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Tynommatidae, n. stat., a family of western North American millipeds: Hypotheses on origins and affinities; tribal elevations; rediagnoses of *Diactis* Loomis, 1937, and *Florea* and *Caliactis*, both Shelley, 1996; and description of *D. hedini*, n. sp. (Callipodida: Schizopetalidea)

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Tynommatidae, n. stat., a family of western North American millipeds: Hypotheses on origins and affinities; tribal elevations; rediagnoses of *Diactis* Loomis, 1937, and *Florea* and *Caliactis*, both Shelley, 1996; and description of *D. hedinii*, n. sp. (Callipodida: Schizopetalidea)

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**Abstract.** Tynommatidae, n. stat., elevated from Tynommatinae, is established as a schizopetalidean family encompassing the western North American callipodidans previously assigned to the Mediterranean Schizopetalidae. It is considered a valid taxon despite somewhat anatomically dissimilar subfamilies, and Colactidinae, Texophoninae, Diactidinae, and Aspidiophoninae constitute tribal elevations and additional new statuses. With a subbasal telopodal prefemoral process, *Diactis hedinii*, n. sp., requires rediagnoses of all three diactidine genera, *Diactis* Loomis, 1937, and *Florea* and *Caliactis*, both by Shelley, 1996, and suggests that telopodal branches ‘B’ in congeners and *Florea* represent distal relocations of the process along the stem. Similarities in the sizes and shapes of the pleurotergal carinae suggest a sister-group relationship with the other, and partly sympatric, New World family, Abacionidae, which is supported by gonopodal similarities between Colactidinae and *Abacion* Rafinesque, 1820. The Western Interior Seaway of the Cretaceous Period, Mesozoic Era, ~141–66 million years ago, appears to have fueled divergence by isolating “proto-abacionid stock” in “Appalachia,” the Eastern North American land mass, which has subsequently spread well into previously inundated areas. The allopatric position of Texophoninae, on the Gulf Coast of south Texas around 1,136 km (710 mi) east of the most proximate familial records, is attributed to this waterway, which eradicated faunal linkages with “proto-Tynommatidae” in “Laramidia,” the Western North American land mass. Texophoninae probably survived the Cretaceous on insular refugia; however, it is rarely encountered anymore and seems destined for imminent extinction. Representatives of the east-Asian families, Caspiopetalidae, Paracortinidae, and Sinocallipodidae, also possess demarcated pleurotergal crests and, implausible though it seems, may share ancestry with the North American taxa vis-à-vis the “Asiamerica” and or “Boreotropic” concepts.

**Key words:** Aspidiophoninae, Colactidinae, Cretaceous, Diactidinae, pleurotergal carinae/crests, prefemoral process, process ‘B’, Texophoninae, Tynommatidae/inae/ini.

## Introduction

On a California field trip in March 2012, RMS visited San Diego during a severe storm that precluded collecting, so CHR transported him to San Diego State University to examine milliped samples amassed over several years by Marshal Hedin in the Biology Department. The holdings were a bonanza, containing far more than one could collect in weeks, among which was a diactidine callipodidan male with a gonopodal prefemoral process. At that time, the only genus with this structure was *Caliactis* Shelley, 1996, but examinations showed that the milliped constitutes a new species of *Diactis* Loomis, 1937, and that telopodal branch ‘B’ in other diactidines apparently represents relocations of the prefemoral

process to distal positions on the telopodal stems. *Diactis hedini*, n. sp., is thus the “missing link” that appears to reveal the nature of branch ‘B’, and we therefore rediagnose all three diactidine genera.

Beyond these accounts and insight on process ‘B’ looms the issue of the familial, subfamilial, and tribal assignments of western North American callipodidans, including the allopatric tribe Texophonini on the Gulf Coast of south Texas, some 1,136 km (710 mi) east of the most proximate familial records, in Durango/Chihuahua, Mexico. Hoffman (1980) assigned *Texophon* Chamberlin, 1946, to Dorypetalidae: Dorypetalinae (in Turkey and the Balkan and Iberian peninsulas) and the other taxa to Schizopetalidae (in Italy, the Balkans, and Turkey). He established Tynommatinae for *Tynomma* Loomis, 1937, and placed *Colactis*, *Diactis*, and *Heptium*, all by Loomis, 1937, in the new tribe Colactidini, subfamily Acanthopetalinae; Shelley (1989) subsequently established Texophonini in this subfamily to accommodate *Texophon*. Shelley (1996) transferred Colactidini to Tynommatinae; erected Diactidini for *Diactis*, *Florea*, and *Caliactis*; and proposed Tynommatini, n. stat., for *Tynomma* and *Idrionaria*, n. gen. Hoffman (1999) retained this arrangement, though labeling Texophonini as “Callipodida of uncertain family position,” as did Shelley (2002a) and Stoev et al. (2008). Shelley (1996) also questioned whether North American and European schizopetalids really are confamilial, as the type-genus, *Schizopetalum* Verhoeff, 1900, occurs in the Balkans. He noted that Tynommatinae is available for a familial name encompassing the North American taxa, an observation reiterated by Shelley (2003), Shear et al. (2003), and Stoev and Shelley (2009). No more new taxa have been proposed from the United States (US/USA), but one tribe and three genera and species have been added from Mexico. Shelley (1997) assigned *Colactoides*, n. gen., to Colactidini and three years later (Shelley 2000) erected Aspidiophonini to accommodate *Aspidiophon*, n. gen. Most recently, Stoev and Shelley (2009) proposed *Mexicopetalum*, n. gen., but declined tribal assignment. We now formally establish Tynommatidae, n. stat., for western North American callipodidans and elevate existing tribes to subfamilies.

Wang and Zhang (1993) erected Paracortinidae for an assemblage of southeast Asian callipodidans, and the taxon has been retained by Wang (1996), Wang and Mauriès (1996), Zhang (1997), Shelley (2003), Shear et al. (2003), Stoev (2004), Stoev and Geoffroy (2004), Stoev et al. (2008), Stoev and Enghoff (2011), and Shear (2011). Gonopodal similarities with *Colactis* were noted by Shear (2000), who therefore assigned a new Vietnamese genus and species to Schizopetalidae; Enghoff et al. (2004) accepted this placement though questioning the generic assignment. Assessment of Paracortinidae is beyond our scope, but if its taxa are found to be confamilial with those in western North America, the name will become either a subfamily or an outright synonym of Tynommatidae, which holds 13 years of priority at the family-group level.

Herein, we elevate Tynommatinae, Colactidini, Texophonini, Diactidini, and Aspidiophonini; chronologically record tynommatid subfamilies and genera; rediagnose *Diactis*, *Florea*, and *Caliactis*; and describe *D. hedini*, n. sp. We also discuss geographic patterns pertinent to Tynommatidae and the other North American/New World family, Abacionidae, which we think reflect the Cretaceous Western Interior Seaway, and discuss how the latter taxon may have become the sole ordinal component east of the Plains. North American callipodidan records that are unpublished or not incorporated into *Abacion* maps (Shelley 1984, McAllister and Shelley 2010) are cited in the Appendix. Repository acronyms are **CAS**, California Academy of Sciences, San Francisco; **CMNH**, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; **FSCA**, Florida State Collection of Arthropods, Gainesville; **GCNP**, Grand Canyon National Park, Arizona; **KMNH**, University of Kansas Museum of Natural History, Lawrence; **MEM**, Mississippi Entomological Museum, Starkville; **NCSM**, North Carolina State Museum of Natural Sciences, Raleigh; **NMNH**, National Museum of Natural History, Smithsonian Institution, Washington, DC; **TMM**, Texas Memorial Museum, Austin; **UCD**, Bohart Entomological Museum, University of California at Davis; **UCR**, Entomology Department, University of California at Riverside; **VMNH**, Virginia Museum of Natural History, Martinsville; **WAS**, private collection of W.A. Shear, Hampden-Sydney, Virginia.

