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Atlas of Myriapod Biogeography. I. Indigenous Ordinal and Supra-Ordinal Distributions in the Diplopoda: Perspectives on Taxon Origins and Ages, and a Hypothesis on the Origin and Early Evolution of the Class

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Atlas of Myriapod Biogeography. I. Indigenous Ordinal and
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“There were no eyewitnesses to the evolutionary changes or the geographical movements hypothesized here. It is nonetheless enjoyable and perhaps even somehow intellectually worthwhile to think about these things and draw inferences.”
George W. Byers (1969:270)

Abstract. The biogeographic significance of Diplopoda is substantiated by 50 maps documenting indigenous occurrences of the 16 orders, the three Spirostreptida s. l. suborders – Cambalidea, Epinannolenidea, Spirostreptidea – and all higher taxa including Diplopoda itself. The class is indigenous to all continents except Antarctica and islands/archipelagos in all temperate and tropical seas and oceans except the Arctic; it ranges from Kodiak Island and the northern Alaskan Panhandle, United States (USA), southern Hudson Bay, Canada, and near or north of the Arctic Circle in Iceland, continental Scandinavia, and Siberia to southern “mainland” Argentina, the southern tips of Africa and Tasmania, and Campbell Island, subantarctic New Zealand. The vast, global distribution is interrupted by sizeable, poorly- or unsampled areas including the Great Basin, USA; the Atacama Desert region of Chile and neighboring countries; southern South American islands; the central Kalahari and Sahara deserts; the Gobi Desert, Mongolia, and all of north-central and western China; from north of the Caspian Sea, Russia, to central Kazakhstan; and the “Outback” of central Australia. Five Arabian countries lack both samples and published records of indigenous diplopods – Bahrain, Kuwait, Oman, Qatar, and United Arab Emirates – as do Turks and Caicos, in the New World, and Mauritania and possibly Egypt, Africa. New records, including the first for Chilognatha from Botswana and the first specific localities from Northern Territory, Australia, are cited in the Appendix. Increased emphasis on mappings in taxonomic research is warranted along with investigations of insular “species swarms” that constitute a microcosm of the early evolution of the class. The largest “species swarm” in the Diplopoda is Diplopoda itself!

Four taxa – Glomerida, Platydesmida, Julida, and Callipodida – occur exclusively in former Laurasian Territory, and seven – Glomeridesmida, Sphaerotheriida, Siphonophorida, Spirobolida, Epinannolenidea, Spirostreptidea, and Stemmiulida – all absent from Europe, are primarily southern/Gondwanan except for secondary dispersals in Mexico/Central America by all but Sphaerotheriida, which are absent from the New World. Siphoniulida and Siphonocryptida, known from only two and four areas, respectively, are declining towards extinction; the former may constitute a relictual intermediate between Colobognatha and Eugnatha. Polyxenida, Polyzoniida, Chordeumatida, and Polydesmida occur on nearly all continents, while Cambalidea, extinct in Europe, inhabit North/Central America and southeast Asia with an isolated area in Iran. Southeast Asia, from southern China to Sumatra, harbors all 16 orders plus Cambalidea and Spirostreptidea. Southern taxa were passively transported to Asia beginning in the Silurian on terranes that rifted from the “proto-Australia” area of the Gondwana deriving from breakup of the supercontinent Pannotia (hereafter “Gondwana I”); they drifted northwards and accreted to Siberia+Kazakhstania/Euramerica,” and later the “proto-Laurasia” part of Pangaea, from the Permian to the Jurassic. Laurasian taxa could not penetrate southeastern Asia until those terranes had accreted and the region was available for colonization; before this, they evolved, differentiated, and dispersed east/southeastward from source areas in Euramerica, as evidenced by detached faunal remnants in present-day Central Asia and the

Himalayas. Southeastern Asia is thus a “mixing area” for northern and southern diplopods as is Mexico/Central America, which Gondwanan forms entered in the Late Carboniferous, ~ 306 ma, when Euramerica collided with the “proto-South America/Africa” region of Gondwana I, thereby forming Western Pangaea. Closure of the Panama Portal in the Pliocene, ~ 5 ma, allowed northward dispersals of South American forms but is too recent to account for occurrences throughout the Central American land bridge and even into the USA, though it probably explains northward spread of Epinannolenidea and the polydesmidan family Paradoxosomatidae to Costa Rica. Occurrence of the latter in Dominica, Lesser Antilles, is regarded as indigenous rather than introduced and probably represents occurrence in the “Proto-Antillean” area before it rifted from northern South America in the Cretaceous/Paleocene, ~ 66 ma.

As the earliest Paleozoic fossil is from Scottish Silurian deposits, an operative hypothesis explaining early diplopod evolution requires origin far enough before then for major dichotomies to have taken place and for ancestral forms to have dispersed and become established relatively simultaneously on both Gondwana I and the northern “micro-continents” (Baltica, Laurentia, and Siberia). Only one source area meets these requirements, the Avalonia terrane of Gondwana I **before** it rifted in the early Ordovician (~ 480 ma) and drifted to and combined with Baltica in the mid-Ordovician (~ 450 ma); 10 my later, Baltica+Avalonia merged with Laurentia to form Euramerica. Presence on Avalonia and neighboring parts of Gondwana I prior to rifting mandates at least **Mid- to Late Cambrian** origin (≤ 524 ma) on or near this terrane with rapid divergence and dispersal onto Gondwana I proper, such that ancestral stock was partitioned when Avalonia rifted. Forms remaining on Gondwana I continued to evolve, differentiate, and disperse, eventually reaching the “proto-east/southeast Asia” terranes before they rifted, while those on Avalonia were confined to this terrane until collisions with Baltica and Laurentia allowed them to colonize these unoccupied lands with numerous vacant niches, which drove evolution in different directions from that taking place simultaneously and in “parallel” on Gondwana I.

Relative ordinal-group ages are postulated as Polyxenida > Polydesmida > Siphoniulida > Siphonocryptida > Spirostreptida *s. l.*/Cambalidea > Chordeumatida \geq Polyzoniida > Glomeridesmida \geq Sphaerotheriida > Epinannolenidea > Stemmiulida \simeq Siphonophorida > Spirobolida > Spirostreptida > Glomerida \simeq Platydesmida > Callipodida > Julida.

Keywords. accretion, Avalonia, Baltica, biogeography, Diplopoda, distribution, Euramerica, “Gondwana I,” Laurentia, Laurasia, maps, Pannotia, rifting, terrane.

Dedication. We dedicate the first consolidated treatment of diplopod biogeography to our late Dutch colleague, Casimir Albrecht Willem Jeekel (1922-2010), a gentleman and scholar whose encyclopedic knowledge of the class and pioneering *Nomenclator generum et familiarum Diplopodorum* (Jeekel 1971) inaugurated the Modern Era in Diplopodology (Shelley 2007a) and ultimately enabled such syntheses.

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Introduction

Important collateral knowledge deriving from systematic research concerns a taxon's geography. In the Diplopoda, however, distributions are frequently ignored; surprisingly, many taxonomic papers lack maps entirely, and a few even lack locality records (Shelley 2007a). Such absences are counter-intuitive because of widespread agreement that millipeds are exceptional biogeographic indicators (Hoffman 1962, 1969a, 1978; Gray and Shear 1992; Hopkin and Read 1992; Golovatch and Kime 2010), and because of their low vagilities, phylogenetic affinities plausibly lie with geographically proximate, rather than distant, taxa. The currency of biogeography is locality data plotted on maps, and without suitable maps, the biogeographic potential of millipeds vis-à-vis documented tectonic events can never be realized. A few authors have partly analyzed modern distributions biogeographically (Hoffman 1962, Kraus 1966, Jeekel 1974, Enghoff 1993a, Nguyen Duy-Jacquemin and Azar 2004, Wesener and VandenSpiegel 2009), but otherwise, this richly promising topic has at best received only superficial attention. Hoffman (1962) stated that millipeds "...have much to teach us, if we have but the patience to unravel the tangled fabric of their present distribution over the face of the earth," and Shear (1999) summarized the situation thusly, "...millipeds might be ideal subjects for biogeographical studies, since vicariance events (such as the rifting of continents and island colonizations) would be the most important factors in their distribution. Regrettably, such studies are hindered because we know so little about the diversity and *distribution* (emphases ours) of millipeds." This contribution, the first in a planned series, attempts to untangle the fabric, remedy the inequity, and rekindle interest in milliped biogeography by providing maps of indigenous occurrences of all 16 orders and higher taxa based on knowledge through June 2010; some of this information is well known but has never been presented in this format or context. Patterns and congruences are evident among chilognath taxa, and ones with similar geographies logically hold similar origins and ages. This is also the first time that biogeographic information on multiple milliped orders has been consolidated, addressed specifically, and depicted on maps that are equivalent and directly comparable. We therefore adopt a novel perspective by treating millipeds as geographic entities and departing from taxonomy, systematics, and cladistics in the strict senses, though the maps may aid construction of area cladograms.

In developing our maps, we utilized a variety of published works and modern electronic sources. The checklists, or listings, for North America, Central America/Mexico, and Caribbean Islands (Chamberlin 1918, 1922a; Chamberlin and Hoffman 1958; Loomis 1968; Hoffman 1999), Africa south of the Zambezi and Kunene rivers (Hamer 1998), and Australia/East Indies/Oceania (in part) (Attems 1914a, Chamberlin 1920), as well as more recent state/provincial and country works (Shelley 1988, 1990a, 2000a, 2001, 2002a, b; Bueno-Villegas et al. 2004; Golovatch et al. 2005; Andersson et al. 2005, 2008), were useful in allowing us to minimize time-consuming searches through what Hoffman (1980a) appropriately labeled a "polyglot literature." Kime (2000) mapped European distributions of Glomerida, Julida, Chordeumatida, and Polydesmida that we accept with modifications from recent sources (Curcic et al. 2001; Kime 2004; Andersson et al. 2005, 2008; Lee 2009), and Golovatch and Kime (2010) addressed northern range limits in Eurasia. Reasonably complete checklists and faunistic works for islands and countries on other continents, too many to list here, were also invaluable resources. The websites on Australian millipeds (<http://www.polydesmida.info/millipedesofaustralia/>) and Tasmanian "multipedes" (<http://www.polydesmida.info/tasmanianmultipedes>), which employ symbols for individual or proximate localities, were invaluable, and we accept these as well. The Fauna Europaea site (<http://www.faunaeur.org/>), however, was less useful because occupied countries are completely highlighted even for marginal occurrences. Finally, we must acknowledge Dr. Jeekel's informative regional and global catalogues (2001a, b, c, 2003a, 2004a, 2006a, 2007), his departing gift to his specialty, which consolidated the literature on these taxa and provided many localities.

Four orders have been previously mapped (incorrectly reported as two by Shelley (2007a)) – Sphaerotheriida (Jeekel 1974, Wesener and VandenSpiegel 2009, Wesener et al. 2010), Julida and Spirostreptida (Jeekel 1985), and Callipodida (Shear et al. 2003; Stoev et al. 2008) – but these maps need updating and initial ones are necessary for other orders and all higher taxa. A number of familial maps are available (listed in the appendix of Shelley (2007a)), some more relevant to ordinal distributions than others, and though not labeled as such, Jeekel (1985) mapped the spirostreptidan suborders as per the taxonomies of Hoffman (1980a) and Shelley (2003a): Cambalidea, Epinannolenidea, and Spirostreptidea.

The basic organization follows the latter classification, but we also map and address these three suborders (hereafter treated as full orders and cited individually, like “Cambalidea”), because they will likely be elevated based in part on the “8th gonopod clade” concept (Shear et al. 2003, Shelley 2007a). Aside from Spirostreptida, we assume that all taxa herein are monophyletic, as opposed to convergences or grades of development.

To complete this effort, we have taken a number of liberties and instituted unique geographic conventions. The word, “continents,” means those inhabited by man and excludes Antarctica, and we intermingle geographical and biogeographical terminologies for the benefit of readers more attuned to one or the other. The boundary between the Nearctic and Neotropical biogeographic realms, particularly in Mexico, is irregular and nebulous. On the west, it lies just north of the tip of the Baja California Peninsula; on the east, it passes through south Florida around Lake Okeechobee. For convenience, we place all of Florida and Baja California in the Nearctic and regard Glomeridesmida and Stemmiulida (Fig. 7, 45) as exclusively Neotropical and Callipodida (Fig. 37-38) as entirely Nearctic. Glomerida, Platydesmida, Julida, Cambalidea, Chordeumatida, and associated higher taxa (Fig. 8-9, 17, 26, 30, 41) are primarily Nearctic/North American, as they extend southward continuously or discontinuously for varying distances through “mainland” Mexico and the spine of Central America before terminating north of South America, the lone exception being relictual chordeumatidan occurrence in Chile (Fig. 41). For simplicity and convenience, we recognize three Asian subdivisions – Middle East, Continental, and Islands – and arbitrarily connect the East Indies and eastern Australia when ranges include both the Island of New Guinea and the Cape York Peninsula, Queensland, which occupy the same tectonic plate and are only ~ 256 km (160 mi) apart, less than the distances between many Indonesian islands. As European countries are comparatively small, they are omitted from world maps to eliminate clutter and emphasize taxon boundaries; countries are included on European enlargements because while insignificant distributionally, their borders constitute important reference lines. Volcanic or coral oceanic islands harboring ostensibly native diplopods represent a special difficulty because there is no evidence that many were ever connected to land masses with substantial indigenous populations. Though different interpretations are possible, we incorporate them with the closest continent(s)/island(s) where native species cluster, except where infeasible as with the remote Republic of the Marshall Islands, the Hawaiian Islands, United States (US/USA), and Kodiak Island, Alaska, USA. All map groupings are also purely geographic; they are not intended to be phylogenetic and should not be misconstrued as such. For our purposes, the geographic position of an ancient land mass is as significant as time, and we emphasize this. To fully grasp diplopod biogeography, simply stating that a fossil is from the Devonian or Carboniferous of a particular modern country is insufficient. Knowing where the land was at that time, which other land masses were drifting and in which directions, which were rifting, etc., is **vital** to understanding how millipeds moved, both actively and passively, for their descendants to inhabit their present locations. Above all, we attempt to present exclusively indigenous occurrences, omitting the multitude of human introductions that mask them, but problematical situations exist where the mode of occurrence cannot be determined; when questionable, we opt for natural origins to avoid omitting indigenous ones. For example in the subclass Colobognatha, order Polyzoziida (Fig. 15, 20), *Rhinotus purpureus* (Pocock, 1894) (Siphonotidae) has been widely introduced, especially on islands (Loomis 1934, 1936; Causey 1965; Hoffman 1977a, 1980a 1999; Mauriès 1980a; Golovatch and Korsós 1992; Shelley 1998a). We suspect that isolated siphonotid occurrences in Sierra Leone and Guinea, Africa, and St. Helena Island, South Atlantic Ocean (Cook 1896, Chamberlin 1920, Hoffman 1977a), represent introduced populations of *R. purpureus*, but without supportive evidence, we consider them native. Systematic studies are lacking in this order and family, leaving no reliable method to infer mode of occurrence other than borrowing the specimens and conducting analyses ourselves, which is beyond our scope and prohibitively time consuming.

The impetus for this >2.5 year study was the desire by RMS to determine **exactly** where the 16 orders occur and where they do not. Geographical allusions, for example to Stemmiulida in India, pervade the literature, but workers need to know precisely where in India without having to spend hours or days scouring reams of publications for scattered records. The intention was to portray complete distributions on world maps for all orders plus spirostreptidan suborders so they can be seen at a glance, in a mental “snapshot,” and higher hierarchical levels were then mapped rather simply, their distributions being additives of subordinate taxa. The original intent was thus simple and straightforward, and only after the maps were finished did their biogeographic potential become evident. Glaring differences – some orders

are widespread while others are restricted, some are conspicuously and puzzlingly absent from certain continents, some are subcontinuous while others are fragmented, etc. – compelled a search for answers that led inexorably to ancient tectonics as reported by geologists and geographers. Clearly, the maps tell a story, broad in scope, that had to be deciphered, which led inevitably to the origin and early evolution of the class. Like the Rosetta Stone, the maps unlock the overriding secrets that no one previously surmised – when and where Diplopoda originated and, as low vagility organisms, what roles dispersals and early tectonic movements played in distributing them so as to generate its modern biogeography and place Paleozoic fossils in their documented locations at the proper times. To terminate this study with only the maps and verbal descriptions of distributions would be a disservice, so we tried to carry it to its logical conclusion and articulate a hypothesis on the origin and early evolution of the class, reconciling clues to ages from fossils, geography, and taxonomy in discussions of each taxon. Beyond being intellectually worthwhile, such efforts yield valuable insight into the organisms themselves.

The contents therefore consolidate accounts of each taxon's geography, thereby complementing those on anatomy by Hoffman (1982a). We then address patterns and congruences ("geographical synapomorphies") between taxa and detail our hypothesis with five accompanying diagrams (Fig. 53-57) of organismal and tectonic movements to try to simplify a complex story. With this knowledge and that of major taxonomic dichotomies (Hoffman 1980a, Shelley 2003a), we provide relative ages drawing on both the fossil record and geography. For geographic completeness, we also report (Appendix) unpublished museum samples (some with only females or juveniles and unidentifiable to genus) that expand ranges and enhance documented occurrences, and incorporate them into the maps and discussions. Though of low taxonomic significance, the samples establish a taxon's presence at a particular place and time, and hence hold biogeographic utility.

Repository codens are **AMNH**, American Museum of Natural History, New York, New York, USA; **AUEM**, Entomology Department, Auburn University, Auburn, Alabama, USA; **BMNH**, The Natural History Museum, London, United Kingdom (UK); **BPBM**, Bernice P. Bishop Museum, Honolulu, Hawaii, USA; **BYUC**, Monte L. Bean Life Science Museum, Brigham Young University, Provo, Utah, USA; **CASC**, California Academy of Sciences, San Francisco, USA; **CMNC**, Canadian Museum of Nature, Ottawa, Ontario, Canada; **CMNH**, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; **CNCL**, Canadian National Collection, Centre for Lands and Biological Resources Research, Agriculture and Agri-Food Canada, Ottawa, Ontario, Canada; **CSCA**, California Department of Food and Agriculture, Sacramento, USA; **DMNH**, Dayton Museum of Natural History, Dayton, Ohio, USA; **EMEC**, Emerson Entomological Museum, University of California, Berkeley, USA; **FMNH**, Field Museum of Natural History, Chicago, Illinois, USA; **FSCA**, Florida State Collection of Arthropods, Gainesville, USA; **LACM**, Los Angeles County (Co.) Museum of Natural History, Los Angeles, California, USA; **MCPM**, Milwaukee Public Museum, Milwaukee, Wisconsin, USA; **MCZC**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; **MEMU**, Mississippi Entomological Museum, Mississippi State University, Starkville, USA; **MHNG**, Muséum d'Histoire Naturelle, Genève, Switzerland; **MNHN**, Muséum National d'Histoire Naturelle, Paris, France; **MTEC**, Entomology Dept., Montana State University, Bozeman, USA; **MZUF**, Museo La Specola, Florence, Italy; **NCSM**, North Carolina State Museum of Natural Sciences, Raleigh, USA; **NMSA**, Royal Natal Museum, Pietermaritzburg, Republic of South Africa; **NSMC**, Nova Scotia Museum, Halifax, Nova Scotia, Canada; **NSSU**, Biology Department (Dept.), National Sun-Yat Sen University, Kaohsiung, Taiwan; **PMNH**, Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA; **PSUC**, Frost Entomological Museum, Pennsylvania State University, College Station, Pennsylvania, USA; **RBCM**, Royal British Columbia Museum, Victoria, British Columbia (BC), Canada; **RMCA**, Royal Museum for Central Africa, Tervuren, Belgium; **SDMC**, San Diego Museum of Natural History, San Diego, California, USA; **SIUC**, Biology Dept., Southern Illinois University, Carbondale, USA; **SWRS**, Southwest Research Station, Portal, Arizona, USA; **TMMC**, Texas Memorial Museum, Austin, USA; **UAIC**, Entomology Dept., University of Arizona, Tucson, USA; **UCDC**, Bohart Entomological Museum, University of California, Davis, USA; **UCRC**, Entomology Dept., University of California, Riverside, USA; **UDCC**, Entomology Dept., University of Delaware, Newark, USA; **UGCA**, Museum of Natural History, University of Georgia, Athens, USA; **UNMC**, Museum of Southwestern Biology, University of New Mexico, Albuquerque, USA; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; **UWBM**, Thomas Burke Museum of Natural History, University of Washington, Seattle, USA; **VMNH**, Virginia Museum

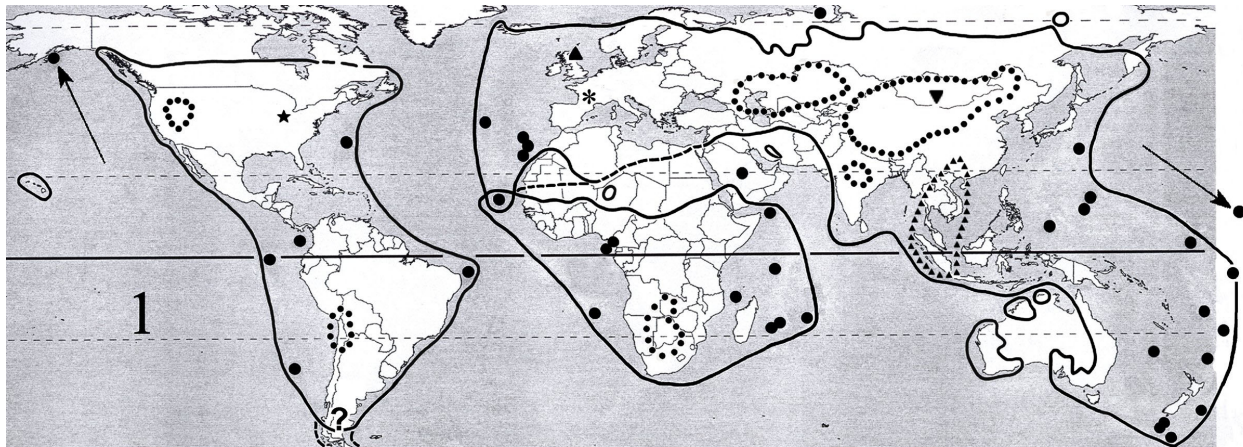


Figure 1. Known (solid lines) and projected (dashed lines) indigenous distributions of the Diplopoda showing locations of significant fossils. The solid line in southern South America shows the extent of diplopod samplings and known occurrences, but we project the organisms for uninvestigated areas south of the southernmost records, in Isla Grande de Chiloé, Chile, and Santa Cruz Prov., Argentina, the unsubstantiated record of the polyxenid from the last (Mauriès 1998), *Propolyxenus patagonicus* (Silvestri, 1903), being indicated by the question mark. Except for records from Kodiak Island, Alaska (Chordeumatida) (left arrow), the Hawaiian Islands (Cambalidea), and the Federal Republic of the Marshall Islands (Polyxenida) (right arrow), oceanic islands and archipelagos harboring ostensibly indigenous forms are grouped with the continent with apparent faunal affinity; the Cape Verde Islands are combined with both Africa and Europe because of dual affinities, Spirostreptidea and Glomerida/Julida, respectively. Only a few records and samples, especially of Chilognatha, are available from the dotted areas in Africa and North America; no extant records and samples are available from those in Eurasia and South America. The southeast Asian area encircled by triangles is the only place where all 16 orders occur indigenously. Upright triangle, site of *Archidesmus macnioli* Peach, 1887, the oldest helminthomorph fossil, from Silurian deposits in Scotland; Star, site of the non-spinose oniscomorph pentazonian Carboniferous fossil at Mazon Creek, Illinois, USA; Inverted triangle, approximate location of *Gobiulus sabulosus* Dzik, 1975, the Cretaceous spirobolidan fossil in Mongolia; Asterisk, location of *Protosilvestria sculpta*, the Oligocene cambalidean fossil from Quercy, France (Mauriès 1992).

of Natural History, Martinsville, USA; **WASC**, private collection of W.A. Shear, Hampden-Sydney, Virginia, USA; **WSUC**, James Entomological Museum, Washington State University, Pullman, USA; **ZMUM**, Zoological Museum of the Moscow State University, Russia; **ZSMC**, Zoologisches Staatssammlung des Bayerischen Staats, Munich, Germany.

POORLY- AND UNSAMPLED AREAS

Sizeable areas on all continents except Europe are essentially unsampled, either lacking collections altogether or having only a few samples. They correspond primarily to hostile environments, either frigid Arctic regions or hot, arid deserts, that are as undesirable for humans to investigate as for millipeds to inhabit. The subcontinuous faunal area stretching from northern Scandinavia to the southern periphery of Africa is interrupted by a nearly empty continent-wide swath through the central Sahara Desert that extends from the Atlantic Ocean to the Red Sea (Fig. 1). The faunas north and south of this barrier are markedly different, though isolated populations of sub-Saharan Spirostreptidea, remnants of a formerly continuous distribution, survive in mountains to the north. This lacuna is wider than it appears because records from oases in southern and central Algeria are of the subclass Penicillata, order Polyxenida (Fig. 1, 3); the gap in the subclass Chilognatha (Fig. 5) arises more northward, near the Mediterranean Coast. That millipeds in general, and chilognathans in particular, probably inhabit pockets throughout this area is indicated by the occurrence of Spirostreptidea (Spirostreptidae, Odontopygidae) in the Air Mountains (Mts.) inselberg of northern Niger (Schubart 1951; Jeekel 1985, fig. 1D). Such Saharan inselbergs as the Tibesti Mts. in northern Chad, the Ahaggar Mts. in southern Algeria, the Adrar des Iforas in northern Mali, and the Jebel Marra in Sudan probably also harbor desert-adapted taxa, but political, financial, and logistical factors render them difficult to investigate. A smaller area, nearly devoid of

samples, exists in southern Africa in the Namib and Kalahari Desert regions of Angola, Botswana, Namibia, and the Republic of South Africa. It is internal and surrounded by sampled areas including the coasts of Namibia and Angola. The few internal records again primarily involve penicillates (Hamer 1998), and we report the first chilognath, a representative of Spirostreptidea (Spirostreptidae), from Botswana (Appendix).

The Saharan lacuna can be regarded as traversing the Red Sea and Persian Gulf and extending eastward to western India. The only records from the Arabian Desert and the Peninsula south of central Israel, the Dead Sea area of Jordan, and southeastern Iraq are *Archispirostreptus transmarinus* Hoffman, 1965 (Spirostreptidea), in the Jabal Al-Hijaz Mts. of southwestern Saudi Arabia and adjacent Yemen, *A. arabs* (Pocock, 1895) from coastal Yemen (Hadramawt), and an unidentifiable female paradoxosomatid (Polydesmida) from a “wadi” in central Saudi Arabia (Shelley 2009, Golovatch and Kime 2010). East of the Persian Gulf, the only records west of the Indian faunal area are of Cambalidea, Callipodida, and Polydesmida from the Zagros Mts. of southwestern Iran and Kermanshah Prov. on the western Iranian periphery (Fig. 30, 37, 39-40, 46) (Jeekel 2004a, Enghoff and Moravvej 2005, Stoev et al. 2008, Appendix). A substantial fauna is anticipated from Iran eastward, but for cultural reasons and because of armed conflicts, it is difficult for non-natives to sample there.

In central India, the northern Deccan Plateau (Fig. 1), located in the rain shadow between the Western and Eastern Ghats Mts., is an arid area with dry deciduous forest and low diversity in all animal groups. We know of no diplopod records from the outlined area.

To the north, the large unsampled area, primarily in central, western, and northeastern China (Manchuria) corresponds closely to the blank area on the map in D. Wang and Mauriès (1996:92, fig. 1) and centers on the Gobi and Taklimakan deserts. It covers north/western Tibet all of Xinjiang Prov., and most of Nei Mongolia, extends northward into southern Mongolia, and depending upon the order, spreads westward for varying distances into Kazakhstan, Kyrgyzstan, Tajikistan, and adjoining Russia. Investigations in this area are a biogeographic priority because of the faunal diversity and palaeogeographic history of north/east/southeastern China, which assembled prior to formation of Pangaea from terranes that rifted from the Gondwana that derived from breakup of the supercontinent Pannotia, ~ 540 million years ago (ma) in the Cambrian Period (Paleozoic Era). Partly because they constituted similar land masses and areas, the same name, “Gondwana,” is assigned to the southern progeny continents that derived from both Pannotia and Pangaea, which arose some 365 million years (my) apart. For convenience and to avoid confusion herein, we henceforth label “Pannotia Gondwana” as “Gondwana I” and “Pangaea Gondwana” as “Gondwana II”; “Gondwanan” refers to southern regions in general.

While Tasmania has been well sampled, records from “mainland” Australia are largely restricted to coastal and adjoining areas, with gaps along the southern and northern peripheries. Sampling has extended inland into the Kimberley Region in northwestern Western Australia. We report the first definite milliped localities from Northern Territory (Polydesmida: Paradoxosomatidae, Haplodesmidae), from near Darwin, but the vast central Australian “Outback,” encompassing the bulk of all “mainland” provinces except Victoria, is blank. According to R. Mesibov (pers. comm. to RMS), substantial samples of Polydesmida and Spirobolida from this area await study in Australian repositories.

In the Western Hemisphere, a large uninvestigated area exists in Canada north of central BC, Alberta, Saskatchewan, Manitoba, Ontario, and Québec. The true northern extent of the indigenous continental fauna is unknown and beyond realistic speculation. Conceivably, millipeds occur in the uninvestigated southern Yukon and Northwest Territories, Canada, substantially farther north than presently known, but diversity is low, individuals are surely highly scattered, and sampling trips for diplopods would not be cost effective. Substantial investigations in Alaska by RMS and associates have established that millipeds in this US state occur exclusively in the coniferous rain forests on the panhandle and Alexander Archipelago, except for the unidentifiable tingupids (Chordeumatida) on Kodiak Island (Shelley et al. 2009a). Otherwise, all Alaskan chilognaths occur along the coast from Yakutat southeastward; even Anchorage vicinity and the lush Kenai Peninsula are devoid of the arthropods, so more northerly regions in central Alaska surely lack them, although polyxenidans plausibly occur there. Because of occurrences in southcentral provinces (Shelley 2002b), diplopods are anticipated farther north in Canada than Alaska, but native North American species surely do not extend as far north as do those in Eurasia and Iceland, where they approach and traverse the Arctic Circle (Fig. 1, 3-4, 14-15, 20, 24-26, 46; Table 2).

The other essentially blank area in North America is the Basin and Range Physiographic Province (= Great Basin) in the western US, a largely uninvestigated “cold” desert that covers most of Nevada and extends eastward into western Utah and northward into southeastern Oregon and southern Idaho. Forested summits, some >3,659 m (>12,000') elevation, in the many inselbergs conceivably harbor diplopods, and the entire Province warrants investigation. The only samples from this Province are from 3,972 m (13,028') Wheeler Peak and nearby caves in the Snake Range of eastern Nevada, in and near present-day Great Basin National Park (Shear 2007, Shear and Shelley 2007a, Shear et al. 2009a).

In South America, the blank area in northern Chile, which spreads into adjoining arid regions of Peru, Bolivia, and Argentina, centers on the Atacama Desert, the world's driest. To the south, the southernmost islands of Chile and Argentina are unsampled, a research objective of RMS, and the southernmost record (here and in the world) is *Propolyxenus patagonicus* (Silvestri, 1903) (Polyxenida: Polyxenidae) from an unknown locality along the Santa Cruz River, Santa Cruz Prov., Argentina (Silvestri 1903, 1905; Mauriès 1998). This site is around 440 km (275 mi) north of the southern extremity of “mainland” South America and 635 km (395 mi) north of Cape Horn. The southernmost chilognath records are some 800 km (500 mi) to the north in the Andes Mts. of Parque Nacional los Alerces, Chubut Prov., Argentina, and on Isla Grande de Chiloé, Chile, at essentially the same latitude (Fig. 5, Table 2). As the southernmost pentazonian locality is 2,080 km (1,300 mi) farther north in southcentral Bolivia (Fig. 6), the southern chilognath border is also that of Helminthomorpha (Fig. 14), which is unknown from the southernmost 1,440 km (900 mi) of both South America (including the southern islands) and the Western Hemisphere. This area is expected to harbor polydesmidans (Dalodesmidae), polyxenidans, and spirobolidans (Rhinocricidae) because of substantial litter layers in the predominant southern beech (*Nothofagus*) forest (H. Heatwole, pers. comm. to RMS).

While taxon boundaries may traverse their borders, indigenous millipeds are unknown from a number of countries, dependent territories, islands, and archipelagos (listed to the best of our knowledge in Table 1). Most absences of records undoubtedly reflect lack of sampling, but they exist and warrant mention; millipeds are known from many oceanic islands and archipelagos, but many faunas are exclusively comprised of widespread, humanly introduced, “tramp” species. We have tried to develop a comprehensive and reasonably exhaustive roster, but incorporating every small island or island group is impossible. Most recently, Saudi Arabia, the largest country that lacked a published indigenous milliped record, was removed from the list (Shelley 2009). From a diplopodological standpoint, the Arabian Peninsula, including the island country of Bahrain in the Persian Gulf, is the most under-investigated region on Earth. Of the eight countries that do not border Iran or the Mediterranean Sea, five – Kuwait, Qatar, Bahrain, United Arab Emirates, and Oman – lack a published milliped record, introduced as well as indigenous. Whereas much of this area is inhospitably xeric and undoubtedly does not harbor diplopods, scattered mountain ranges and desert “wadis” or valleys are promising localities especially during and immediately after seasonal rains (Shelley and Crawford 1996, Shelley 2009).

Beside each country and territory in Table 1 is the known or presumed explanation for the lack of indigenous records. Some oceanic island nations, for example the Republic of Kiribati in the Pacific, are too remote from regions with indigenous forms to contain native millipeds and are known or expected to harbor only introduced species. Although a “city state,” Vatican City is the only independent European country lacking published milliped records; Mauritania and possibly Egypt (including the Sinai Peninsula) are the only ones in Africa; and the aforementioned five Arabian nations are the only ones in Asia. The island nation, Turks and Caicos, is the only independent country in the Western Hemisphere from which no millipeds, native or introduced, have been recorded.

TAXON DISTRIBUTIONS

Class Diplopoda (Fig. 1, 2)

“Throughout the temperate and tropical regions of the world, wherever local climatic conditions permit the accumulation of humus layers, the megascopic fauna of the forest floor is often dominated by species of the arthropod class Diplopoda.” So said R.L. Hoffman (1969a), and while millipeds also inhabit deserts, savannas, and prairies, geographic documentation of this statement is now, finally, available (Fig. 1). Diplopoda is truly a global taxon that is indigenous, or presumed so, to all continents and continental islands, all of the East and West Indies, Iceland and Macaronesian islands in the Atlantic

Ocean, Madagascar and small islands in the Indian Ocean, both major islands of New Zealand, and scattered, remote islands in the Pacific Ocean. It is unknown from Arctic Ocean islands, Antarctica, and subantarctic islands (Hopkin and Read 1992, Minelli and Golovatch 2001, Golovatch and Kime 2010); the most proximate locality to the Antarctic Peninsula, of Penicillata/Polyxenida, lies some 1,680 km (1,050 mi) to the north-northwest in Santa Cruz Prov., Argentina, while that of Chilognatha, in Chubut Prov., Argentina, is some 2,960 km (1,850 mi) distant. Because of their minute sizes, light, non-calcified bodies, and the potential to be blown by winds and incidentally transported by birds (Tajovsky et al. 2001), Polyxenida is the only order that plausibly may someday be discovered on either the Antarctic Peninsula or subantarctic islands.

Diplopoda occupy enormous areas in both the New and Old Worlds. There are two in the former, an isolated point locality on Kodiak Island, Alaska, USA, in the North Pacific Ocean, and a continuous area extending from Yakutat, Alaska, USA, and the “Haines Triangle,” Stewart, and Dawson Creek, BC, Ft. Severn, Hudson Bay, Ontario, southern Labrador, and northern Newfoundland, Canada, to southern Argentina and Chile. The latter encompasses all the continental US including the Channel Islands, off southern California, all of Mexico and Central America, all of the Bahamas and the Greater and Lesser Antilles, and all of South America except for southernmost Argentina/Chile and the Atacama Desert and adjoining arid areas in northern Chile and vicinity. We incorporate three Pacific Islands and archipelagos into this area – Cocos Island, Costa Rica; the Galapagos Islands, Ecuador; and the Juan Fernandez Islands, Chile – along with Fernando de Noronha, in the Atlantic off the eastern tip of Brazil, and we project Diplopoda for Turks and Caicos, Penicillata for Antigua and Barbuda, and Chilognatha for St. Kitts and Nevis. Several chilognath taxa potentially inhabit the first and last island nations, so we do not project orders.

In sub-Saharan Africa, Diplopoda exhibit a curvilinear northern border that extends from the Atlantic Ocean/Senegal River, in the west, to the Red Sea at the Sudan/Eritrea border, in the east. We expand this area eastward to encircle southwestern Saudi Arabia/Yemen, Sokotra, the Comoros and Seychelles Islands, and Mauritius, Rodriguez, and Madagascar; on the west/Atlantic, we include Bioko (=Fernando Po), São Tomé and Príncipe, St. Helena, and the Cape Verde Islands, the last shared with “Euroaustralasia” because of potentially indigenous taxa with Afrotropical and Palaeartic/European affinities.

