereby compelling individuals to slightly hump their bodies for the lobes to clear the substrate during walking. While plesiomorphic acropodites are simple and structurally unmodified, they are actually rotated 180° *in situ* so that the cannulae that arise mediad in confamilial forms arise laterad instead, and the acropodites thus project caudad and overhang the caudal, rather than the anterior, aperture margins. Bizarre apomorphies are not limited to males as the small and non-descript cyphopodal valves of most xystodesmids are larger, with the caudal corners modified into low ridges, short prolongations, or long, flexible, dactyliform projections that protrude through the cyphopodal apertures *in situ*. The longest and most striking are on *E. dactylocyphus*, and Shelley (1990a) suggested that they may function as "feelers" to detect the proper male aperture before mating, and that of this species is the largest in the subtribe, spreading across nearly the entire metazonum. Xystodesmid cyphopodal modifications reach their zeniths in *Parafontaria*, where the cyphopod is recessed in a large, membranous invagination, and the sternum and second coxae are also modified (Hoffman 1978e). Gonopodal acropodites are also long and doubly curled, but Hoffman's proposal (1978e) of a new subfamily focused on the female condition that is unique to Polydesmida. Not having studied *Parafontaria*, we cannot evaluate his action, but full subfamilial status for such seems excessive, as there are multitudinous male analogs for which he did not do such. However, he did originally propose subfamilial status for Orophini (Hoffman 1964b), which we consider appropriate particularly if *Parafontaria* truly warrants such.

The final example of "obverse" xystodesmid evolution involves Chonaphini, where the relative sizes and complexities of the acropodites and "prefemoral processes" are reversed. In all other xystodesmids with two or more telopodital projections, the "prefemoral process" is smaller and secondary to the

acropodite. Chonaphini reverses this pattern with the "prefemoral process" being longer, elaborate, and hence the dominant telopodital projection while the acropodite is curled, coiled, acicular, and even inconspicuous (Shelley 1994). However, this condition appears to have evolved from the traditional one in Xystodesmini through the transitional genus *Selenocheir*.

Conclusion and Summary

   With the incorporations of Euryuridae and Eurymerodesmidae, as per the respective concepts of Hoffman (1998a) and Shelley (1990a), into Xystodesmidae and Devilleini already there, all Holarctic leptodesmidean families are now included in Xystodesmidae with three exceptions. They are Sphaeriodesmidae (Sphaeriodesmoidea), a Neotropical immigrant represented by two species of *Desmonus* Cook (Desmoninae) in the southcentral/southeastern Nearctic (Cook 1898; Causey 1958; Chamberlin and Hoffman 1958; Hoffman 1969, 1999; Shelley 2000a); Chelodesmidae (Chelodesmoidea) represented by two Iberian genera and species, the cavernicolous *Cantabrodesmus liorioli* Mauriès and the epigean *Macellolophus excavatus* Verhoeff (Fig. 21, red line and stars) (Mauriès 1971; Hoffman 1980; Luque and Labrada 2017), and Oxydesmidae represented by the two species of *Libanaphe* Hoffman in Lebanon and Israel (Hoffman 1963, 1990; Tabacaru 1995; Golovatch 2007) (Fig. 21, green triangles). Neither a single character nor a combination of them defines Xystodesmidae, which therefore becomes the Holarctic analog to the primarily Neo-/Afrotropical Chelodesmidae (Hoffman 1962a, 1978a, 1980) in comprising numerous loosely connected tribal and subfamilial taxa with few common features but with each component linking to others through one or a few characters to form a common whole. Despite its host of apomorphies, Eurymerodesmidae is a xystodesmid through its connection with Nannariini, an unquestioned component, and the East-Nearctic Euryuridae and Mediterranean Melaphinae are such through their common connection with Eurymerodesmidae. RMS has found it impossible to define full families, separate and distinct from Xystodesmidae, for the West-Nearctic tribes Chonaphini, Sigmocheirini, and Xystocheirini (Shelley 1994, 1995b, 1996, 1997), the east-Asian Parafontariinae (Hoffman 1978e; Tanabe et al. 2001; Tanabe 2002), and the east-Asian/West-Nearctic Orophini and Xystodesmini (Hoffman 1964b; Tanabe 1988, 1990, 1994; Tanabe and Shinohara 1996). Additionally, the last also transitions to Chonaphini through *Selenocheir* (Shelley 1994).

   We believe that Xystodesmidae arose on Baltica 450 mya after collision with Avalonia, enabling rapid divergent evolution when the latter's xystodesmoidean stock spread onto the former and penetrated and occupied the multitude of open and available niches. The extant subfamilies Euryurinae (Melaphina) and Xystodesminae (Devilleini), or their ancestors, arose then along with possible extinct taxa. This process recurred ten million years later, when stock on Baltica + Avalonia invaded and occupied niches in eastern Laurentia. As Laurentia was a substantially larger land mass with logically more niches, it is not surprising that the North American/Nearctic fauna, with seven (sub)tribes, is significantly larger than that of the Mediterranean/West-Palearctic, with two (sub)tribes.