**Taxonomy** (taken in part from Hoffman [1980], Shelley [1996, 2003], Stoev et al. [2008], and Shear [2011]).

**Superorder Nematophora Verhoeff, 1913****Order Callipodida Pocock, 1894****Suborder Schizopetalidea Hoffman, 1973****Family Tynommatidae Hoffman, 1980, new status**

Tynommatinae Hoffman, 1980:120; 1999:200. Shelley, 1996:30; 2002a:105. Shelley et al. 2000:60. Stoev et al., 2008:35. Stoev and Shelley, 2009:160–161.

**Diagnosis** (adapted from that in Stoev and Shelley [2009]; terminology of Shelley [1996]). Small- to moderate-size Schizopetalidea with or without light lateral stripes along pleurotergal suture in addition to middorsal one. Carinae large and prominent, transition point varying from pleuroterga 7–19. Gonosterna with or without lateral sternal laminae and variable caudal sternal processes; gonocoxae also with or without processes. Telopodites weakly sclerotized, arising caudally or anteriorly from coxae, generally long, slender, fragile, and sublinear, subupright or leaning, not strongly bent near midlength or distad, with or without true prefemoral processes and proximal projections, divided distad (division point) into two or three branches; solenomere branch usually subterminal, subdivided into ventral solenomere and dorsal branch ‘A’; distal telopodal branch (tibiotarsus) short, configuration varying from expanded and laminate to narrow and gently curved, with or without a third branch, ‘B’, apparently representing relocated prefemoral process.

**Components.** Five subfamilies – Tynommatinae and Colactidinae both by Hoffman, 1980; Texophoninae Shelley, 1989; Diactidinae Shelley, 1996; and Aspidiophoninae Shelley, 2000 – the last four constituting tribal elevations and **new statuses**.

**Distribution.** Tynommatidae inhabit three or perhaps four disjunct areas (Shelley 1989, 1996; Hoffman 1999; Shear et al. 2003; Stoev et al. 2008; Shelley and Golovatch 2011). The smallest extends along the Gulf Coast of south Texas from San Patricio to Cameron counties (cos.) and is occupied by the two species of *Texophon* (Texophoninae). As only three specific localities are involved, two in Cameron and one in San Patricio cos., some 224 km (140 mi) apart, texophonines do not seem continuous but are considered so herein. The second largest area surrounds San Francisco Bay, California, extends along the Pacific coast from northcentral Sonoma to San Luis Obispo cos., ranges inland to San Joaquin Co., and is occupied by the three species of *Tynomma*. The third and largest area, harboring all other taxa, extends discontinuously from Kern and Los Angeles cos., California, USA, to southern Baja California Sur and Durango/Sinaloa, Mexico. Extensive sampling has taken place to the north in coastal California and in the Dixie and Fishlake National Forests (Nat. Fors.), in southwestern/southcentral Utah, such that northern range limits in these states seem well defined, but the eastern boundary in New Mexico, USA, and the southern in Durango/Sinaloa, Mexico, are nebulous. Tynommatidae probably occupy adjoining Nyarit, Jalisco, and Zacatecas, and Texophoninae may inhabit coastal Tamaulipas, particularly across the Rio Grande opposite Brownsville, Cameron Co., Texas.

**Relationships.** See concluding section.

**Remarks.** Though five names, four elevated herein, have been validly proposed, subfamilial categories in Tynommatidae are actually uncertain, and we endorse the decision (Stoev and Shelley 2009) not to assign *Mexicopetalum*. Except for Nevada, areas in the US that are reasonably potential for Tynommatidae have been sufficiently sampled that all generic- and higher-level taxa have probably been discovered, but the same cannot be said about potential areas in Mexico. Vast regions in states known to harbor tynommatids (Baja California Norte and Sur, Sonora, Chihuahua, Durango, Sinaloa) are poorly sampled for diplopods in general, so new tynommatids surely await discovery; as more and more Mexican forms are found, bizarre and unique telopodites that appear to warrant new genera, tribes, and perhaps even subfamilies are virtually guaranteed. The overall picture of Mexican Tynommatidae will gradually become evident, so to avoid having to synonymize superfluous supra-generic names, we think new ones should be deferred until gonopodal patterns come into focus. The three most recent discoveries required monotypic genera – *Colactoides*, *Aspidiophon*, and *Mexicopetalum* – but only the first



was assignable to an established higher category, Colactidini (now Colactidinae) (Shelley 1997, 2000; Stoev et al. 2008; Stoev and Shelley 2009). The monotypic tribe Aspidiophonini (now Aspidiophoninae) was erected for its namesake, and one could have been justified for *Mexicopetalum* had the authors so chosen. Tynommatids possess complex, plastic gonopods (Hoffman 1980), and as *D. hedinii* indicates for the diactidine prefemoral process, sub-structures have been added, lost, rearranged, reconfigured, and relocated, creating a tangled, intricate picture. Until more Mexican tynommatids are available, gonopodal patterns are better understood, and informed supra-generic categories can be proposed, we think that erecting them “piece-meal,” essentially a new one for each newly discovered form, is imprudent. Deferring them seems preferable to individual proposals and having to combine and synonymize names years later.

#### **Subfamily Tynommatinae Hoffman, 1980**

Tynommatini Shelley, 1996:49; 2002a:106. Hoffman, 1999:205. Shelley et al. 2000:60. Stoev et al., 2008:38.

*Tynomma* Loomis, 1957, type-genus. Three species, central coastal California, USA (Loomis 1937; Chamberlin and Hoffman 1958; Buckett 1964; Buckett and Gardner 1969; Jeekel 1971; Gardner 1973; Hoffman 1980, 1999; Shelley 1996, 2002a; Stoev et al. 2008).

*Idrionaria* Shelley, 1996. One species, southwestern Utah, USA (Shelley 1996, Hoffman 1999, Shelley et al. 2000, Stoev et al. 2008).

#### **Subfamily Colactidinae Hoffman, 1980, new status**

Colactidini Hoffman, 1980:121; 1999:200. Shelley, 1996:30–31; 2002a:105. Shelley et al. 2000:57. Stoev et al., 2008:35.

*Colactis* Loomis, 1937, type-genus. Four species, southern Nevada and Utah, USA, to southern Baja California Sur, Tiburon Island (Gulf of California), Sonora, and northwestern Durango, Mexico (Chamberlin 1923, 1958; Loomis 1937; Chamberlin and Hoffman 1958; Hoffman 1954, 1980, 1999; Buckett 1964; Loomis 1968; Jeekel 1971; Shear 1974; Shelley 1996, 2002a; Bueno-Villegas et al. 2004; Stoev et al. 2008).

*Heptium* Loomis, 1937. Two species, southernmost California, USA (Loomis 1937; Chamberlin and Hoffman 1958; Buckett 1964; Jeekel 1971; Hoffman 1980, 1999; Shelley 1996, 2002a; Stoev et al. 2008).

*Colactoides* Shelley, 1997. One species, southwestern Chihuahua, Mexico (Shelley 1997, Hoffman 1999, Shelley et al. 2000, Bueno-Villegas et al. 2004, Stoev et al. 2008).

**Remarks.** Female as well as male colactidines can be readily distinguished from sympatric diactidines by their substantially longer and more robust bodies (Shelley 1996), which lack stripes and also seem more supple and flexible. Colactidines resemble abacionids more than other tynommatids in these attributes.

#### **Subfamily Texophoninae Shelley, 1989, new status**

Texophonini Shelley, 1989:382–383. Hoffman, 1999:206–207. Shelley et al. 2000:60. Stoev et al. 2008:38.

*Texophon* Chamberlin, 1946, type-genus. Two species, Gulf Coast of south Texas, USA (Chamberlin 1946; Causey 1954; Chamberlin and Hoffman 1958; Jeekel 1971; Hoffman 1980, 1999; Shelley 1989, 1996; Stoev et al. 2008).

#### **Subfamily Diactidinae Shelley, 1996, new status**

Diactidini Shelley, 1996:40; 2002a:106. Hoffman, 1999:203. Shelley et al. 2000:57. Stoev et al., 2008:36.