The enormous “Euroaustralasian” area begins in the Atlantic with Iceland, Madeira, the Azores, Canary, and Cape Verde islands, and encompasses all North/Baltic Sea and Mediterranean islands, all of the UK and Ireland, and all of continental Europe except northernmost Scandinavia and Russia. The irregularly curvilinear northern border extends across Siberia and Asian Russia, drops southward in the Far East to the Sea of Okhotsk, and crosses the heart of Kamchatka. With a detached site in central Saudi Arabia, the southern border extends through two parts of Mediterranean Africa, across the Middle East (central Israel and southern Jordan/Iraq) into Iran, curves northward into southern Afghanistan and northcentral Pakistan, and then turns abruptly southward through western India to encompass Sri Lanka, the Maldive/Andaman/Nicobar islands, in the Indian Ocean, and all of Indonesia including islands offshore of Sumatra and Java. To the north, the eastern border curves around the Kurile and Bonin Islands, Pohnpei (=Ponape), Federated States of Micronesia, Samoa, Tonga, and Fiji, and we continue it southward to incorporate New Zealand, Tasmania, and southern and eastern Australia. Although the Deccan Plateau, India, western China/Mongolia, and parts of the Central Asian Republics lack records,

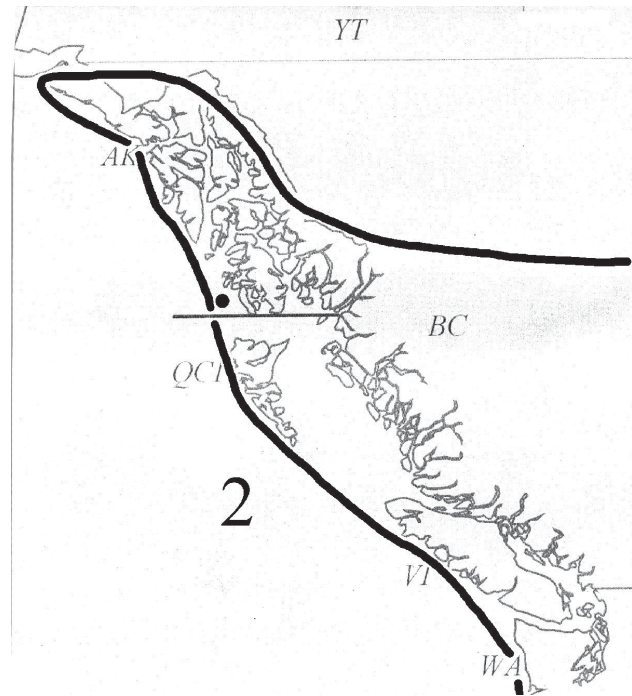


Figure 2. Distributions of Diplopoda, Chilognatha, Helminthomorpha, and Eugnatha in northwestern North America. The dot denotes Forrester Island, Alaska, USA.

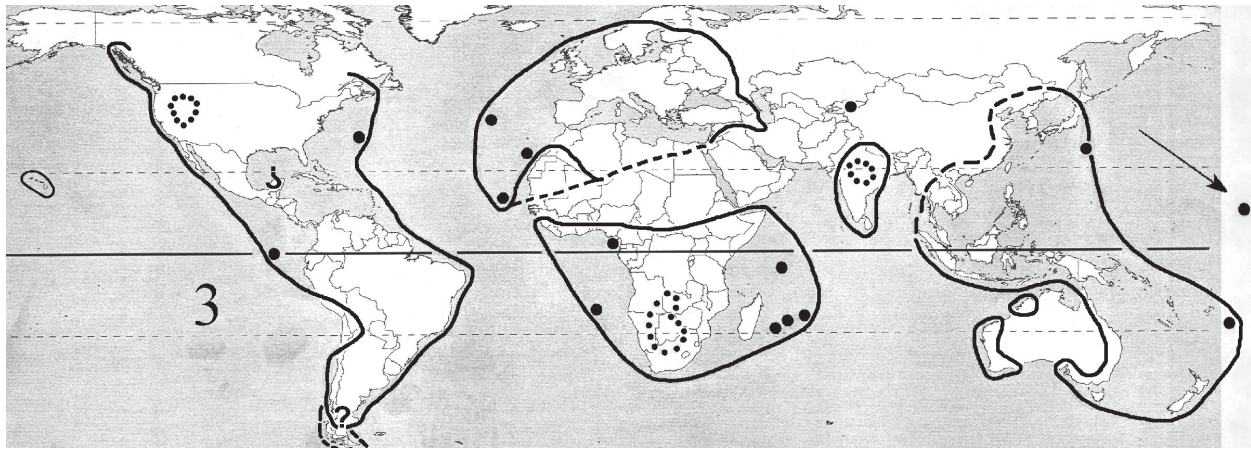


Figure 3. Known (solid lines) and projected (dashed lines) indigenous distributions of the Subclass Penicillata and Order Polyxenida. The arrow denotes the record from the Federal Republic of the Marshall Islands; the upright question mark (?) denotes the unsubstantiated record of *Propolyxenus patagonicus* (Silvestri, 1903) from Santa Cruz Prov., Argentina (Mauriès 1998); and the inverted question mark (¿) indicates uncertain occurrence on the Yucatan Peninsula, Mexico. Other parameters as in Fig. 1. Too few records exist from Canada to project a northern boundary in North America, and the isolated record from central Asia (Kyrgyzstan) is too distant to be combined with an area where records cluster. No records are available from the dotted areas in India and North America, and the only one from that in Africa is *Chilixenus schultzei* (Attems, 1909) from Botswana (Hamer 1998).

the Asian part of this area includes all of Tajikistan, Nepal, Bhutan, Bangladesh, Myanmar, Thailand, Japan (including the Ryukyu Islands), Taiwan, the Philippines, Singapore, Indonesia, Papua New Guinea, Vanuatu, New Caledonia, the Solomon Islands, and New Zealand plus the Indochina, Malay, and Korean peninsulas,

Diplopoda are known from three small Australian areas in addition to the eastern and southern coastlines, included with Eurasia. The largest is the westernmost coastal region of Western Australia, which spreads inland and along the northern and southern coasts, and there are two smaller “outlier” areas to the northeast, one in the Kimberley Region and another on the coast of Northern Territory that ranges 50 km (31.3 mi) inland.

Kodiak Island, Alaska (denoted by the left arrow in Fig. 1), the Hawaiian Islands, and the Federal Republic of the Marshall Islands (indicated by the right arrow) cannot be feasibly combined with one of the continents and are shown as separate.

The ranges of Diplopoda and Chilognatha (Fig. 1, 5) are nearly identical; Penicillata’s (Fig. 3) impact on the former is minimal. It extends the class’ range southward beyond Chilognatha in both South America and North Africa, where it accounts for the bulk of the area by its occurrence in a Saharan oasis in southern Algeria. It is also responsible for the record from Federal Republic of the Marshall Islands and accounts for the coastal part of the Kimberley Region in Western Australia. With these few exceptions, the taxon Penicillata is entirely subsumed within the much larger area of Chilognatha.

Subclass Penicillata (Fig. 3-4)

With only one component order, Penicillata have the same distribution as Polyxenida (Fig. 3-4), detailed below (Fig. 3-4).

Order Polyxenida (Fig. 3-4)

The distribution of Polyxenida, the most poorly known of the major global/subglobal orders, is based more on inference, projection, and conjecture than are those of other taxa. Polyxenidans are best sampled by Berlese techniques, but most collectors, RMS included, search instead for readily visible chilognaths

that can be gathered by hand. Aside from Europe and the continental US, for which we document nine new states (Appendix), only scattered records exist, particularly from Asia, where they are unknown from Thailand (Enghoff 2005); for the Philippines, Y. Wang (1951) stated, "The subclass Pselaphognatha (= Penicillata) (is) represented in the Palaearctic and Oriental regions but (has) not so far been found in the Philippine Islands." Despite these difficulties, we postulate broad, global occurrence for Polyxenida that encompasses five major areas, two smaller regions of Western Australia, and point sites in Kyrgyzstan, the Hawaiian Islands, and the Republic of the Marshall Islands (Ailinglapalap Atoll) (Silvestri 1904; Chamberlin 1947a; Nishida 1994, 2002).

The northern borders are nebulous to varying degrees, so we show them by solid (Europe) or dashed (Asia) lines and omit that in North America because too few Canadian records exist to project a position. According to Palmén (1949), the northernmost European locality was at 63° 30'N, but Polyxenida occur now at 65°N on Vikna Island near Rörvik, North-Trøndelag, Norway (Ellingsen 1910, Meidell 1970), just south of the Arctic Circle (66° 33' 39"N). It probably occurs farther north along the warmer, more moist Norwegian coast than deeper into Eurasia, but 65°N is a convenient northern meridian for Europe if not also North America. The southernmost record, *Propolyxenus patagonicus*, in Santa Cruz Prov., Argentina (Silvestri 1903, 1905; Condé and Massoud 1974; Mauriès 1998; Nguyen Duy-Jacquemin and Geoffroy 2003; Short and Huynh 2010), is ~ 50°S, some 16° north of the Antarctic Circle (66° 33' 39"S), which crosses the northern Antarctic Peninsula. Based on the known occurrence at 65°N and the presence of southern beech (*Nothofagus*) litter layers, Penicillata/Polyxenida should be expected on Isla Grande de Tierra del Fuego and possibly even at Cape Horn (55° 58'S). Investigating this possibility is a research objective of RMS.

In the New World, Polyxenida are known from southern Québec and the northern Alaskan Panhandle to Santa Cruz Prov., Argentina (Fig. 3). The northernmost site is Haines, Alaska (Fig. 4) (59° 14' 09"N) (Shelley 1990a), and in Canada, the order is also known from Nova Scotia and Ontario (Jawłowski 1939a, Judd 1967, Kevan 1983, Shelley 1988, 2002b). It also occupies Bermuda, and with occurrence on New Providence Island, Bahamas (an obscure record in Condé and Terver (1965)), and published localities from all Greater and several Lesser Antilles, Polyxenida can be reasonably projected for all Caribbean islands including Turks and Caicos. Fewer records exist from Mexico and Central/South America but enough to project it throughout the continental land mass southward to Santa Cruz Prov., aside from the Atacama Desert region. The western border encompasses the Galapagos Islands (Shear and Peck 1987), the Channel Islands of southern California (Shelley 2002a), Vancouver and the Queen Charlotte Islands, BC, and the Alexander Archipelago, Alaska. For North America *per se*, the new records (Appendix) coupled with the few published localities, summarized in Condé (1996), point to widespread occurrence in the Continental US and suggest the same through border regions of adjacent Canadian provinces. Palmén (1952) did not report Polyxenida from Newfoundland, possibly because of improper sampling, but the island lies well below the northernmost European latitude and it should be expected there, farther north along the Atlantic Coast (Labrador and Québec), and maybe in southern Greenland. References with general or specific records include California (Buckett 1964, Shelley 2002a), Florida (Shelley 2001), Michigan (Kane 1981, Snider 1991), Montana (Loomis and Schmitt 1971, Nguyen Duy-Jacquemin 1976), New England (Blake (1931), New York (Bailey (1928), Texas (Chamberlin and Mulaik 1941; Chamberlin 1943, 1947b; Stewart 1969), and North Carolina (Shelley 1978, 2000a). Additional Canadian records for BC

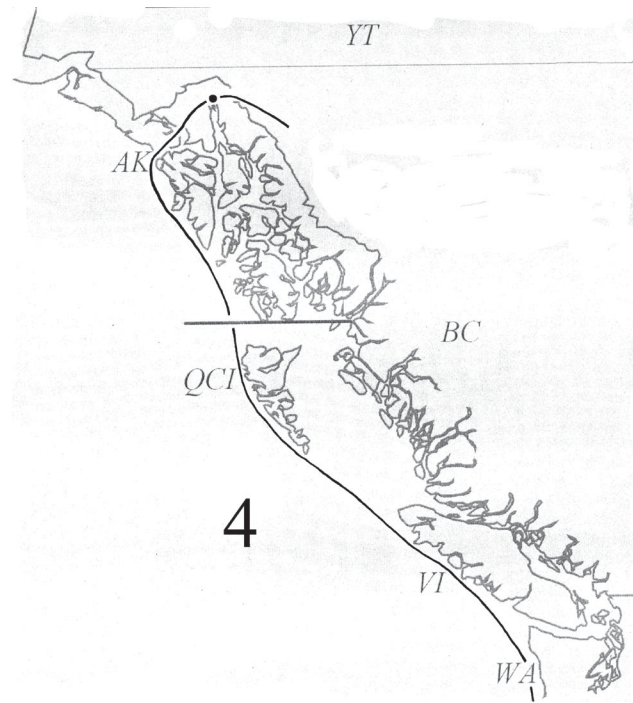


Figure 4. Distributions of Penicillata and Polyxenida in northwestern North America. The dot represents the northernmost record, from Haines, Haines Borough, Alaska, USA.

(“mainland” and Vancouver Island), Ontario, and Nova Scotia are available in (Kevan 1983; Shelley 1988, 1990a, 2002b).

Polyxenida have been collected less frequently in Mexico/Central America. In the former, they are known only from Baja California Sur, Nuevo León, and Veracruz (Loomis 1966a, 1968; Hoffman 1999; Bueno-Villegas et al. 2004), and in Central America, they have been reported from Guatemala, Costa Rica, and Panama (Condé and Terver 1964; Loomis 1964, 1968). A map and table documenting *Ancistroxenus* Schubart, 1947, and *Lophoturus* Brolemann, 1931, in Nicaragua and Costa Rica is available in Nguyen Duy-Jacquemin (2002), which also covers the Greater and Lesser Antilles. In addition to Hoffman (1999), works lacking maps that report Polyxenida for the New World include Cuba (Loomis 1933, Condé and Terver 1965; de la Torre y Callejas 1974; Gonzalez Oliver and Golovatch 1990); Hispaniola (Haiti and the Dominican Republic including Beata Island) (Loomis 1936, Condé and Terver 1965, Pérez-Asso and Pérez-Gelabert 2001, Pérez-Gelabert 2008); Puerto Rico including Mona Island (Chamberlin 1950a, Vélez 1967); Jamaica (Loomis 1975; Condé and Terver 1979); Cayman Islands (Grand Cayman) (Hounscome 1994); Bermuda (Condé 1972); Bahamas (New Providence) (Condé and Terver 1965); US Virgin Islands (St. John) (Loomis 1970); St. Eustatius (Condé and Terver 1965, 1979); St. Martin (Condé and Terver 1979); St. Barthélemy (Condé and Terver 1979); St. Kitts (Loomis 1933); Guadeloupe (Condé and Terver 1979, Nguyen Duy-Jacquemin 2002); Martinique (Nguyen Duy-Jacquemin 2002); St. Vincent (Loomis 1933, Condé and Terver 1979); the Grenadines (Mustique) (Loomis 1933, Condé and Terver 1979); Tobago (Nguyen Duy-Jacquemin 2002); and Trinidad (Nguyen Duy-Jacquemin 2002).

South American countries with records, but not maps, include Surinam (Condé and Terver 1964), Brazil (Mello-Leitão 1925, Nguyen Duy-Jacquemin and Condé 1967, Brandão et al. 1991, Diniz and Brandão 1993), and Peru (Condé 1980), and the map and table of occurrences in Nguyen Duy-Jacquemin (2002) covers northern Brazil, Colombia, Venezuela, Surinam, and French Guiana. The southernmost record, along the Santa Cruz River, Santa Cruz Prov., Argentina, is ~ 800 km (500 mi) south of that of Chilognatha, in Parque Nacional los Alerces, Chubut Prov.

We enclose the Azores, Cape Verde, and Canary islands (Enghoff 1993b, Vicente and Enghoff 1999); Polyxenida are unknown from Iceland, but the 65th parallel crosses the northern tip of the island and occurrence is plausible. Nearly all of Europe is occupied, or potentially so, including Great Britain, Ireland, and all Mediterranean and Aegean Islands. The northern border drops southward in Finland, swings eastward in Russia to near Moscow, and then angles southward into the Caucasus region and south of the Caspian Sea in northwestern Iran (Enghoff and Moravvej 2005). In North Africa, the range spreads southward into the Sahara Desert in southern Algeria and probably extends directly southwestward to the Atlantic, though no records exist. Condé (1954a) documented Polyxenida in Morocco, and we project it for Libya, Egypt, the Gaza Strip, Israel, and northern Syria and Iraq. Enghoff (2006) cited localities in western Turkey, some mapped by Short and Huynh (2010), and we project the order throughout the country.

Kime (2000) did not map European Polyxenida, so we scoured papers for records. Ones with maps document occurrences in Scandinavia (Palmén 1949, Meidell 1970, Enghoff 1976, Ishii 1988, Andersson et al. 2005), British Isles (Blower 1985), Switzerland (Pedroli-Christen 1993a), Hungary (Korsós 1994a), and Belgium (Kime 2004). Documentations without maps include Balearic Islands (Enghoff and Vicente 2000), Balkan Peninsula (Ceuca 1992, Mauriès et al. 1997, Curcic et al. 2002), France (Geoffroy 1996), Germany (Schubart (1925, 1934a), Italy (Stasser and Minelli 1984, Foddai et al. 1995), Luxembourg (Kime 1996), Netherlands (Jeekel 1953), Poland (Jawlowski 1938, 1939b; Jedryczkowski 1982), Portugal (Ladeiro 1943), and Switzerland (Pedroli-Christen 1992). References documenting Polyxenida in eastern Europe, European Russia, and the former Soviet Republics include the Carpathians (Loksina and Golovatch 1979), “Russian Plain” (Loksina and Golovatch 1979; Golovatch 1992a), Georgia (Lohmander 1936, Loksina and Golovatch 1979, Kobakhidze 1965, Talikadze 1984), Crimea (Loksina and Golovatch 1979; Golovatch 1990a, 2008), and Ukraine (Chorny and Golovatch 1993).

Polyxenida probably inhabit oases and high elevation inselbergs across the Sahara so as to occur subcontinuously from northern Scandinavia to southernmost Africa. It would be the only diplopod order to do so, but lacking published records from the desert heartland, we recognize a separate sub-Saharan region that extends into both the Atlantic and Indian Oceans and encloses Madagascar (Condé and Nguyen Duy-Jacquemin 1962, Nguyen Duy-Jacquemin and Condé 1967, Enghoff 2003). The northern border traverses Sierra Leone, Liberia, Ivory Coast, Nigeria, Chad, Central African Republic, southern Sudan,

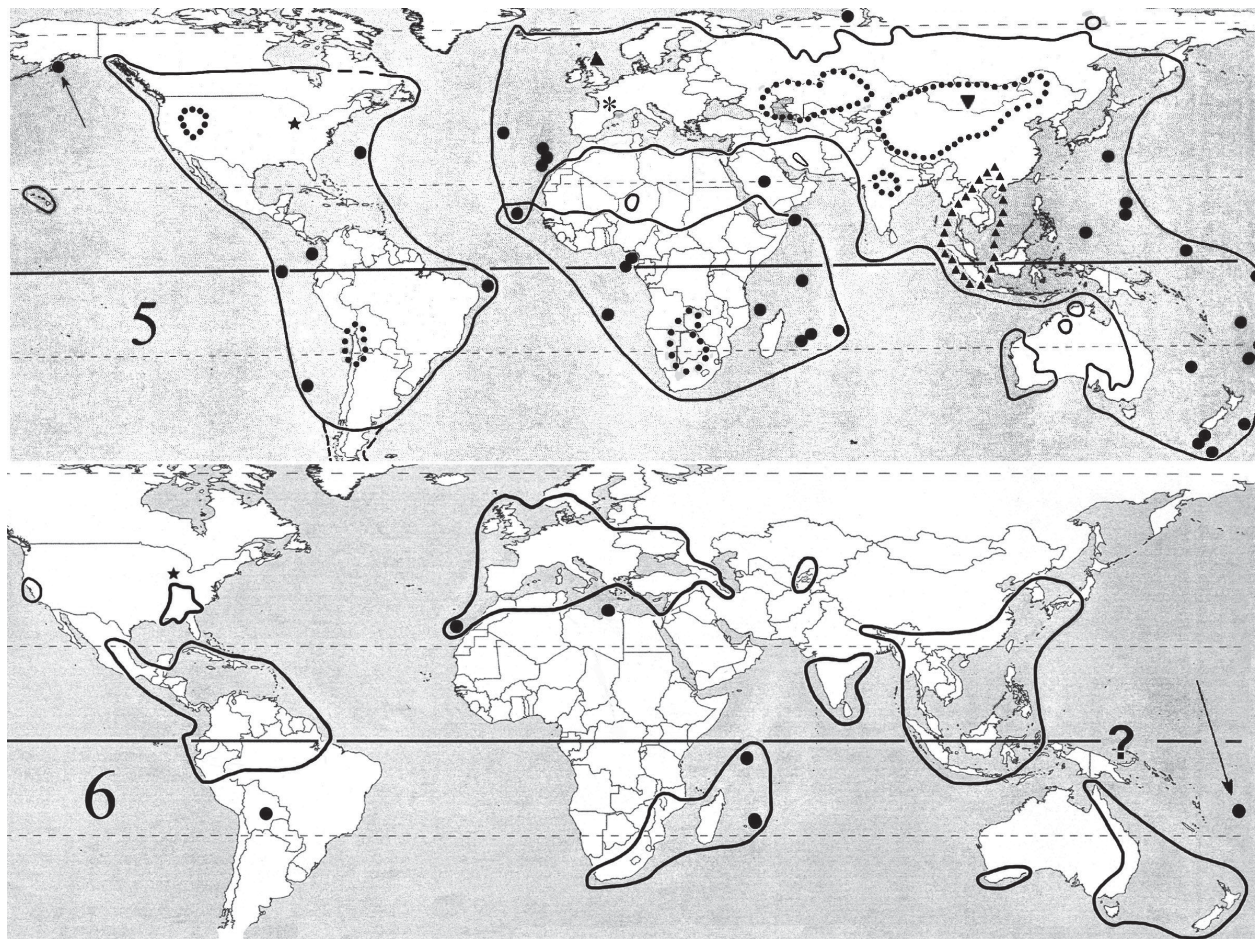


Figure 5-6. Distributions. **5)** Known (solid lines) and projected (dashed lines) indigenous distributions of the Subclass Chilognatha showing the locations of significant fossils, parameters as in Fig. 1. It is essentially identical to that of the Infraclass Helminthomorpha (Fig. 14), the only difference being imperceptibly greater eastward expansion for Chilognatha on the southern coast of Western Australia. At present, this is the only place in the world where the Infraclass Pentazonia (Fig. 6) influences the overall distribution of a higher diplopod taxon. Upright triangle, site of *Archidesmus macnioli* Peach, 1887, the oldest helminthomorph fossil, from Silurian deposits in Scotland; Star, site of the non-spinose oniscomorph pentazonian Carboniferous fossil at Mazon Creek, Illinois, USA; Inverted triangle, approximate location of *Gobiulus sabulosus* Dzik, 1975, the Cretaceous spirobolidan fossil from Mongolia; Asterisk, location of *Protosilvestria sculpta*, the Oligocene cambalidean fossil in Quercy, France (Mauriès 1992). **6)** Distribution of the Infraclass Pentazonia, which presently excludes the Yucatan Peninsula, Mexico. The question mark represents the unconfirmed Oniscomorpha (Sphaerotheriida) record from Papua New Guinea (Attems 1943), and the arrow denotes the new Limacomorpha/Glomeridesmida locality in Fiji (Appendix). Star, site of the non-spinose oniscomorph Carboniferous fossil at Mazon Creek, Illinois, USA.

and Ethiopia, reaching the Red Sea at the Eritrea/Djibouti border. Excluding Sokotra, it swings around the Seychelles (Golovatch and Korsós 1992), Rodriguez (Condé and Nguyen Duy-Jacquemin 1962; Nguyen Duy-Jacquemin and Condé 1967), Mauritius (Condé and Nguyen Duy-Jacquemin 1962, Mauriès and Geoffroy 1999, Enghoff et al. 2004), and Réunion islands (Condé and Nguyen Duy-Jacquemin 1962, Nguyen Duy-Jacquemin and Condé 1967, Enghoff 2003) in the Indian Ocean and encompasses St. Helena in the Atlantic (Enghoff et al. 2004). Documented sub-Saharan occurrences include: Botswana (Condé 1959, Hamer 1998), Ethiopia (Chalande 1908, Ribaut 1922), Kenya (Chalande 1908, Ribaut 1922, Nguyen Duy-Jacquemin and Condé 1967), Liberia (Turk 1947), Mozambique (Condé 1959), Republic of South Africa (Condé 1959; Nguyen Duy-Jacquemin and Condé 1967; Hamer 1998), and Uganda (Nguyen Duy-Jacquemin and Condé 1967). The polyxenidan from Lehututu, in the Kalahari Desert, is the only milliped record

from Botswana, so we add the first chilognath, an unknown spirostreptidean (*Spirostreptidae*) from Ngamiland (Appendix).

In Asia, there is an isolated record in Kyrgyzstan (Read and Golovatch 1994), and we join ones from India (Almora and Bombay) (Turk 1947, Nguyen Duy-Jacquemin and Condé 1967, Golovatch and Martens 1996), Nepal (Golovatch and Martens 1996), and Sri Lanka (Pocock 1892a) into a separate region on the Indian Subcontinent, which likely connects with that in east/southeastern Asia, whose inner/western border is nebulous. We merge the latter with eastern Australia/Tasmania, New Zealand, and western Oceania, but the Marshall and Hawaiian Islands are too remote. The northernmost Asian sites are in Honshu, Japan, and the Maritime Prov., Russia, and we incorporate the eastern periphery of China, all of the Indochina and Malay peninsulas, and most of Thailand, although (Enghoff 2005) cited no polyxenidans. The area extends eastward around the Bonin and Ryukyu Islands, Taiwan, all of Indonesia, Papua New Guinea, the Solomon Islands, New Caledonia, and Tonga. The only map, in Nguyen Duy-Jacquemin and Condé (1982), depicts records in the text. Other works with records cover Cambodia (Enghoff et al. 2004), China (D. Wang and Mauriès 1996; provinces and localities are not provided), Indonesia (Java) (Nguyen Duy-Jacquemin and Condé 1967, Murakami 1975a), Japan (mainland and Ryukyu Islands) (Nguyen Duy-Jacquemin and Condé 1967; Murakami 1975a, b; Ishii 1988; Tsurusaki 2002), Eastern Malaysia (Sabah/Sarawak) (Condé and Nguyen Duy-Jacquemin 1984, Lewis 1984a), Papua New Guinea ("mainland" and the Bismarck Archipelago) (Enghoff et al. 2004), Asian Russia (Mikhaljova 1993, 1998, 2004, 2010), Singapore (Ishii 1988), Taiwan (Korsós 2004), and Vietnam (Nguyen Duy-Jacquemin and Condé 1967, Enghoff et al. 2004). We project Polyxenida for the Philippines and eastern Myanmar.

Australian records, from the Australian milliped website and Short and Huynh (2010), include a coastal strip from Cape York to Tasmania and southeastern South Australia. Additional areas, both in Western Australia, are in the Kimberley Region and along the west/southwestern coasts.

Subclass Chilognatha (Fig. 2, 5)

The geography of Chilognatha (Fig. 5) is also that of Diplopoda except for north Africa and Western Australia; additionally, this subclass is not known from the Republic of the Marshall Islands. Instead of spreading southward into the Sahara, Chilognatha cuts across Morocco, Algeria, and Tunisia, heads into the Mediterranean, angles into the Benghazi region of coastal Libya, east of the Gulf of Sidra, then back into the Mediterranean again. Consequently, the northern Africa area south of this line in Diplopoda (Fig. 1) is solely attributable to Penicillata. In Western Australia, the chilognath area in the Kimberley Region is exclusively interior, in contrast to that in Diplopoda as a whole (Fig. 1).

Infraclass Pentazonia (Fig. 6)

Pentazonia occupy 12 areas that span both Tropics and the Equator, involve all continents plus Oceania, Madagascar, and Indian Ocean islands, and possibly the Bismarck Archipelago, Papua New Guinea (Fig. 6). Areas in the US, Europe, northern and southern Africa, Madagascar and Indian Ocean islands, central and southeastern Asia, and Australia/New Zealand refer solely to Oniscomorpha, as does the Carboniferous fossil in Illinois, USA (Fig. 6, 8-10 star). The Fiji site represents Limacomorpha as does, primarily, the Neotropical area, though Mexican occurrence is mostly Oniscomorpha. Conversely, Indian occurrence is primarily oniscomorphan except for more northerly limacomorph extension along the Bay of Bengal. In east/southeastern Asia, the superorders occur sympatrically, with Limacomorpha enclosed within Oniscomorpha.

Superorder Limacomorpha (Fig. 7)

With only one extant order, Limacomorpha presently have the same distribution as Glomeridesmida (Fig. 7), detailed below.

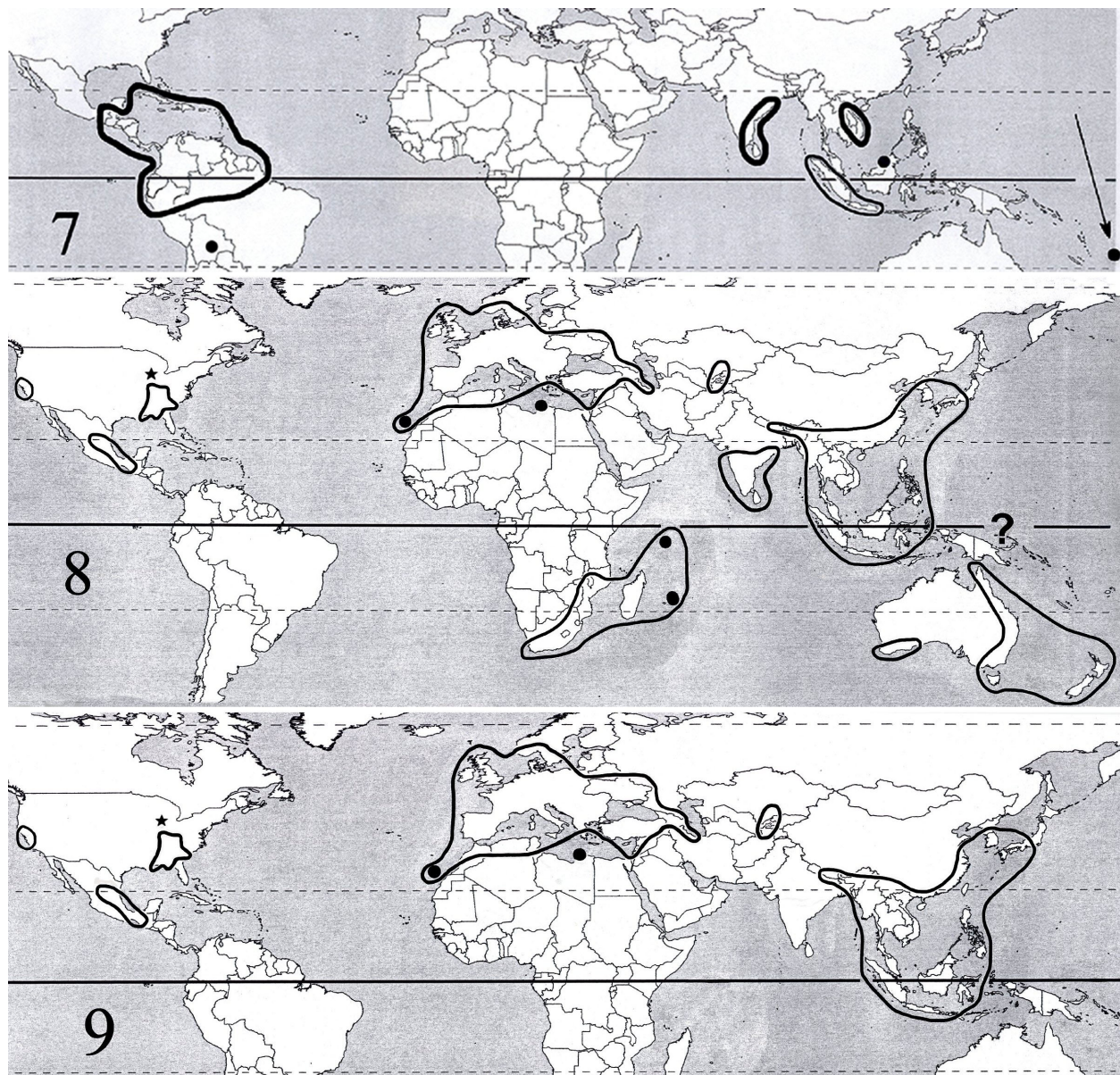


Figure 7-9. Distributions. **7)** Distributions of the Superorder Limacomorpha and the order Glomeridesmida, at present excluding the Yucatan Peninsula, Mexico. The arrow denotes the new record from Fiji (Appendix). **8)** Distribution of the Superorder Oniscomorpha. Star, site of the non-spinose Carboniferous fossil from Mazon Creek, Illinois, USA. **9)** Distribution of the Order Glomerida, parameters as in Fig. 1, 6.

Order Glomeridesmida (Fig. 7)

Glomeridesmida is a tropical taxon inhabiting seven widely separated areas, two straddling the Equator. A reasonably complete summary (Jeekel 2003a) is available along with a map in Mauriès (1988a).

In the New World, Glomeridesmida straddle the Equator but most records occur to the north in Caribbean Islands, Mexico/Central America, and northern South America. They are known from both Greater (Hispaniola [Haiti], Jamaica, Puerto Rico) and Lesser (Dominica, Grenada, Guadeloupe, Martinique, St. Vincent) Antilles (Hoffman 1960, 1999; Jeekel 2003a), sufficient to encircle all Caribbean Islands except the Bahamas and Turks and Caicos. The northernmost continental records are from Chiapas and Tabasco, Mexico (Shear 1973a, Hoffman 1999, Jeekel 2003a); we provide new ones (Appendix) from Peru and Brazil that extend the range continuously southward, but the southernmost is from

Santa Cruz Prov., Bolivia, some 1,600 km (1,000 mi) southeast of the contiguous range. It is so detached that we show a point locality (Fig. 6-7), not knowing how or whether it links with the northern area. The easternmost record is Labba Creek Sand Hills, Guyana (Chamberlin 1923; Adis et al. 2002; Jeekel 2003a), and occupied countries include Guatemala, Costa Rica, Panama, Colombia, Ecuador, Venezuela, and Trinidad and Tobago (Trinidad) (Campos-Rebeiro 1926; Loomis 1968, 1972; Jeekel 1986a, 2003a; Hoffman 1999). As the new record from Pará, Brazil, is in the eastern Amazon Basin, we project occurrence in Surinam and French Guiana.

Available records document four detached Old World regions plus the new sites in Fiji and Eastern Malaysia/Sarawak (Appendix) – the Bengali Coast/southern India/Sri Lanka, coastal Vietnam, and Singapore/western Indonesia (Sumatra/Java). The Indonesian region straddles the Equator, but most Old World localities are to the north. Other published citations include Sumatra in general (Y. Wang and Tang 1965) and Mt. Honba, Khanh Hoa Prov., Vietnam (Enghoff et al. 2004).

Superorder Oniscomorpha (Fig. 8)

Oniscomorpha occupy ten areas on all continents except South America, with a questionable sphaerotheriidan record from the Bismarck Archipelago, Papua New Guinea (Attens 1943). They traverse the Equator and both Tropics, and terminate in southern Scandinavia well south of the Arctic Circle. The detached Libyan site is near Benghazi, east of the Gulf of Sidra.

Areas in the New World, Europe/north Africa, and central Asia attribute solely to Glomerida as may the Paleozoic/Carboniferous fossil from Illinois, USA (Fig. 8-9, star); those in southern Africa/Madagascar/Indian Ocean, Australia/New Zealand, and India/Sri Lanka represent Sphaerotheriida; and that in east/southeastern Asia represents both orders, which are sympatric and highly congruent here (compare Fig. 9 and 13). Both encompass the Indochina and Malay peninsulas, Thailand, Myanmar, Indonesia from Sulawesi westward, and the Philippines. Both also exhibit a narrow dactyliform extension that runs westward through eastern India, Bhutan, and the eastern half of Nepal. Sphaerotheriida ranges farther eastward in Indonesia, around Halmahera, and Glomerida spread substantially farther north, encircling Taiwan, coastal China to the Shangdong Peninsula, most of the Korean Peninsula, and the Ryukyu Islands and “mainland” Japan northward to central Honshu. The northernmost sphaerotheriidan locality is Fuzhou, Fujian Prov., China, ~ 1,080 km (675 mi) south of the northernmost glomeridan, but Sphaerotheriida extend farther inland.