   In contrast to its African counterparts, Oxydesmidae and Gomphodesmidae (Hoffman 1990, 2005), the plesiomorphic xystodesmid acropodite is a simple, sublinear, and slender structure that bends or curves distad at varying positions and possesses varying lengths and densities of hairs on the "inner" and/or "outer" surfaces. This structure manifests itself differently in different taxa, and a multitude of apomorphies (complexities, ornamentations, and modifications) have evolved in North American and east-Asian taxa. Of the acropodital forms extant today, we consider those of Euryurini, which curve/bend around midlength to resemble the number "7," possess moderately long hairs on the "inner" surfaces that arise from a "prefemoral elongation" and then from the acropodite itself, to be the most plesiomorphic. We classify Eurymerodesmina, whose acropodites possess long, wavy hairs on the "inner" surfaces and curve/bend subapically in plesiomorphic forms, in the same subfamily and group them with Nannariina in the tribe Eurymerodesmini, because plesiomorphic forms of the latter share the "stick-like" acropodital configuration and hair positions of the former. Additionally, as Nannariina also possesses the ventrodistal spines on the ambulatory prefemora that exist in Rhysodesmini and the East-Nearctic endemics, Apheloriini and Pachydesmini, but are absent from primarily West-Nearctic and East-Palearctic taxa – Chonaphini, Orophini, Sigmocheirini, Xystocheirini, Xystodesmini, and Parafontariinae – we believe that Nannariina may constitute a lineage that is basal to the endemic

East-Nearctic taxa currently placed in Xystodesminae. Indeed, the solenomere/"primary telopodite" in *Pachydesmus* (Pachydesmini) derives from the plesiomorphic, "stick-like" condition, and the acropodital tibiotarsus or "secondary telopodite" has effectively moved proximad from distal in *Dicellarius,* to midlength in *Thrinaxoria*, to basal in *Pachydesmus* (Hoffman 1958; Shelley and Filka 1979; Filka and Shelley 1980; Shelley 1984a, 2002c; Shelley and McAllister 2006). These observations have profound ramifications because they suggest that if Apheloriini and Rhysodesmini truly are xystodesmines, then their prefemoral spines are convergent with those of Nannariina, which seems unlikely. Conversely, if the prefemoral spine constitutes a true synapomorphy with Nannariina, then they must be admitted to Euryurinae as Xystodesminae must be accorded to its namesake, the Oriental genus *Xystodesmus*, which necessitates taxonomic reshuffling. Comparative molecular study of Nearctic and East-Palearctic taxa seems to be the only technique to resolve these queries.

Devilleini, however, possesses a short, curled/looped acropodite with short hairs on the "outer" surface of the partial prefemoral extension plus a few proximad on that of the acropodite and a secondary projection on the "inner" surface of the stem. Both the structure itself and its origin on the acropodite, rather than separately from the prefemur, are remarkably similar to those in *Rhysodesmus* and *Stenodesmus* Saussure (Xystodesminae: Rhysodesmini), suggesting that they plus *Devillea* may be contribal, which further suggests that other rhysodesminines and the putative ones in the southeastern US are not so and require at least two and perhaps even more new tribes. Regardless of configuration or origin, secondary telopodital projections throughout Xystodesmidae are routinely labeled "prefemoral processes" and we retain this term even though homology has never been demonstrated; lacking a reason for change, we also conserve Devilleini as a tribe of Xystodesminae.

In the occupied New World areas, the acropodital patterns of Melaphina, Euryurina, and Eurymerodesmina are evident even though masked by the multitudinous modifications and ornamentations. In the east-Nearctic tribe Pachydesmini, what Hoffman (1958) called the "primary telopodite" is really the solenomere with the "secondary telopodite" being the acropodital tibiotarsus, subsequently labeled accessory, femoral, and tibial process (Shelley 1984a, 2002c; Shelley and McAllister 2006). Additionally, the "stick-like," subapically curved acropodital configuration in plesiomorphic eurymerodesminines is evident in *Pachydesmus* and particularly in *P. clarus* (Chamberlin). It can particularly be seen in the subspecies of *P. crassicutis* (Wood), though the configuration is partly obscured by the broadened, lightly scalloped inner margin (Hoffman 1958; Shelley and Filka 1979; Filka and Shelley 1980; Shelley 2002c; Shelley and McAllister 2006).

The recently discovered, disjunct, relictual Appalachian species of *Rhysodesmus*, some 1,957 km (1,223 mi) NE of the major area stretching from southern Texas to El Salvador (Hoffman 1966, 1970, 1998b, 1999; Loomis 1968; Shelley 1987, 1999; Shelley et al. 2011; Marek et al. 2014), prove that *Rhysodesmus* is significantly older than representatives of Apheloriini and Pachydesmini, both of which are comparatively restricted and cohesive. Prior to the mid-Cretaceous, *Rhysodesmus* had to be (sub)-continuous throughout this vacant area, but just as the Western Inland Sea split Chonaphini into one genus/species east of the Plains and the others in the Pacific northwest, the embayment did likewise to *Rhysodesmus*, except its distribution is oriented northeast/southwest. The part of this area that was dry and in Appalachia at this time may or may not harbor more species of *Rhysodesmus*, but we think that the arisal of *Cherokia*, and its penetration southward into formerly inundated areas, swamped and largely eradicated *Rhysodesmus*, which was unable to compete with the younger and more successful genus. The Appalachian species are clearly relictual and probably have restricted ranges.

Acknowledgments

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