**Type-genus.** *Diactis* Loomis, 1937

**Diagnosis.** (adapted from that of Diactidini by Shelley [1996]). Small-bodied Tynommatidae with conspicuous lateral stripes; median primary crests on pleuroterga 3–5 diverging caudad, transition to full complement of dorsal carinae on segments 7–8. Males smaller than females; 7<sup>th</sup> male legs subequal to 6<sup>th</sup>, 6<sup>th</sup> and 7<sup>th</sup> segments noticeably inflated; gonopodal aperture large and conspicuous, telopodites protruding *in situ*, widely separated from 7<sup>th</sup> legs. Gonocoxae narrowly segregated by variably narrow sternum, expanding laterad into broad laminae extending to lateral side of, and enveloping, coxa, also expanding anteriorly across base of telopodal stem, without anterior sternal plates, flagella, caudal sternal processes, and coxal processes. Telopodites arising anteriorly from coxae, with or without true prefemoral processes; stems divided distal to midlengths into slender tibiotarsi, solenomere branches, and processes 'B' apparently representing relocated prefemoral processes; solenomere branches usually redivided, processes 'A' usually present.

**Components.** *Diactis* Loomis, 1937; *Florea* Shelley, 1996; *Caliactis* Shelley, 1996.

**Distribution** (adapted from Shelley [1996]). Southwestern California and the Sierra Juarez in the adjacent interior periphery of Baja California Norte, primarily in canyon biotopes (Loomis 1937; Chamberlin and Hoffman 1958; Buckett 1964; Shelley 1996, 2002a; Hoffman 1980, 1999; Bueno-Villegas et al. 2004; Stoev et al. 2008). The Santa Monica mountains, Los Angeles Co., constitute the northern limit along the coast, and the northernmost interior record is an unidentifiable female from the Mojave Desert, central Kern Co.; the eastern boundary is the San Jacinto Range, Riverside Co. The distribution encompasses the region of southern California with the most rainfall and forests, and extends about 182 km (114 mi) east-west and 342 km (214 mi) north-south.

**Genus** *Diactis* Loomis, 1937

*Diactis* Loomis, 1937:110–111. Chamberlin and Hoffman, 1958:112. Buckett, 1964:14. Jeekel, 1971:97. Hoffman, 1980:121; 1999:203. Shelley, 1996:40–41; 2002a:106. Stoev et al. 2008:37. *Etiron* Chamberlin, 1941:21. Chamberlin and Hoffman, 1958:113. Buckett, 1964:15. Jeekel, 1971:98.

**Type-species.** *D. soleata* Loomis, 1937, by original designation.

**Diagnosis** (adapted from that of Shelley [1996]). Telopodal stem sublinear to gently curved, with either subbasal prefemoral process or process 'B', apparent homologue, arising distad; tibiotarsus slender and gently curved, either distalmost projection, coaxial and subcontinuous with stem, or shorter than solenomere branch and subperpendicular to stem; solenomere branch redivided, process 'A' present and variably long, either perpendicular to stem and longer than tibiotarsus or coaxial with latter and directed distad to form distalmost projection, solenomere longer than process 'A'; process 'B', apparently representing relocated prefemoral process, variable in both position and configuration, either arising basally from solenomere branch or from telopodal stem at level of, or proximal to, latter.

**Species.** Eight are known in addition to *D. hedini* – *D. soleata*, *frondifera*, and *triangula*, all by Loomis (1937); and *D. amniscela*, *cupola*, *jacinto*, *procera*, and *strumella*, all by Shelley (1996) – but more surely exist within the subfamilial range area.

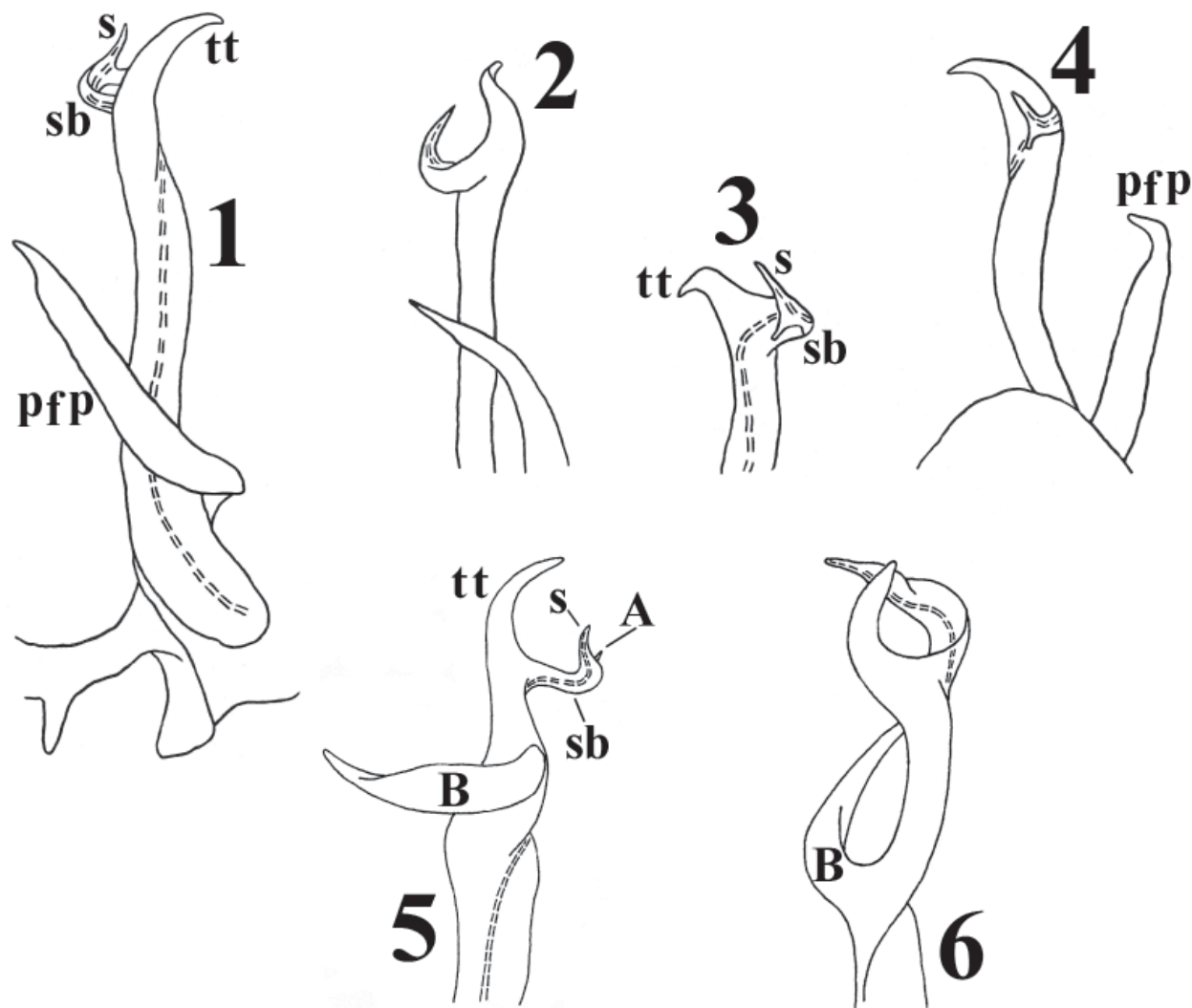
**Distribution.** Same as that of the subfamily.