Order Glomerida (Fig. 9-12)

Glomerida are north temperate and tropical oniscormorphs that occupy six areas (Fig. 9), three each in the New and Old Worlds. Those in the former are widely segregated with the two in the US wholly north of the Tropic of Cancer and the other spanning this meridian over a swath of Mexico and Guatemala (Fig. 10). The Old World areas in Europe/North Africa and east/southeastern Asia are large and irregular, and the third is ovoid in Central Asia, primarily Kyrgyzstan and Tajikistan. The European region, eastwardly lobate, expands through Ukraine, indents slightly westward then spreads eastward again to the Caspian Sea and northwestern Iran; it also expands southward to Israel and, on the west, the Canary Islands. The southeast Asian region spans both the Tropic of Cancer and the Equator, extending roughly

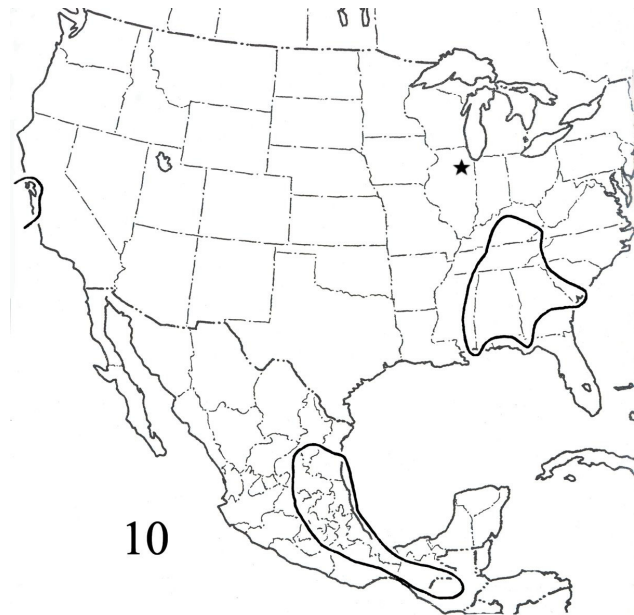


Figure 10. Distributions of Oniscomorpha and Glomerida in North America/the Western Hemisphere. Star, site of the non-spinose fossil from Mazon Creek, Illinois, USA. .

from 40°N in North Korea to 6°S in Indonesia; overall, the northern limit is 60°N in Norway. The Central Asian area is equidistant from the others, each of which points generally to it with a subdactyliform extension. It therefore appears to be a remnant of a prior connection of the European and southeast Asian faunas that ran along the southern Laurasian/Eurasian border through what is now the Himalayan region of northern India, Pakistan, and Afghanistan, and perhaps lower mountain areas in Uzbekistan and north-eastern Iran.

The US regions, separated by ~ 2,880 km (1,800 mi), include an irregularly shaped one in the southeast and a small one around San Francisco and Monterey Bays, California. The former comprises two unrevised genera – *Onomeris* Cook, 1896, with two species, and the monotypic *Trichomeris* Loomis, 1943 – but the actual number of genera and species is unknown and surely substantially larger. A taxonomic study of southeastern glomerids is a major need in Nearctic diplopodology that can largely be accomplished with VMNH material, where the great majority of samples are housed. The area extends ~ 816 km (510 mi) in both dimensions, ranging, north-south, from the Ohio River in central Kentucky to the Florida panhandle and Gulf Coast of Alabama/Mississippi and, east-west, from the Atlantic Coast of Georgia/South Carolina to eastern Mississippi. It covers parts of nine states and essentially all of Alabama (Fig. 10), and we provide records in the Appendix. The unknown but non-spinose, glomeridan-like, onicsomorph fossil from Illinois is compatible with the present area, lying just to the north. It may therefore represent an ancestral form from the radiation that occurred when Laurentia collided with Baltica+Siluria in the early Silurian.

The Californian and Mexican regions harbor 17 species of *Glomeroides* (Chamberlin 1922b), but only *G. primus* (Silvestri, 1929) occupies the former, a narrow coastal strip ~ 240 km (150 mi), north/south, and 56 km (35 mi), east/west. We add new records (Appendix) to the three published localities – Mill Valley and S.P. Taylor State Park, Marin Co., and Pfeiffer Big Sur State Park, Monterey Co. (Silvestri 1929, Shear 1986, Hoffman 1999).

The Mexican area, primarily south of the Tropic of Cancer, is ~ 1,306 km (816 mi) long, 304 km (190 mi) wide, and extends from southern Nuevo León/Tamaulipas, Mexico, to Alta and Baja Verapaz Depts., Guatemala. Sixteen species have been described from this region, eight known only from caves, and we add records in the Appendix to those reported by Shear (1982, 1986), Hoffman (1999), and Bueno-Villegas et al. (2004).

The European distribution follows Kime (2000), to which we add the Caucasus region, the Middle East, Mediterranean Islands, coastal northwestern Africa, and the Canary Islands (Fig. 9, 11). Works with or without maps cover the Balearic Islands (Mauriès and Vicente 1976), British Isles (Blower 1985), Canary Islands (Golovatch 1987a, Golovatch and Enghoff 2003), Caucasus (Golovatch 1989a, b, 1990b), Cyprus and Greece (Mauriès and Karamaouna 1984; Thaler 1987, 2000), Iran (Golovatch 1981a, 1989a, b, 1990b;



Figure 11. Distributions of Oniscomorpha and Glomerida in Europe, the Middle East, and North Africa.

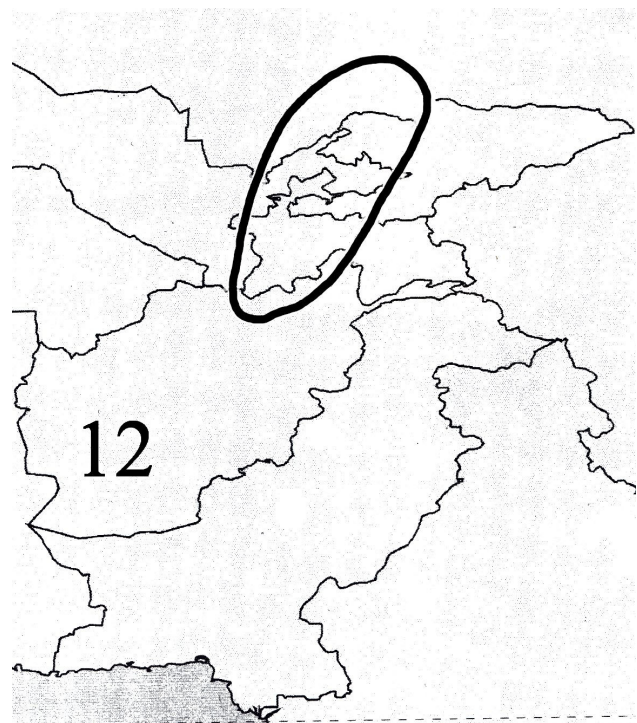


Figure 12. Distributions of Oniscomorpha and Glomerida in Central Asia.

Enghoff and Moravvej 2005), Israel and Syria (Golovatch 2003), the Maltese Islands (Enghoff and Schembri 1989), Turkey (Thaler 1987, 2000; Golovatch 1989a, b, 1990b; Enghoff 2006); and Ukraine (Golovatch 2010). African representatives are summarized by Golovatch et al. (2009); we project occurrences in Portugal and northern Tunisia.

The Central Asian region is mapped by Golovatch et al. (2006); localities in Kyrgyzstan were reported by Read and Golovatch (1994).

In southeast Asia, Glomerida spread eastward to Weber's Line and western "Wallacea"; partial maps are available in Golovatch (1975) and Golovatch et al. (2006). Golovatch (1983a) addressed southeast Asia in general; other papers treat India, Nepal, and the Himalayas (Golovatch 1987b, Golovatch and Martens 1996), the Korean Peninsula (Mikhaljova and Lim 2006a), Sarawak and the Philippines (Y. Wang 1951, 1961), Taiwan (Korsós 2004), Thailand (Enghoff 2005), and Vietnam (Enghoff et al. 2006).

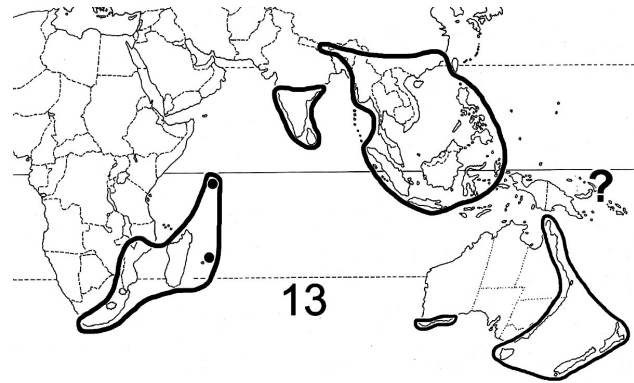


Figure 13. Distribution of the Order Sphaerotheriida. The question mark represents the unconfirmed record from Papua New Guinea (Attems 1943).

Order Sphaerotheriida (Fig. 13)

One of four orders to have been mapped (Jeekel 1974, Wesener and VandenSpiegel 2009, Wesener et al. 2010), Sphaerotheriida span the Tropics of Cancer and Capricorn and the Equator but are primarily tropical. Regional maps are available for Africa and Madagascar (Alderweireldt 1997; VandenSpiegel 2002; Wesener and Sierwald 2005a, b; Wesener and VandenSpiegel 2007), and Jeekel (2001a) cataloged the Asian fauna.

In Jeekel's map (1974), African occurrences encompassed Lesotho, part of the Republic of South Africa, and Swaziland (though no records exist from the last), with a few localities from coastal Mozambique (Attems 1928). Since then Sphaerotheriida have been documented from Malawi (Jocqué 1984, VandenSpiegel 2002) and Zimbabwe (Alderweireldt 1997), with species listings, complete at the times, by Hamer (1998) and VandenSpiegel et al. (2002); we enclose these areas in Fig. 13.

The Madagascar fauna is documented by Butler (1878), Jeekel (1999), Enghoff (2003), Wesener and Sierwald (2005a, b), Wesener and VandenSpiegel (2007, 2009), and Wesener et al. (2010); those in India and Southeast Asia are addressed by Jeekel (1974, 2001a). India comprises parts of both regions, which are separated by ~ 832 km (520 mi); the southern Indian range extends southward around Sri Lanka from a line roughly connecting Mumbai and Bhubaneshwar, south of Cuttack.

The southeast Asian region, the largest for the order and highly congruent with Glomerida, extends from north of the Tropic of Cancer, as far as Fuzhou, Fujiang Prov., China, to south of the Equator in Indonesia (Java). It extends eastward around Halmahera to "Lydekker's line" in the north and "Wallace's line" in the south; a northwestern, finger-like projection extends through northeast India (Assam/Sikkim) and Bhutan, into Nepal, the northwesternmost locality being Chitlong (27.67°N, 85.15°E) (Attems 1936). This area encompasses all of the Philippines, both parts of Malaya, Thailand, Laos, Cambodia, and Vietnam, and most of Myanmar. Sphaerotheriida have been reported from Indonesian islands off the west coast of Sumatra but not from the Nicobar and Andaman Islands to the north, which logically are inhabited. In addition to Jeekel (1974, 2001a), relevant works include Golovatch (1983b), Golovatch and Martens (1996), Mauriès (2001), Enghoff et al. (2004), and Enghoff (2005).

Sphaerotheriida occupy two parts of Australia. The larger extends narrowly along the eastern periphery from the Torres Strait/Cape York Peninsula to southern coastal Victoria southeast of Melbourne; it includes all of Tasmania and both major New Zealand islands. Additionally, *Cynotelopus* Jeekel, 1986, and *Epicyllosoma* Silvestri, 1917, inhabit southern coastal Western Australia (Jeekel 1986b, Black 1997), some 2,624 km (1,640 mi) to the west, which is shown on the Australian milliped website but not on the maps of Wesener and VandenSpiegel (2009) and Wesener et al. (2010). Jeekel (1981) mapped localities up to that time in eastern Australia and Tasmania. The eastern coastal strip extends ~ 160 km (100 mi)

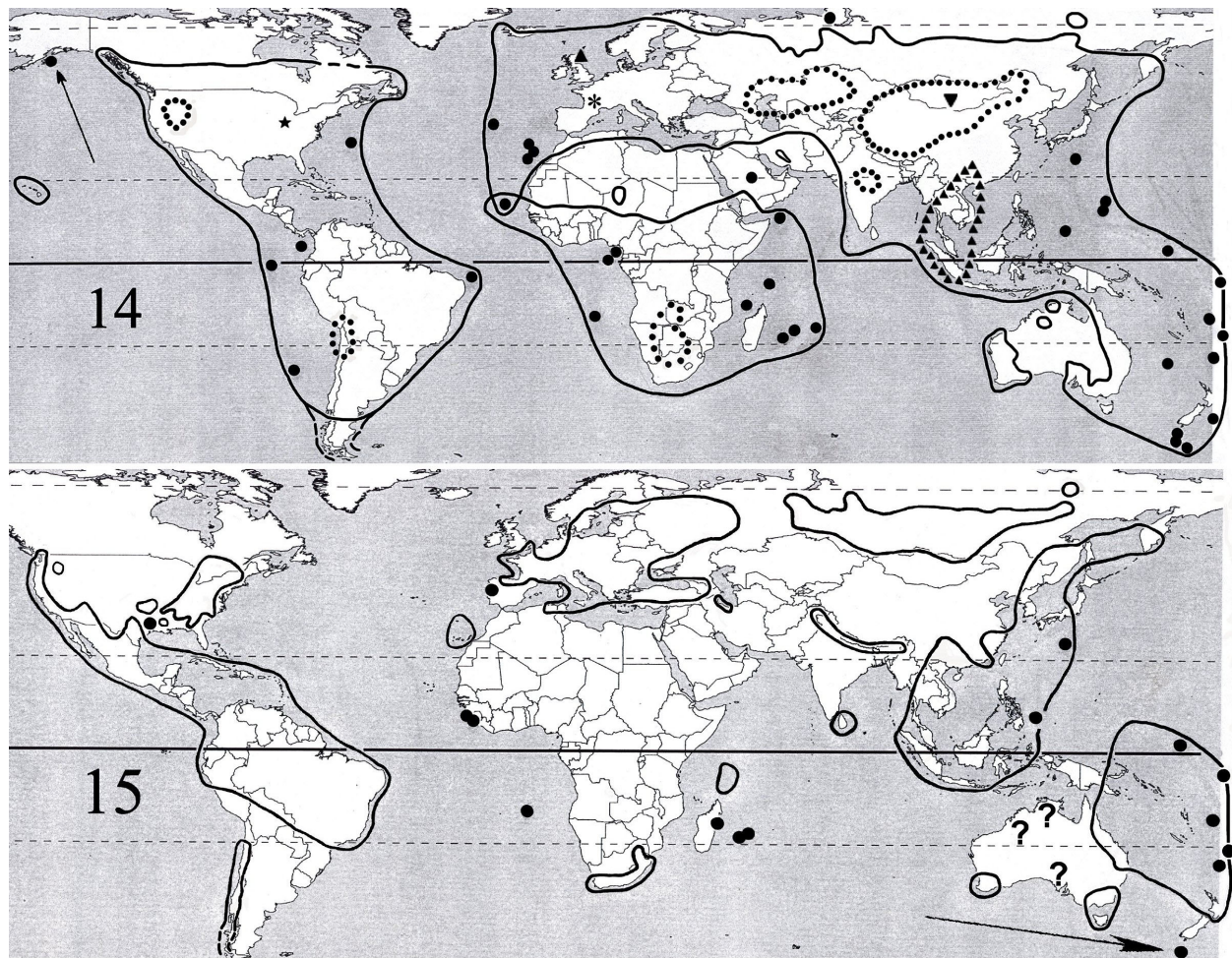


Figure 14-15. Distributions. **14)** Known (solid lines) and projected (dashed lines) distributions of the Infraclass Helminthomorpha showing the locations of significant fossils, parameters as in Fig. 1. It differs from that of the Subclass Chilognatha (Fig. 5) in the imperceptibly shorter length along the southern coast of Western Australia, the only place where Pentazonia have been taken without helminthomorphs. Upright triangle, site of *Archidesmus macnioli* Peach, 1887, the oldest fossil, from Silurian deposits in Scotland; Inverted triangle, approximate location of *Gobiulus sabulosus* Dzik, 1975, the Cretaceous spirobolidan fossil from Mongolia; Asterisk, location of *Protosilvestria sculpta*, the Oligocene cambalidean fossil in Quercy, France (Mauriès 1992). **15)** Known (solid lines) and projected (dashed lines) distribution of the Subterclass Colobognatha. The question marks in Australia represent generalized records from Northern Territory, South Australia, and “Upper Western Australia” by Black (1997). Some point localities probably represent the ubiquitous, introduced polyzoniidan (Siphonotidae), *Rhinotus purpureus* (Pocock, 1894).

inland to Gayndah, Queensland, becoming narrower to both the north and south. The “Torres Straits” record is from Butler (1878), and Sphaerotheriida are widespread in Tasmania (Mesibov 2000). In New Zealand, Chamberlin (1920) cited the order from Cape Maria Van Diemen, at the northern tip of the North Island, to Dunedin, on the southern coast of the South Island, and we project Sphaerotheriida for Stewart Island.

An obscure record of *Pulusphaera fera* (Attems, 1935) also exists from an unspecified site in the “Bismarckarchipel” (Attems 1943, Jeekel 2001a); with even the island unknown, we represent it by a question mark in Fig. 6, 8, 13.

Infraclass Helminthomorpha (Fig. 2, 14)

The distribution of Helminthomorpha (Fig. 14) is nearly identical to that of Chilognatha (Fig. 5), to which readers are referred for details, as Pentazonia barely impact the latter's range; the New World, Eurasian, sub-Saharan African, and oceanic occurrences are identical. The only difference, barely perceptible, is in coastal Western Australia, where Helminthomorpha do not extend quite as far eastward along the southern coast. Most helminthomorph occurrences are attributable to Eugnatha (Fig. 24); Colobognatha (Fig. 15) have minimal impact and are largely subsumed within the former's area. Colobognatha extend Helminthomorpha westward in the Atlantic to encompass St. Helena and north of the Arctic Circle in Asian Russia; otherwise, helminthomorph distribution is attributable to Eugnatha alone.

Archidesmus macnioli Peach, 1887, the earliest helminthomorph fossil (Fig. 1, 5, 14, upright triangle), from Silurian deposits in Scotland, came from either Avalonia itself or Laurentia after it collided with Baltica+Avalonia. It is not definitely assignable to either a modern or an extinct order.

Subterclass Colobognatha (Fig. 15-16)

Colobognatha span the Equator and both Tropics and are scattered over 28 areas on all continents; some point records, however, probably reflect human introductions of *R. purpureus* (Polyzoniida). As no one has studied this species, reviewed global occurrences, or attempted to deduce its native area, the only way to distinguish indigenous from introduced occurrences is a lengthy examination of preserved specimens, which is well beyond our scope. We exclude known introductions but include occurrences of uncertain origins.

The seven New World areas include a continuous one involving the three major components (Platydesmida, Polyzoniida, Siphonophorida) that spans both Tropics and the Equator. Omitting Vancouver Island, the large area extends southward along the Pacific Coast of North America from Vancouver (city), BC (Fig. 16), to Mexico, re-enters the US in both Arizona and Texas, and continues southward through Central America and the Antilles to blanket the northern half of South America and terminate at a southeastward slanted line running through central Peru and Bolivia, and southern Brazil. There is also a detached area in Chile that spreads southward to Isla Grande de Chiloé and surely beyond, where no samples are available. Moreover, there are five additional regions in North America, three exclusively representing Platydesmida (Fig. 17-18) – the point locality in Texas (Shelley et al. 2005), the small subcircular area in Louisiana/Mississippi, and the larger subtriangular one in Arkansas and adjacent states. The detached area in northern Idaho represents both Platydesmida and Polyzoniida, as does the large eastern area extending from Québec to the Florida Panhandle and, east-west, from the Atlantic Coast to western Arkansas.

There are two regions in Europe and environs – a point site in Portugal and a large, irregular, lobate one stretching from northern Spain, western France, and southeastern England to the Caspian Sea and the Ural Mts. of Russia. North-south, it ranges from southern Sweden, Finland, and Karelia, Russia, to southern Turkey, “mainland” Greece, and northern Tunisia/northeastern Algeria, enclosing Sicily, Malta, and northern Aegean Islands but omitting Cyprus, Crete, Sardinia, and Corsica. Madeira and the Canary Islands, depicted separately in Fig. 15, contain the rare order Siphonocryptida (Fig. 23). The point lo-

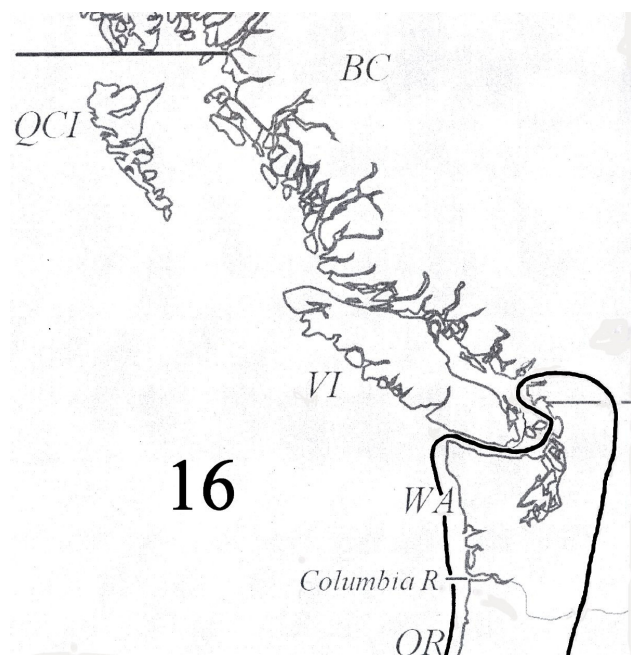


Figure 16. Distributions of Colobognatha and Polyzoniida along the Pacific Coast of northwestern North America

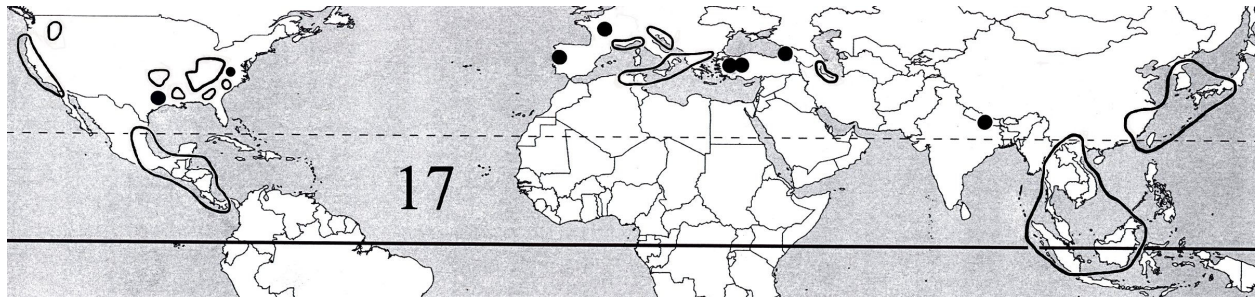


Figure 17. Distribution of the Order Platydesmida.

cality in Sierra Leone represents a polyzoniidan species described by Cook (1896) that may also occur on St. Helena (Hoffman 1977b), but both may also reflect introduced *R. purpureus*, as may the site just off the coast of Guinea. The southern coastal band in the Republic of South Africa, the only definitely indigenous sub-Saharan occurrence, involves both Polyzoniida and Siphonophorida; both orders also inhabit the Seychelles, while the former occupies Mauritius and Réunion.

Asian occurrences include Sri Lanka (Siphonophorida), narrow strips along the southwestern Caspian Sea from Azerbaijan to Iran (Platydesmida) and the Himalayas from northern Pakistan through Nepal and Bhutan to eastern India and perhaps northern Myanmar (Polyzoniida, Siphonophorida). A small detached circular area (Polyzoniida) straddles the Arctic Circle in Yakutia, Russia (Mikhailjova 2004, Golovatch 2009), lying north of a long, irregular, east-west band that spreads across subarctic Siberia/central Russia and dips southward into Mongolia. The final Eurasian area, containing all four components, extends from Kamchatka, Sakhalin, and Far Eastern Russia to southern Indonesia (Sumatra to Flores) and, east/west, from the Bonin Islands and Halmahera to eastern Myanmar, excluding parts of coastal China, northern Honshu and Hokkaido, Japan, and the Kurile Islands, Russia.

Colobognatha occupy the southwestern and southeastern corners of Australia with generalized records from Northern Territory, South Australia, and northern Western Australia. A large area, representing Polyzoniida and Siphonophorida, encircles the North Island of New Zealand, central coastal Queensland, Australia, Pohnpei, Federated States of Micronesia, Samoa, Tuvalu, Tonga, and Fiji. It crosses the eastern arm of the Island of New Guinea (Papua New Guinea) and may join with the southeast Asian area, but without records from Irian Jaya and western Papua New Guinea, we consider them separate.

Order Platydesmida (Fig. 17-19)

Like Glomerida, Platydesmida are exclusively Laurasian; the order occupies 21 areas primarily north of the Tropic of Cancer but also in the New and Old World Tropics and south of the Equator in southeast Asia (Indonesia), its largest region (Fig. 17). It is absent from South America, Australia/New Zealand, and Africa except for northern Tunisia and the adjacent northeastern corner of Algeria. Most areas are comparatively small, with six being point localities; 10 are in the Western Hemisphere (North and Central America), six are Asian, and five are European, one drifting across the Mediterranean into a sector of Mediterranean Africa. No consolidated catalog exists for Platydesmida nor were European occurrences depicted by Kime (2000). However, Shelley et al. (2005) mapped *Brachygybe* Wood, 1864 (Andrognathidae), the dominant Nearctic and northeast Asian genus, and these maps apply di-



Figure 18. Distribution of Platydesmida in North America/the Western Hemisphere.

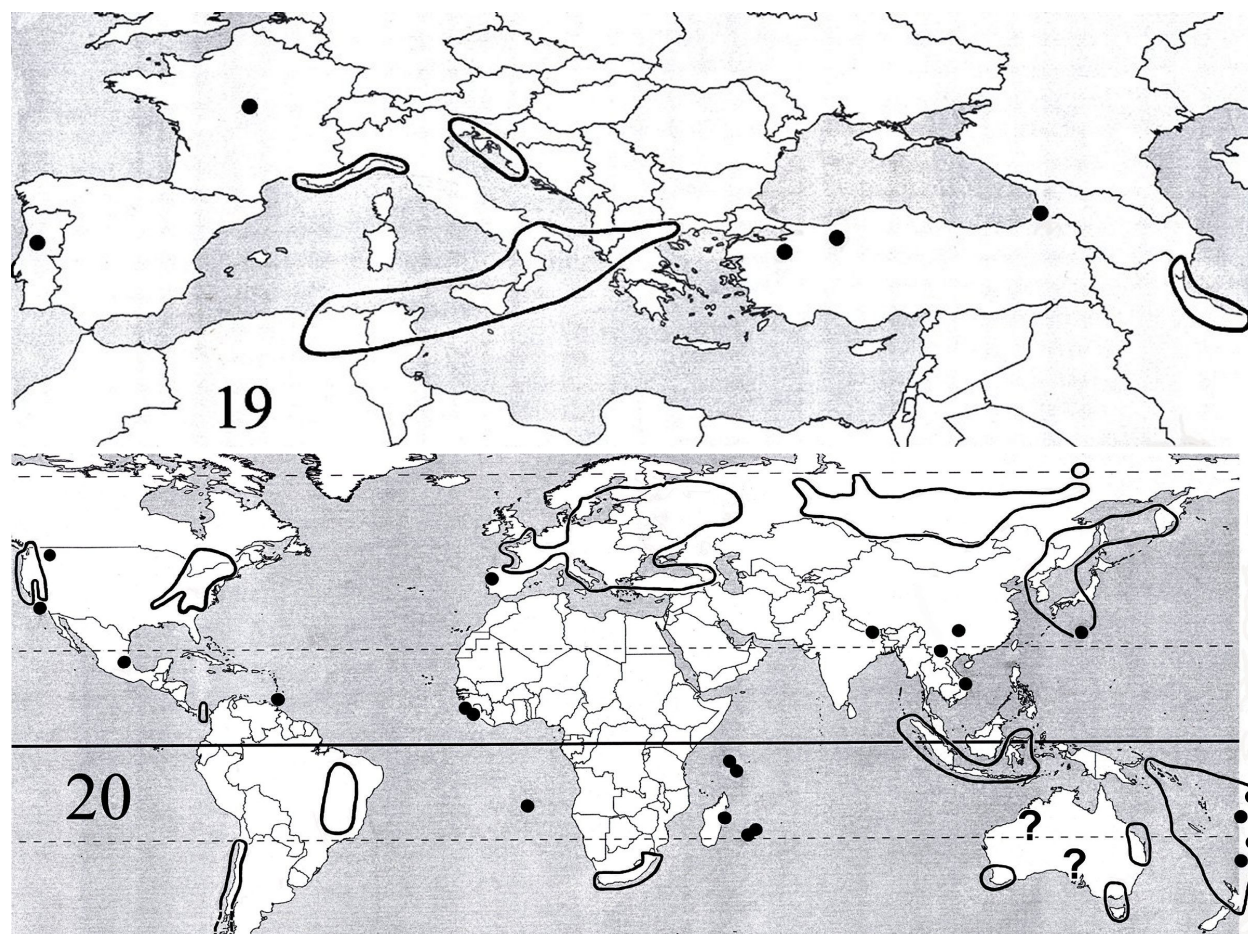


Figure 19-20. Distributions. 19) Distribution of Platydsmida in Europe, the Middle East, and North Africa. 20) Known (solid lines) and projected (dashed lines) distribution of the Order Polyzoniida, parameters as in Fig. 15.

rectly to the present focus when other familial genera are incorporated. We then scoured the literature, consolidated records, incorporated significant unpublished ones (Appendix), and determined ranges of non-US andrognathids and the nominate family, whose area encloses the only Mexican andrognathid (Shear and Marek 2009). Papers with records and/or maps include Sinclair (1901), Chamberlin (1945), Chamberlin and Wang (1953), Y. Wang and Tang (1965), Buckett and Gardner (1969), Gardner (1975), Minelli (1976), Loksina and Golovatch (1979), Golovatch (1980a, 1981b), Strasser and Minelli (1984), Lewis (1984a, b), Ceuca (1992), Golovatch and Martens (1996), Mauriès et al. (1997), Mikhaljova et al. (2000), Korsós (2004), Enghoff et al. (2004), and Enghoff (2005, 2006). Additional literature citations are available in Causey (1954), Gardner (1975), and Shelley (2000a, 2002a).

Represented solely by Andrognathidae, Platydsmida occupy nine regions of the US. Shelley et al. (2005) documented five areas of *Brachycybe* in the east/southeastern US, which increases to seven when *Andrognathus* Cope, 1869, is included (Fig. 18, Appendix). The three westernmost lie primarily west of the Mississippi River, while the large central area slightly crosses it in southeastern Missouri. The point locality in Virginia and the eastern area in North Carolina, which dips into South Carolina, represent *Andrognathus*, which also expands the ranges of the central area and that in southwestern Georgia and adjacent Florida. Distributions of other western US andrognathids consolidate the areas of *Brachycybe* in California and Oregon into a continuous one that arises at the Mexican border in San Diego Co., California, and extends northward to Benton Co., Oregon; occurrence in the northwestern corner of Baja California Norte, Mexico, is virtually certain. There is also a small area in northern Idaho, first reported by Causey (1954), that probably spreads westward into southeastern Washington and northeastern Oregon.

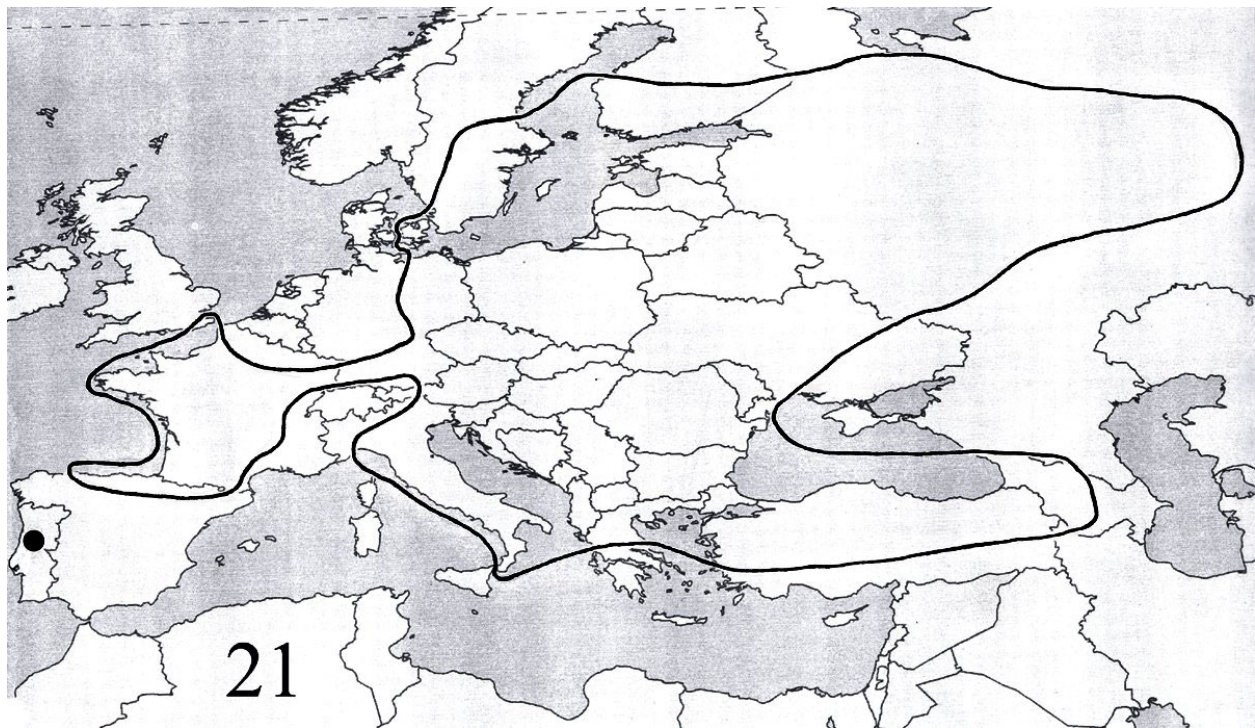


Figure 21. Distribution of Polyzoziida in Europe and the Middle East.

The southernmost New World area (Fig. 17-18), representing the entire distribution of Platydesmidae, traverses the Tropic of Cancer and extends from central Nuevo León, Mexico, to the Former Canal Zone, Panama. It includes all or nearly all of Guatemala, Honduras, El Salvador, Nicaragua, and Costa Rica, but excludes the Yucatan Peninsula. Hoffman (1999) cited the order and nominate family from every Central American country except Belize, which we add (Appendix).

In Europe, Platydesmida/Andrognathidae occupy five areas (Fig. 17, 19), the two westernmost being point localities in Portugal and central France. Narrow strips extend along the Mediterranean Coast of northwestern Italy/southeastern France and the Adriatic Coast of northeastern Italy/Croatia. The largest area arises in northern Greece, traverses Albania and southern Italy (including Sicily), and crosses the Mediterranean into North Africa (northern Tunisia and northeastern Algeria) (Pocock 1892b, Silvestri 1898a; Brolemann 1921).

We recognize six faunal regions of Platydesmida/Andrognathidae in Asia. Two are in Turkey (Enghoff 2006), the more western comprising two point localities, and a narrow strip extends along the southwestern Caspian Sea from Azerbaijan to northwestern Iran. No locality was published, but Golovatch and Martens (1996) reported Platydesmida from Nepal. The largest areas are in east and southeastern Asia. The northern extends, north/south, from central Honshu through Taiwan, nipping the Tropic of Cancer and ranging westward over central coastal China and most of the Korean Peninsula (Shelley et al. 2005). The southeast Asian region is entirely tropical and the only one spanning the Equator. It includes the Indochina and Malay peninsulas and western Indonesia, extending from northern Vietnam (and doubtlessly also adjacent Yunnan Prov., China) to Sumatra, the Island of Borneo, and Wallace's Line.

Order Polyzoziida (Fig. 16, 20-21)

Polyzoziida occur natively and somewhat sporadically on all continents (Fig. 20), traversing the Equator and both Tropics. Like Platydesmida, no catalog exists, but Shelley (1996a, 1998b) and Shelley et al. (2010) mapped Hirudisomatidae in the Americas and Polyzoziidae worldwide, which essentially represent ordinal occurrences as the only significant additions are from South and North Korea (Mikhailjova and Lim 2006b) and the new ones in the Appendix. Completing the ordinal map thus required determining hirudisomatid occurrences elsewhere and indigenous ones worldwide of Siphonotidae, but the latter

are problematical because they are masked by widespread introductions of *R. purpureus*. Determining native siphonotid records is virtually impossible, but those in Brazil and Chile are plausibly so.

Another impediment to determining polyzoniidan distribution is that many are so small as to be overlooked in field sampling. Records are spotty with only a few from certain countries and regions such that a consolidated range cannot be postulated as, for example, continental Asia aside from Russia and the Korean Peninsula, where the efforts of E.V. Mikhailjova produced the areas outlined by Shelley (1998b). Otherwise, only scattered hirudisomatid and siphonotid localities, some far removed from each other, exist from Asia, which we show with dots in Fig. 20.

The ordinal range in North America is basically that of Polyzoniidae (Shelley 1998b); the only effects of Hirudisomatidae are to place the order in Idaho and extend the Pacific Coastal area northward into southwestern “mainland” BC (Fig. 16) (Shelley (1990a, 1996a, 2002b; Shelley et al., 2010). The most recently described polyzoniid and the first familial record north of the Columbia River, *Stenozonium leonardi* Shelley and Shear, 2005, lies within the range of *Octoglena anura* Cook, 1904, and does not impact the ordinal distribution (Shelley and Shear 2005). To the south, the Veracruz, Mexico, locality (Hirudisomatidae) is definitely indigenous, and three species of *Rhinotus* have been recorded from the Former Canal Zone and Panama (Chamberlin 1940; Loomis 1961, 1964, 1970; Hoffman 1999) that we consider native.

Mauriès and Silva (1971) mapped 10 species of *Siphonotus* Brandt, 1837, in Chile to which we add those described by Chamberlin (1947b). Brazilian localities are provided by Schubart (1944, 1947), Attems (1951), and Hoffman (1977a), and we include Port of Spain, Trinidad (Silvestri 1898b), based on the *S. virescens* record that may represent *R. purpureus*. Polyzoniida thus occupy two general areas of continental South America – the central 2/3 of Chile, extending an unknown distance southward, and an ovoid area in eastern Brazil, extending southward to near Rio de Janeiro and São Paulo.

The only definitely native African occurrence is a band along the Indian Ocean in the Republic of South Africa, whose eastern edge extends inland between Lesotho and Swaziland. Records are summarized by Hamer (1998), and because so few are known, we add three in the Appendix. Two closely proximate records from west Africa are potentially *R. purpureus*, that of *S. africanus* from Sierra Leone (Cook 1896) and that of the order from Tamara Island, Îles de Los, off the coast of Conakry, Guinea (Chamberlin 1920).

Kime (2000) did not depict polyzoniidan occurrences in Europe, so we scoured the literature for hirudisomatid records to add to Shelley’s (1998) polyzoniid map and found several for Italy, two for France and Spain, and one each for Portugal, Slovenia, Greece, and European Turkey (Verhoeff 1901, 1940; Mauriès 1960, 1964; Strasser and Minelli 1984; Mauriès and Barraqueta 1985; Ceuca 1992; Foddai et al. 1995; Geoffroy 1996; Enghoff 2006). Strasser and Minelli (1984) summarized Italian records, and Polyzoniida occurs throughout the “boot” except for the north/northwestern borders (Fig. 21). We include occurrences in Turkey and the Caucasus with Europe, as hirudisomatids occur along the Denizi and Black Sea Coasts of the former up to ~ 100 km (62 mi) inland (Enghoff 2006). General records exist from the Caucasus of Georgia and vicinity (Talikadze 1984, Loksina and Golovatch 1979) but not specific localities.

In the Indian subcontinent, Shelley (1996b) documented Polyzoniida/Hirudisomatidae from central Nepal.

Besides Kamchatka, Sakhalin Island, and southeastern mainland Russia (Mikhailjova 1979, 1981, 1993, 1998, 2001, 2004; Mikhailjova and Basarukin 1995; Shelley 1998b; Mikhailjova and Golovatch 2000; Mikhailjova and Marusik 2004), ordinal records from far eastern Asia include Hirudisomatidae in Japan and South Korea and Siphonotidae in Indonesia and Vietnam (Hoffman 1980a). D. Wang and Mauriès (1996) did not report the order from China, but the type locality of *Angarozonium amurense* (Gerstfeldt, 1859) (Polyzoniidae) is the delta of the Songhua Jiang (= Sungari) River, Heilongjiang Prov., Manchuria (Mikhailjova 1993; Shelley 1998b), and this or congeneric species plausibly occur in Liaoning and Jilin provs. near the North Korean border. We report Siphonotidae from Sichuan Prov. (Appendix), and the family is expected in southern Yunnan based on occurrence in adjacent northern Vietnam (Enghoff et al. 2004). Polyzoniida are known through most of North Korea, extending to south of Pyongyang (Golovatch 1980b, Mikhailjova and Kim 1993, Mikhailjova et al. 2000, Mikhailjova and Korsós 2003), and we project them for South Korea. In Japan, Shinohara (1973) reported *Orsiboe ichigomensis* Attems, 1909, (Hirudisomatidae) from lava caves near Mt. Fuji, central Honshu, and Tsurusaki (2002) recorded *Kiusiozonium okai* (Takakuwa and Miyosi, 1949) (Hirudisomatidae) from Matsuyama City, Shikoku. In

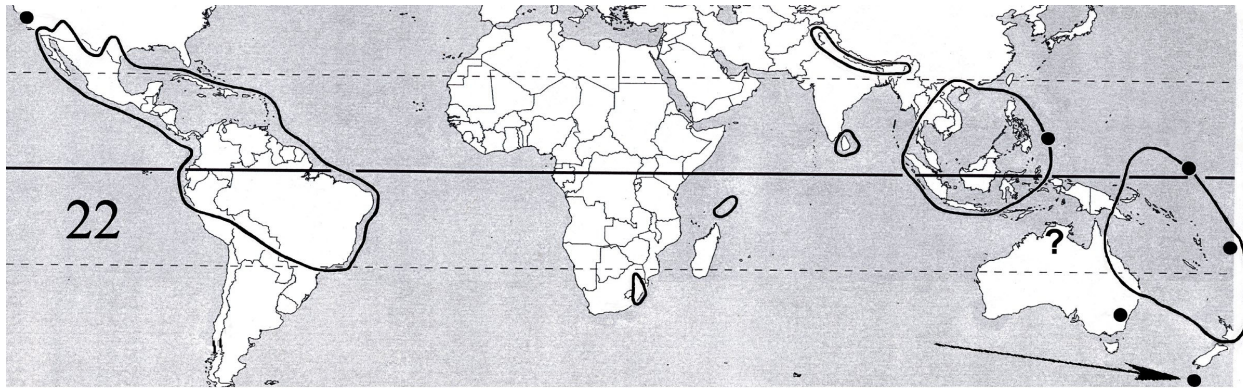


Figure 22. Distribution of the Order Siphonophorida; the dot in North America/USA (California) signifies the type and only known locality of *Illacme plenipes* Cook and Loomis, 1928 (Siphonorhinidae), the world's "leggiest" animal (Cook and Loomis 1928; Shelley 1996c, d; Marek and Bond 2006). The question mark represents the generalized record from Northern Territory, Australia (Black 1997), and the arrow denotes the locality of Siphonophoridae on Auckland Island, New Zealand (Johns 1964).

Indonesia, Y. Wang and Tang (1965) reported five species of *Siphonotus* from Sumatra, and Hoffman (1980a) added Java and Flores. We encircle these islands plus Sulawesi in Fig. 20, and the area's eastern border coincides roughly with Weber's Line.

Occurrences in Australia, all of Siphonotidae (<http://www.qvmag.tax.gov.au/zoology/millipedes/index.html>), are in the southwestern corner of Western Australia, the coast of southern Queensland, and Melbourne vicinity, Victoria. Without giving a genus or species, Black (1997) recorded the family in general from New South Wales, South Australia, and northern Western Australia.

Many oceanic records clearly represent *R. purpureus* (Shelley 1998a), but distinguishing which do and do not from literature accounts is impossible, and the specimens need restudying. Attems (1914a) summarized ones from Pacific Islands; Chamberlin (1920) proposed 10 new species from Fiji and the Solomon Islands and repeated prior records from the Loyalty Islands. Carl (1926) described three new species from New Caledonia, the Loyalty Islands, Vanuatu, and the North Island of New Zealand, and Golovatch (1994a) reported *Rhinotus* from Tonga and Samoa (Eua and Upolu islands). While *R. purpureus* has been reported from Indian Ocean Islands (Shelley 1998a), congeneric species have been described and recorded from Mauritius and Silhouette, Praslin, and Mahé islands, Seychelles (Mauriès 1980b, Golovatch and Korsós 1992, Mauriès and Geoffroy 1999).

Order Siphonophorida (Fig. 22)

We recognize nine areas of Siphonophorida, three in Asia and Australia/New Zealand/Papua New Guinea/Oceania, two in the New World, and one each in Africa and Indian Ocean Islands (Fig. 22).

The New World distribution, comprising a large area and a point locality to the north in California, was mapped by Shelley (1996c); the former traverses the Equator and Tropic of Cancer and extends southward to the Tropic of Capricorn. The detached northern site, of *Illacme plenipes* Cook and Loomis, 1928 (Siphonorhinidae), the world's "leggiest" animal, is also the northernmost for the order and the only familial locality in the Western Hemisphere. Known only from the area of the type locality (Cook and Loomis 1928; Chamberlin and Hoffman 1958; Shelley 1996c, d; Hoffman 1999), it was recently rediscovered by Marek and Bond (2006). The large area encompasses all Greater and Lesser Antilles (excluding the Bahamas and Turks and Caicos), Mexico, and Central America, and terminates at a southeastward slanted border that passes through central Peru and Bolivia but excludes Paraguay and the three southernmost Brazilian states: Paraná, Santa Catarina, and Rio Grande do Sul.

The lone African occurrence, of Siphonorhinidae, is restricted to KwaZulu Natal and Mpumalanga provs., Republic of South Africa; it was mapped by Shelley and Hoffman (2004). The order also occurs in the Seychelles (Mauriès 1980b, Jeekel 2001b).

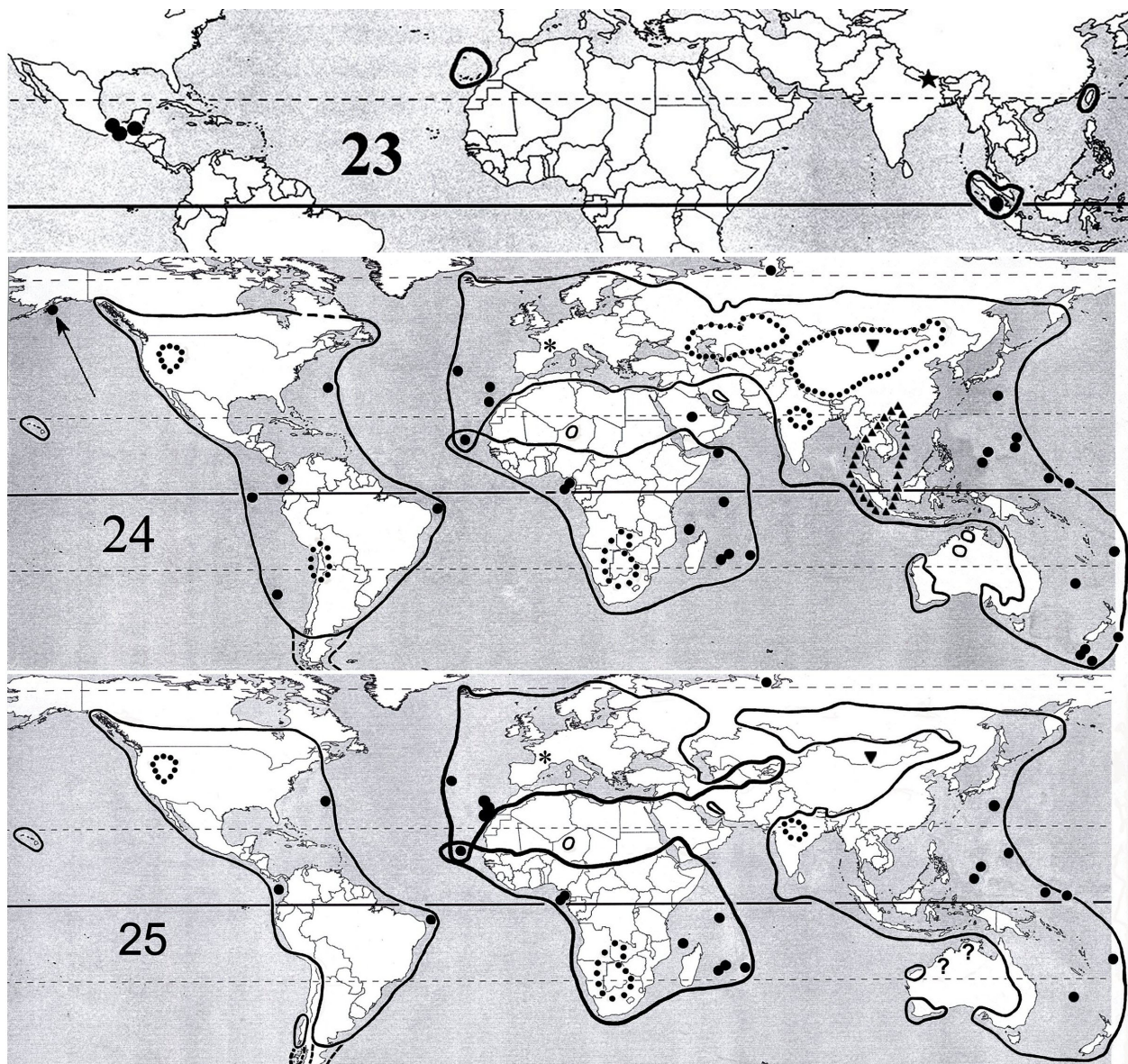


Figure 23-25. Distributions. **23)** Distribution of the “minor” orders. Star/Circled Areas, Siphonocryptida (Colobognatha); Dots, Siphoniulida (*Helminthomorpha incertae sedis*). **24)** Known (solid lines) and projected (dashed lines) distributions of the Subterclass Eugnatha showing the locations of significant fossils. The arrow points to the Kodiak Island, Alaska, USA, record of Chordeumatida (Tingupidae). Inverted triangle, approximate location of *Gobiulus sabulosus* Dzik, 1975, the Cretaceous spirobolidan fossil from Mongolia; Asterisk, location of *Protosilvestria sculpta*, the Oligocene cambalidean fossil in Quercy, France (Mauriès 1992). **25)** Known (solid lines) and projected (dashed lines) distributions of the Superorder Juliformia showing the locations of significant fossils. Parameters as in Fig. 1 except no records or samples are available from the dotted area in North America, the Great Basin Physiographic Province, western USA. Inverted triangle, approximate location of *Gobiulus sabulosus* Dzik, 1975, the Cretaceous spirobolidan fossil from Mongolia; Asterisk, location of *Protosilvestria sculpta*, the Oligocene cambalidean fossil in Quercy, France (Mauriès 1992). The question mark indicates the generalized record of Epinannolenidea from Northern Territory, Australia (Black 1997).

Records are sporadic, but we recognize six areas in Australasia that include western/southern Oceania. Sri Lanka, on the Indian Subcontinent, is one, but unlike Sphaerotheriida, Spirobolida, Chordeumatida, and Stemmiulida (Fig. 13, 28, 41, 46), no records exist from peninsular India itself. We unite isolated records from northern Pakistan, the northernmost Asian occurrence (Golovatch 1991, Jeekel 2001b), northern India, the Darjeeling District in eastern India, and Assam (Appendix) into a narrow continuous

strip through the Himalayas and adjacent southern lowlands. While varying in lengths, strip-like occurrences here, contiguous or detached from southeast Asian areas, are shown by Glomerida, Sphaerotheriida, Julida, and Chordeumatida (Fig. 9, 13, 26, 41), and the point localities here in other colobognaths (Platydesmida, Polyzoniida, Siphonocryptida) (Fig. 17, 20, 23), constitute extreme manifestations of this phenomenon. Because of these patterns, we project siphonophoridan occurrence eastward into northern Myanmar. The third Asian area encompasses all of the Malay and most of the Indochina peninsulas, spreads eastward around the Philippines to the Republic of Palau (Takakuwa 1942), and then swings southward around Indonesia as far east as Halmahera and Flores. Although we could not find records, we project Siphonophorida for Sulawesi and Borneo as the order occurs on proximate islands in all directions and extends eastward to Lydekker's Line. To the southeast, we unite the eastern arm of the Island of New Guinea (Port Moresby region, Papua New Guinea), eastern Queensland, the North Island of New Zealand, New Caledonia and the Loyalty Islands, Fiji, the Solomon Islands, and Pohnpei, Federated States of Micronesia (Takakuwa 1942), into one area. Black (1997) recorded the order and nominate family from Northern Territory, Australia, in general, and Hoffman (1980a) and Mesibov (2009:90) cited the former from New South Wales. The New Zealand sites are near Wellington and well to the south on Auckland Island, the southernmost for Siphonophorida as a whole. Johns (1964) reported a juvenile *Siphonophora* from Auckland I. without comment, while simultaneously reporting many specimens of *Schedotrigona* n. sp. (Chordeumatida) from Campbell I. that he strongly suspected were introduced from New Zealand proper. Lacking information to the contrary, we regard the lone siphonophoridan as indigenous, include Auckland I. here (Fig. 22), but exclude Campbell I. on the Chordeumatida map (Fig. 41). The Australian and southeast Asian areas conceivably join, but without records from the gap, we leave them separate. Jeekel (2001b) summarized ordinal occurrences in Asia, and the only subsequent work is on Vietnam (Enghoff et al. 2004). Enghoff (2005) did not record Siphonophorida from Thailand, but we project them for the east and south. Siphonophorida occur in peninsular Myanmar, and occurrence to the north is plausible. Without providing localities and provinces, D. Wang and Mauriès (1996) cited Siphonophorida from China based on an unpublished record of the first author, but we know of no published Chinese records. Extrapolating southeast Asian localities suggests occurrence in southernmost coastal China, Hainan Island, and southern Guangxi and Guangdong provs.

Order Siphonocryptida (Fig. 23)

The second rarest diplopod order, behind Siphoniulida, Siphonocryptida are known from four widely separated Old World regions that span both the Equator and the Tropic of Cancer; distances between them vary from ~ 2,880 km (1,800 mi) to ~ 12,100 km (7,560 mi). Twenty-one localities are known – four in Taiwan, one in Nepal, three in Indonesia (Sumatra), one in peninsular Malaya, nine in the Canary Islands, and three in Madeira (Pocock 1894; Hoffman 1980a; Enghoff 1992; Enghoff and Golovatch 1995; Vicente and Enghoff 1999; Korsós 2004; Korsós et al. 2008, 2009). As noted by Korsós et al. (2008, 2009), this relictual distribution pattern indicates great age; the only plausible explanation is a once continuous Gondwanan fauna that has either become extinct in intervening areas of modern Asia and Africa or is still undiscovered there. While new records and localities may be found in India and southeast Asia, as suggested by the recent discovery in Nepal (Korsós et al. 2009), most of the hiatus between India and Macaronesia seems too arid for these small millipeds. Perhaps Siphonocryptida's continued existence in Macaronesia reflects the moist climate on these islands in contrast to the aridity of northern/Mediterranean Africa.

Subterclass Eugnatha (Fig. 2, 24)

Eugnatha occupy the entire global distributions of Diplopoda, Chilognatha, and Helminthomorpha except for St. Helena Island in the south Atlantic Ocean; otherwise, they completely overlie Colobognatha. Juliformia account for most eugnathan occurrences, particularly in the Western Hemisphere, where they cover the entire range except for Kodiak Island, Alaska, and northeastern Canada, occupied by Nematophora, and the Galapagos, Juan Fernandez Islands, and the northern half of Chile, covered by Merocheta. Likewise in Europe, sub-Saharan Africa, Indian Ocean Islands, and the Middle East, Juliformia occupy the entire eugnathan range except for Sokotra Island and central Saudi Arabia, occupied by Merocheta.

Juliformia are absent from western Asian Russia, a gap partly covered by Merocheta, which also account for eugnathan continuity through western India, central Pakistan, and Afghanistan. The three superordinal components occur together throughout much of eastern and southeastern continental Asia, Japan, the Philippines, and Indonesia, while Juliformia and Merocheta account for eugnathan occurrence in Oceania. All three superorders occupy New Zealand and eastern Australia, though Merocheta account for most of the latter and Nematophora inhabit three localized patches. Merocheta also account for the entire eugnathan range in Western Australia and Northern Territory, though the other taxa inhabit parts of the former.

All three eugnathan superorders occupy enormous continuous areas with a single major one in the Western Hemisphere (Fig. 25, 35, 46). Broad European areas, which expand westward in the Atlantic to the Azores and southward to Madeira (Merocheta) and the Cape Verde Islands (Juliformia, Nematophora), become narrower in the east and are discontinuous with Asian areas in the last two taxa (Fig. 25, 35), where they extend eastward as narrow strips south of the Caspian Sea then expand latitudinally into central Asia. All three also occupy east/west bands in Siberia that lie atop Mongolia but differ in origins. That of Merocheta arises from the European part of the range; that in Juliformia arises from the Asian; and that in Nematophora is independent.

Superorder Juliformia (Fig. 25)

Juliformia occur broadly across all continents except Australia, where they occupy the eastern and southeastern margins and two small coastal areas in Western Australia, with generalized records from Northern Territory, South Australia, and “Upper Western Australia” (Black 1997). The taxon spans the Equator and both Tropics in the Western Hemisphere and Australasia, slightly crossing the Arctic Circle in Iceland and Europe (Scandinavia). Its known or projected area encompasses all Caribbean, Mediterranean, Atlantic, and Indian Ocean islands occupied by Eugnatha except Sokotra, and all of the East Indies, the Bismarck Archipelago, the Solomon Islands, and New Caledonia and associated islands. Juliformia are native to numerous small oceanic islands and archipelagos: Bermuda, Fernando Noronha, Madeira, the Azores, Canaries, Cape Verdes, Bioko, both São Tomé and Príncipe, Cocos I., the Hawaiians, Fiji, Palau, Truk, Pohnpei, Ulithi Atoll, Saipan, Guam, Lord Howe, Mauritius, Rodriguez, the Maldives, Nicobars, Seychelles, and Comoros. While some representatives thrive in harsh, arid environments (for example spirostreptideans in the Namib and Kalahari deserts of Africa and the Sonoran and Chihuahuan in the US/Mexico), others do not, so the largest gaps in what would otherwise be subcontinuous global occurrences are in deserts like the Atacama in South America, the Sahara in Africa, the Arabian in the Middle East, the Gobi in Asia, and the interior deserts of Australia. New World occurrence is primarily attributable to Julida (Parajulidae), in North America, and Spirostreptidea (Spirostreptidae) and Spirobolida (Rhinocricidae) in Central/South America and the Caribbean. Occurrences in Europe, the Mediterranean coast of Africa, and the Middle East are almost exclusively Julida (particularly Julidae); Spirostreptidea (Spirostreptidae) occur sympatrically along the eastern Mediterranean coast and alone account for part of the superordinal area in northwestern Africa (Morocco). Sub-Saharan African distribution is nearly exclusively attributable to Spirostreptidea, while those in Asia, Australia, the East Indies, and Oceania involve combinations of taxa.

All three ordinal components – Julida, Spirobolida, and Spirostreptida *s. l.* (Fig. 26, 28-29) – occupy large, continuous areas in the Americas of varying dimensions, with three smaller spirostreptidan regions and a point locality of Spirobolida. Julida are restricted to the Northern Hemisphere, approaching the Equator in southeast Asia only (Enghoff 1993a). Spirobolida and Spirostreptida *s. l.*, however, inhabit substantial areas in the Southern Hemisphere, traverse the Tropic of Capricorn, and occupy the South Temperate Zone on all three southern continents, but Spirostreptida/Spirostreptidea do not show the large southwest African indentation in Spirobolida. Both orders are represented in the Indian Subcontinent, in contrast to Julida, whose only Indian occurrence is Assam, though it also exhibits a small, detached area in Nepal (Fig. 26).

As the order Spirostreptida (*sensu* Hoffman 1980a, Shelley 2003a) seems likely to be dismembered, we discuss and map all three presently recognized suborders.

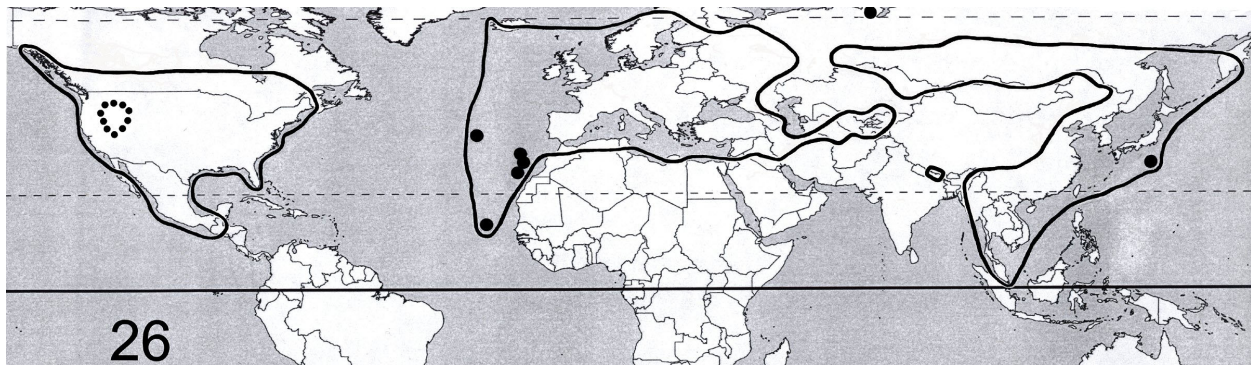


Figure 26. Distribution of the Order Julida.

Order Julida (Fig. 26-27)

According to Hoffman (1969b) and Enghoff (1993a), Julida is basically a Holarctic order occurring north of the Tropic of Cancer. Along with Glomerida and Platydesmida, we characterize it as Laurasian, North Temperate, and Tropical, but not Holarctic, as southeast Asia and northern Central America lie in the Indo-Malay and Neotropical realms, respectively. We recognize five areas (Fig. 26), the three major ones – North America/Mexico/northern Central America, Europe/Middle East/central Asia/north Africa/Atlantic Islands, and northcentral/east/southeastern Asia – extending southward into the Tropics, with the last even touching the Equator. At the northern extreme, Julida nip the Arctic Circle in Iceland, where *Proteroiulus fuscus* (Am Stein, 1857) (Blaniulidae) is the only indigenous diplopod (Tuxen 1941, Eason 1970), crosses it again in Scandinavia/Norway, and a point locality of this species in central Russia lies north of this line in the southern Yamal Peninsula. Finally a disjunct area exists in eastern Nepal. The order is absent from Caribbean Islands, most of Central America and all of South America, sub-Saharan Africa, Madagascar and Indian Ocean Islands, the Indian Subcontinent, Indonesia/Philippines/Papua New Guinea/Australia/New Zealand, and Oceania except for a questionable record from the Bonin Islands.

In contrast to most orders, ten maps, a veritable plethora, exist for Julida. Jeekel (1985) depicted the entire ordinal distribution, and Kime (2000) did likewise for Europe. Enghoff (1993a) mapped familial and superfamilial components, and Shelley (2008) mapped Parajulidae in North/Central America. The maps of Kime (2000) and Shelley (2008) show country boundaries, but the others lack these reference lines, so precise boundaries are difficult to determine in central Asia.

The distribution of Parajulidae in North/Central America (Shelley 2008) constitutes that of the order in the Western Hemisphere, as the other families with indigenous components – Aprosphylosomatidae, Blaniulidae, Chelajulidae, Nemasomatidae, Okeanobatidae, Paeromopodidae, Telsonemasomatidae – lie wholly within its range.

The European and Icelandic distributions depicted by Kime (2000) still appear accurate. Occurrences in Macaronesia (Enghoff 1992, 1993b, c; Vicente and Enghoff 1999) and North Africa represent the same basic fauna and are grouped with Europe. Both Jeekel (1985) and Enghoff (1993a) depict the range in Tunisia, Algeria, and Morocco; additional records (Enghoff 1995, Read 2005) lie within this area, and Akkari et al. (2010a) summarized North African occurrences. The Middle Eastern area encompasses Crete and Cyprus, all of Turkey, Lebanon, and Syria, northern Israel

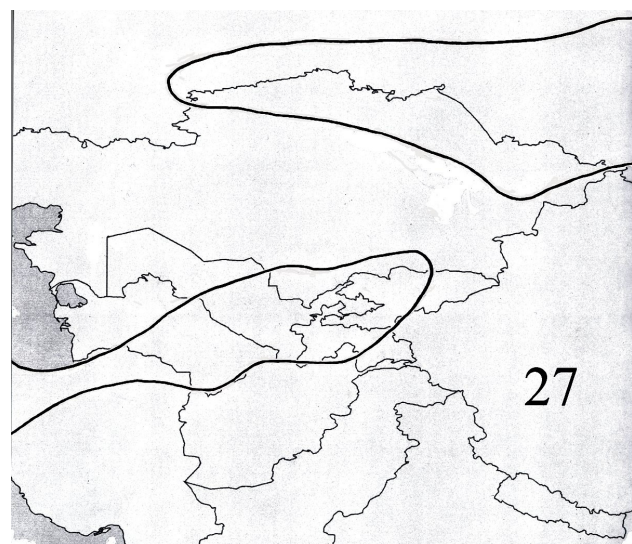


Figure 27. Distribution of Julida in central Asia.

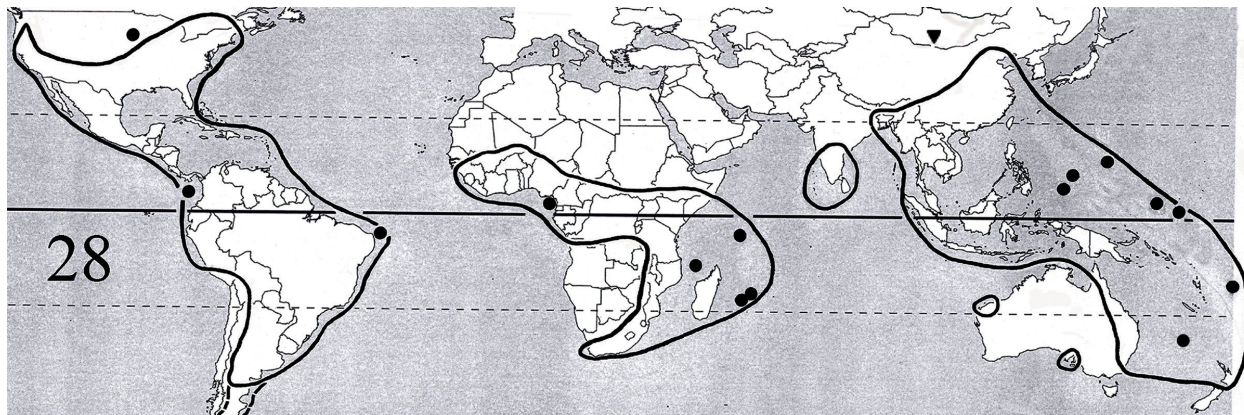


Figure 28. Distribution of the Order Spirobolida, parameters as in Fig. 1. Inverted triangle, location of *Gobiulus sabulosus* Dzik, 1975, the Cretaceous fossil from Mongolia.

and the West Bank, and northern Iraq (Enghoff 1993a, 1995, 2006; Kime 2000; Golovatch et al. 2004). In eastern Europe, the area extends to the Ural Mts., overhangs western Kazakhstan (Loksina and Golovatch 1979, Golovatch 1992a, Kime 2000, Enghoff 1993a), and then swings westward and southeastward through the Caucasus to the Caspian Sea (Enghoff 1984a, Golovatch and Enghoff 1990, Read 1992, Hoy Jensen et al. 2002). It spreads southward in western Iran to near the Persian Gulf (Enghoff 1995, Enghoff and Moravvej 2005), and an eastward projection expands latitudinally through the Central Asian Republics (Enghoff 1985, Read 1994, Read and Golovatch 1994).

The primary Asian area consists of long eastern and northern arms that meet in the northeast at an acute angle. The former extends from Kamchatka and “mainland” Asian Russia to the Equator at Singapore, expanding westward through Myanmar into Assam; the northern arm spreads westward through southern Siberia and northeastern Kazakhstan, where it overhangs the eastward projection of the European area. These central Asian “distributional peninsulas” (Fig. 27) are not known to join but are only ~ 704 km (440 mi) apart at their closest points. This overall area encompasses islands like Sakhalin, the Kuriles, all of Japan and the Ryukyus, Taiwan, and Hainan but excludes the Philippines, Indonesia, and Borneo/eastern Malaya. Maps are available in Enghoff (1987), Mikhaljova (1993, 1998), Mikhaljova and Basarukin (1995), and Korsós (2001), while species lists with at least countries of occurrence are provided by Enghoff (1986, 2005), Korsós (1994b, 1996, 2004), D. Wang and Mauriès (1996), Mikhaljova and Nefediev (2002), Mikhaljova and Marusik (2004), Enghoff et al. (2004), and Mikhaljova et al. (2007). No published records are available for Bangladesh, southwestern Myanmar, and central and southern India, so we draw the boundary considerably to the north of that in Enghoff (1993a). Bonin Island occurrence is documented by Verhoeff (1939), Enghoff (1986), Mikhaljova and Kim (1993) and Korsós (1996), although Paik (1958) thought it represented mislabeling.

Order Spirobolida (Fig. 28)

Spirobolida occupy seven areas (Fig. 28), three large and four small; one of the latter is a point locality in the northcentral US (Minnesota) (Shelley et al. 2006). Two small coastal areas in Australia, subequal in size, enclose Barrow Island and a “mainland” site in Western Australia and the Adelaide region of South Australia, and a larger one in Asia encompasses southern peninsular India, Sri Lanka, and the Maldive Islands. Large areas exist in the Western Hemisphere, sub-Saharan Africa, and east/southeastern Asia/eastern Australia/North Island of New Zealand/western Oceania.

The continuous range in the Western Hemisphere arises in Québec, Canada, and Maine and Washington states, USA, and extends southward through Mexico/Central America and the Antilles (excluding the Bahamas and Turks and Caicos) to central Argentina. Shelley and Bauer (1997) and Shelley (2010a) mapped Tylobolinae (Spirobolidae) and showed it angling inland in northern California and extending northward to Klickitat Co., Washington, to which we add adjacent Skamania Co. (Appendix). *Narceus Rafinesque*, 1820 (Spirobolidae: Spirobolinae), the most common diplopod genus in eastern North America, ranges from Québec and Maine to the south Florida Keys and westward to the Central Plains (Keeton

1960, 1966; Shelley et al. 2006), and Atopetholidae and Allopecoekiidae arise in eastcentral and south Texas, respectively (Hoffman and Orcutt 1960; Hoffman 1969b, 1999; Shelley and Hoffman 1995). The former spread westward to the Pacific Coast and southward into Baja California and “mainland” Mexico, where they intermingle with Allopecoekiidae, the spirobolid genus *Aztecobolus* Chamberlin, 1943, and four additional families – Hoffmanobolidae, Messicobolidae, Spirobolellidae, and Rhinocricidae, the dominant Neotropical family – to produce a continuous range on the continental land mass extending into southern South America. Bueno-Villegas et al. (2004) summarized Mexican records, the southernmost in Baja California Sur, *Eurhinocricus fissus* Verhoeff, 1937 (Rhinocricidae) being near the southern tip of the peninsula, and the order also occurs on islands in the Gulf of California. While Spirobolida have not been recorded from the Bahamas and Turks and Caicos, Rhinocricidae are widespread in the Greater and Lesser Antilles, where they occur sympatrically with Spirobolellidae (Hoffman 1969c, 1999; Pérez-Asso 1998).

The global distribution of Rhinocricidae has been mapped three times (Kraus 1966, 1978; Marek et al. 2003); all omit Chile and are similar except for northern borders in both the New and Old Worlds. From Cuba and Central America southward, the familial distribution is essentially that of the order, for which we adopt the latest map (Marek et al. 2003). An obscure publication (Hounscome 1994) reported Rhinocricidae from the Cayman Islands (Grand and Little Cayman); Chamberlin (1950b) recorded the family from Cocos Island, Costa Rica, misreported as Cocos (Keeling) island in the Indian Ocean (Marek et al. 2003); and Pocock (1890) and Hoffman (1979a) documented Pachybolidae from Fernando de Noronha. The only remaining question is the southern boundary of the order and family in South America. Chamberlin (1957) transferred two Chilean species described by Gervais from *Julus* to *Rhinocricus* but added that the assignment was tentative because recent Chilean collections had not contained representatives of either the family or order; without authentic documentation, we too exclude Chile as well as adjoining desert regions of Peru and Bolivia. Chamberlin (1950b) reported Rhinocricidae from Santa Fe and San Luis provs., Argentina; the latter is in the west around the latitude of Buenos Aires, so the boundary lies substantially west of where it is shown in prior maps. Farther south, we report (Appendix) Rhinocricidae from Parque Nacional los Alerces, on the Chilean border in the Andean Cordillera of Chubut Prov. (42°48'27" S, 71°53'56" W), which along with Isla Grande de Chiloé, Chile, are the southernmost localities of Chilognatha and all subordinate taxa in the Western Hemisphere. Neither colleagues nor searches in ecological as well as taxonomic literature revealed more southerly records, so for now the southern boundaries of Chilognatha and Spirobolida are at this latitude.