***Diactis hedini*, new species**

Figures 1–4

**Type specimens.** M holotype and F paratype (NCSM) collected by M. Hedin, 17 December 2005, 4 km (2.5 mi) N of Interstate Highway 8 along SR 79, 1.9 km (1.2 mi) NE Descanso Jct., NW side of Guatay





**Figures 1-6.** *Diactis* spp. 1) *D. hedini* holotype, right gonopod, caudal view. 2) *D. hedini* holotype, right gonopod, telopodite of the same, medial view. 3) *D. hedini* holotype, right gonopod, the same, lateral view. 4) *D. hedini* holotype, right gonopod, distal extremity of the same, anterior view. 5) Telopodite of right gonopod of *D. frondifera* male from Los Angeles Co., California, lateral view. 6) Telopodite of right gonopod of *D. triangula* male from San Bernardino Co., California, anterior view. A, process 'A'; B, process 'B'; pfp, prefemoral process; s, solenomere; sb, solenomere branch; tt, tibiotarsus.

Mountain (32°51'16"N, 116°35'68"W), elevation 1,080 m (3,600 ft.), San Diego Co., California.

**Diagnosis** 50 rings including epiproct. Gonosternum with dactyliform, medial projection. Telopodal stem of subequal width throughout most of length, tapering apically to acuminate tip; prefemoral process short and broad, directed distolaterad. Distal processes arising subapically; tibiotarsus a broad continuation of telopodal stem curving opposite to solenomere branch; latter bending caudolaterad, process 'B' absent, apparently represented by prefemoral process (Fig. 1-4).

**Ecology.** The types were retrieved from a berlesate of Coast Live Oak (*Quercus agrifolia* Nee) litter adjacent to Samagatuma Creek in a Western Sycamore (*Platanus racemosa* Nutt.) riparian corridor forest that runs through coastal sage and chaparral habitat. This is the southernmost US locality for the salamander, *Ensatina eschscholtzii klauberi* Dunn, 1929, and investigating other localities where it is known (e.g., Sierra San Pedro Martir, Baja California Norte, Mexico) may provide more diactidine callipodidans and perhaps even *D. hedini*.

**Etymology.** We are pleased to name this species for Dr. Hedin, who graciously allowed RMS to search through his collection, take samples of interest, and add them to the invertebrate research holdings at the NCSM. The types of this species are deposited in the primary type collection.

**Distribution.** Known only from the type locality, in the Cleveland Nat. For., southcentral San Diego Co., near the center of the generic range. The site is also the community of Guatay, approximately 40 km (25 mi) east of downtown San Diego.

**Remarks.** *Diactis hedini* belongs to the “*D. triangula* species group” with *D. triangula* and *D. frondifera*. While differences exist in the distal telopodal configurations and branches, the major distinction between the components is the position of the third projection, subbasal and a true “prefemoral process” in *D. hedini* and shorter and progressively more distal in *D. frondifera* and *D. triangula*, hence labeled process ‘B’ (Fig. 5–6). Though longer in *D. hedini*, the projections seem to represent the same structure in all species; its telopodal position is what changes. Consequently, *D. hedini* clarifies process ‘B’, whose apparent identity was not evident when *D. triangula* and *D. frondifera* were the only group components.

### Genus *Florea* Shelley, 1996

*Florea* Shelley, 1996:46; 2002a:106. Hoffman, 1999:205. Shelley et al. 2000:58. Stoev et al, 2008:38.

**Type-species.** *F. sinuata* Shelley, 1996, by original designation.

**Diagnosis** (adapted from that in Shelley [1996]). Transition to full number of dorsal carinae on segment 8. Telopodal stem long, slender, and strongly sinuate, without true prefemoral process; division point apical and with basal lobe, with three apical or slightly subapical projections directed generally horizontally, subperpendicular to stem. Tibiotarsus directed subcaudad, moderately long, subequal in length to solenomere branch; latter directed subanteriad, not redivided and thus constituting the solenomere itself, process ‘A’ absent; process ‘B’, apparently representing relocated prefemoral process, subapical, shorter than other projections, directed generally horizontally but curving ventrad near midlength.

**Species.** One.

**Distribution.** Known definitely only from the Trabuco Ranger District, Cleveland Nat. For., Orange Co., California; it probably also occurs near the San Juan Guard Station in this forest (Shelley 1996, 2002a; Hoffman 1999; Shelley et al. 2000; Stoev et al. 2008).

### Genus *Caliactis* Shelley, 1996

*Caliactis* Shelley, 1996:47–49; 2002a:106. Hoffman, 1999:203. Shelley et al. 2000:57. Stoev et al., 2008:36.

**Type-species.** *C. bistolata* Shelley, 1996, by original designation.

**Diagnosis** (adapted from that in Shelley [1996]). Transition to full number of dorsal carinae on segment 7. Gonosternum narrow, particularly mediad. Telopodal stem gently sinuate, distally broad and clavate, without division point, with long and variably broad prefemoral process angling across anterior face, narrowing subapically and tapering to acuminate tip. Distal processes arising (sub)apically on stem. Tibiotarsus moderately long, apically acuminate and directed laterad, a narrow projection arising from medial side of distal margin and overhanging solenomere branch. Latter short, arising from lateral margin and bending anteriomedial, divided into distal solenomere and slightly shorter and more proximal process ‘A.’

**Species.** One.

**Distribution.** Known only from Mission Viejo, Orange Co., California (Shelley 1996, 2002a; Hoffman 1999; Shelley et al. 2000; Stoev et al. 2008).

### **Subfamily Aspidiophoninae Shelley, 2000, new status**

Aspidiophonini Shelley, 2000:85. Stoev et al., 2008:35.

*Aspidiophon* Shelley, 2000, type-genus. One species, southwestern Sinaloa, Mexico (Shelley 2000, Bueno-Villegas et al. 2004, Stoev et al. 2008).

### **Tynommatidae of uncertain tribal position**

*Mexicopetalum* Stoev and Shelley, 2009. One species, southern Sonora, Mexico (Stoev and Shelley 2009).

### **Biogeography**

Callipodida's distribution has been mapped three times (Shear et al. 2003, Stoev et al. 2008, Shelley and Golovatch 2011), and North American/New World occurrences are depicted by Shelley (1979, 1984, 1989, 1996) and Stoev and Shelley (2009). One of four exclusively Laurasian diplopod orders, Callipodida had to arise from ancestral nematophoran stock **after** the Avalonia terrane rifted from "Gondwana I" (deriving from breakup of Pannotia around 540 million years ago [mya]) in the early-Ordovician Period, Paleozoic Era, ~480 mya (Shelley and Golovatch 2011). Origin was on either the drifting Avalonia terrane itself, the mini-continent Baltica after collision with Avalonia in the late-Ordovician, ~450 mya, or Laurentia after it merged with Baltica + Avalonia to form Euramerica in the early-Silurian, ~440 mya. Because of the extensive callipodidan fauna in Europe, which partly derives from Baltica, Shelley and Golovatch (2011) postulated origin there in the late-Ordovician, ~445 mya. Callipodida's origin in North America/New World, however, was no earlier than the early-Silurian, ~440 mya, when ancestral stock on Baltica + Avalonia dispersed onto Laurentia, and Tynommatidae and Abacionidae eventually evolved. The latter has not been taken in Canada, the south Florida Keys, Delmarva, or eastern Virginia and North Carolina, but it otherwise blankets the eastern US from southern New York, Michigan, Wisconsin, and Minnesota to the tip of peninsular Florida, the Gulf Coast, and northeastern Mexico (Coahuila, Nuevo León, and Tamaulipas) and extends westward in the Plains to western Kansas, the Texas panhandle, and west of the Pecos River (Shelley 1984, 1988, 1989, 2001a, 2002b; Shear et al. 2003; Stoev et al. 2008; Stoev and Shelley 2009; McAllister and Shelley 2010; Shelley and Golovatch 2011). Except for relictual occurrence in south Texas (Shelley 1989, 1996; Hoffman 1999), where Texophoninae are sympatric with Abacionidae/*Abacion texense* (Loomis, 1937), Tynommatidae occur well to the west (Shelley 1989, 1996; Stoev and Shelley 2009; Shelley and Golovatch 2011). The questions therefore arise as to how, with the exception of Texophoninae, the families now occupy mutually exclusive areas, and where their affinities lie.