The only indigenous African family is Pachybolidae, and maps in Lawrence (1967), Enghoff (1977), and Wesener et al. (2008) supplement the list by Hamer (1998). The northernmost locality is Tombouctou, Mali, and the curvilinear border passes through Sierra Leone, Guinea, Mali, Niger, Nigeria, Cameroon, Central African Republic, Sudan, Ethiopia, and Somalia. A surprise to us is the absence of authentic records from southern Democratic Republic of the Congo, all of Zambia, Angola, Botswana, and Namibia, and the northern 1/3 of the Republic of South Africa; consequently, the range exhibits a strong indentation in southern Africa with a north/south lacuna of ~ 2,816 km (1,760 mi) along the west coast. It extends inland for fully of the breadth of the continent (~ 2,240 km [1,400 mi]); continuity between occurrences in the Cape Region of the Republic of South Africa and the transcontinental area arising in Tanzania is a variably narrow strip (~ 640 km [400 mi] wide) along the Indian Ocean through Mozambique, Malawi, and eastern Zimbabwe. Indigenous representatives of Spirobolida also occur on Bioko, Zanzibar, Madagascar, Mauritius, Rodriguez, the Seychelles, and Comoros Islands (Butler 1876, 1879; Mauriès 1980b; Golovatch and Korsós 1992; Mauriès and Geoffroy 1999; Enghoff 2003; VandenSpiegel and Golovatch 2007; Appendix).

For Asia, we added spirobolidan localities cited by Jeekel (2001c), Enghoff et al. (2004), and Enghoff (2005) to the rhinocricid map of Marek et al. (2003). Localities cluster in southern peninsular India and Sri Lanka without connecting to the northeastern area, so we show them as separate and incorporate records from the Maldivian and Lakshadweep Islands that we consider indigenous although they may represent human introductions. Apparently native spirobolidans inhabit even smaller and more isolated islands in western Oceania, so the probability that these represent indigenous occurrences seems greater. The large Asian area lying southeast of the Mongolian Cretaceous fossil, *Gobiulus sabulosus* Dzik, 1975 (Fig. 1, 5, 14, 24-25, 28, inverted triangle), excludes the main Japanese islands and the Korean Peninsula, angles southwestward from north of Beijing through Sichuan Prov., China, northern Myanmar,

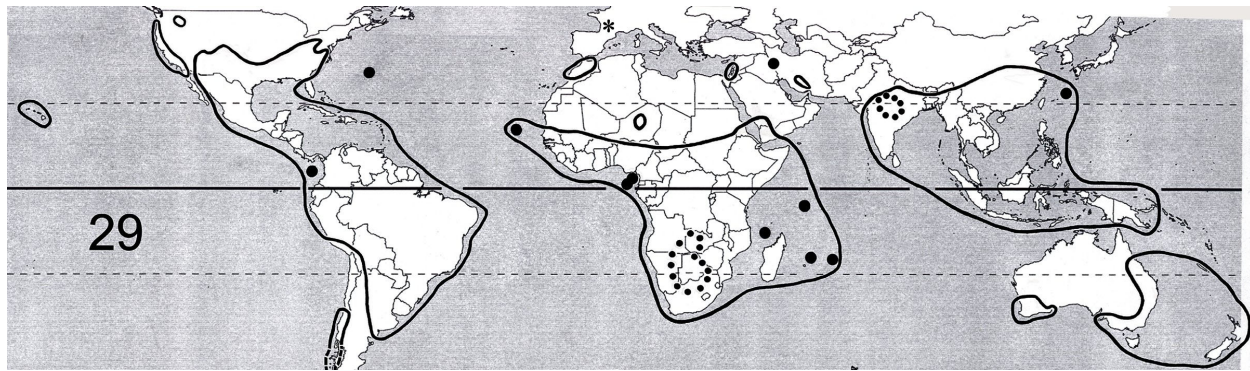


Figure 29. Known (solid lines) and projected (dashed lines) distributions of the Order Spirostreptida *s. l.* (*sensu* Hoffman 1980a, Shelley 2003a), parameters as in Fig. 1. Asterisk, location of *Protosilvestria sculpta*, the Oligocene fossil from Quercy, France (Mauriès 1992).

Bhutan, and eastern India (Assam, Darjeeling District, West Bengal (Appendix)), then angles southeastward encompassing all of Myanmar, the Malay and Indochina peninsulas, and all of Indonesia, while excluding the Anadaman and Nicobar Islands. The Ryukyu Islands, Taiwan, the Philippines, Papua New Guinea, and the Solomon Islands are included along with eastern Australia, Lord Howe Island, the North Island of New Zealand, and such western Oceanic islands as Fiji, Truk/Pohnpei/Ulithi Atoll, Federated States of Micronesia, Guam/Saipan, Commonwealth of the Northern Marianas Islands, and the Republic of Palau. Finally, this area includes a moderately broad strip along the east coasts of Queensland and New South Wales that extends to Cape York.

Order Spirostreptida *s. l.* (Fig. 29)

Spirostreptida *s. l.* (*sensu* Hoffman 1980a, Shelley 2003a) occur on all continents except Europe (Fig. 29). They span the Equator and both Tropics in the New World and Africa, the former being continuous and the latter, discontinuous, the Tropic of Cancer and Equator in Asia, and the Tropic of Capricorn in Australia. They also inhabit islands in the Atlantic (Cape Verdes, Bioko, both São Tomé and Príncipe [Appendix]) and Indian (Comoros, Madagascar, Seychelles, Mauritius, Rodriguez) Oceans, which we combine with sub-Saharan Africa; except for the Hawaiian Islands, they are absent from Oceania. Spirostreptida also inhabit Bermuda, which is isolated because occurrence is not ubiquitous in the eastern US.

The New World distribution comprises four areas, the smallest in the northern Rocky Mts. of the US. An elongate region along the Pacific Coast, extending from southwestern Washington to northern Baja California Norte, includes the Channel Islands, and another elongate strip, with unknown southern limit, occupies central Chile. Finally, there is a large area that encompasses most of the southeastern and south-central United States, all Caribbean Islands except the Bahamas and Turks and Caicos, all of Mexico and Central America except the Baja California Peninsula, and extends south-southeastward in South America to east-central Argentina. Arising in western Pennsylvania and northern Virginia, the area ranges southward to the panhandle and north-central Florida, but it does not penetrate the peninsula and also excludes the Outer Banks/Coastal Plain of North Carolina. It angles southwestward to Oklahoma, curves north westward into the Rocky Mts. of Colorado, dips into northern Arizona, then heads southward through “mainland” Mexico (Sonora) into the Gulf of California, incorporating Tiburon Island. It encompasses the northern 1/2-2/3 of South America, as the western border slants through southern Peru and southwestern Bolivia north of the Atacama Desert. In Argentina, Spirostreptida veer south-southeastward away from the Andes and terminate north of Spirobolida.

Distributions in Africa, the Middle East, and Indian Ocean islands represent the nominate suborder. Restricted to the coastal region of the Republic of South Africa (Fig. 32), Epinannolenidea are entirely subsumed by spirostreptideans. The Iranian area represents Cambalidea (*Chiraziulus* Mauriès, 1983), whereas that in India/southeast Asia combines Cambalidea and Spirostreptidea. It extends from the vicinities of Mumbai and New Delhi to Shanghai and encloses Taiwan, the Philippines, all of Indonesia and Papua New Guinea, the Andaman and Nicobar Islands, and peninsular India and Sri Lanka. We

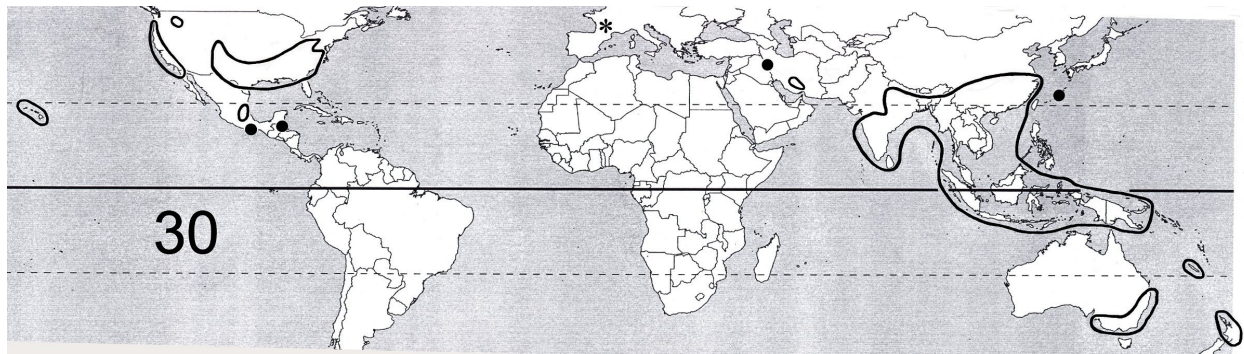


Figure 30. Distribution of the Suborder Cambalidea. Asterisk, location of *Protosilvestria sculpta*, the Oligocene fossil from Quercy, France (Mauriès 1992).

recognize a separate area in east/southeastern Australia that represents Cambalidea and Epinannolenidea, spreads eastward around New Zealand and New Caledonia, and is detached from the small range in southwestern Western Australia.

Spirostreptida s. l. are extinct from Europe. Past occurrence is shown by the Oligocene French fossil, *Protosilvestria sculpta* (Cambalidea), redescribed by Mauriès (1992).

Taxonomists differ as to the constitution of *Spirostreptida s. l.*, and Shear et al. (2003) and Shelley (2007a) promoted the “8th gonopod clade” concept that, if substantiated, will disrupt the concepts of Hoffman (1980a) and Shelley (2003a) and potentially elevate the component suborders to full orders. To cover this possibility, we map and discuss the distributions of Cambalidea, Epinannolenidea, and Spirostreptidea (Fig. 30, 32, 34) separately; they demonstrate decidedly different patterns with little congruency, which supports elevating the first two to full orders.

Suborder Cambalidea (Fig. 30-31)

Cambalidea occur in the North Temperate, Tropical, and South Temperate zones of North/Central America, Asia, and Australia plus the North Island of New Zealand, New Caledonia, and the Hawaiian Islands (Fig. 30); they are extinct in Europe, as evidenced by the Oligocene fossil, *Protosilvestria sculpta*, from Quercy, France (Mauriès 1992). The largest area, in south/southeastern Asia, is substantially larger than the second, in the east/central/southern US. Five smaller areas occur in the continental US, Mexico, and northern Central America, two being point localities. The suborder also inhabits two regions of Iran that likely connect, the Zagros Mts. and a site on the Iraqi border, and another point locality exists on Okinawa. Cambalidea are absent from South America, Africa, Europe, and Caribbean, Atlantic, and Indian Ocean Islands aside from Sri Lanka.

In the New World, Cambalidea (Cambalidae) (Fig. 31) extend southwestward from Pennsylvania and Virginia to New Mexico then turn northward into the Rocky Mts. of Colorado. Eastern Virginia and North Carolina are excluded along with peninsular Florida and south Texas/Rio Grande Valley; the southernmost records in central Texas are from Bexar, Menard, Uvalde, and Val Verdes. The Pacific Coastal area, which includes the Channel Islands, ranges from southwestern Washington to the northwest corner of Baja California Norte and inland up the western slopes of the Sierra Nevada and Cascade Mts.; a detached area

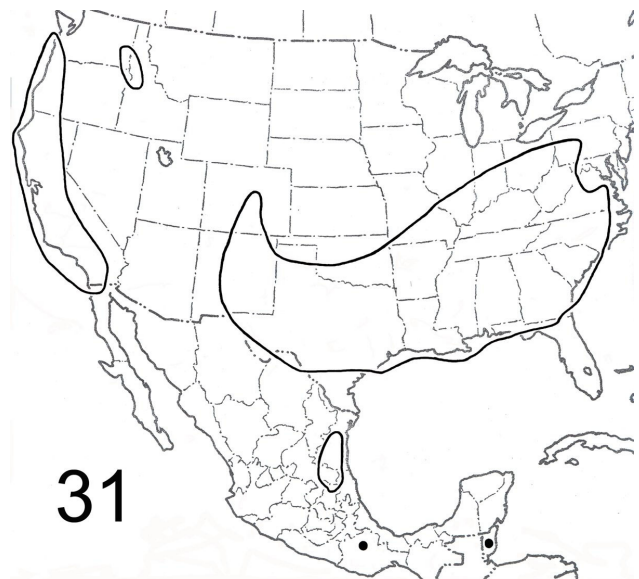


Figure 31. Distribution of Cambalidea in North America/Western Hemisphere.

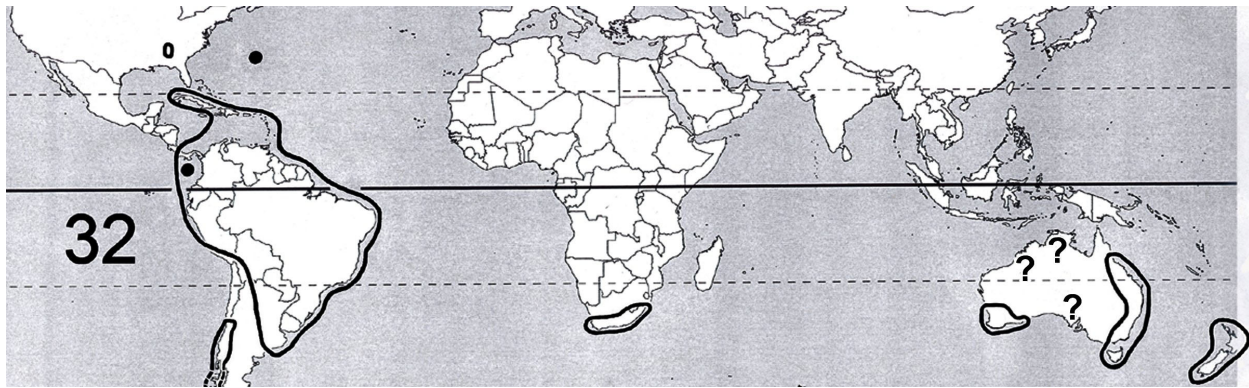


Figure 32. Known (solid lines) and projected (dashed lines) distributions of the Suborder Epinannolenidea. Parameters are as in Fig. 1, except the question marks in Australia represent general records from Northern Territory, South Australia, and northern Western Australia (Black 1997).

occurs in western Idaho and the adjacent corners of Oregon/Washington. In Mexico, the suborder and family occupy a small area from central Tamaulipas to eastern San Luis Potosí, with point localities to the south in Oaxaca and Belize. In addition to Hoffman (1980a, 1999) and Jeekel (1985), publications with maps and/or records include Shelley (1979) and Jeekel (2004a). In Hawaii, Cambalidea (Cambalidae) are native to Kauai, Lanai, Maui, Molokai, and Oahu (Silvestri 1904; Nishida 1994, 2002; Jeekel 2004a), the only spirostreptidan occurrence in Oceania. While the Hawaiian forms have never been studied, they relate anatomically to those on the Pacific Coast of the US; one of the great mysteries in diplopodology concerns their origin on these volcanic islands, which have never been connected to a continental land mass and are among the most isolated and remote in the world. An extreme, implausible rafting event of some 4,806 km (2,691 mi) seems required, although Jeekel (1985) suggested origin involving the hypothetical continent Pacifica (=Lemuria), and Fig. 30 shows that Cambalidea are indeed oriented around the Pacific, rather than the Atlantic, oceans.

In the Old World, the families Cambalopsidae and Pericambalidae cover a broad, subcontinuous area in southeast Asia extending from Nepal, Assam, and eastern China to southern Indonesia and, east/west, from the Bismarck Archipelago to central India and the vicinity of Mumbai. The area excludes the Philippines, Taiwan, and the Andaman and Nicobar Islands. Papers with maps and/or records include D. Wang and Mauriès (1996), Mauriès (1997a), Jeekel (2004a), Enghoff et al. (2004), Enghoff (2005), and Golovatch et al. (2007a, b); the last two mapped occurrences in China, Thailand, Java, the Malay and Indochina peninsulas, and Indonesia. Here, the problem of distinguishing between indigenous and anthropochoric records again arises because of two widespread introductions, *Hypocambala helleri*

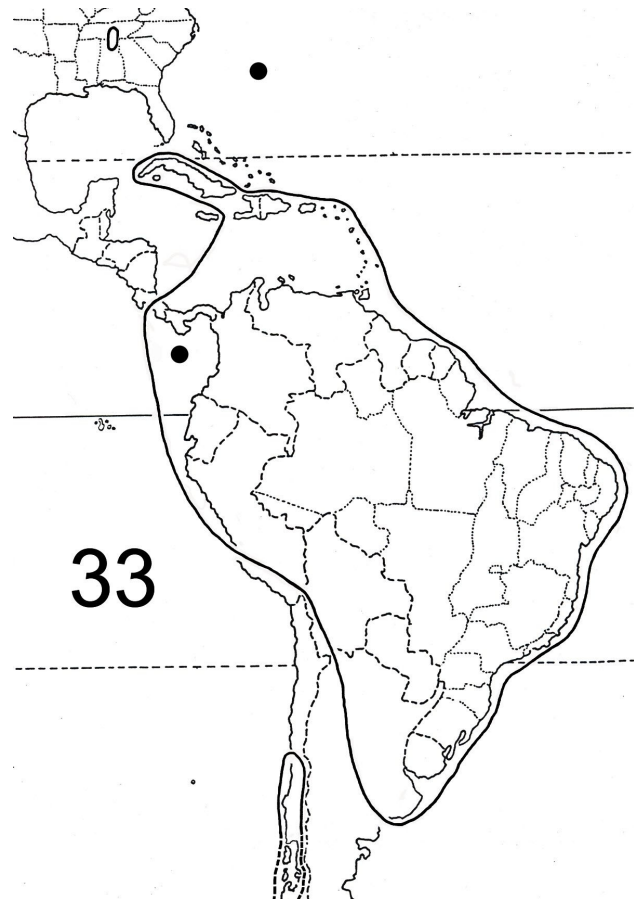


Figure 33. Known (solid lines) and projected (dashed lines) distributions of Epinannolenidea in the Western Hemisphere and associated oceanic islands, parameters as in Fig. 1.

Silvestri, 1897, and *Glyphiulus granulatus* Gervais, 1847 (both Cambalopsidae); accordingly, we exclude records from remote oceanic islands because of the likelihood that they are allochthonous. Taiwanese samples were assigned to *G. granulatus* by Korsós (2004), hence the distribution excludes this country and associated islets. The isolated record of *Dolichoglyphius asper* Verhoeff, 1898, from Okinawa, Ryukyu Islands, is consistent with an introduction and hence is shown as a separate dot. There is also an isolated area in the Zagros Mtns., Iran (Mauriès 1983, Golovatch 1983c, Jeekel 2004a, Enghoff and Moravvej 2005), and we add a detached site on the Iraqi border (Appendix).

Indigenous records also exist from southeastern coastal Australia and the North Island of New Zealand, and we treat New Caledonia records of *Hypocambala caledonica* (Carl, 1926) as native.

Suborder Epinannolenidea (Fig. 32-33)

Primarily a Neotropical, Gondwanan taxon, where it occupies a large area and a detached one in Chile, Epinannolenidea also inhabit both major islands of New Zealand, and small, isolated regions in the southeastern US (Tennessee and Alabama, Choctellidae) (Hoffman 1965a, 1999; Appendix), Bermuda (presumed indigenous), the Republic of South Africa, and three coastal patches of Australia. Jeekel (1985) mapped the distribution and (Jeekel 2004a) included the suborder in his bibliographic catalog of the “Cambaloidea,” which summarized localities.

While again excluding the Bahamas and Turks and Caicos, we project Epinannolenidea for all the Greater and Lesser Antilles except Jamaica (Fig. 32-33); they are known from Cuba, Hispaniola, Puerto Rico, US Virgin Islands (St. Thomas), Guadeloupe, Marie-Galante, and Barbados, to which we now add (Appendix) St. Croix, US Virgin Islands, and Barbuda. Works with localities and/or species listings since Mauriès (1980a) and Hoffman (1999) include Hispaniola (both Haiti and Dominican Republic) (Pérez-Asso and Pérez-Gelabert 2001, Pérez-Gelabert 2008) and Brazil (Trajano et al. 2000; Adis et al. 2002; Golovatch et al. 2005). The large Neotropical area traverses central Costa Rica, encompasses Cocos Island, and slices through southern Peru and southwestern Bolivia north of the Atacama Desert. Mauriès (1974a) mapped Neotropical occurrences but missed some Peruvian records, so we put the boundary south of his localities to include all records in Chamberlin (1955) and Kraus (1954, 1955, 1957, 1959). Distributions in Argentina (Pseudonannolenidae) and Chile (Iulomorphidae) are the same as Spirostreptida s. l.; Chilean localities extend from Valparaiso and Santiago, in the north, to the Golfo de Aucud, in the south (Chamberlin 1957). The suborder’s hemisphere biogeography indicates origin in South America and spread onto the “proto-Antillean Arc” (excluding Jamaica) before it split from the present-day Guianas/northeastern Brazil coastline area of Gondwana II in the Late Cretaceous. Present concepts place Choctellidae in Epinannolenidea (Hoffman 1980a, Jeekel 1985, Shelley 2003a), and Shelley and Whitehead (1986) suggested that they may represent the former northern component of a once contiguous mosaic complex (Fig. 33). Paleogeography, however, shows that continuity was extremely ancient if it ever existed, which we now question with no evidence that the Cumberland Plateau region of the US was ever directly connected to South America/“proto-Antilles.” Thus, from milliped biogeography and knowledge of tectonic movements, this placement warrants revisiting; Choctellidae substantially antedate modern epinannolenideans and truly constitute a mystery taxon, tucked away in the Cumberland Plateau of Tennessee and Alabama and unrelated to anything remotely proximate. It is clearly ancient and the sole surviving relict of something, but what? Perhaps it is a remnant of the original radiation on Laurentia after collision with Baltica+Avalonia in the early Silurian.

Jeekel’s map (1985) of Iulomorphidae remains reasonably accurate for Africa and Australia, although Edward and Harvey (2010) expanded the area in Western Australia. In Africa, Epinannolenidea (Iulomorphidae) are restricted to Lesotho and the southern periphery of the Republic of South Africa (Hamer 1998, 1999). Korsós and Johns (2009) recorded the taxa from New Zealand and mapped occurrences on both major islands. With generalized records from Northern Territory, South Australia, and “Upper Western Australia” (Black 1997), the taxa are still known from only three definite areas of the continent – southwestern Western Australia, Perth vicinity to east of Esperance (Edward and Harvey 2010); along the Queensland coast from near Cairns to Brisbane; and northeastern Victoria and Tasmania. We join the last two with New Zealand.

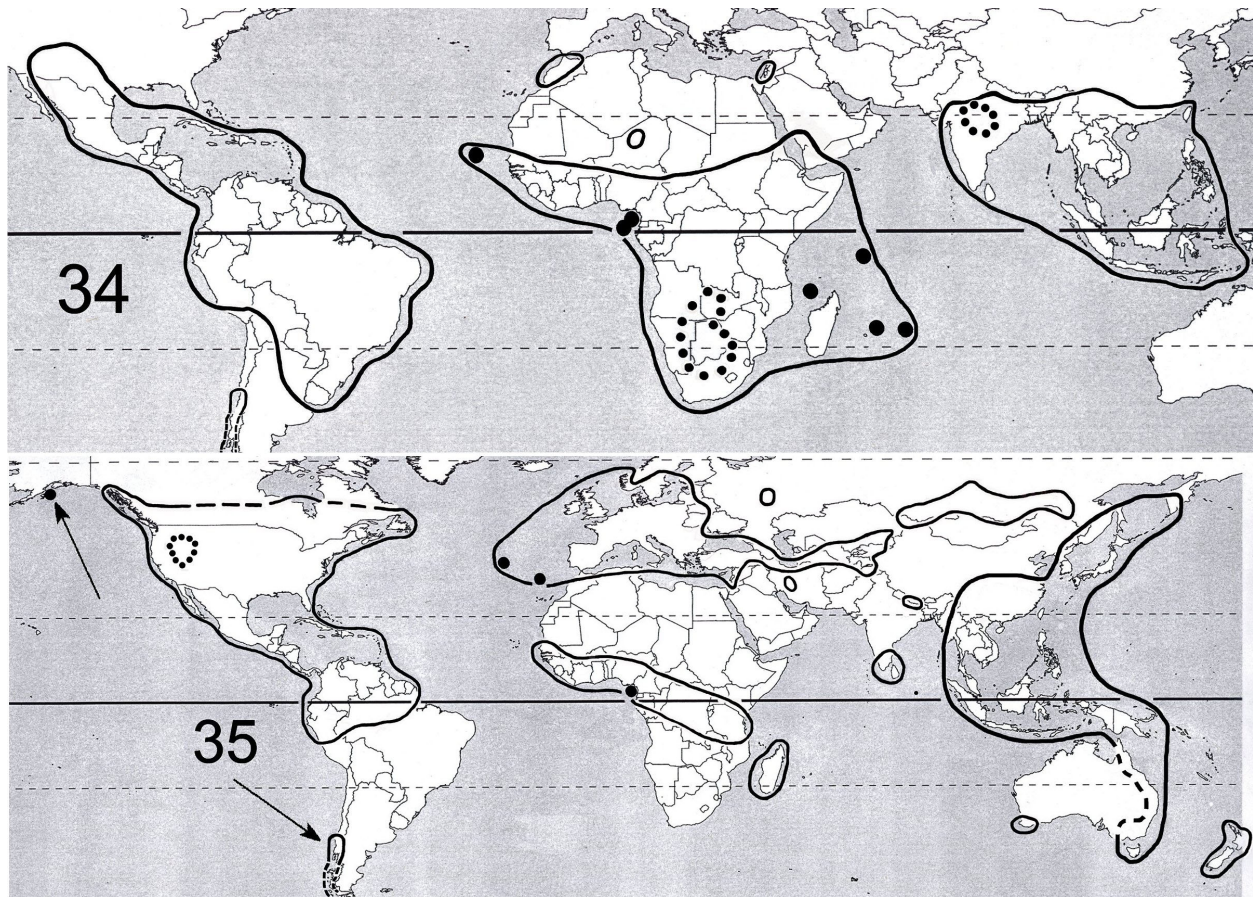


Figure 34-35. Distributions. **34)** Known (solid lines) and projected (dashed lines) distributions of the Suborder Spirostreptidea, parameters as in Fig. 1. **35)** Known (solid lines) and projected (dashed lines) distributions of the Superorder Nematophora, parameters as in Fig. 1; a few records are available from the dotted area in North America. The upper arrow denotes the Chordeumatida (Tingupidae) record from Kodiak Island, Alaska, USA, and the lower one denotes the known and projected distribution of Chordeumatida (Eudigonidae) in Chile.

Suborder Spirostreptidea (Fig. 34)

The nominate suborder occurs in the North and South Temperate Zones and the Tropics. It is absent from Europe and Australia/New Zealand, and occupies seven areas – two in the New World, three in Africa, one in the Middle East, and one in south/southeastern Asia; three are large and four are restricted. Jeekel's ordinal map (1985) and the earlier ones of Kraus (1966) of Harpagophoridae and Spirostreptidae correspond to Spirostreptidea for our purposes; additional maps exist in Crawford (1979) and Kraus (1978).

In the New World, the suborder and nominate family reach their northern limits in the southwestern and southcentral US (Arizona, New Mexico, the Texas Panhandle, and Oklahoma), as depicted by Causey (1975); the western limit is the Colorado River in the US and the eastern side of the Gulf of California, in Mexico, as *Orthoporus ornatus* (Girard, 1853) occurs on Tiburon Island, Sonora. In an inset map, Causey (1975) depicted occurrences in southern California and throughout Baja California, so it flagrantly contradicts the adjacent, larger map, which is accurate to our knowledge. RMS has not seen an authentic spirostreptid from either of these reasonably well sampled areas, and as large, abundant, and active as these millipeds are, it is reasonable to conclude that one would have been collected by now if they occurred there. We also have not seen US samples from outside the area in Causey's large map; the northernmost locality on the Texas Coast is in Victoria Co. (Causey 1964a). We cite *O. ornatus* from Sonora, Coahuila, and Chihuahua, Mexico (Appendix) to supplement records of Causey (1964a, 1975); localities for the first two states are particularly important because she cited and mapped only one record from each.

Published records do not exist from every country and Mexican state to the south. We report (Appendix) Campeche, Mexico, and Belize/El Salvador, but continuous spirostreptidean occurrence can be reasonably assumed throughout central and southern “mainland” Mexico, the Yucatan Peninsula, and all of Central America as shown by Jeekel (1985). Spirostreptidea are absent from the Bahamas, Turks and Caicos, peninsular Florida, and the Keys. In the Antilles, they have been reported (as *Orthoporus* spp.) from Jamaica, Cuba, Hispaniola, Puerto Rico and Culebra, Guadeloupe, Marie-Galante, Dominica, Barbados, St. Vincent, Carriacou, Grenada, Tobago, and Trinidad (Pocock 1888; Chamberlin 1918, 1922a; Loomis 1968; de la Torre y Callejas 1974; Mauriès 1980a, b; Krabbe and Enghoff 1985; Gonzales Oliver and Golovatch 1990; Hoffman 1999; Pérez-Asso and Pérez-Gelabert 2001; Pérez-Gelabert 2008), to which we add St. Thomas, US Virgin Islands (Appendix). The distribution continues through South America to northeastern Argentina, slicing across Peru and Bolivia north of the Atacama Desert and through northern San Luis and central Córdoba provs. Again, the question arises as to the southern limit, and we concur with Jeekel (1985) that it lies around Buenos Aires and Montevideo, Uruguay, with a small, disjunct area in Chile (Demange and Silva 1971) that is subsumed within the larger Chilean area of Epinannolenidea (Fig. 32-33). Hoffman (1968a, 1980b) mapped the distribution of *Urostreptus* Silvestri, 1897, but the southernmost Argentinean locality that we can find is Candelaria, San Luis Prov., for “*Spirostreptus*” *bovei* (Silvestri, 1895), which was designated a *nomen dubium* by Krabbe (1982). The southern terminus of Spirostreptidea in South America is therefore north of those of both Epinannolenidea (Fig. 32-33) and Spirobolida (Rhinocricidae) (Fig. 28). However, Spirostreptidea’s New World distribution is largely congruent with that of Epinannolenidea; both even have small, detached regions west of the Andes in Chile.

Spirostreptidea comprise three families in Africa and the Middle East – Spirostreptidae, Harpagophoridae, and Odontopygidae – and occupy four areas, three small and one large, that collectively span the Equator and both Tropics. The small, detached areas represent Spirostreptidae exclusively; two lie north of the Tropic of Cancer – those in Israel/West Bank/Lebanon, partly mapped by Shelley (2009), and in the Atlas Mts. of coastal Morocco – and the third is in the Air Mts., an inselberg in the central Sahara Desert in Niger (Schubart 1951). We recognize a large, continuous area in sub-Saharan Africa that lies south of the Tropic of Cancer, spans the Equator and Tropic of Capricorn, and corresponds to the distribution of Odontopygidae (maps in Kraus 1960a, 1966), as Spirostreptidae and Harpagophoridae cover smaller areas within this larger one. It stretches from the Senegal River on the Senegal/Mauritania border in the west, to Eritrea in the east, curves gently northward on both ends, sags southward in the interior, and passes through Senegal, Mali, Burkina, Niger, Nigeria, Chad, Sudan, and Eritrea. We extend it across the Red Sea to encompass spirostreptid occurrences in the southwestern Arabian Peninsula (Saudi Arabia and Yemen) (Shelley 2009, Golovatch and Kime 2010), then southward into the Indian Ocean to encircle Madagascar plus the Seychelles, Comoros, Mauritius, and Rodriguez islands but excluding Sokotra, though the taxon may yet be found there. In the Atlantic, we enclose Bioko, São Tomé and Príncipe, and the Cape Verde Islands, though odontopygid occurrence in the last may be exogenous (Enghoff 1993b). Jeekel’s map (1985) still depicts ordinal and subordinal distributions reasonably accurately in Africa and the Middle East; other papers with maps/locality listings include Kraus (1960a, 1966), Hoffman (1965b, 1991), and Hoffman and Howell (1996), but the type locality of *Spirostreptus multisulcatus* Demange, 1957, appears to be in the Central African Republic instead of Chad (Demange 1957). Pierrard (1972) published highly useful maps that show odontopygid localities in relation to political boundaries, enabling us to place the northern border. Forty-four endemic spirostreptidean (Spirostreptidae) species occur on Madagascar (Enghoff 2003), and indigenous, if not endemic, species also inhabit the Seychelles, Rodriguez, Mauritius, and the Comoros islands (Butler 1876, 1879; Mauriès 1980b; Golovatch and Korsós 1992; Mauriès and Geoffroy 1999; VandenSpiegel and Golovatch 2007). Hoffman (1993) characterized familial ranges in sub-Saharan Africa.

In Asia, Spirostreptidea occur on the Indian subcontinent (west to Mumbai and New Delhi), Myanmar, the Malay and Indochina peninsulas, southern China, Taiwan (Appendix), the Philippines, and Indonesia eastward through Halmahera; they have not been reported from the Island of New Guinea. Harpagophoridae comprise the entire area, with the one adiaphorostreptid occurring near Mumbai. The area spans both the Tropic of Cancer and Equator and lies south of the highest Himalayan peaks but slips across the mountains in Myanmar into Sichuan and Yunnan provs., China. On the east, it extends to Wallace’s Line and includes southern Indonesia, islands off the west coast of Sumatra, and the Nicobars, and we

project Spirostreptidea for the Andaman Islands. In addition to Jeekel's map (1985), a map of the border area in southeast Asia is provided by Hoffman and Burkharter (1978). Species lists are available for the Himalayas (Golovatch and Martens 1996), Thailand (Enghoff 2005), Vietnam (Enghoff et al. 2004), and China (D. Wang and Mauriès 1996), in addition to the catalog of Asian harpagophorids (Jeekel 2006a).

Superorder Nematophora (Fig. 35-36)

Primarily Holarctic, Nematophora also inhabit the Tropics and South Temperate Zone. They occupy 14 areas on all six continents and span the Equator in South America, Africa, and Indonesia, but are absent from Oceania and nearly so from oceanic archipelagos in general, except for the Azores and Madeira, in the Atlantic, and Kodiak Island, Alaska, USA, in the North Pacific Ocean (Fig. 35). Area sizes vary from large – in the New World, Europe/Central Asia, and east/southeastern Asia – to the isolated point locality on Kodiak I. Chordeumatida, the dominant component and along with Polydesmida one of the two most speciose orders, occur globally, alone comprise 11 of the 17 nematophoran regions including the five southernmost, in Chile, Madagascar, Australia, and New Zealand, and occupy half or more of the three largest by themselves, particularly northern sectors. By themselves, the primarily Holarctic Callipodida and the pantropical Stemmiulida comprise only one area each, although the latter order is the sole nematophoran in the South American and Antillean parts of the primarily North American area.

Most of the northern border is uncertain, but the large New World area, comprising all three orders, extends continuously from Hudson Bay, Ontario, and the "Haines Triangle," BC (Fig. 36), through the entire continental US, all of Mexico and Central America, and all Caribbean Islands (except the Bahamas and Turks and Caicos) to central Peru and south of the Amazon River in Brazil; additionally, a small, detached area with an unknown southern border exists in southcentral Chile. Nematophora doubtlessly occur farther south in Peru and Brazil, but no records are available; they also occupy Madagascar, both major islands of New Zealand, angle completely across sub-Saharan Africa in a broad, angled swath, and occupy a narrow, curvilinear region in Siberia along the Chinese/Mongolian borders. Smaller areas exist in southern India/Sri Lanka, Nepal, Iran, European Russia, and the east/southeast and southwestern coasts of Australia. The Asian part of the Australasian area, also comprising all three components, extends from Kamchatka, Sakhalin, and the Maritime Prov., Russia, to southern Indonesia and Papua New Guinea, encompassing the Kurile Islands, the Ryukyus and "mainland" Japan, Taiwan, and the Philippines; it expands westward through central China to the longitude of central Myanmar. The European/Central Asian area, comprising Callipodida and Chordeumatida, stretches eastward from the Azores through Europe and part of northern Africa to southern Kazakhstan and northern Pakistan, narrowing latitudinally at the Black and Caspian seas. It dips southward in Israel/West Bank, but connection with the detached Zagros Mts., Iran, cannot now be demonstrated.