Disjunct east-west distribution patterns in North America, as exhibited by Tynommatidae, suggest impact of the Western Interior Seaway (embayment), that divided the "proto-continent" into eastern and western halves (thirds when coupled with the Hudson Seaway in Canada) during the Cretaceous Period, Mesozoic Era, ~141–66 mya. At its maximum, the waterway traversed central North America in a south-southeastward direction from the present-day Arctic Ocean at Yukon/Northwest Territories, Canada, to the Gulf of Mexico at Texas/ Louisiana, USA, and northeastern Mexico, spreading eastward to the Atlantic Ocean in South Carolina (Fig. 7). Maximal dimensions were about 970 km (600 mi) wide, 3,200 km (2,000 mi) long, and 760 m (2,500 ft) deep (Stanley 1999). Continuous pre-Cretaceous faunas that ranged across this area prior to inundation were divided and evolved in different directions on each side. The waterway thus fueled divergence, and its impacts are shown in modern diplopod distributions (Shelley, in prep.). Taxa with allopatric components in eastern and western North America **antedate**

the Cretaceous; they had to be present in these areas and fully evolved **before** the seaway arose, eradicated the faunal connections, and isolated the allopatric taxa that exist today. Taxa that occur on only one side of this ancient waterway **may or may not** antedate it; they may have arisen earlier but lacked the time and/or mobility/vagility to disperse that widely, or they may have arisen later and not dispersed into this area for temporal or ecological reasons. Taxa that occur in the area of the seaway itself had to spread there **after** the water receded.

North American callipodidan distributions demonstrate such patterns and *Texophoninae*, isolated on the Texas coast, constitutes evidence that *Tynommatidae* antedates the embayment. Cretaceous maps that we have seen do not show land where *Texophoninae* occurs, but small, near-shore islands existed (Stanley 1999) and one or more must have been in this area and served as refugia because the taxon cannot reflect post-Cretaceous dispersion. In this case, *tynommatid* populations would be anticipated in the lacuna, which has been sampled by many arthropodologists without one individual's being found. Consequently, *Texophoninae*, with two allopatric species some 225 km (141 mi) apart, appear to be truly relictual and declining toward extinction. In multitudinous visits to virtually every continental repository, RMS has encountered only three samples of *T. nessium* Chamberlin, 1946, and 13 of *T. aransas* Shelley, 1989, all taken at the type locality in 1980, and he did not find any individuals during a 1986 visit there. *Tynommatidae* therefore antedate the Cretaceous, and we postulate origin no later than the mid-Jurassic, >173 mya, to allow time for dispersal across the gap prior to the seaway's formation.

Lacking allopatric populations and faunas, *Abacionidae* could have arisen before the embayment; subsequent expansions into areas that were submerged suggest that, if they had existed earlier, they would have spread far enough westward to leave an isolated component analogous to *Texophoninae*, but none seem to exist. We suggest that *Tynommatidae* and *Abacionidae* may be sister-taxa and that the embayment promoted divergence by isolating "proto-abacionid stock" in "Appalachia," the Eastern North American land mass, away from "proto-tynommatids" in "Laramidia," the Western. During the embayment, *Abacionidae* withdrew, perhaps to the area south of the present Great Lakes, but afterwards, it spread through much of the eastern North America of today. The seaway began closing in the south, so abacionids spread in this direction, and *A. texense*, the westernmost species, expanded into vacant niches of the emergent Plains to now occur in southeastern South Dakota, halfway across Kansas/Oklahoma, and well westward in Texas (Loomis 1937, 1968; Chamberlin and Hoffman 1958; Hoffman 1980, 1999; Shelley 1984; McAllister and Shelley 2010; Shelley and Golovatch 2011; Shelley and Snyder 2012).

Did *Tynommatidae* occur east of the seaway prior to submergence, perhaps even east of the present Mississippi River, and might they do so today? We think the answers are negative because thousands of callipodidans have been collected in the heavily sampled eastern states, and every individual is an abacionid; even females can be confidently identified by their large, flexible bodies. We think at least **one** definite *tynommatid* would have been encountered by now if they truly inhabit eastern North America.



**Figure 7.** North America showing approximate maxima of the Cretaceous Western Interior and Hudson Seaways, which divided the continent into three separate land masses, Appalachia and Laramidia, the Eastern and Western North American land masses, respectively, being relevant herein (adapted from Stanley (1999)).

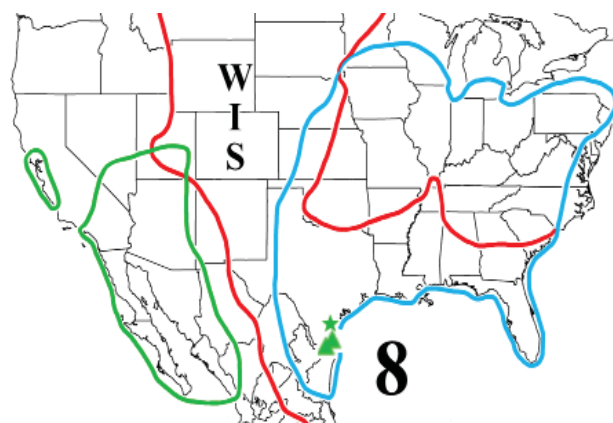


If tynommatids did occur farther east, perhaps on one or more insular refugia, they have since been displaced by highly successful abacionines, which can penetrate and adapt to virtually every biotope, even urban ones, and are virtually ubiquitous within their ranges. If tynommatids occurred east of the Plains and somehow escaped inundation, they could not have competed with the more successful abacionids, which have supplanted them throughout this area. Texophoninae still, barely, survive, but with only three known localities and sympatry with *A. texense*, they are surely rare; if not already extinct, this status seems imminent. Fortunately, Texophoninae were extant and collected in the mid-20<sup>th</sup> Century, because their presences provide a more accurate picture of “pre-Cretaceous” callipodidans and enable clearer inferences into evolutionary scenarios than would otherwise be possible.

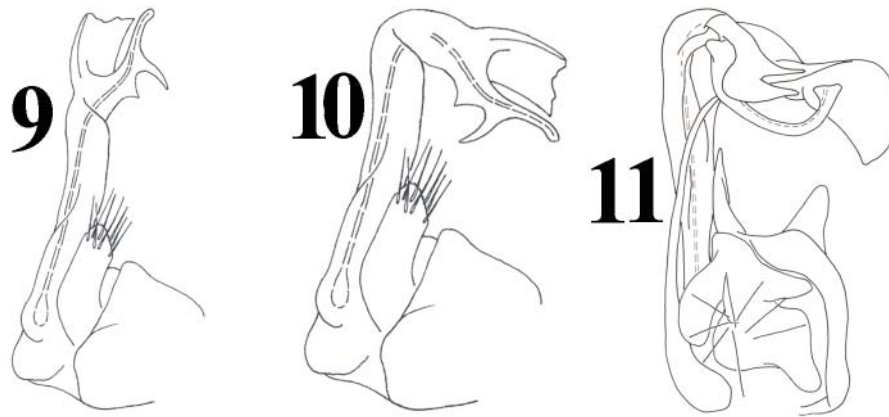
Except for Texophoninae and the eastward bulge (of Colactidinae/*Colactis utorum* [Chamberlin, 1925]) in Utah, Tynommatidae occur exclusively within former Laramidia (Fig. 8). As both the family and Colactidinae inhabit deserts, the fact that they have not spread farther eastward since the Cretaceous suggests low vagility, and the late Cretaceous origin of the Rocky Mountains surely blocked expansion in eastern Utah and Colorado. Abacionidae have spread well beyond the southern and western margins of former Appalachia to the tip of peninsular Florida and southern Tamaulipas. Northward expansion, however, has been minimal, particularly compared to other taxa (Polyzoniidae [Polyzoniida], Parajulidae [Julida], Spirobolidae [Spirobolida], Caseyidae and Conotylidae [Chordeumatida], and Polydesmidae and Xystodesmidae [Polydesmida]) that have spread into Canada and even to James and Hudson Bays since retreat of the Wisconsin glaciation 12,000 years ago (Keeton 1960; Shelley and Whitehead 1986; Shelley 1988, 1994, 1998, 2001a, 2002b, c, 2008; Shelley and LeSage 1989, 1996; Shelley and McAllister 2005, 2007; Shelley et al. 2006; McAllister et al. 2009; Shelley and Snyder 2012). Although Abacionidae have certainly had time to penetrate Ontario, they have not done so (Shelley 1984, 1988, 2002b). Their far greater southward expansion than northward suggests low tolerance to cold climates and that temperature is the limiting factor in Abacionidae’s northward occurrence. Indeed, the entire order Callipodida primarily inhabits warm-temperate and even subtropical climatic zones of the Northern Hemisphere and former Laurasian land mass (Shelley and Golovatch 2011).