The nematophoran orders – Callipodida, Chordeumatida, and Stemmiulida (Fig. 37, 41, 45) – exhibit less commonality and geographical congruence than do those of Juliformia, perhaps indicating a less sound cladistic foundation. All inhabit areas in the Western Hemisphere of greatly different sizes that cover different regions. Callipodida and Chordeumatida occupy sizeable parts of Europe and smaller areas; conversely, Stemmiulida, the lone African representatives, are absent from this continent. Chordeumatida exhibit Gondwanan elements in Chile, Madagascar, peninsular India/Sri Lanka, and

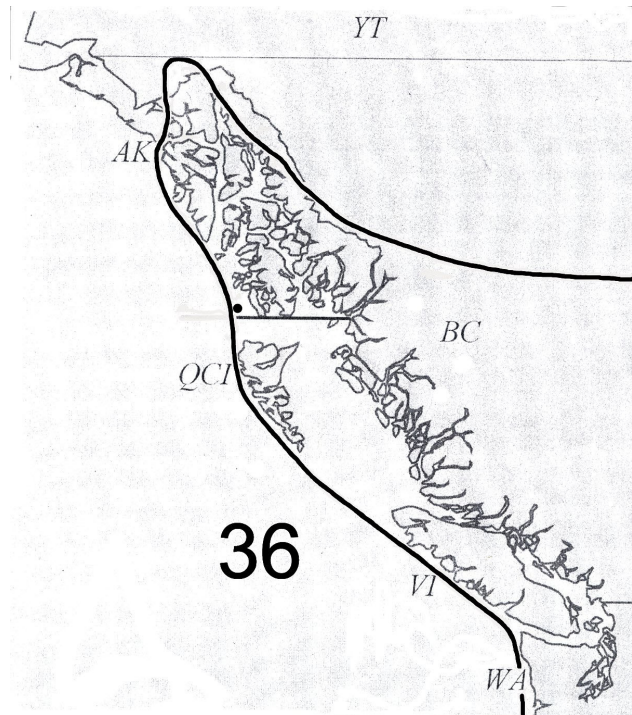


Figure 36. Distributions of Nematophora and the Order Chordeumatida in northwestern continental North America.

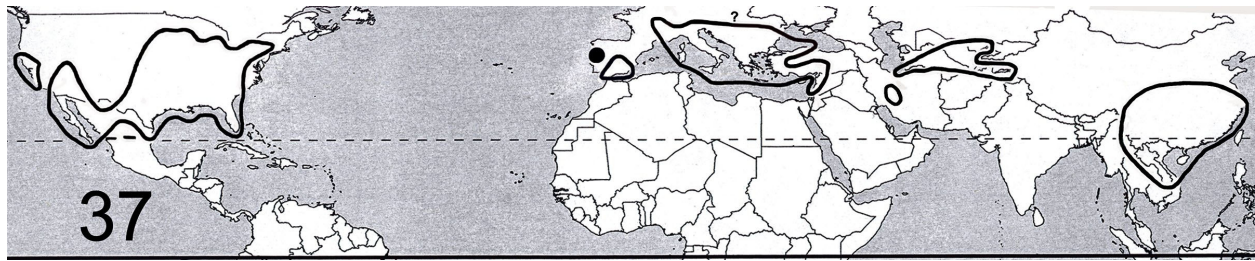


Figure 37. Known (solid lines) and projected (dashed line) distributions of the Order Callipodida. The question mark denotes the record from Budapest, Hungary, whose origin is uncertain.

Australia/New Zealand; Stemmiulida are sympatric in India/Sri Lanka, partly congruent in Indochina, and absent from the others. Chordeumatida are widespread in east/southeastern Asia and the East Indies, whereas Stemmiulida are known only from Vietnam, the Island of New Guinea, and Halmahera. The discovery by SIG of Stemmiulida in northern Vietnam (Appendix), expanding the recent discovery in southern Vietnam (Mauriès et al. 2010), suggests that their southeast Asian occurrences may be greater than presently realized. Chordeumatida and Stemmiulida may be more congruent here than our maps show.

Order Callipodida (Fig. 37-40)

Like Glomerida, Platydesmida, and Julida, the order Callipodida is basically a Laurasian taxon that penetrates the Tropics in southeast Asia and approaches this zone in the Western Hemisphere. It is absent from Central and South America, Africa, Australia/New Zealand, and all islands except some in the Adriatic, Aegean, Ionian, and Mediterranean Seas and the Gulf of California; we project it for Hainan Island, China (Fig. 37). Modern maps exist for Callipodida that we combine and update in Fig. 37 with a new California locality (Appendix). The order has been mapped globally twice (Shear et al. 2003, Stoev et al. 2008); Kime (2000) depicted the European distribution; and Stoev and Shelley (2009) did likewise for Mexico.

In the New World, Callipodida are known exclusively north of the Tropic of Cancer in North America, but they surely extend southward in “mainland” Mexico. The two large, formerly segregated areas in the eastern and southwestern US and adjacent Mexico (Shelley 1996e) were joined through northern Mexico by Stoev and Shelley (2009) to form an irregular, but continuous, area (Fig. 37-38). Additionally, a small, detached region exists along the California coast around San Francisco and Monterey Bays that we extend ~ 200 km (125 mi) southward to include San Luis Obispo Co. (Appendix). In the east, the distribution extends, north-south, from southern New York, Michigan, Wisconsin, and Minnesota to the tip of peninsular Florida, the Gulf Coast, and southward through eastern and central Texas to southern Tamaulipas and Nuevo León (Fig. 38). Callipodida are unknown, and possibly absent, from the south Florida Keys; the eastern halves of North Carolina, Virginia, and Maryland; southern New Jersey; and all of Delaware. East-west, the range extends from the Atlantic Coasts of New Jersey and South Carolina-Florida to central Nebraska, where it angles progressively southwestward onto the Edwards Plateau of westcentral Texas and spans the Pecos River near its confluence with the Rio Grande (McAllister and Shelley 2010). The boundary then crosses into Mexico (Coahuila and Chihuahua), turns back northward into the US, crossing the southwesternmost corner of New Mexico, eastern Arizona, and southeastern Utah,

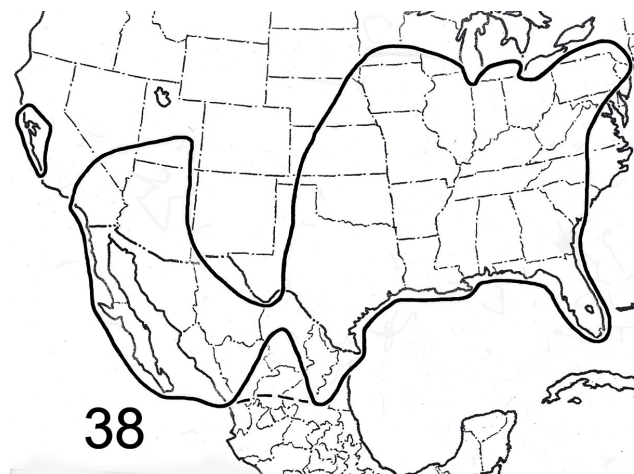


Figure 38. Known (solid lines) and projected (dashed line) distributions of Callipodida in North America/Western Hemisphere.

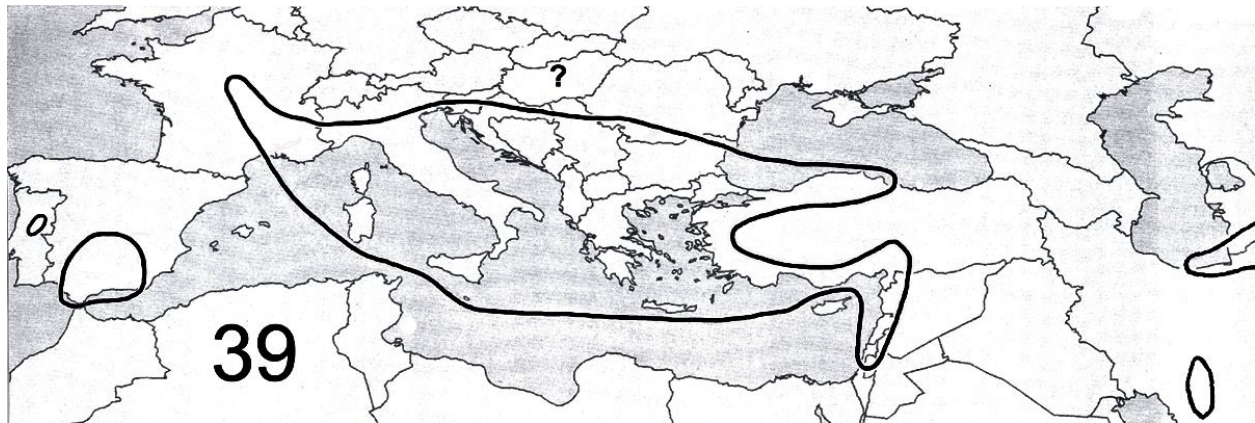


Figure 39. Distribution of Callipodida in Europe and the Middle East. The question mark denotes the record from Budapest, Hungary, whose origin is uncertain.

where it turns southwestward and curves through Nevada and California touching the Pacific Coast north of Los Angeles. The area encircles Baja California and the Gulf of California, and enters “mainland” Mexico in southern Sinaloa; present records indicate a gap between southern Durango and southeastern Nuevo León, where we project occurrence. While new discoveries may move the border northward in New Mexico, we believe the lacuna in this state, west Texas, and southern Colorado is real because substantial sampling in the southern Rocky Mts. (Sangre de Christos) of Colorado, the Sierra Blancas and Sacramentos in New Mexico, around El Paso, and in the Guadalupe, Davis, and Chisos Mts. of Texas have not yielded specimens.

We recognize three callipodidan areas in Europe (Fig. 39) with two on the Iberian Peninsula – a small one in northcentral Portugal and a larger one in southcentral Spain that does not traverse the Strait of Gibraltar. We unite other localities into a broad area that covers parts or all of the Mediterranean, Adriatic, Aegean, and Ionian seas from the Rhone River Delta, France, to northcentral Turkey, with a southward extension in the Middle East to central Israel and the West Bank. Inland, the area pervades central France, but not as far as Paris, where the one record is surely an introduction (Demange 1946, Stoev et al. 2008). We are uncertain about the occurrence of *Dorypetalum degenerans* (Latzel, 1884) in and near Budapest, Hungary, as the literature is ambivalent. It is ~ 192 km (120 mi) north of the continuous callipodidan range in Europe and could represent an indigenous but allopatric population or a human introduction, so we indicate it by a question mark (?) in Fig. 37 and 39 (Korsós 1992, 1994a; Korsós et al. 2002; Stoev and Enghoff 2006; Stoev et al. 2008). The northern border then curves through the Po River Valley of Italy into Slovenia, and angles through the Balkans to the Black Sea in northeastern Bulgaria. The range in Turkey is coastal and hence appears “bifid.” Callipodida inhabit many European islands including Corsica, Sardinia, Sicily, Malta, Crete, and most Adriatic, Ionian, and Aegean islands but are not known from Cyprus. Papers with maps or lists of species include Hoffman and Lohmander (1964), Stoev and Enghoff (2003, 2006, 2008), and Enghoff (2006).

We also recognize three regions in Asia (Fig. 37, 40), the smallest in the Zagros Mts. Iran. To the north, a subtriangular area stretches from the southern Caspian Sea and Kopetdagh Mts. of Turkmenistan to Punjab Prov., Pakistan, and far western China; north-south, it extends from Uzbekistan to northern Pakistan. Callipodida doubtlessly occur in northeastern Iran and are known from caves in Tajikistan and northern Afghanistan; they are also expected in Kyrgyzstan and projected for Xinjiang Prov., China. The third

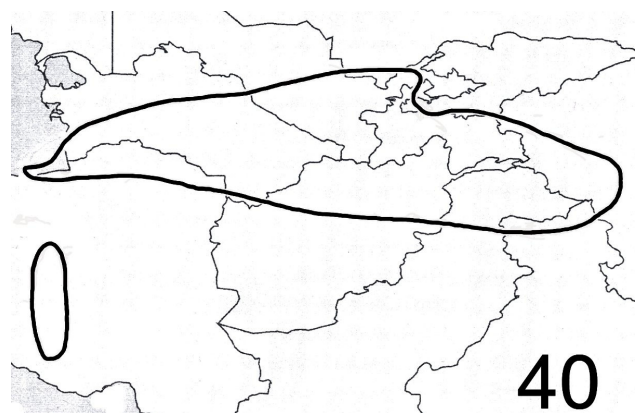


Figure 40. Distribution of Callipodida in Central Asia.

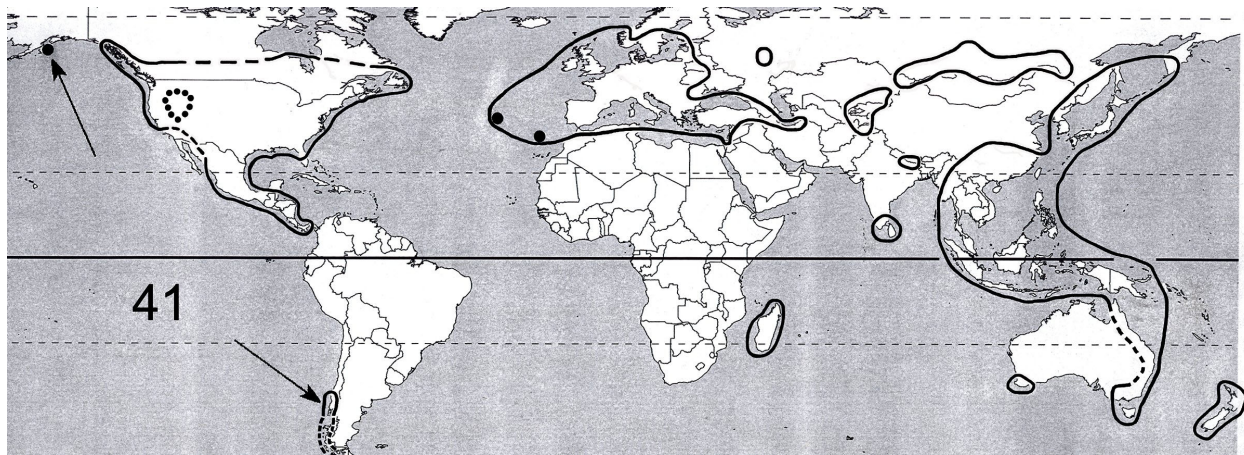


Figure 41. Known (solid lines) and projected (dashed lines) distributions of the Order Chordeumatida, parameters as in Fig. 1; a few records are available from the dotted area in North America. The upper arrow denotes the Tingupidae record from Kodiak Island, Alaska, USA, and the lower one indicates the known and projected ranges of Eudigonidae in Chile.

and largest area, in continental southeastern Asia, is the least known and conceivably larger, likely spreading farther west in Myanmar and southward onto the Malay Peninsula. North-south, it extends roughly from China north of Shanghai to central Cambodia and eastern Thailand; east-west, it ranges from the East China Sea to around eastern Tibet and northern Myanmar. Papers mapping or detailing this fauna include D. Wang and Mauriès (1996), Stoev (2004), Stoev and Geoffroy (2004), Enghoff et al. (2004), Stoev and Enghoff (2005), and Stoev et al. (2007).

Order Chordeumatida (Fig. 36, 41-44)

Chordeumatida inhabit the Tropics in both the Western Hemisphere and east/southeastern Asia, traversing the Equator in the latter; they also straddle the Tropic of Capricorn in Madagascar and occur in the South Temperate Zone in Australia, New Zealand, and South America (Chile). They are prominent, if not dominant, in harshly cold environments and, except for the Himalayas, dominate high montane faunas of Europe and Central Asia, occurring among ice and snow in rocky crevices above the timberline in the Alps (Geoffroy 1981, Pedrolí-Christen 1993b, Read and Golovatch 1994, Spelda 1996, Kime and Golovatch 2000, Mikhaljova 2004, Golovatch and Kime 2010). We recognize 13 faunal areas (Fig. 41) on all continents, with minor representation in South America and Africa (Mediterranean Coast). Sizes vary from a point locality (Kodiak I.) to large, continuous areas in North/Central America, Europe/western Asia/Middle East/North Africa, and east/southeastern Asia/East Indies. The seven southernmost areas, small and scattered, are in southern Chile (the only representation in South America), Madagascar, Australia, and New Zealand (both major islands); they represent Gondwanan remnants as does that north of the Equator in Sri Lanka and southernmost peninsu-



Figure 42. Known (solid lines) and projected (dashed lines) distributions of Chordeumatida in North and Central America; a few records are available from the dotted area, primarily the Great Basin Physiographic Province.

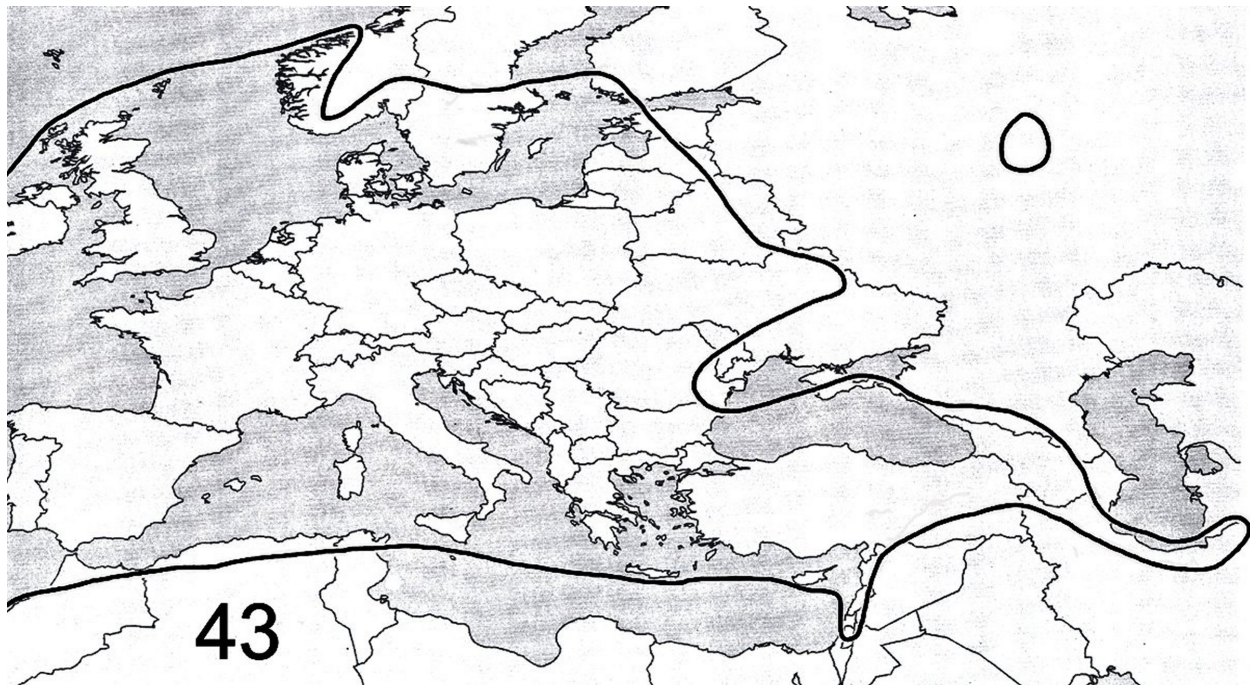


Figure 43. Distribution of Chordeumatida in Europe, North Africa, and the Middle East.

lar India. Some of the most boreal chilognath records are chordeumatidans, which range northward in Scandinavia, Siberia, and Canada to areas that are beneath ice and snow for most of the year. Chordeumatida occur on Kodiak I., in the North Pacific Ocean, Madeira and the Azores in the Atlantic, Madagascar and Sri Lanka in the Indian, Indonesia and Papua New Guinea, and the following European islands: Balearic, Corsica, Sardinia, Sicily, Malta, Crete, Cyprus, and islands of the Adriatic, Ionian, and Aegean seas. While present on Newfoundland, Canada, Chordeumatida are absent from Caribbean islands, ones in the Atlantic (Iceland, Bermuda, Canaries, Cape Verdes, Bioko, São Tomé and Príncipe, and Fernando Noronha), the Seychelles, Comoros, Réunion, Mauritius, Rodriguez, Maldives, Andamans, and Nicobars in the Indian, and Cocos, the Galapagos, Hawaiians, and all of Oceania in the Pacific. The boundary in the East Indies is uncertain because of a paucity of records; we encircle Papua New Guinea, but Chordeumatida plausibly occupy the geographically proximate Solomons and possibly expand southward to New Caledonia.

Kodiak I., harboring Tingupidae, is the westernmost diplopod locality in North America/ New World (Shelley et al. 2009a), and a large continuous area with an indefinite northern limit spans the continent from ocean to ocean. It extends southward from the northern Alaskan Panhandle and the “Haines Triangle,” BC, Hudson Bay, Ontario, and Newfoundland/Labrador, to north of Lake Okeechobee, Florida, the Gulf Coast, Los Angeles, California, southwestern Arizona, and Chiriquí and Bocas del Toro provs., Panama (Fig. 42). The area thus terminates west of the Former Canal Zone and omits southern peninsular Florida, the Channel Islands, California, and the Yucatan and Baja California peninsulas; we project exclusion from most or all of Sinaloa and Colima and western Sonora, Nayarit, and Jalisco. The northern boundary, essentially those of the families

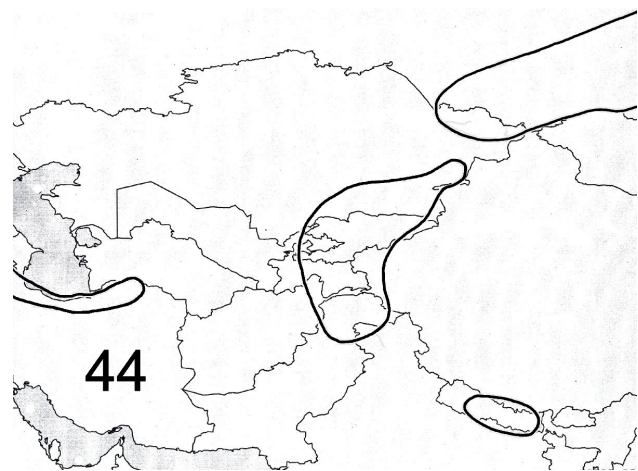


Figure 44. Distribution of Chordeumatida in central Asia.

Caseyidae, Conotylidae, and Tingupidae (Shelley 1993a; Shear and Shelley 2007b; Shelley et al. 2007, 2009a, b), curves south-southeastward from the “Haines Triangle,” BC, through Haines, Juneau, and Hyder, Alaska, then heads eastward to Dawson Creek and Tupper, BC, and northcentral Alberta. We project it continuing curvilinearly to Ft. Severn, on Hudson Bay, Ontario, then through southcentral Québec, southern Labrador, and encircling Newfoundland and Nova Scotia (Shelley 1988, 2002b), where Caseyidae occur; we also encircle New England even though no indigenous records exist from coastal Maine, New Hampshire, and Rhode Island. However, records (Appendix) are available from central New Jersey, northern Delaware, the “eastern shore” of Maryland, and near or on the coasts of Virginia, North and South Carolina, and Georgia, the North Carolina ones being from Hatteras Island. Chordeumatida cover northern peninsular Florida, the southernmost records being from Highlands Co. north of Lake Okeechobee (Loomis 1966b, Shear 1972, Hoffman 1999, Shelley 2001, Appendix). The border then extends along the Gulf Coast to Tabasco, Mexico, where it cuts across the Yucatan Peninsula but encompasses Belize, where we report the first locality (Appendix), and continues to Panama (Loomis 1964, 1968; Shear 1972; Hoffman 1999). Substantial sampling as has taken place on Barro Colorado Island, and the lack of chordeumatidans suggests that the order is absent from the Former Canal Zone.

The western boundary curves southward from Gustavus/Glacier Bay, Alaska, and encompasses the Alexander and Queen Charlotte Archipelagos and Vancouver and associated islands, BC (Shelley 1990a, 2002b; Shear 2004; Shelley et al. 2007, 2009b). The southernmost California localities are in the Santa Monica, San Gabriel, and San Bernardino Mts., so Chordeumatida are unknown south of metropolitan Los Angeles and are absent from Orange, Riverside, San Diego, and Imperial cos. Records are sporadic, so we project the border through Yuma, Arizona, before crossing into Mexico around Nogales. The westernmost records in northern Mexico are from western Chihuahua and Durango, so we angle the border south-southeastward to intersect the coast at Michoacan. In addition to new records (Appendix), works detailing occurrences, with or without maps, include Cook (1904), Palmén (1952), Causey (1961), Shear (1971, 1972, 1973b), Kevan (1983), Eskov and Golovatch (1986), Shelley (1988, 1990a, 1993a, 2002b), Gardner and Shelley (1989), Shear (1999), Shelley et al. (2007, 2009a, b), and Shear and Shelley (2007b).

The other ordinal occurrence in the Western Hemisphere, and the only one in South America, is Eudigonidae in southcentral Chile; the southernmost locality is on Isla Grande de Chiloé (Appendix), but the true southern limit is unknown. Maps are available in Golovatch (1986a) and Shear (1988), and no additional records, published or unpublished, exist. The most proximate ordinal locality is in central Panama, ~ 4,640 km (2,900 mi) to the north.

European occurrences (Fig. 43), basically as depicted by Kime (2000), stretch eastward from the Azores and Madeira (Demange 1970) to Ukraine, Belarus, the Balkan States, and Finland (Loksina and Golovatch 1979). North/south, the area extends from southwestern Norway and southern Sweden to the Atlas Mts. and Mediterranean coast of Morocco, Algeria, and Tunisia, the only ordinal occurrence in Africa (Pocock 1892b; Silvestri 1896; Brolemann 1920, 1921; Hoffman 1980a; Mauriès 1990; Akkari et al. 2010b). In the southeast, the distribution extends eastward through Crimea and the Caucasus, tapering into a finger along the southern Caspian Sea in northern Iran and Turkmenistan (Enghoff and Moravvej 2005). The southern border of this extension cuts through southeastern Turkey and turns abruptly southward to include coastal Syria, Lebanon, northern Israel, and the West Bank. Vicente and Enghoff (1999) reported *Ceratophys poculifer* (Brolemann, 1920) from the Canaries but speculated that it was introduced because it had not been taken there previously. Occurrence in the Balearic Islands was reported by Enghoff and Vicente (2000). Curcic et al. (2001, 2007) and Makarov et al. (2007) mapped occurrences in the Balkans, western Turkey, and Aegean islands. Additionally, a small, detached, circular area exists in Russia west of the Ural Mts. (Golovatch 1992a, Mikhaljova 2004).

While absent from sub-Saharan Africa, Chordeumatida occur on Madagascar; distributions were mapped by Mauriès (1994, 1997b) in addition to the species list of Enghoff (2003). No other island off Africa harbors this order.

No prior, consolidated map exists for chordeumatidan distributions in Asia, so we combined species and generic maps with unmapped records. We recognize four areas in central Asia (Fig. 41, 44) beginning with Sri Lanka and southernmost peninsular India (Tamil Nadu and perhaps part of Kerala), also Gondwanan in origin. The next small area is in Nepal and may pervade adjacent India and China (Shear 1979, 1987; Golovatch 1986b; Mauriès 1988b; Golovatch and Martens 1996). To the northwest, a larger, irregular area arises in Kashmir that curves through mountainous terrain in Pakistan, Afghanistan,

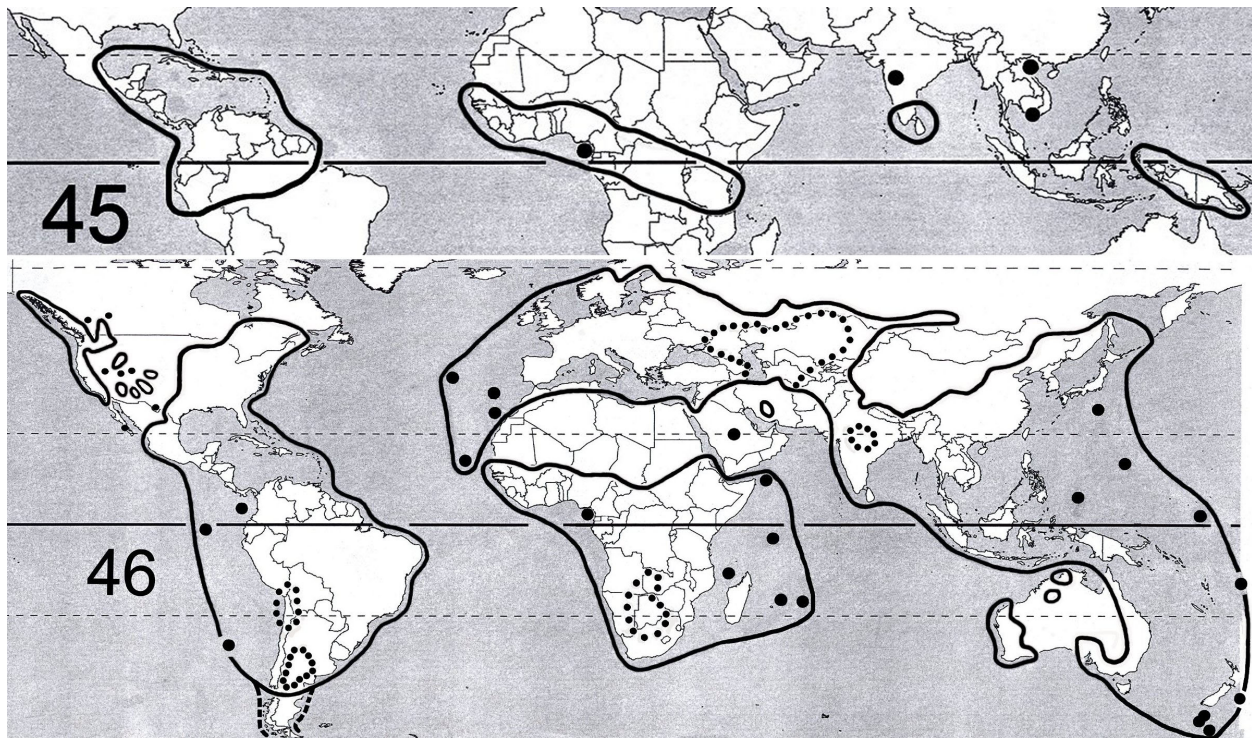


Figure 45-46. Distributions. **45)** Distribution of the Order Stemmiulida. **46)** Known (solid lines) and projected (dashed lines) distributions of the Superorder Merocheta and the Order Polydesmida, parameters as in Fig. 1. No records or samples are available from the dotted areas.

Tajikistan, Kyrgyzstan, and western China (Xinjiang) to eastern Kazakhstan (Shear 1979, Read and Golovatch 1994, Golovatch and Martens 1996). Finally, a slender, transverse, curvilinear area exists in Siberia atop the Mongolian and Chinese borders from northeastern Kazakhstan to the Amur River Region of Far Eastern Russia (Golovatch 1980c, Shear 1990, Shelley 1993a, Mikhaljova 1998, 2004, 2010). The western corner of the Siberian and the northern one of the Central Asian areas are only ~ 480 km (300 mi) apart, but continuity has not been demonstrated.

A large, irregularly crescent-shaped area covers eastern and southern, continental and insular Asia and eastern Australia. It extends, north/south, from southern Kamchatka, Sakhalin Island, and the Maritime Prov., Russia, through southcentral China, eastern Myanmar, southern Indonesia, and eastern Papua New Guinea, and along the east coast of Australia to Tasmania. It encompasses the Kurile and Ryukyu Islands, Japan, Taiwan, the Philippines, and the Korean Peninsula, where the western border angles southward into the Yellow and East China seas before expanding westward into China at the Yangtze Delta. From there, the border extends westward into Sichuan Prov. then curves through eastern Tibet into Myanmar and southward along the Irrawaddy River to the Andaman Sea (east of the Andaman and Nicobar Islands) and Indian Ocean around Sumatra, Java, and southern Indonesia. Publications with records and/or partial maps include Murakami and Kawasawa (1976), Loksina and Golovatch (1979), Golovatch (1986b), Eskov and Golovatch (1986); Shear (1990, 1999), Mikhaljova (1993, 1998, 2000, 2004, 2010), Shear and Tanabe (1994), Mikhaljova and Basarukin (1995), Shear et al. (1997), Mikhaljova and Nefediev (2002), Mikhaljova and Korsós (2003), Korsós (2004), Enghoff et al. (2004), and Enghoff (2005).

In Australia, we project continuous occurrence along the entire eastern coasts of Queensland, New South Wales, and Victoria, and all of Tasmania. Chordeumatida also occupy a small, detached area in the southwestern corner of Western Australia. While now obviated by the Australian and Tasmanian websites, Golovatch (1986a) and Shear and Mesibov (1997) mapped Metopidiotrichidae in Tasmania, and though no maps are presented, Shear (2002) addressed *Metopidiotrichix* Attems, 1907, geographically. Shear (1999) also mapped the superfamily Heterochordeumatoidea globally, including areas in Australia and New Zealand, for which we encircle both major islands although records appear to be lacking from the North Island. We exclude Campbell I., subantarctic New Zealand, because of Johns' (1964) suspicion that the

Schedotrigona sp. occurring there was introduced from New Zealand proper. Golovatch's (1986a) work on the then superfamily Conotyloidea is also relevant.

Order Stemmiulida (Fig. 45)

In contrast to its nematophoran counterparts, the order Stemmiulida is a purely tropical, Gondwanan taxon that inhabits seven regions, those in the New World, Africa, and eastern Indonesia/Papua New Guinea straddling the Equator. It contains only one component family and three genera (Mauriès and Golovatch 2006. Mauriès et al. 2010), and the occupied areas vary from point localities in Vietnam and India to a sizeable region in the northern Neotropics that encompasses northern South America, all Caribbean islands, southern Mexico, and Central America.

The New World distribution lies primarily north of the Equator, approaches the Tropic of Cancer in Cuba and eastern Mexico, and is known in the southern Tropics as far south as central Peru (Huanuco Dept., Appendix) and south of the Amazon in Brazil. In the Caribbean, Stemmiulida may be expected on all the Greater Antilles and the larger Lessers, being known specifically from Cuba and Isle of Pines; Hispaniola (both Haiti and the Dominican Republic); Puerto Rico and Culebra; St. John, US Virgin Islands; Tortola, British Virgin Islands; Guadeloupe; and Tobago (Chamberlin 1918, 1922a; Loomis 1934, 1936, 1941, 1970; Velez 1967; de la Torre y Callejas 1974; Mauriès 1980a; Gonzalez Oliver and Golovatch 1990; Hoffman 1999). On the continental land mass, the northernmost record appears to be Xalapa, Veracruz, Mexico (Silvestri 1916, Loomis 1968, Hoffman 1999), and stemmiulidans are also known from Chiapas (Silvestri 1916, Loomis 1968, Reddell 1971, Hoffman 1999, plus unpublished samples examined by RMS). Stemmiulida are anticipated throughout Central America and have been recorded from Guatemala, Honduras, Costa Rica, and Panama including the Former Canal Zone (Silvestri 1916; Chamberlin 1922a; Loomis 1964, 1968, 1972; Hoffman 1999). In South America, they are known from Colombia, Ecuador, Brazil (Amazônas Est., Manaus region), Venezuela, Surinam, and Trinidad, which we include here because of its proximity to the continent (Silvestri 1897, 1898b; Chamberlin 1918; Campos-Rebeiro 1926; Loomis 1934, 1968; Jeekel 1963, 1986a; Mauriès 1979, 1984; Hoffman 1999). Manaus and the Amazon River itself lie south of the Equator, so we project occurrence in French Guyana and draw the boundary across northern Brazil at the latitude of the River, though stemmiulidans surely occur farther south there as in Peru.

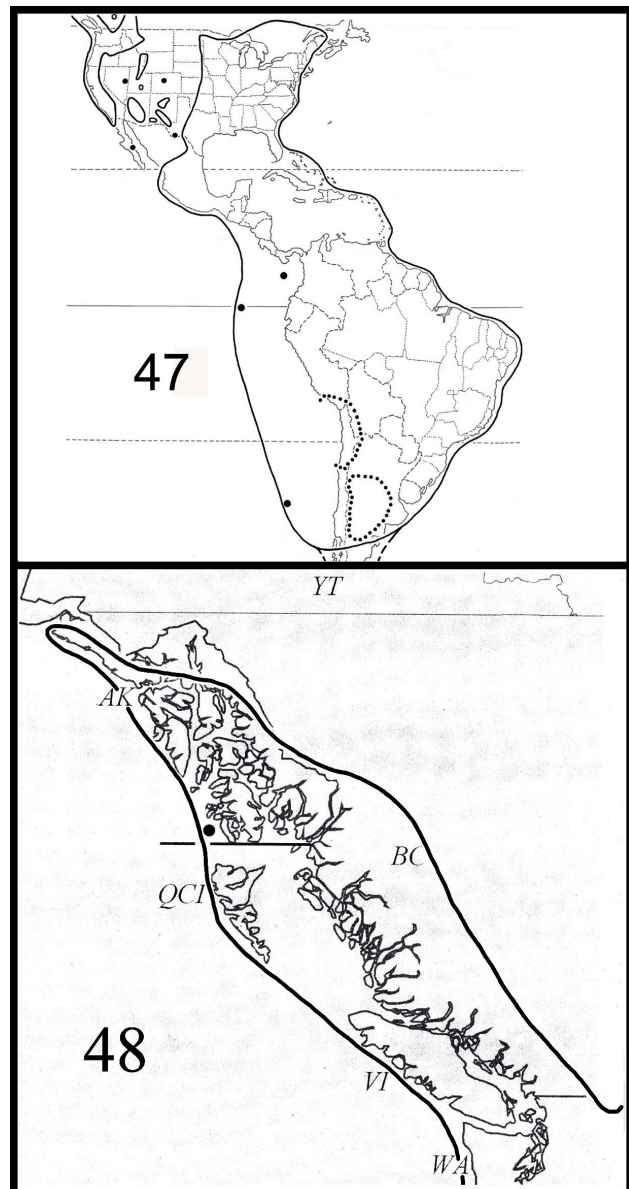


Figure 47-48. Distributions. **47)** Known (solid lines) and projected (dashed lines) distributions of *Merocheta*/*Polydesmida* in the Western Hemisphere from southern Canada southward. Dotted lines demarcate areas lacking both records and samples. **48)** Distributions of *Merocheta*/*Polydesmida* in northwestern North America; the dot denotes Forrester Island, Alaska, USA.

The African/sub-Saharan distribution, again primarily north of the Equator, stretches south-eastward from Senegal to Kenya, Tanzania, and northern Malawi. We accept the maps of Mauriès (1985, 1989), which are supplemented by Kenyan records in VandenSpiegel (2001) and a new site on Bioko (Appendix). Readers are referred to these papers and ones cited therein for details.

The Indian region encompasses Sri Lanka and the southern tip of the peninsula (Kerala and Tamil Nadu), to which we add a detached site in Maharashtra near Mumbai (Appendix). Carl (1941) published the only prior records of Indian stemmiulidans, and Mauriès (1981) reviewed Sri Lankan species.

We record (Appendix) a new locality north of Hanoi, northern Vietnam, to supplement that from the south (Mauriès et al. 2010).

Stemmiulida occupy an ovoid area in the East Indies that lies primarily south of the Equator and encircles Halmahera, Indonesia. Silvestri (1916) recorded the order from Mt. Hanseman, Madang Prov., Papua New Guinea, and ninety years later, Mauriès and Golovatch (2006) described a species from Halmahera; we project occurrence in Irian Jaya. Though unknown, we anticipate stemmiulidans on other Indonesian islands, for example Sulawesi, which is inadequately sampled.

Superorder Merocheta (Fig. 46-50)

With only one component order, the superorder Merocheta has the same distribution as Polydesmida (Fig. 46), detailed below.

Order Polydesmida (Fig. 46-50)

Generally considered the most speciose order, though second to Chordeumatida in the number of families (Shelley 2003a, 2007a), Polydesmida occur natively on all continents and on islands in all oceans and seas; they are particularly dominant in the Himalayas, where over half of the ~ 200 species are polydesmidans (Golovatch and Kime 2010). While not crossing the Arctic Circle as do Polyxenida, Polyzoniida, and Julida (Fig. 3, 20, 26), and hence not representing the northern limit for either Diplopoda or Chilognatha, Polydesmida include the southernmost diplopod, *Notonaia campbellensis* Johns, 1970 (Dalodesmidea: Dalodesmidae), on Campbell I. (52° 36' 18"S) in the subantarctic islands of New Zealand (Johns 1964, 1970).

We recognize 21 areas for Polydesmida (Fig. 46) that vary in size from point localities in North America and Saudi Arabia to large, continuous areas in the Western Hemisphere (eastern North America to southern South America), sub-Saharan Africa, and eastern Atlantic islands to Australia/New Zealand/Oceania. The northernmost localities are Yakutat, Alaska, USA, Steinkjer, Norway, and Östersund and Längselo, Sweden, and while Polydesmida inhabit many islands, they are notably absent from Bermuda, Newfoundland, Iceland, and the Hawaiians. Works with global familial maps, all obsolete, include Jeekel (1968, Paradoxosomatidae), (Mauriès 1974b, Platyrrhacidae *sensu* Hoffman (1980a)), Hoffman (1962, 1978, Chelodesmidae, Xystodesmidae, Platyrrhacidae *sensu* Hoffman (1980a)), Simonsen (1990, Pyrgodesmidae, Trichopolydesmidae, Nearctodesminae, Macrosterodesminae, Fuhrmannodesmidae, Dalodesmidae,

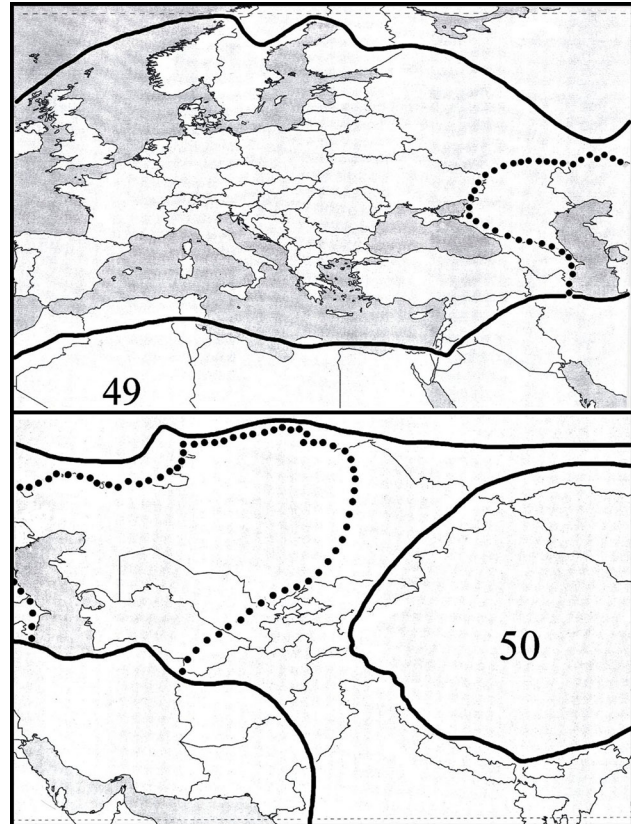


Figure 49-50. Distributions. **49)** Distributions of Merocheta/Polydesmida in Europe, North Africa, the Middle East, and western Asia; the dotted line circumscribes an area lacking both records and samples. **50)** Distributions of Merocheta/Polydesmida in Central Asia; the dotted line circumscribes an area lacking both records and samples.

Polydesmidae, Cyrtodesmidae), Simonsen (1992, Cryptodesmidae, Haplodesmidae), Golovatch (1996a, Pyrgodesmidae, on a blank map without reference lines), and Djursvoll et al. (2000, Polydesmidae).

The map of the order/nominate family by Simonsen (1990) shows Polydesmida as continuous throughout North America from southern Canada southward, but such is not the case. Continuity is through the forested biomes of eastern North America only; 13 separate areas of varying sizes exist in the west, seven of which are point localities with two being from caves. The eastern area joins with “mainland” Mexico, Central America, Caribbean and eastern Pacific Islands, and South America to form a large area extending from southern Québec and James Bay, Ontario, to southern Chile (Isla Grande del Chiloé) and Argentina (Nequen/Rio Negro provs.). It lies generally east of Lake Superior in Canada and east of the central Plains in the US, with the western border angling south-southwestward in Texas to the Rio Grande west of the confluence with the Pecos River. The northernmost record is *Pseudopolydesmus canadensis* (Newport, 1844) (Polydesmidae), from the Albany River at James Bay, Ontario, from which the area slopes southwestward to Sault Ste. Marie and southeastward through Québec to the Gaspé Peninsula (Fig. 47). The eastern border cuts across New Brunswick and Maine to the Atlantic coast and then across Massachusetts and Connecticut to Long Island Sound. No polydesmidans are known from Long Island itself, but they do occur in southern New Jersey, Delmarva, and Cape Hatteras National Seashore and Bald Head Island, North Carolina. The eastern border then encircles the Bahamas (Shelley 2003c, 2007c) and the Antilles, but excludes Turks and Caicos, while the western traverses northern Minnesota to Fargo, North Dakota, then heads southward through eastern South Dakota and Nebraska before angling south-southwestward to the Rio Grande, northeastern Coahuila, and passing through Zacatecas and Nayarit to the Pacific at Jalisco.

Of the 13 western areas in the US and Canada, only one is substantial in size and continuity. It extends along the Pacific Coast from Yakutat and Gustavus/Glacier Bay, Alaska (Fig. 48), to south of Ensenada, Baja California Norte, Mexico, encompassing all of the Alexander Archipelago and the Queen Charlotte, Vancouver, and associated islands but excluding the Channel Islands, California. Its inner boundary extends through Hyder, Alaska, and Stewart, Terrace, and Manning Provincial Park, BC, into Washington; from the south, it extends northward through San Diego, Riverside, and San Bernardino cos., California, angles through the Tehachapi Mts., and runs along the crest of the Sierra Nevadas and Cascades to central Oregon. There, the boundary turns eastward through the Blue Mts., Oregon, and the Bitterroots, Idaho, and nips the Continental Divide in Montana. It then heads westward/northward into Canada along the Divide and the BC/Alberta border to Yoho National Park, where it swings westward into BC and southward into Washington. Two detached areas exist in western Canada, a point locality east of the Divide in Jasper National Park, Alberta (Shelley 2007b), and a small one in the Shuswap Highlands, BC (Shelley 1994a).

Polydesmida occupy nine smaller areas in the western US, one in the Rockies of eastern Idaho/western Wyoming that curves through the Wasatch Mts. to south of Great Salt Lake, Utah. A few localities cluster in the Henry Mts., Utah, and there are cave localities to the east and west in Colorado and Nevada. To the south, a slightly larger area covers most of Arizona with scattered sites on forested mountaintops and around springs and rivers, extending from the Colorado River/Grand Canyon National Park, in the northwest, to the Chiricahua and Graham Mts., in the southeast. Three regions of New Mexico are occupied – the Manzano and Sandia Mts. in the north-center, the Black Mts. and associated ranges in the southwest, and a narrow area extending from the Capitans and Sierra Blancas to the Guadalupe in Texas. Additionally, there are point localities in the Chisos Mts., Big Bend National Park, Texas, and on the Gulf of California, Baja California Sur. Other than the last site and northwestern Baja California Norte, no polydesmidans are known from the Baja Peninsula; maps showing continuous ranges here for Pyrgodesmidae (Simonsen 1990, Golovatch 1996a) are erroneous.

Works with maps, some outdated, include Hoffman (1962, Xystodesmidae, Platyrhacidae *sensu* Hoffman (1980a)), Buckett and Gardner (1968, Xystodesmidae), Shelley (1980, 1982, 1987, 1990b, c, 1992, 1993b, c, d, e, f, 1994a, b, 1995, 1996f, g, 1997a, b, c, 2000b, c, 2003b, c, 2004, Eurymerodesmidae, Euryuridae, Nearctodesmidae, Platyrhacidae, Polydesmidae, Pyrgodesmidae, Rhachodesmidae, Sphaeriodesmidae [Desmoninae], Xystodesmidae), Shear (1984, Polydesmidae), Withrow (1988, Polydesmidae); Whitney and Shelley (1995, Nearctodesmidae), Shelley and Whitehead (1986, Xystodesmidae), Shelley and Shear (2006, Nearctodesmidae), Shear and Shelley (2007a, Macrosterodesmidae), and Shelley and McAllister (2007,

Xystodesmidae). Ordinal limits in eastern Canada are depicted by Shelley (1988), and Hoffman (1979a) reported Chelodesmidae from Cocos Island, Costa Rica.

South American occurrence is continuous with that to the north, and we expand the border westward in the Pacific to incorporate the Galapagos and Juan Fernandez Islands, where indigenous, if not endemic, species have been recorded in Pyrgodesmidae and Dalodesmidae, respectively (Shear and Peck 1987, Chamberlin 1957). The area encompasses the entirety of all countries but Argentina and Chile, as the southernmost records, all in Dalodesmidae, are *Tsagonus muermo* Chamberlin, 1957, from de los Lagos Dist., Chile (Chamberlin 1957), and *Anaulacodesmus lacustris* and *Monenchodesmus inermis nahuelhuapiensis*, both by Schubart, 1954, from Parque Nacional Nahuel Huapi, Neuquén and Rio Negro provs., Argentina (Schubart 1954, Demange 1963, Mauriès 1998). We could not find records from two areas; the more northern, also blank for the class, encompasses the Atacama Desert and arid regions in Chile and adjacent Peru and Bolivia. It lies west of Lake Titicaca, as Kraus (1954) described *Catharosoma titicacaensis* (Paradoxosomatidae) and *Cryptogonodesmus peruvianus* (?Fuhrmannodesmidae) from the western side of the lake; later, he (Kraus 1960b) recorded *Mestosoma alticolum* (Attems, 1930) and described *M. orobium* (Paradoxosomatidae) from the lake region in general. The second blank area is in central Argentina east of the Andean Cordillera and west of Buenos Aires. Works with maps include Jeekel (1968, Paradoxosomatidae), Demange and Silva (1976, Dalodesmidae), Hoffman (1982b, 1990a, Chelodesmidae), Simonsen (1990, Cyrtodesmidae), and Vohland (1998, Aphelidesmidae); ones with species lists and localities, particularly for southern South America, include Kraus (1956), Jeekel (1965a), and Golovatch (2005).

In sub-Saharan Africa, Polydesmida occur generally south of the Senegal and Niger rivers, the curvilinear border passing through Mali, Niger, northern Nigeria, and southern Chad, then angling northward through Sudan to the Red Sea in Eritrea. The entire area south of this line is occupied including Bioko, except for the dotted area that encompasses western Zambia, southeastern Angola, eastern Namibia, northern Republic of South Africa, and all of Botswana. To some degree this void reflects lack of sampling, but it also corresponds to the preponderance of the generally hot, dry, and inhospitable Kalahari and Namib deserts. Polydesmida also occur on Madagascar, Sokotra, and the Comoros, Mauritius, Rodriguez, and the Seychelles Islands (Butler 1876, 1879; Mauriès 1980b; Hoffman 1990b; Golovatch 1992b; Mauriès and Geoffroy 1999; Enghoff 2003, VandenSpiegel and Golovatch 2007). Works with maps include Schiøtz (1966, Campodesmidae), Jeekel (1968, Paradoxosomatidae), Hoffman (1968b, 1978, 1990b, 2004, 2005, Paradoxosomatidae, Oxydesmidae, Gomphodesmidae), Simonsen (1990, Ammodesmidae), Mauriès and Heymer (1996, Fuhrmannodesmidae), Shelley and Crawford (1996, Paradoxosomatidae), Alderweireldt and Enghoff (1998, Oxydesmidae), and VandenSpiegel and Golovatch (2003, Ammodesmidae). Oxydesmidae and Fuhrmannodesmidae occupy Sokotra (Hoffman 1990b, Golovatch and Mauriès 2007), and Cryptodesmidae occur on Bioko (Hoffman 1975), to which we add Pyrgodesmidae (Appendix). Chamberlin (1952) listed chelodesmid (prepodesmine) species with countries or regions of occurrence as did Jeekel (2003b, 2004b, 2006b) for Paradoxosomatidae, and valuable species lists exist in Cook (1898) and Hoffman (1953, 1968b).

Occurrence in the European part of the Euroaustralasian area, which extends around Atlantic islands and the northern periphery of Africa, follows Kime (2000) with modifications in Russia and eastern Europe. In North Africa, Polydesmida occupy the Atlantic and Mediterranean coasts of Morocco, extending inland into the Atlas Mts. and the Mediterranean coasts of Algeria, northern Tunisia, and the Benghazi region of Libya. Tabacaru (1995) and Golovatch (2007) reported Oxydesmidae from Israel, and Shelley (2009) mapped paradoxosomatid occurrences, thereby accounting for the eastern Mediterranean dip.

The European and Asian parts of this area connect through an “isthmus” in Pakistan and Afghanistan (Jeekel 2003c) that extends westward south of the Caspian Sea, curves southward through Iraq, Syria, and Jordan, then northward through Israel to the Mediterranean. The eastern border curls northeastward through the Central Asian Republics (Spelda et al. 1998) and around uninvestigated western China, then expands eastward as a narrow “peninsula” in Siberia atop western Mongolia. A substantial area east, north, and west of the Caspian Sea lacks records; it expands westward into eastern Ukraine and eastward into central Kazakstan, Uzbekistan, and Turkmenistan. Two sites are sufficiently detached to be shown separately, that near Riyadh, Saudi Arabia (Shelley 2009), and in the Zagros Mts., Iran.

The eastern and southern Asian section expands curvilinearly northeastward through central China and Manchuria into Khabarovsk Prov., Russia, crossing into the Sea of Okhotsk north of Sakhalin Island. It then turns southeastward through the Kurile Islands and traverses the Pacific east of Bonin, the Marshall Islands, Micronesia, Fiji, and New Zealand. Fiji has no endemic or presumably indigenous Paradoxosomatidae (Jeekel 1972), but he (Jeekel 1980) regarded their Cryptodesmidae as native, so we draw the Oceania border east of Fiji and Chatham Island, New Zealand (Appendix). From the isthmus in Central Asia, the border curves southward through western India to encompass the entire Indian Peninsula, Sri Lanka, all of southeastern continental Asia, the Andaman and Nicobar Islands, and all of Indonesia and Papua New Guinea. We continue this area through eastern and southern Australia, including nearly all of Victoria and Capital Territory and about halfway into South Australia. Polydesmida occupy the westernmost coastal region of Western Australia, a small interior area in the Kimberley Region, and Darwin vicinity (Paradoxosomatidae, Haplodesmidae, Appendix), the first precise diploped localities from Northern Territory.

A bibliographic catalog on Platyrrhacidae (Jeekel 2007) is available for the Asian/Australian part of this area. Papers with maps regarding the continent and islands include Jeekel (1965b, Paradoxosomatidae), Hoffman and Lohmander (1968, Paradoxosomatidae, Xystodesmidae), Johns (1979, Polydesmida as a whole), Hoffman (1973, 1975, 1997, Cryptodesmidae, Platyrrhacidae), Golovatch (1979, 1986b, 1987b, c, 1988, 1990c, d, 1992b, 1994b, c, 1996b, Fuhrmannodesmidae, Opisetretidae, Paradoxosomatidae, Polydesmidae), Simonsen (1990, Haplodesmidae [=Doratodesmidae], Opisetretidae), Golovatch and Enghoff (1994, Paradoxosomatidae), Tanabe and Shinohara (1996, Xystodesmidae), Mikhailjova (1998, Paradoxosomatidae, Polydesmidae), Tanabe (2002, Xystodesmidae), Mesibov (2002, 2003a, b, c, 2004a, b, c, 2005a, b, Dalodesmidae, Haplodesmidae), Golovatch and Nguyen Duc (2006, Platyrrhacidae). Jeekel (1973, 2000) listed species from the Solomon Islands, and Attems (1914a), Jeekel (1967), and Hoffman (1980a) reported *Eustrongylosoma* (Paradoxosomatidae) from Pohnpei, Federal Republic of Micronesia. In addition to Enghoff (2006) and Enghoff and Moravvej (2005), Iranian and Caucasus records are available in Golovatch (1981a), and Jeekel (2006c) published New Zealand dalodesmid localities. We report Dalodesmidae (P. Johns, pers. comm. to RMS) from Chatham I. in the South Pacific Ocean, ~ 1,136 km (710 mi) east of the South Island. To the best of our knowledge, this is the first report of Polydesmida from this archipelago.

Order Siphoniulida *incertae sedis* (Fig. 23)

The rarest order, the monofamilial Siphoniulida are known from only two areas some 19,200 km (12,000 mi) apart on opposite sides of the world. It was first discovered on Sumatra at essentially the same site as Siphonocryptida, and there is a small area in southern Mexico/Guatemala (Fig. 23) (Pocock 1894; Hoffman 1979b, 1980a, 1999; Sierwald et al. 2003; Bueno-Villegas et al. 2004). All locations are tropical, that in Sumatra lying essentially on the Equator and the New World site being to the north; aside from the discoveries of the order and the holotype of *Siphoniulus albus* Pocock, 1894, Siphoniulida have not been encountered again in the Old World. While additional populations may await discovery, the present limited and vastly disjunct occurrences indicate great age, relictual status, and decline toward extinction (Golovatch and Kime 2010). The most informative works are Hoffman (1979b) and Sierwald et al. (2003); the latter readdressed affinities but could not resolve them. The combination of a juliformian body and colobognathan head suggests that Siphoniulida may be a remnant of an early intermediate lineage. Could Siphoniulida be the sole surviving remnant (a “living fossil”) of a transition stage between Colobognatha and Eugnatha? We have no answer but suggest that dissection and SEM examinations of siphoniulid mandibles, as well as molecular studies, might be meaningful.

PATTERNS AND CONGRUENCES AMONG CHILOGNATHA

A host of geographical patterns, both broad, at global or hemisphere levels, and narrow, at (sub)continental levels, manifest themselves when distributions are carefully mapped. We believe they hold evolutionary significance and indicate relative ages when correlated with documented palaeogeographic events. In this section, we identify discernible patterns while attempting to exclude those that reflect

inadequate sampling; sampling uniformities are unknown, and for practicality we assume (sub)continuous occurrences throughout taxon areas. From personal experiences and knowledge of the literature, we believe that pentazonian and eugnathan taxa occur reasonably continuously throughout their occupied areas; we also believe the same holds for Colobognatha, but we cannot personally attest to such for forms in the Southern Hemisphere. Discoveries in ordinal lacunae can never be wholly discounted, but neither can they be predicted or anticipated; one can only analyze, or draw inferences from, existing data and evidence. Observations and conclusions presented here therefore concede the caveat that future findings may necessitate alterations.

Broad/Global Patterns

1) Continuous versus Fragmented Distributions. Shelley and Whitehead (1986) observed that geographical (and anatomical) discontinuities reflect extinctions and that fragmented distributions are consistent with greater age. We concur and consider relative degrees of fragmentation, based on a subjective combination of the number of occupied areas and distances between them, as a measure of relative ages. The contrast between continuous and discontinuous geographies is an obvious and striking feature of the maps; every taxon, even Diplopoda itself, exhibits some fragmentation of continental ranges. Chordeumatida's occurrence on Kodiak, a "continental" North American island, is ~1,440 km (900 mi) west of continuous ranges in the Alaskan panhandle (Fig. 1, 3, 14, 24, 35, 41), and the two Russian areas on/north of the Arctic Circle are narrowly detached from the same (Fig. 1, 5, 14, 15, 20, 24-26). Detached regions in Niger and Iran represent occurrences in inselbergs, and that in Saudi Arabia is in one of many desert "wadis." If the numerous uninvestigated inselbergs and wadis in the Saharan, Arabian, Iranian, Pakistani, and Indian deserts were sampled during wet seasons, Diplopoda, Chilognatha, and Helminthomorpha might prove to be substantially continuous through these harsh environments and actually occur subcontinuously throughout the Old World.

Substantially continuous distributions are exhibited by all taxa at the "class-group" hierarchical level except for the infraclass Pentazonia and subterclass Colobognatha (Fig. 6, 15), and an unknown number of the latter's point records from coastal sites probably refer to *R. purpureus*. Excluding such records, Polyzoziida (Fig. 20) are only slightly more fragmented than Platydesmida, 24 areas versus 21; by contrast, Siphonophorida (Fig. 22), with only eight areas and three large ones, are surprisingly continuous, particularly in the Western Hemisphere as shown by hundreds of unpublished museum samples. The most fragmented colobognath, however, is Siphonocryptida (Fig. 23, circles, star), known from only four regions.

All pentazonian taxa inhabit at least five areas, and the Gondwanan origin of Sphaerotheriida, in contrast to the northern of Glomerida (Fig. 9, 13), is evident. The only Laurasian occurrence of the former is southeast Asia, derived from terranes from Gondwana I (Hall 1998, 2009; Metcalf 1998).

Ranking the extant helminthomorph orders from most to least fragmented derives the following sequence: Siphoniulida > Siphonocryptida > Polyzoziida > Platydesmida > Chordeumatida > Callipodida = Siphonophorida > Stemmiulida > Spirostreptida *s. l.* > Polydesmida > Spirobolida > Julida. The eight most fragmented taxa include all those with prolonged, pyriform or rostrate heads and all colobognaths and nematophorans, suggesting greater age for these taxa than for components of Juliformia and Merocheta. Pentazonians are even more fragmented, and incorporating them into the equation yields, for Chilognatha as a whole: Siphoniulida > Siphonocryptida > Glomeridesmida > Sphaerotheriida > Glomerida > Polyzoziida > Platydesmida > Chordeumatida > Callipodida = Siphonophorida > Stemmiulida > Spirostreptida *s. l.* > Polydesmida > Spirobolida > Julida. Both Pentazonia and Helminthomorpha contain extinct orders, like Amynilyspedida (Pentazonia) and Euphoberiida (Helminthomorpha), but overall, the latter infraclass has been more successful, generated more lineages, and apparently colonized more territory. As suggested by Enghoff's (1990) reconstruction of the hypothetical ancestral chilognath, Glomeridesmida may really be the sole surviving limacomorph order rather than the only one that ever existed. Likewise, one or more extinct orders of Penicillata, in addition to extant Polyxenida, seem plausible, but all traces of these have vanished because of the inability of these soft-bodied organisms to form impression fossils.

2) Diminished Ordinal Diversity at Higher Latitudes. Golovatch and Kime (2010) observed that Polyzoziida, Julida, Chordeumatida, and Polydesmida are more "cold tolerant" and extend farther into higher latitudes and colder climates than other orders; our study substantiates this fact. We discuss below the situations in the Northern and Southern Hemispheres in both the New and Old Worlds, respec-

tively. Readers are also directed to the listing of Milliped Extremes (Table 2), which cites northern- and southernmost millipeds and those occurring at the highest (coldest) elevations. For completion, we include Polyxenida (Fig. 3-4) in the table but limit the ensuing discussions to Chilognatha.

A) Northern Hemisphere.

1) North America. Ranges extend farther north along the Pacific Coast than in the interior, and unlike Eurasia, no order is known near the Arctic Circle. Arbitrarily selecting the western US/Canadian border (49°N) as a reference line, only 5 of the 12 chilognath orders in the continental US also inhabit Canada, two of which, Polyzoniida (Fig. 20) and Spirobolida (Fig. 38), are limited. Both occur in the east, primarily in southern Ontario south of 49°N; Spirobolida are restricted to the east while Polyzoniida also nip the southwestern corner of mainland BC but exclude Vancouver Island. Polyzoniida do not extend nearly as far north in North America as in Eurasia; conversely, Spirobolida range farther north in the New World with minimal presence in Eurasia, being absent from Europe, the Middle East, and Central Asia, and present today only in the Indian Subcontinent and from coastal/eastcentral China southward. There is also a fossilized Cretaceous spirobolidan, *Gobiulus sabulosus*, from Mongolia (Fig. 28, inverted triangle) (Dzik 1975), which is consistent with east Asian ordinal occurrence, though as nearly as we can determine, the site is detached from the modern range by ~ 1,120 km (700 mi). Thus in North America, only three orders – Julida, Chordeumatida, and Polydesmida (Fig. 26, 41-42, 46-47) – extend significantly northward into Canada and the Alaskan Panhandle, a dramatic drop in diversity from the eight in both the northwestern US (Washington/Idaho) and Ohio, and only 25% of the diversity occurring across the southern US.

2) Eurasia. Eight orders are represented in the European part of the Eurasian land mass (west of the Ural Mts.) (Table 5). All eight occur from Denmark and the North/Baltic seas southward; six inhabit Norway, Sweden, and Finland, but only Julida, plus Polyxenida, touch or cross the Arctic Circle. Including Polyxenida, 13 orders occupy Asia north of the Tropic of Cancer, the Palearctic Realm (Table 4), but only four are known from Russia north of Mongolia and Kazakhstan, and only two, Polyzoniida and Julida, extend to or beyond the Arctic Circle. While expected, Polyxenida have yet to be documented from Siberia, as indicated by the dashed inner line in Fig. 3.

B) Southern Hemisphere.

1) South America. No political boundary is a natural reference line here as the US/Canada border, well north of the Tropic of Cancer, is in North America; the equivalent, 49°S latitude is in the uninvestigated southernmost “mainland,” where the only recorded milliped is the polyxenidan, *Propolyxenus patagonicus*, at ~50°S, in Santa Cruz Prov., Argentina (Mauriès 1998). A different reference point, south of the Tropic of Capricorn, is needed, and to avoid choosing a nebulous spot in Argentina/Chile, we select the latitude of Buenos Aires/southern Uruguay, or the mouth of Rio de la Plata at ~39°S. Fewer orders/suborders are present in this continent than in North America, 10 as opposed to 15, and six plus Chordeumatida (restricted to Chile) occur south of Buenos Aires. Greater diversity exists to the north, but only three more orders occur there: Glomeridesmida, Siphonophorida, and Stemmiulida. Thus, the decrease in diversity with increasing latitude is less here, but South America does not extend as far into higher latitudes. While North America and Eurasia are bisected by the Arctic Circle (66° 33' 44"N), the Antarctic Circle, at the same southern latitude, lies south of South America and crosses the Antarctic Peninsula. Cape Horn, the southernmost point of land associated with South America, is at 55° 58' 47"S, only 6+° farther south than the US/Canadian border is north. The equivalent latitude in Alaska lies south of Kodiak I., north of Ketchikan, and passes through the southern Alaskan Peninsula, central Prince of Wales I., and Hyder. In Canada, it runs through Stewart and Dawson Creek, BC; Spirit River, Alberta; Beauval and La Ronge, Saskatchewan; Thompson, Manitoba; Fort Severn and southern Hudson Bay, Ontario; and uninhabited regions of northern Québec and Labrador. In Eurasia, this latitude passes through Edinburgh, Scotland; Copenhagen, Denmark; and Moscow, Omsk, northern Lake Baikal, the Sea of Okhotsk north of Sakhalin I., and the heart of Kamchatka, Russia.

In both northern land masses, millipeds have been recorded at or north of the southernmost latitude of South America. Chordeumatida (Caseyidae) have been taken at Fort Severn, Ontario (Causey 1952; Shelley 1988, 1993a), and in Alaska, the distributions of Julida, Chordeumatida, and Polydesmida, plus Polyxenida and associated higher taxa, spread well to the north on the Panhandle and Kodiak I. (Fig. 1-

5, 14, 24-26, 35-36, 41-42, 46). In Eurasia, the ranges of Glomerida, Polyzoniida, Julida, Chordeumatida, and Polydesmida, as well as Polyxenida and associated higher taxa (Fig. 1, 3, 5-6, 8-9, 11, 14-15, 20-21, 24-26, 35, 41, 43, 46, 49-50) also lie north of this latitude. While millipeds surely occur in the southern beech (*Nothofagus*) forests on southern South American islands, land mass limitations physically prohibit occurrences at higher latitudes in the Southern Hemisphere than the North. Consequently, the northernmost milliped records in the Northern Hemisphere are also the highest latitude ones in the world.

2) Sub-Saharan Africa. Africa terminates north of the southern extremities of South America, Australia, and New Zealand. The southernmost point, Cape Agulhas at 34°50'00"S, is only ~ 11° south of the Tropic of Capricorn and slightly north of Buenos Aires and Sydney; this latitude in the Northern Hemisphere is roughly that of Los Angeles, Atlanta, Rabat, Tripoli, Osaka, and Xuzhou, China (south of the Shangdong Peninsula). Thus, Africa does not extend far enough south to show a diminishing fauna with high latitudes, and this is indeed the case. Of the nine African orders south of the Equator, eight occur in the Republic of South Africa, and two, Polyzoniida and Siphonophorida (Fig. 20, 22) are restricted to the southern periphery of this nation. The only African order that is absent from this country is Stemmiulida (Fig. 45), which is tropical throughout its range and only approaches the Temperate Zone in Cuba and Mexico.

3) Australia/New Zealand. New Zealand and its associated subantarctic islands lie wholly south of the Tropic of Capricorn, so we likewise only consider the area of Australia south of this meridian. Including Polyxenida, nine ordinal taxa inhabit this region; all occur on the North Island of New Zealand, and eight, all but Siphonophorida, occur along the east/southeastern Australian coast from Cape York to near Adelaide. Additionally, Spirobolida and Cambalidea are absent from southwestern Western Australia, leaving only six orders in this corner of the continent. Tasmania and the South Island of New Zealand, located between 40° 44' 53"– 43° 38' 12"S and 40° 32' 47"– 46° 39' 47"S, respectively, harbor the same five orders, but only two chilognaths, Siphonophorida and Polydesmida, occupy the subantarctic islands of New Zealand, where to our knowledge, Polyxenida has not been reported. Furthermore, indigenous occurrence of Siphonophorida on Auckland I. is doubtful (Johns 1970) because the only individual encountered was a juvenile siphonophorid (Johns 1964), and Siphonorhinidae, not the nominate family, inhabit the North Island. Consequently, Polydesmida is probably the only indigenous order in the subantarctic islands, and we assume so for this discussion.

Thus in New Zealand, four orders (44% of the ordinal diversity) are lost between the North and South Islands, only 20 km (12.5 mi) apart, four more orders (80% of the South Island's diversity) are lost between the South and subantarctic islands, and eight orders (89% of the country's diversity) are lost between the North and subantarctic islands. This loss is not entirely attributable to increasing latitude/coldness because the subantarctic islands are minute and substantially segregated from the two major New Zealand islands. Australia and Tasmania are only ~ 360 km (225 mi) apart, and there are three fewer orders and 38% less ordinal diversity in the latter. Again, the much smaller size and insular nature of Tasmania surely are factors, but increasing latitude may be as well.

Old World Patterns

1) Himalayan Connections. Discounting the sizeable uninvestigated regions, Diplopoda, Chilognatha, Helminthomorpha, and Eugnatha (Fig. 1, 5, 14, 24) connect through the Himalayas and peninsular India to broadly expanded southeast Asian areas that we continue through the East Indies, eastern Australia, and New Zealand into Oceania. This primarily reflects the influence of Merocheta/Polydesmida (Fig. 46), but other orders show evidence of prior European-southeast Asian connections through what is now the Himalayas that reveal this to be a major congruency and pattern in the class.

Short, eastward projections of European ranges, extending for varying distances through northern Iran and along the southern shore of the Caspian Sea, are shown by Glomerida and Chordeumatida (Fig. 9, 11, 41, 43-44); the extension continues, and expands latitudinally, with Julida in central Asia (Fig. 26-27), requiring equivalent configurations on maps of higher taxa – Pentazonia, Oniscomorpha, and Juliformia (Fig. 6, 8, 25). Another central Asian expansion, congruent with those in Juliformia/Julida, exists in Nematophora, where the Caspian extension in Chordeumatida combines with isolated central Asian occurrences in this order and Callipodida (Fig. 35, 37, 41). Furthermore, the central Asian callipodidan area (Fig. 37, 40) is narrow on the west, extends along the southern Caspian Sea in Iran, and expands east-

ward through northern Afghanistan and Pakistan toward Kashmir and Xinjiang Prov., China. There are also point localities or narrow, detached, Himalayan faunal strips in Platydesmida, Polyzoniida, Siphonophorida, Siphonocryptida, Julida, and Chordeumatida that also appear on maps of higher taxa (Fig. 15, 17, 20, 22-23, 26, 35, 41, 44). Glomerida (Fig. 9, 12) also exhibit a detached, isolated central Asian remnant (Tajikistan, Kyrgyzstan) that is manifested in Oniscomorpha and Pentazonia (Fig. 6, 8). Dactyliform strips from southeast Asia, primarily in the Himalayas, are displayed by Glomerida, Sphaerotheriida, and Julida that are also manifested in maps of higher taxa (Fig. 6, 8-9, 13, 26). Finally, Platydesmida, and accordingly Colobognatha (Fig. 15, 17), display detached areas, remnants of prior European connections, along the southern Caspian Sea in northern Iran and southeastern Azerbaijan.

Consequently, a number of distributional stages testify to past and present faunal connections between latitudinally expanded distributions in Europe and southeast Asia. These are manifested through an existent faunal linkage (Merocheta/Polydesmida, Fig. 46, 50), attached relictual “fingers” of varying breadths pointing in both directions (Glomerida, Sphaerotheriida, Julida, Chordeumatida, and associated higher taxa, Fig. 6, 8-9, 13, 26-27, 35, 41), and detached, isolated remnants of prior faunal connections (Glomerida, Platydesmida, Polyzoniida, Siphonophorida, Siphonocryptida, Julida, Callipodida, Chordeumatida, and associated higher taxa, Fig. 6, 8-9, 12, 15, 17, 19, 20, 22-23, 26, 35, 37, 40-41, 44). Cumulatively, they constitute *prima facie* evidence of faunal connections between Europe and Asia via what are now the Himalayas, the Central Asian Republics, and the southern Caspian Sea region that antedate the Eocene to Oligocene collision of the Indian subcontinent with Asia. The maps show conclusively that a European-southeast Asian connection through what are now the Himalayas is a fundamental geographical pattern in the subclass Chilognatha. As shown by the recent discovery of Siphonocryptida (Korsós et al. 2009), the area of Kashmir, Nepal, Sikkim, and Bhutan is a logical place to search for “missing links” and additional forms of such orders as Glomerida and Callipodida.

2) Eastern European/Asia Minor Indentations. All five orders and associated higher taxa with large European ranges that do not connect to ones in Asia are congruent in exhibiting noticeable range indentations on the eastern margins in some or all of the following areas: the Black Sea, western Russia, the Caucasus Republics, Ukraine, and Turkey. Inadequate sampling, shown by the western dotted area in Fig. 1, only partly explains this gap because the rest of it has been substantially investigated. The pattern is strongest and most obvious in Glomerida/Oniscomorpha/Pentazonia and Polyzoniida/Colobognatha (Fig. 6, 8-9, 11, 15, 20-21), moderately expressed in Callipodida/Chordeumatida/Nematophora (Fig. 35, 37, 39, 41, 43), and weakest in Julida/Juliformia (Fig. 25-26). By itself, the indentation in Julida would not be notable, but with stronger expressions of the same feature in congruent taxa, its expression in Julida manifests a true geographical pattern applicable to Chilognatha as a whole.