## Relationships

Perhaps the most inscrutable of the 12 helminthomorph orders, Callipodida have defied phylogenetic organization. Except for the necessary additions of southeast Asian Paracortinidae and Sinocalipodidae, the three 21<sup>st</sup> century taxonomies (Shelley 2003, Stoev et al. 2008, Shear 2011) are basically that of Hoffman (1980), who disliked his own arrangement: “The higher classification remains entirely unsettled...the only point about which I feel at all confident is the basic division into two (now three) suborders. The arrangement given here is eminently unsatisfactory, at best a kind of collage of Verhoeffian schemes with recently described taxa stuck on at what seem to be suitable places....” He noted the obvious telopodal plasticity, and we surmise that callipodidan gonopods may be replete with homoplasies/convergences and that similar conditions may have evolved independently in different parts of the world. Overall patterns are difficult to discern, or stated differently, one can discern practically any pattern (s)he chooses to discern. Hoffman (1980) also stated that the gonopodal structure of *Tynomma*



**Figure 8.** North American/New World distribution of Callipodida in relation to the Cretaceous Western Interior Seaway (WIS). Red lines, margins of Appalachia and Laramidia during the embayment maximum. Blue line, present distribution of Abacionidae. Green lines, present distribution of Tynommatidae except Texophoninae, represented by green symbols. Triangles, known occurrences of *Texophon nessium*. Star, known occurrence of *T. aransas*.



**Figures 9-11.** Colactidinae/Abacionidae comparison. **9)** left gonopod of male of *Colactis utorum* from Utah, lateral view. **10)** Adobe photoshop reconstruction of the same with telopodite bent  $>90^\circ$  caudad. **11)** left gonopod of *Abacion tessellatum* male from Ohio.

is “totally different from that of all other genera,” that *Texophon* (only *T. nessium* was then known) and the Balkan genus *Dorypetalum* “are more closely related to each other than to other callipodids despite the wide geographic separation,” and that *Bollmania* Silvestri, 1896, occurring from Iran to China, and *Abacion* “seem closely related.” While our knowledge is largely restricted to New World taxa, we disagree with Hoffman’s statements. In surveying published photos and drawings of their gonopods (Hoffman and Lohmander 1964; Hoffman 1972; Spelda 1993; Stoev 2008; Stoev and Enghoff 2003, 2004, 2005, 2008), the only broad patterns we discern are that telopodites in many different taxa possess variably long, bifurcate “solenomere branches” with variably long solenomeres separated for varying distances and depths from variable opposing branches ‘A’. Additionally, the solenomere branches are often shielded to varying degrees by enlargements/expansions of the tibiotarsi and other aspects of the telopodites. Given the wide phylogenetic and geographic distributions of these features, we interpret them as symplesiomorphies and phylogenetically uninformative. Hoffman (1980) did not mention the similarities he detected between *Texophon/Dorypetalum* or *Abacion/Bollmania*, but perhaps they too constituted symplesiomorphies rather than synapomorphies. Reassessing illustrations ourselves, we do not detect potential synapomorphies between these generic pairs, and Shelley (1996) did not find *Tynomma*’s gonopod to be unique beyond normal, generic-level attributes. Adult body lengths tend to differ, around 2 and 10 cm for Tynommatidae (excepting Colactidinae) and Old World forms, respectively, and anatomical differences exist. In Tynommatidae and Abacionidae, pleurotergal rings are ornamented with prominently demarcated longitudinal carinae of at least two lengths, “primary” and “secondary,” whereas all European and Middle Eastern callipodidans that we have seen conform to Spelda’s (1993) characterization for *Eurygyrus* (Schizopetalidae), “convex swellings separated by furrows.” Hoffman (1982) also noted this distinction, characterizing callipodidan metazona as “smooth or longitudinally carinate.” His over-simplification of schizopetalid telopodites as “typically short and massive” excludes tynommatids in which they are usually long and slender, yet he included most of them in the family.

As stated by Stoev and Enghoff (2011), resolution of callipodidan affinities awaits cladistic and/or molecular analyses, which are beyond the scope of our study. In the meantime, no harm is done by seeking clues from geographic factors, which are particularly relevant to organisms that can neither run, fly, swim, nor float; consequently, phylogenetic affinities more likely lie with proximate, rather than distant, taxa (Shelley and Golovatch 2011). We do **not** suggest that this is **necessarily the case**, only that when assessing relationships among poorly vagile organisms, the **first** taxa to consider are those that are closest geographically (Hedin et al. 2011), and the most proximate family to Tynommatidae is Abacionidae. Sharing North America, they may be sister-taxa, but we can offer little supportive anatomical evidence other than the similar, and perhaps synapomorphic, pleurotergal ornamentations.

While tynommatid and abacionid telopodites generally differ, similar and potentially synapomorphic configurations exist between those of Colactidinae and Abacionidae. Their gonopodal tibiotarsi are



expanded and laminate, being (sub)upright and continuous with the stem in the former and strongly bent and angular in the latter. The solenomere branch in *C. utorum* is shielded anteriorly by the tibiotarsus, and if the stem is artificially bent 90° caudolaterad at the base of these structures using Adobe Photoshop, the resultant configuration resembles those in the five species of *Abacion* (Fig. 9–11; also see Shelley 1984, figs. 1, 4, 7, 10, and Shelley et al. 2003:4, fig. 2). Could Colactidinae be the phylogenetic link between Tynommatidae and Abacionidae? Could the taxon actually be a subfamily of Abacionidae and hence a component west of the Cretaceous embayment that denotes greater age for the family than is presently evident? As the largest-bodied tynommatids, colactidines conform to abacionids in this regard, and so strikingly do their short gonopodal telopodites contrast with the long ones of other tynommatids that confamilial status (Hoffman 1980, 1999; Shelley 1996, 2002a; Stoev et al. 2008) seems based more on geographical concordance than shared anatomical traits. The phylogenetic position of Colactidinae therefore needs reevaluation.

While anatomical differences exist, we believe that Tynommatidae and Abacionidae may be sister-taxa and more closely related to each other than to other schizopetalidean families. Divergence was fueled by the Western Inland Seaway, which segregated “proto-abacionid stock” in Appalachia, where it evolved in a different direction from the “proto-tynommatids” inhabiting Laramidia. Telopodites differ markedly, and an obvious distinction is the abruptly bent distal half in abacionids as opposed to subcontinuous and upright/gently curved in Tynommatidae. Either condition could have generated the other (Fig. 9–11), and despite differences among the two tribes and three genera, abacionid telopodites are clearly recognizable by this feature. Consistent with geographical continuity, Abacionidae show greater anatomical continuity and gonopodal stability. They truly blanket their occupied area, and meticulous field sampling would surely reveal specimens in every county. The relative lack of anatomical and geographical discontinuities in Abacioninae/*Abacion* reflects younger age and too little time for extinctions to generate such (Shelley 1984); both exist in Delophoninae/*Delophon*, suggesting greater age (Shelley 1979). Diactidine, colactidine, and tynommatine gonopods are so different that separate familial statuses could be advocated, but we favor the present arrangement because all forms could have derived from a shared ancestor with narrow, continuous, subupright telopodites. Colactidines have short telopodites with distally expanded, laminate tibiotarsi; tynommatines also exhibit the latter, but solenomere branches arise from the tibiotarsi instead of basal to them and telopodal stems are elongated. Diactidines also have prolonged stems but, except for *Caliactis*, tibiotarsi are continuous and subequal in breadths instead of expanded. We cannot address the monospecific Aspidiophoninae, erected prematurely, and with two dissimilar species, one with a moderately expanded tibiotarsus and the other without such, Texophoninae are characterized primarily by the prominent coxal and prefemoral processes in both component species. Uniting these telopodally dissimilar, allopatric species in one supra-generic taxon is preferable to placing each in its own, particularly since both are rare and may already be extinct. Although Colactidinae is the most geographically proximate subfamily, Texophoninae are more closely related to Diactidinae based on gonopodal conditions of their component species.

The strongly demarcated pleurotergal carinae shared by Tynommatidae and Abacionidae are also exhibited by east-Asian Caspiopetalidae/*Bollmania*, Paracortinidae, and Sinocallipodidae (Shear et al. 2003:10, fig. 5; Stoev 2004; Stoev and Geoffroy 2004; Stoev and Enghoff 2005:1878, figs. 1–3, 2011; Stoev et al. 2007), though they are lower and more rounded in the last, which also lacks secondary and tertiary crests. To our knowledge these are the only other callipodidans with distinct carinae, and gonopodal similarities exist between paracortinids and colactidines (Shear 2000). Implausible though it seems, do these shared attributes constitute synapomorphies between Paracortinidae/Sinocallipodidae and Tynommatidae despite their vast separation of some 11,350 km (7,094 mi) across the Pacific Ocean, South China Sea, and Taiwan Strait? We think this possibility warrants consideration vis-à-vis the “Asiamerica” and/or “Boreotropic” concepts (Lavin and Luckow 1993, Graham 1999, Hedin et al. 2011). While this manuscript was in review, RMS discovered an unidentifiable female callipodidan, presumably a paracortinid, from Nanjing, Jiang-Su Province, China (NMNH), that closely resembled a tynommatid; if unlabeled, it could readily have been housed with North American specimens. Shelley (in prep.) details the applicability of the aforementioned concepts to Diplopoda. We recommend that participants in the milliped phylogenomics initiative investigate the position of Colactidinae and potential affinities between Tynommatidae, Abacionidae, Caspiopetalidae, Paracortinidae, and Sinocallipodidae in their molecular-based research.

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APPENDIX. Unpublished and unmapped tynommatid and abacionid records; missing data were not provided on vial labels. All known samples of *Tetracion* spp. are cited since there are so few published records. Hoffman (1956) recognized two subspecies of his newly described *Tetracion jonesi* but elevated *T. j. antraeum* Hoffman, 1956, to a full species in 1999. We find only slight differences between *T. jonesi* and *T. antraeum* and hence combine records in the *T. jonesi* listing.

## TYNOMMATIDAE

### Tynommatinae

*Tynomma mutans* (Chamberlin, 1910). **USA, CALIFORNIA**, Glenn Co., Mendocino Nat. For., F, 39 March 1997, J. Schweikert (CAS).

### Colactidinae

*Colactis protenta* Loomis, 1937. **MEXICO, BAJA CALIFORNIA NORTE**, Rosarito Beach, 2F, 12 November 1956, E.S. Ross (CAS).

*Colactis quadrata* Loomis, 1937. **USA, ARIZONA**, Cochise Co., 1.6 km (1 mi) E Portal, juv., 26 July 1955, W.J. Gertsch (AMNH); Painted Canyon Ranch W Portal, MM, FF, 20 June 1954, M.A. Cazier (AMNH); and Huachuca Mts., Montezuma Pass, M, F, 4 June 1952, M.A. Cazier, W.J. Gertsch, R. Schrammel (AMNH). *Pinal/Santa Cruz cos.*, Santa Rita Mts., Madeira Canyon, M, 3F, 27 July 1949, W.J. and J.W. Gertsch (AMNH).

*Colactis utorum* (Chamberlin, 1925). **USA, ARIZONA**, Coconino Co., Grand Canyon Nat. Pk., E Boucher Spg., M, 1 October 2002, L.E. Stevens (GCNP), mouth of Boucher Cr., riparian habitat, 710 m, M, 30 March 2001, L.E. Stevens (GCNP), E Grapevine Spg., rocky talus slope, F, 23 October 2000, L.E. Stevens (GCNP), Vasey's Paradise Cr., mile 31.7, 2F, 26 March 2001, L.E. Stevens (GCNP), and Grand View Trail, 1,950 m, under rock, M, 29 April 2001, L.E. Stevens (GCNP). **CALIFORNIA**, San Bernardino Co., near Amboy, SE end Bristol Mts., M, 6 February 1994, G.R. Ballmer (UCR). **NEVADA**, Nye Co., Mercury, F, March 1960 (NMNH). **UTAH**, Grand Co., Moab, M, FF, 8 April 1946, G.F. Knowlton (AMNH).

*Heptium scamillatum* Loomis, 1937. **USA, CALIFORNIA**, San Bernardino Co., Providence Mountains St. Rec. Area, Visitor Center vic., pitfall, M, 3 April 1991, R.L. Aalbu (CAS).

### Texophoninae

*Texophon aransas* Shelley, 1989. **USA, TEXAS**, San Patricio Co., 11.2 km (7 mi) N Sinton, Welder Wildlife Ref., unburned and 1 year old burned clay soil, 14M, 3F, 1 March – 16 July 1980, D.K. Hoffmaster (FSCA, NCSM, TMM).

*Texophon nessium* Chamberlin, 1946. **USA, TEXAS**, Cameron Co., "southernmost palm grove," F, 16 February 1941, L.I. Davis (AMNH).

### Diactidinae

*Diactis triangula* Loomis, 1937. **USA, CALIFORNIA**, Los Angeles Co., near Claremont, San Antonio Canyon, M, F, 1 July 1956, W.J. Gertsch, V. Roth (AMNH). *San Diego Co.*, 3.2 km (2 mi) E Pine Springs, M, 26 April 1961, W.J. Gertsch (AMNH); and William Heise Co. Pk., M, C.H. Richart, E. Tyler, T. Ebañez (WAS).

## ABACIONIDAE

### Abacioninae

*Abacion lactarium* (Say, 1821). **USA, Alabama**, Morgan Co., Decatur, M, 1 June 1899, Kirsch (NMNH). **District of Columbia**, Washington, 2M, May 1893, F.C. Pratt (NMNH); and "Eastern Branch," M, F, 1 May 1924, H.S. Barber (NMNH). **Florida**, Alachua Co., Oleno St. Pk., F, 1958, N.B. Causey (FSCA). *Bay Co.*, along FL hwy. 20 at Ecofina Cr., F, 16 April 1997, R.M. Shelley (NCSM). *Collier Co.*, Collier-Seminole St. Pk., F, May 1931, O.F. Cook (NMNH); and Immokalle, frags., 1958, N.B. Causey (FSCA). *DeSoto Co.*, W of Arcadia, juv., and Myakka River St. Pk., F, 1958, N.B. Causey (FSCA). *Duval Co.*, Paradise Key, 2F, 19 February and 4 March 1919, H.S. Barber (NMNH); and Hacksonville, Memory



Gardens, 4F, 8 June 1959, N.B. Causey (FSCA). *Hamilton Co.*, Suwannee River St. Pk., 3F, 29 May 1958, N.B. Causey (FSCA). *Highlands Co.*, Avon Park, F, May 1931, O.F. Cook (NMNH); Brighton, frags., 8 December 1920, O.F. Cook (NMNH); Between Arcadia and Okeechobee, juvs., 10 May 1927, O.F. Cook (NMNH) and Highlands Hammock St. Pk., 4F, 1 April 1958, N.B. Causey (FSCA). *Leon Co.*, Tall Timbers Res. Sta., Woodyard Hammock, M, 9-15 May 1972, D.L. Harris (FSCA). *Manatee Co.*, Bradenton, F, October 1958, Hoya (FSCA). *Marion Co.*, Ocala Nat. For., 2F, 10 October 1929, O.F. Cook (NMNH); and 16 km (10 mi) N Ocala, M, March 1931, O.F. Cook (NMNH). *Miami-Dade Co.*, Coral Gables, Chapman Field Park, 2F, November 1930 and May 1931, O.F. Cook (NMNH); Everglades Nat. Pk., Royal Palm Hammock and 1.5 km (0.9 mi) NW of same, 3F, 28 June 1985 – 24 February 1986, S. and J. Peck (NCSM); and S. Miami, 7900 SW 176<sup>th</sup> St., Old Cutler Hammock, MM, FF, juvs., 15 November 1985 – 26 July 1986, 2M, 2F, juvs., S. and J. Peck (NCSM). *Pasco Co.*, Dade City, M, F, 8 December 1929, O.F. Cook (NMNH). *Putnam Co.*, Palatka and Ravine Gardens, 2M, F, 1 November, 1958, N.B. Causey (FSCA); Interlachen, 2F, 4 December 1982, D.T. Corey (NCSM). **Illinois**, *Vermillion Co.*, Danville, M (NMNH). **Indiana**, *Harrison Co.*, Wyandotte, M, F (NMNH). **Kentucky**, *Jefferson Co.*, Louisville, M, 19 April 1993, J. Jeseo (FSCA). **Maryland**, *Montgomery Co.*, Potomac R., Plummers Island, M, 15 April 1915, H.S. Barber, Shannon (NMNH). **New Jersey**, *Essex Co.*, Short Hills, M, 13 June 2008, L.F. Barnum (AMNH). **Ohio**, *Hocking Co.*, M, September 1961, A.A. Weaver (NCSM). *Wayne Co.*, Wooster, MM, FF, 23 April 1962 – 26 May 1966, A.A. Weaver (NCSM). **Pennsylvania**, *Bucks Co.*, 3.2 km (2 mi) E Jamison, Neshaminy Cr., M, 2F, 22 May 1962, J. and W. Ivie (AMNH). *Montgomery Co.*, Wyncote, M, F (NMNH).

*Abacion magnum* (Loomis, 1943). **USA, Alabama**, *DeKalb Co.*, DeSoto St. Pk., M, 19 May 1990, R. Brown, J. McGown (MEM). *Lee Co.*, Wright's Mill nr. Auburn M, F, January 1896 (NMNH); and Opelika, M, C.F. Baker (NMNH). **Kentucky**, *Carter Co.*, Bat Cave, M, F, March 1948 (NCSM). **Pennsylvania**, *Allegheny Co.*, Pittsburgh, M, F (CMNH); and Seawickley, 2M, 2F, July 1993, L.B. Wallace (NMNH). *Bucks Co.*, 3.2 km (2 mi) E Jamison, Neshaminy Cr., M, F, September 1953, J. and W. Ivie (AMNH). **South Carolina**, *Berkeley Co.*, 8.2 km (5.1 mi) NNE Cainhoy, Francis Marion Nat. For., M, 6 March 1999, J.C. Beane, P.D. McMillan (NCSM). *Charleston Co.*, James I., Dill Refuge, M, 2F, 28 November 1995, C.L. Whitney (NCSM). *Clarendon Co.*, 3.0 km (1.9 mi) WNW Foreston, Bennett's Bay, M, 5 March 1999, J.C. Beane, P.D. McMillan (NCSM). *Colleton Co.*, 8.6 km (5.4 mi) SSW Jacksonboro, Hope Plantation, Ted Turner Property, M, 22 March 2004, J.C. Beane et al. (NCSM).

*Abacion tessellatum* Rafinesque, 1820. **USA, Alabama**, *Butler Co.*, 4.8 km (3 mi) NW McKenzie, M, 29 April 1983, R.M. Shelley, P.B. Nader (NCSM). *Dale Co.*, 9.0 km (5.6 mi) NE Ozark, AL hwy. 105 at Judy Cr., M, 29 April 1983, R.M. Shelley, P.B. Nader (NCSM). **Arkansas**, *Pulaski Co.*, Camp Robinson, M, 1958, N.B. Causey (FSCA). **Florida**, *Jackson Co.*, Marianna, Florida Caverns St. Pk., 2M, 2 April 2964, A.A. Weaver (NCSM). **Georgia**, *Fulton Co.*, Atlanta, M, 12 November 1958, A.L. Cohen (FSCA). *Jenkins Co.*, S of Perkins, along US hwy. 25, 5.3 km (3.3 mi) S Burke Co. line, "Geomys burrow pitfall," M, 19 October 1997, P.E. Skelley, P. Kovarik (FSCA). *Muscogee Co.*, Ft. Benning, M, 24 October 1943, D.E. Beck (NMNH). **Indiana**, *Marion Co.*, 16 km (10 mi) S Indianapolis, M, 21 November 1970, R.F. Wilkey (UCD). *Parke Co.*, Turkey Run St. Pk., MM, FF, 1963 (FSCA). **Kansas**, *Cherokee Co.*, Baxter Springs, M, 28 September 2002, R.M. Shelley (NCSM). *Wyandotte Co.*, Kansas City, M, 2F, 8 June 1933, W. Ivie (NMNH). **Michigan**, *Livingston Co.*, Pinckney, E.S. George Res., M, 3 May 1960, W. Suter (FSCA). **Mississippi**, *Chariton Co.*, M (NMNH). *Grenada Co.*, "T21N, R2E, Sec. 12, 13N," MM, FF, 10 July – 4 September 1991, M.W. MacGown (MEM). *Oktibbeha Co.*, Dorman Lake, M, 1-7 July, 1989, T.L. Schiefer (MEM); and Black Belt Prairie, M, 11 May – 1 June 1992, J.A. MacGown (MEM). *Pearl River Co.*, 9.6 km (6 mi) W Poplarville, 2M, 2F, 1 February 1980, A.K. Johnson (NCSM). *Webster Co.*, 11.2 km (7 mi) W Wathall, The Cove "T20N, R8G, Sec. 12," M, 1-7 July 1988, T.L. Schiefer (MEM). **Missouri**, *Howell Co.*, Mountain View, M, 29 May 1993, S. Hubbell (NCSM). **Ohio**, *Greene Co.*, Yellow Springs, M, 1886, W.S.M. (NMNH).

*Abacion texense* (Loomis, 1937). **USA, Kansas**, *Douglas Co.*, Lawrence, Low Nature Park, F, 15 May 2011, Z.H. Falin (KMNH).

*Tetracion jonesi* Hoffman, 1956. **USA, Alabama**, *Colbert Co.*, 6.4 km (4 mi) S Margerum, McCluskey Cave (Cv.), M, 21 December 1965, S.B. Peck (FSCA). *Jackson Co.*, 1.6 km (1 mi) N Paint Rock, Crossing Cv., MM, FF, 5 August 1967, S.B. Peck (FSCA); 4.8 km (3 mi) NW Limrock, Shiffman Cv., 3M, 3F, 24 January 1967, S.B. Peck (FSCA, NCSM); 8 km (5 mi) SW Scottsboro, House of Happiness Cv., M, 4

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September 1968, S.B. Peck (FSCA, NCSM); Langstone Cv., F, 9 October 1988, A. Grubbs (TMM); and 3.2 km (2 mi) E Russell Cv., Montague Cv., juv., 15 October 1988, A. Grubbs (TMM). *Madison Co.*, nr. New Hope, Cave Spring Cv. (Hering Cv.), on ceiling up to 2,000 ft. from entrance, 5F, 31 October 1948, B.D. Valentine, E.O. Wilson (VMNH). *Marshall Co.*, 7.2 km (4.5 mi) S Grant, Dunham Cv., 6M, 2F, 18 August 1967, A. Fisk, J.E. Cooper (FSCA, NCSM).