3) Gondwanan Remnants. Small, isolated occurrences in certain “southern” areas are interpreted as relictual occurrences of Gondwanan faunas. They contrast markedly with larger occurrences in the same or similar regions that are continuous with northern areas. These remnants occur in four regions, three lying south of the Equator.

a) Chile. Variably long, strip-like occurrences of Polyzoniida, Epinannolenidea, Spirostreptidea, Chordeumatida, and associated higher taxa (Fig. 15, 20, 25, 29, 32-35, 41) in Chile south of the Tropic of Capricorn are detached from larger ordinal areas in South America and contrast with those of Polydesmida/Merocheta (Fig. 46-47), which are continuous through Chile, Argentina, and northern countries. The longest is that of Polyzoniida (Siphonotidae)/Colobognatha (Fig. 15, 20), and the smallest, in Spirostreptidea (Fig. 34), is enclosed within Epinannolenidea (Fig. 32-33) and does not influence the spirostreptidan and juliformian areas (Fig. 25, 29). The Chilean occurrence of Chordeumatida (Eudigonidae)/Nematophora (Fig. 35, 41), the only ordinal occurrence in South America, is congruent with those of Polyzoniida, Epinannolenidea, and Spirostreptidea. The Chilean areas of the last two appear to have been separated from those in the rest of South America by the rise of the Andean Cordillera and desertification of the Atacama region.

b) Republic of South Africa. Small or narrow remnants of Polyzoniida, Siphonophorida, and Epinannolenidea (Fig. 20, 22, 32), all south of the Tropic of Capricorn, constitute the only definitely indigenous occurrences of these taxa on both the African continent and the Afrotropical realm. The first two coalesce in Colobognatha, whose eastern corner extends northward to accommodate Siphonophorida (Fig. 15, 22), but Epinannolenidea are subsumed within Spirostreptidea, reversing the situation in Chile, and do not impact the ordinal map (Fig. 29, 34). A more extensive, non-relictual version of this southern

African Gondwanan phenomenon is that of Sphaerotheriida and associated higher taxa (Fig. 6, 8, 13), which straddle the Tropic of Capricorn and extend northward into Malawi and Mozambique; we expand this area eastward into the Indian Ocean to encompass Madagascar, Mauritius, and the Seychelles. The south/southeastern range of Spirobolida in Africa (Fig. 28) is congruent with the entire sphaerotheriidan area in that a westward-projection angles along the Indian Ocean in the Republic of South Africa that encloses the same faunal area in Mozambique, Malawi, and Indian Ocean islands. However, the northern spirobolidan area is continuous with a broad swath that spreads across central and western sub-Saharan Africa, which is congruent with the African range of Stemmiulida (Fig. 28, 35, 45).

c) Southern Peninsular India and Sri Lanka. Though north of the Equator, Glomeridesmida, Sphaerotheriida, Siphonophorida, Spirobolida, Chordeumatida, Stemmiulida, and associated higher taxa (Fig. 6, 7, 13, 15, 22, 28, 35, 41, 45) inhabit southern regions of the Indian subcontinent that are isolated from the rest of their ranges. The areas vary in size from Sri Lanka alone (Siphonophorida; Fig. 15, 22) to Sri Lanka plus southernmost India (Sphaerotheriida, Chordeumatida, Stemmiulida; Fig. 13, 35, 41, 45), to a broader area extending around the Republic of the Maldives in the Arabian Sea (Spirobolida; Fig. 28), to a narrow, coastal sliver extending northward along the Bengali Coast to ~ 320 km (200 mi) south of Kolkata (Glomeridesmida; Fig. 7). The sphaerotheriidan area is reflected in Oniscomorpha (Fig. 28), but the eastern margin of Pentazonia (Fig. 6) extends farther northward to accommodate Glomeridesmida.

d) Madagascar. Besides Sphaerotheriida's occurrence in Madagascar and Indian Ocean islands as part of its African area (Fig. 6, 8, 13), Chordeumatida/Nematophora (Fig. 35, 41) show unequivocal, relictual Gondwanan occurrence in Madagascar. The latter taxa are absent from both sub-Saharan Africa and neighboring Indian Ocean Islands, so the Madagascan fauna, which straddles the Tropic of Capricorn, is both isolated and insular. The most proximate occupied area is that north of the Equator in southern peninsular India and Sri Lanka, ~ 3,896 km (2,435 mi) to the northeast.

4) Europe-North Africa Connections. European faunal areas overlap varying areas of northern/Mediterranean Africa in Glomerida, Platydesmida, Julida, Chordeumatida, Polydesmida, and associated higher taxa (Fig. 9, 11, 17, 19, 26, 41, 43, 46, 49). The African areas include the Atlas Mts. and both the Mediterranean and northern Atlantic coasts of Morocco, the coastal 1/8-1/4 of Algeria, the northern 1/2-2/3 of Tunisia, and one or more records from the Benghazi region of Libya in Glomerida, Julida, and Polydesmida (Fig. 9, 11, 26, 46, 49). Chordeumatida (Fig. 41, 43), however, are absent from Libya and more peripheral in the other countries, and Platydesmida (Fig. 17, 19) occupy only the northern 1/3 of Tunisia and the adjoining corner of Algeria. Conversely, Callipodida (Fig. 37, 39) are proximate to Africa in southern Spain and Malta/Sicily but are unknown from northern Morocco and Tunisia, and while Polyzoniida (Fig. 20-21) occur widely in Europe, they too do not occupy North Africa and are absent from Malta, Sicily, Sardinia, and other western Mediterranean islands. The only southern/Gondwanan taxon occurring in Mediterranean Africa is Spirostreptidea (Fig. 29, 34) in the Atlas Mts. and coastal Morocco, and like Callipodida, it too does not span the Strait of Gibraltar and penetrate Spain. Taxa occurring on both continents are considered older than those on only one because the connections are likely Pangaeian, when "proto-Mediterranean Europe" adjoined this part of Africa. Callipodida and Spirostreptidea spread into Iberia and North Africa, respectively, after Laurasia and Gondwana had split, and neither could extend into the other continent. Alternatively, southern Spain has also been part of both Europe and North Africa since the Pliocene (~ 5 ma) because of repeated openings and closing of the Straits of Gibraltar and Guadalquivir, which allowed land organisms to interchange between the two continents (Hsü 1972).

5) Gondwanan/African taxa that are absent from Europe. The ordinal-group taxa, Sphaerotheriida, Siphonophorida, Spirobolida, Epinannolenidea, Spirostreptidea, and Stemmiulida (Fig. 13, 22, 28, 32, 34, 45) occupy varying parts of Africa but are absent from Europe. Sphaerotheriida, Siphonophorida, and Epinannolenidea (Fig. 13, 22, 32) are only in southern Africa and well removed from the Mediterranean, while Spirobolida and Stemmiulida (Fig. 28, 45) traverse the continent and the northern Afrotropical realm immediately south of the Sahara. Spirostreptidea cross this barrier and inhabit Morocco but no part of Europe, not even southernmost Spain. Spirostreptidea's occupation of Morocco therefore antedates xerification of the Saharan region that partitioned the Moroccan population from the rest of the suborder.

6) Eastern Mediterranean Dip. The European ranges of the orders Glomerida, Callipodida, Chordeumatida, Polydesmida, and associated higher taxa (Fig. 6, 8-9, 11, 35, 37, 39, 41, 43, 46, 49), all of which are continuous, are congruent in dipping southward for short distances (~ 488 km [305 mi]) along

the eastern Mediterranean coasts of Syria, Lebanon, and Israel, terminating in the northern Negev Desert. They range eastward for even shorter distances, 80 km (50 mi), into western Jordan and Syria east of the Golan Heights, and are so narrow in the east-west dimension that they cannot be accurately depicted on a world map. Substantial enlargement is necessary, as done by Shelley (2009) to depict localities of *Archispirostreptus syriacus* (Saussure, 1859) in Israel and the West Bank. Instead of European/Palaearctic, this spirostreptidean derives from the continuous, subordinal, Afrotropical area and represents a northward extension of the fauna in the southwestern Arabian Peninsula (Shelley 2009, Golovatch and Kime 2010).

7) Central Asian Peninsulas. To some degree they represent sampling artifacts, but the central Asian areas of Nematophora and Juliformia/Julida (Fig. 25-26, 35) show similarly configured, geographical “peninsulas” extending east-northeastward from the southern Caspian Sea that nearly unite with longitudinally oriented regions in northern Asia. Nematophora do not extend as far north in Europe or north/south in the Atlantic, nor do they range continuously eastward through Ukraine, Belarus, the Balkan states, and European Russia. However, the detached area in the Ural Mts. north of the Caspian Sea and western Kazakhstan suggests prior continuity, which may have been disrupted in the Pleistocene (Markova et al. 2008).

8) Southeast Asian Expansions into Indonesia/East Indies. This pattern is exemplified by Glomerida, Sphaerotheriida, and associated higher taxa (Fig. 6, 8-9, 13). Both may occur east of their present areas, for example on the Island of New Guinea, and the Asian and eastern Australian sphaerotheriid regions may connect. Their similarly configured distributions, including even the westward pointing, dactyliform, Himalayan projections, exemplify congruence resulting from different origins. The glomeridan projection is a remnant from eastward dispersal along the coastal southern Laurasian margin, while that of Sphaerotheriida represents spread from southeast Asia after accretion of the terranes. The other pentazonian order, Glomeridesmida (Fig. 7), comprises three southeast Asian populations including a new record from Sarawak (Appendix), so if these regions are ever joined, a smaller but similarly configured and congruent area to that of the oniscomorphs will result.

Platydesmida (Fig. 17) also expand east-west in southeastern Asia/Indonesia as do siphonophoridans (Fig. 22), which also encompass the Philippines. While siphonocryptidan regions (Fig. 23) are smaller and more remote, southeast Asia is still the area of highest concentration.

Among juliformians, this pattern is demonstrated by Spirobolida, Cambalidea, and Spirostreptidea (Fig. 28-30, 34); the Asian and eastern Australian areas connect in the first, and hence also Juliformia (Fig. 25). Southeast Asian expansions of Chordeumatida and Nematophora (Fig. 35, 41), including all of Papua New Guinea but excluding Cape York, Australia, are congruent with those of Spirostreptida and Cambalidea (Fig. 29-30).

9) Southeast Asia/East Indies/Eastern Australia Connections. As explained in the Introduction, we connect the East Indies and eastern Australian ranges when they include documented occurrences on both the Island of New Guinea and the Cape York Peninsula, Queensland. This connection exists in Spirobolida, Polydesmida, and all higher taxa (Fig. 1, 5, 14, 24-25, 28, 46), and indeed, is continuous with southeastern continental Asia. If Sphaerotheriida are ever documented from the Island of New Guinea and siphonophoridans and chordeumatidans, from Cape York, connections will exist in these orders and their higher taxa as well (Fig. 6, 8, 13, 15, 22, 35, 41). Discovery of Epinannolenidea on Cape York, however, would link Asia and Australia in Spirostreptida *s. l.* but not in the suborder itself (Fig. 29, 32). These taxa are already known from so close to the gap on which we base separate versus continuous areas that a few records from the hiatus will join them.

10) Restricted vs. widespread occurrences in Japan. Six chilognath orders inhabit the four main Japanese islands: from south to north, Kyûshû, Shikoku, Honshu, and Hokkaidô. Julida, Chordeumatida, and Polydesmida, and associated higher taxa (Fig. 1, 5, 14, 24-26, 35, 41, 46) occur throughout all of them, whereas Glomerida, Platydesmida, Polyzoniida, and associated higher taxa (Fig. 6, 8-9, 15, 17, 20) cover all of Kyûshû and Shikoku but extend northward only to midlength of Honshu, around Tokyo/Mt. Fuji. These southern occurrences are virtually identical, so 50% of the Japanese diversity is lost from Tokyo northward, including all of Hokkaido.

11) African/Afrotropical Patterns. The Gondwanan remnants in the Republic of South Africa – Polyzoniida, Siphonophorida, Epinannolenidea, and associated higher taxa (Fig. 15, 20, 22, 32) – have been mentioned as has the large, curious, western indentation in southern Africa in Spirobolida (Fig. 28).

Spirostreptidea, Polydesmida, and associated higher taxa (Fig. 25, 29, 34, 46) occupy all of sub-Saharan Africa and the continental part of the Afrotropical realm, occurring in both wet and dry biotopes. With such congruent distributions over all of sub-Saharan Africa, the narrow, transcontinental, northwest/southeastern band of Stemmiulida (Fig. 45) through the northern 1/3 of the area stands out in stark contrast. Though narrower and slanted more southeastward, this stemmiulidan band is remarkably congruent with the transcontinental spirobolidan occurrence (Fig. 28) in the same region. Spirobolida extend more due east to west and hence coincide more with the southern Saharan and northern Afrotropical borders, but their congruence is still close. Their transcontinental bands are equivalent in breadth and roughly as wide in west Africa as the breadth of the sub-Saharan/Afrotropical area from the Atlantic Coast of Senegal to central Mali and Niger.

12) Australia/New Zealand. We do not attempt to address Australian patterns because they are too likely to be overturned when extant samples from the gaping voids are studied (R. Mesibov, pers. comm. to RMS) and when more sampling takes place. The only region that has been reasonably well sampled is the eastern/southern periphery extending from Cape York to Adelaide, including nearly all of Victoria. The limited occurrences of Siphonophorida, Cambalidea, and associated higher taxa (Fig. 22, 29-30), and the segregated east/southeastern areas of Polyzoniida, Epinannolenidea, and Chordeumatida (Fig. 15, 20, 32, 35, 41) appear real. Equally interesting is the fact that Sphaerotheriida, Epinannolenidea, Chordeumatida, Polydesmida, and associated higher taxa (Fig. 6, 8, 13, 32, 41, 46) occupy both major islands of New Zealand while Polyzoniida, Siphonophorida, Spirobolida, and Cambalidea (Fig. 15, 20, 22, 28, 30) are restricted to the North Island, only ~ 20 km (12.5 mi) from the South Island at their closest points. Similarly, the gap between Sri Lanka and India is only ~ 61 km (38 mi), but Colobognatha and Siphonophorida (Fig. 15, 22) are restricted to the former.

13) East Indian Faunal "Lines." From present records, the hypothetical borders separating Asian and Australian faunas in Indonesia (Wallace's, Weber's, and Lydekker's "lines") hold little relevance for diplopods. Of the four exclusively Laurasian orders, only Glomerida and Platydesmida (Fig. 9, 17) expand into the East Indies/Indonesia, as Julida and Callipodida (Fig. 26, 37) terminate on the southeast Asian continent. In the north, Glomerida spread eastward to Weber's line, between Sulawesi and Halmahera, while the southern edge conforms roughly to Wallace's line. Platydesmida, however, extend to Wallace's line between Borneo and Sulawesi while the southern border passes between Sumatra/Java and corresponds to nothing. We would not expect these "lines" to be operative for the Gondwanan representatives, which were carried passively to southeast Asia by the terranes, and this is indeed the case. The only taxon conforming precisely to one of these hypothetical boundaries is Spirostreptidea, derived from Gondwana I, whose eastern border matches Lydekker's line completely. While future discoveries may alter East Indian taxon borders, hypotheses like these lines may not apply to low vagility organisms like millipeds, whose geographies are so dependent on geological events; conformity of Spirostreptidea may therefore be coincidence.

New World Patterns

1) North and South American Continuity. Glomeridesmida, Siphonophorida, Spirobolida, Epinannolenidea, Spirostreptidea, Stemmiulida, Polydesmida, and associated higher taxa (Fig. 6-7, 15, 22, 25, 28-29, 34-35, 45, 46-47) are continuous to varying degrees on the continental land mass between North/Central and South America. Connection is via the Central American land bridge; all are also on the apparent "stepping stones" of the Antillean Arc, a more figurative than literal connection in Epinannolenidea because of the ~ 1,360 km (850 mi) gap between Choctellidae, in the US, and Pseudonannolenidae, in Cuba. Their Caribbean presences, however, date back to the Cretaceous/Paleocene boundary, ~ 66 ma, when both the Greater and Lesser Antilles were joined to the "proto-Guianas/northeastern Brazilian" region of Gondwana II, where these taxa existed when this area rifted and split into the islands that their descendants inhabit today. Similarly, the occurrence of the polydesmidan family Paradoxosomatidae on Dominica is explainable by prior presence in this "proto-Antillean area" before it rifted from Gondwana II; we therefore believe the Dominican occurrence to be native instead of introduced, as suggested by Hoffman (1977c, 1999). As no Antillean diplopod taxon has been found natively on peninsular Florida or the Keys, even via rafting the short distance from Cuba, no evidence exists that the Antilles were ever an operative route into North America. Epinannolenideans have actively spread northward up the spine of Central America, but only for ~ 880 km (550 mi) to central Costa Rica. Colobognatha extend continuously from

South America to southwestern “mainland” BC (Fig. 16) through the Siphonophorida/Polyzoniida connection. The distributions of Glomeridesmida and Stemmiulida in the northern Neotropics (Fig. 7, 45) are congruent; the latter range farther northward in Mexico, and both may occur substantially farther south than we show, as central and westcentral Brazil have received little attention.

It is tempting to attribute this northward Central American occurrence to active dispersal after closure of the Panamanian Portal in the Pliocene, ~ 5 ma; this appears to be true for Epinannolenidea (Fig. 32-33) and the polydesmidan family Paradoxosomatidae (Hoffman 1977c, 1999), which have only spread to central Costa Rica. However, ~ 5 my is insufficient time to account for occurrences of Glomeridesmida, Siphonophorida, Spirobolida, Spirostreptidea, and Stemmiulida throughout Central America, partly (Glomeridesmida, Stemmiulida [Fig. 7, 45]) or completely (Siphonophorida, Spirobolida, Spirostreptidea [Fig. 22, 28, 34]) through “mainland” Mexico excluding the Yucatan (see below), and varying distances for the last three in the southwest/western US and through the eastern US into Canada (Spirobolida [fig. 28]). We believe these expansions date back to the Late Carboniferous, ~ 306 ma, when Euramerica collided with the “proto-South America” part of Gondwana I forming West Pangaea, the first step in assembling Pangaea itself. This merging enabled the independently evolving faunas of these land masses to intermingle for the first time. The Mexican part of Euramerica abutted against northern South America (present day Colombia and Venezuela), enabling forms of Siphonophorida, Spirobolida, and Spirostreptidea that were present there to cross directly into what is now Mexico and then disperse both northward, into the present southwest/western US, and southward into Central America as it developed and grew in succeeding paleogeological eras. When the Panamanian isthmus did close and form a continuous “land bridge” between South and North America, forms spreading northward from the former encountered ones of their own orders dispersing southward, which quickly filled Central American gaps. Evidently, Epinannolenidea had not arisen by the Carboniferous, or had not spread into northern South America, so it was not able to cross directly into Mexico, and subsequently the US and northern Central America, and hence does not inhabit these regions today. Its entire Central American occurrence represents northward, post-Pliocene dispersal, which only covers the southernmost part of this “land bridge.”

2) Central American Congruence among North American Taxa. Ranges of the first three are dissected, but Glomerida, Platydesmida, Cambalidea, Julida, Chordeumatida, and associated higher taxa (Fig. 8-9, 17-18, 26, 30-31, 41-42) extend southward for varying distances in Mexico/Central America, avoiding the Yucatan Peninsula (see below). Platydesmida and Chordeumatida (Fig. 17-18, 41-42) extend substantially farther, terminating abruptly at the Former Canal Zone; Glomerida and Julida (Fig. 8-9, 26) terminate equally abruptly but well to the north, in Guatemala/El Salvador, respectively, the general area also occupied by Siphoniulida (Fig. 23). Central America is truly a transitional area or “bridge” between the two large continents on either side. Glomeridesmida, Siphonophorida, Spirobolida, Spirostreptidea, Stemmiulida, Glomerida, Platydesmida, Julida, and Chordeumatida, intermingle in, for example, southern Mexico/Guatemala, but overall, the first five orders are dispersing northward, and the last four are moving south. Polydesmidans are also part of the mix, but their Central American occurrences are attributable to spread in both directions from both North and South America.

All South American taxa that extend northward to North America/US through Central America also inhabit the Antillean Arc with the exception of Epinannolenidea, which is primarily Antillean and only ranges to central Costa Rica. Conversely, no North American taxon spreads southward completely to South America, and those that go even part way do so via Central America, as the Antillean paleogeographic origin excludes them as a north-south pathway. No primarily North American taxon inhabits even part of the Antilles. As they have spread throughout peninsular Florida, Callipodida (Abacionidae) and Julida (Parajulidae) come close (Shelley 1984, 2000d, 2008; Hoffman 1999), but they are absent from even the Keys, much less Cuba, ~ 250 km (156 mi) to the south across the Straits of Florida, and the Bahamas, ~ 128 km (80 mi) to the east.

3) Presences and Absences in the Yucatan Peninsula, Mexico. Though highly vegetated, the Yucatan, especially the northern half, is dry with thin litter layers. It is suboptimal milliped habitat, in contrast to the thick, moist humus layers in the rain forests of Chiapas, Mexico, and Belize. Only five orders and associated higher taxa are known from the Yucatan – Siphonophorida, Spirobolida, Spirostreptidea, Stemmiulida, and Polydesmida (Fig. 15, 22, 24, 28-29, 34, 45, 46-47) (Chamberlin 1938, Loomis 1968, Causey 1977, Reddell 1981, Hoffman 1999, Bueno-Villegas 2001, Bueno-Villegas et al. 2004) – the last being widespread and the first four being primarily Gondwanan/South American. Glomeridesmida

and even the widespread Polyxenida (Fig. 3, 7) are unknown from the Yucatan. Chordeumatida (Fig. 41), another global order, and the three northern/Laurasian orders that range southward beyond its latitude – Glomerida, Platydesmida, Julida, and associated higher taxa (Fig. 8-9, 17-18, 26) – bypass this readily available peninsula, presumably for ecological reasons. Whereas Mexico/Central America is an area in which northern/Laurasian and southern/Gondwanan taxa intermingle, this does not seem to be true for the Yucatan; excepting Polydesmida, its fauna exclusively comprises forms with southern origins. Indeed, except for Glomeridesmida, all Gondwanan orders that have spread northward to this latitude inhabit the Yucatan, whereas none of the Laurasian orders that have spread southward to this latitude do so. We have no explanation as to why this wide, broadly attached peninsula is somehow suitable for southern, but not northern, taxa.

4) East-West Expansion in South America. As they are Gondwanan, Siphonophorida/Colobognatha and Spirostreptidea (Fig. 15, 22, 34) occupy narrower areas in North America than South America, where they blanket the breadth of the continent. This pattern suggests that expansion into at least the US is relatively recent and that insufficient time has elapsed for greater longitudinal dispersal. While Polydesmida (Fig. 46-48) have spread across the breadths of both continents, aridification has dissected its western North American area into 13 units, seven being point localities. The continuous area, from the Central Plains eastward, is narrower than that in South America, which we expand westward to encompass Cocos I. and the Juan Fernandez and Galapagos archipelagos in the Pacific. Polydesmida also occur throughout the Antilles, including the Bahamas (Shelley 2003c, 2007c).

5) East-West Segregation in the US/North America. Glomerida, Platydesmida, Polyzoniida, and associated higher taxa (Fig. 6, 8-10, 15, 17-18, 20) occupy widely separated areas in east/southeastern and western North America, primarily in the US (Gardner 1975, Shelley 1998b, Hoffman 1999, Shelley et al. 2005). The eastern faunas lie generally east of the Central Plains, while the western ones are west of the crest of the Sierra Nevada and Cascade Mts.; lacunas vary from ~ 2,248 – 2,976 km (1,405 – 1,860 mi) in Platydesmida and Glomerida, respectively. All three orders inhabit Pacific Coastal regions of California, particularly around San Francisco and Monterey Bays, that extend varying distances north and south. These are relatively old, declining taxa that occurred (sub)continuously across “proto-North America” before the Cretaceous embayment, ~ 94 ma, extending between what are now the Arctic Ocean and the Gulf of Mexico (Smith et al. 1981, 1994), split the land mass and segregated the faunas. Eastern and western areas of Spirobolida, Cambalidea, Callipodida, and associated higher taxa (Fig. 28-31, 37-38) are widely segregated in the north but join in the south, either in Texas or northern Mexico (Coahuila, Chihuahua). As spirobolidans and callipodidans are relatively mobile millipedes, the southern continuities probably represent post-embayment dispersals that have closed the lacunae in these taxa. Cambalideans seem less mobile and have taken refuge in caves in parts of the hiati (Causey 1964b, 1971; Shear 1969; Shelley 1979; Hoffman 1999), which are cool and moist in contrast to the hot, dry deserts and prairies.

A smaller east-west disjunction exists in Polydesmida that is negligible when one considers the point locality in the Chisos Mts., Big Bend National Park, west Texas; excluding this record, the distance between the continuous eastern area and the closest non-point western area is only around 320 km (200 mi). While the embayment surely affected Polydesmida as well, and subsequent dispersal of eastern forms closed some of the gap, desertification in the southwestern US and adjacent Mexico appears more significant. By reducing forested areas to (sub)boreal remnants at high elevations on inselberg summits, desertification created uninhabitable gaps in the formerly continuous fauna that remain today.

6) Detached areas in the northwestern US interior. This pattern is shown by Platydesmida, Polyzoniida, Cambalidea, and associated higher taxa (Fig. 15, 17-18, 20, 29-31), while the rest of their western distributions are west of the crest of the Cascades or along the Pacific Coasts of Oregon and Washington. All three orders occur in the northern Rocky Mts. of northern Idaho; sites are not superimposed, and Polyzoniida are known only from a point locality (Shelley et al. 2010) while Platydesmida and Cambalidea occupy small areas that nip the corners of Oregon and/or Washington (Causey 1954; Chamberlin and Hoffman 1958; Gardner 1975; Shelley 1979, 1981, 1996a, 1998b, 2010b; Hoffman 1999; Shelley et al. 2005). Spirobolida (Fig. 28) exhibit the same coastal pattern, extending northward from Mexico to southern Washington, but do not have a detached population in Idaho or anywhere west of the Continental Divide.

7) Northward Extensions along the Pacific Coast of North America. The moist, forested, coastal environments, some true rainforests, that extend from south of Big Sur, Monterey Co., California,

to Yakutat, Alaska, constitute ideal diplopod habitat. Consequently, it is no surprise that six orders range farther north along the Pacific coast than inland. This pattern manifests in Diplopoda itself and is exhibited by Polyzoniida, Siphonophorida, Julida, Chordeumatida, Polydesmida, and associated higher taxa (Fig. 1-2, 5, 14-16, 20, 22, 24-26, 35-36, 41-42, 46-48), necessitating enlarged mappings of this corner of New World ranges. Conversely, the northernmost platydesmidan records (Fig. 17-18) are inland in Idaho and southeastern Washington. Platydesmida, Siphonophorida, Julida, Spirobolida, Cambalidea, Polydesmida, and associated higher taxa arise in coastal Mexico, either in the northwest corner, from Tijuana-Ensenada (Platydesmida, Cambalidea, Polydesmida; Fig. 17-18, 29-31, 46-47), or varying distances down the Baja California Peninsula (Siphonophorida, Julida, Spirobolida; Fig. 15, 22, 25-26, 28). Chordeumatida (Fig. 41-42) originates in the Santa Monica Mts., Los Angeles, California, and the coastal point locality of Polyzoniida (Fig. 20), in southern Monterey Co. (Shelley 1998b), is farther north. Distributions are narrower to both the south and north; they are primarily confined to coastal canyons south of Los Angeles, expand inland/eastward up the western slopes of the Sierra Nevada and Cascade Mts. from central California to southern BC, and narrow to west of the Coast Range and then the coast itself in northern BC and Alaska. While Polyzoniida arise in a moderately detached point locality, Siphonophorida (Fig. 22) terminate in such, the type and only known locality of *I. plenipes*, the only representative of Siphonorhinidae in the Western Hemisphere (Cook and Loomis 1928; Chamberlin and Hoffman 1958; Shelley 1996c, d, 2002a; Hoffman 1999; Marek and Bond 2006). The ordinal area to the south, exclusively Siphonophoridae, is subcontinuous through Central America and the Antilles to the west-to-east sloping terminus at the Tropic of Capricorn in Brazil.

8) Northward Extensions in Eastern North America. Because eastern North America, from the Central Plains eastward, is more moist and continuously forested than the west, fewer taxa extend noticeably farther north in the east in general or along the Atlantic Coast. As shown by Callipodida (Fig. 37-38), they range essentially as far northward around the Great Lakes as on the coast. Spirobolida (Fig. 28) is an exception, curving noticeably northward through the Great Lakes into Ontario and Québec from its nadir in west Texas and New Mexico. Though less dramatic, Cambalidea (Fig. 29-31) demonstrate the same pattern, curving northward to northern Virginia and western Pennsylvania from its southernmost level in the Texas Panhandle. From eastern North Dakota, Polydesmida (Fig. 46-47) turn abruptly eastward through Minnesota and Wisconsin then curve northward through Ontario and Québec, reaching their northern limit at James Bay.

9) Southward Extensions in Eastern South America. In South America, the southern borders of the contiguous ranges of Siphonophorida, Spirobolida, Epinannolenidea, Spirostreptidea, and associated higher taxa (Fig. 15, 22, 25, 28-29, 32-34) extend farther south on the Atlantic Coast than on the Pacific. Colobognatha and Siphonophorida (Fig. 15, 22) slant southeastward from central Peru to São Paulo/Santos, Brazil, while Juliformia, Spirobolida, Epinannolenidea, and Spirostreptidea (Fig. 25, 28-29, 32-34) drop precipitously southward east of the Andean Cordillera and the Lake Titicaca region of Peru/Bolivia to termini in Argentina south of Buenos Aires. While differing in lengths and breadths, these steep southward extensions are congruent, and Epinannolenidea and Spirostreptidea occupy detached areas of undetermined lengths in central Chile.

SÃO TOMÉ and PRINCIPE

Before it is lost, a major, international effort is underway to document baseline biodiversity on the Gulf of Guinea Islands, Africa (Bioko and Annobón, Equatorial Guinea; and São Tomé and Príncipe [ST and P]), which lie in the Atlantic off the coasts of Nigeria, Cameroon, and Gabon. Bioko is a continental island with a diverse diplopod fauna, whereas the others are classical oceanic islands; ST and P also constitute an independent nation of the same name, one of the world's smallest, that is situated between Bioko and Annobón. Spelda (1993) summarized the Diplopoda of São Tomé, reporting three indigenous spirostreptideans (Spirostreptidae) and one introduced spirobolidan and polydesmidan each. As they inhabit similar environments, R.C. Drewes (CASC) hand sampled macroscopic millipeds in addition to his herpetology specialty for six weeks on ST and P in early 2010, but the samples, sent to RMS for preliminary determinations, consisted of only one order, family, and genus – Spirostreptida: Spirostreptidea: Spirostreptidae: *Globanus* Attems, 1914 (see Appendix). *Globanus integer* and *marginescaber*, both by Karsch (1884), the former subsequently reported by Attems (1914b), Krabbe (1982), and Spelda (1993),

were apparently recovered along with one new species. No other order or family of macroscopic millipedes that logically might be indigenous to these islands and, indeed, inhabit Bioko – Spirobolida (Pachybolidae), Stemmiulida (Stemmiulidae), Polydesmida (Chelodesmidae [Prepodesminae], Cryptodesmidae [Pterodesminae], Gomphodesmidae, Oxydesmidae, Paradoxosomatidae) – was found. A drop in diversity with greater distance from the African continent was expected, but not a total loss except for *Globanus*! Large bodied polydesmidans are conspicuous, ornate, and/or brightly colored, so an experienced field biologist, even a non-specialist, could hardly miss seeing them if they were present, and not a single individual was encountered. These findings suggest that *Globanus* “species swarms” may inhabit ST and P, that the islands were devoid of macroscopic diplopods and form(s) of *Globanus* somehow reached them, plausibly by rafting from the African continent (Measey et al. 2007), encountered a plethora of vacant niches, and radiated explosively to fill them in the absence of competition. Species swarms in Glomerida (Glomeridae) and Julida (Blaniulidae, Julidae) have been documented on other Atlantic islands (Madeira, Canaries, Cape Verdes) (Enghoff 1982, 1983, 1993b, c, 2002; Golovatch 1987a; Read 1989; Vicente and Enghoff 1999; Golovatch and Enghoff 2003; Arndt et al. 2008), and while further work on ST and P is necessary, *Globanus* “species swarms,” if confirmed, will constitute the first examples of such in Spirostreptidea. For more information, readers are directed to the following two blogs that are appropriately titled, “Island Biodiversity Race” (<http://islandbiodiversityrace.wildlifedirect.org/>; <http://www.calacademy.org/medialibrary/blogs/gulfofguinea/?p=181>).

THE SPECIAL CASE OF SOUTHEAST ASIA

Tables 3-5 list occupied continents and biogeographical realms for each ordinal taxon and vice versa. What they do not show *per se*, but do in combination with the maps, is that only one region in the world harbors all 16 diplopod orders and higher taxa, southeast Asia. This small corner of the world’s largest land mass – southeastern China, the Indochina and Malay peninsulas, and Sumatra (Fig. 1, 5, 14; encircled by triangles) – is **the only place** where all 16 orders and higher taxa occur indigenously; the only taxon treated here that is absent is Epinannolenidea. This situation developed in June 2010, when Mauriès et al. (2010) described *Eostemmiulus caecus*, the first southeast Asian stemmiulidan, from southern coastal Vietnam, and we report *Stemmiulus* (Appendix) from north of Hanoi. Siphoniulida and Siphonocryptida, the two rarest orders, occur essentially sympatrically in western Sumatra, the former at Lake Maninjau (0° 23’S, 100° 12’E) and the latter on Mt. Singgalang (0° 23’S, 100° 19’E), and were described by Pocock (1894) from material collected on the 1888 Netherlands East Indies expedition led by Prof. Max Carl Wilhelm Weber, University of Amsterdam. This corner of Asia, ~ 3,240 km (2,025 mi) long and 1,568 km (980 mi) wide, is **the key area worldwide for Diplopoda**, and elucidating the origin of its fauna assumes paramount importance because of potential insights into Diplopoda as a whole. First, however, we summarize salient aspects of tectonic drift pertaining to the region.

As tectonic plates drift atop the Earth’s mantle of magma, they converge periodically to form supercontinents. Seven, dating back ~ 3.6 billion years (by), are known, the most recent being Pangaea, which began forming ~ 250-240 ma, during the Permian (Paleozoic), and rifted into two progeny continents, Laurasia and Gondwana II, ~ 152 ma during the Jurassic (Mesozoic). Around 1.1 ba, in the Precambrian period (Neoproterozoic Era), long before metazoan life evolved, the supercontinent Rodinia formed, surviving until ~ 750 ma. Approximately 600 ma, still during the Precambrian, the short-lived supercontinent Pannotia formed, lasting until ~ 540 ma, in the early Cambrian, when it rifted into Gondwana I and Baltica, Laurentia, and Siberia. Avalonia, an arc shaped terrane that rifted from the “proto-South America/Africa” region of Gondwana I in the early Ordovician (~ 480 ma), coalesced with Baltica ~ 30 my later (~ 450 ma) in the late Ordovician, and ~ 10 my later (~ 440 ma), in the early Silurian, the two fused with Laurentia to form “Euramerica.” Beginning in the late Silurian, ~ 35 my later (~ 415 ma), terranes began rifting sequentially from the “proto-Australia” region of Gondwana I, drifting northwards, and accreting first to Siberia+Kazakhstan and then to Siberia+Kazakhstan+Euramerica beginning in the Carboniferous. These terranes form present-day north and south China, Tibet, Indochina, the Malay Peninsula, and Indonesia east to Borneo; the accretion process continued with Pangaea after it formed in the Permian and lasted into the Jurassic, when Pangaea itself began rifting. Metcalf (1998), Hall (1998, 2009), and <http://www-personal.une.edu.au/~imetcalf2/Palaeogeog.html> depict this complex, “jig-saw puzzle”

arrangement, and though derived from Gondwana I, “proto-southeast Asia” was thus in the northern or Laurasian part of Pangaea and subsequently in Laurasia itself.

The 17 ordinal-group taxa occupying the defined sector of southeast Asia are classified thusly:

- entirely northern/Laurasian – Glomerida, Platydesmida, Julida, Callipodida (Fig. 9, 17, 26, 37);
- entirely southern/Gondwanan – Sphaerotheriida (Fig. 13);
- entirely southern/Gondwanan excepting Central America/Mexico and primarily the southern US/North America – Glomeridesmida, Siphonophorida, Spirobolida, Spirostreptidea, Stemmiulida (Fig. 7, 22, 28, 34, 45) (see below);
- mixed Gondwanan/Laurasian but with limited or no occurrence in Africa and/or South America – Polyzoniida, Cambalidea, Chordeumatida (Fig. 20, 30, 41);
- mixed Gondwanan/Laurasian and widespread in both areas – Polyxenida, Polydesmida (Fig. 3, 46); globally relictual – Siphonocryptida, Siphoniulida (Fig. 23).

In item 3, US/North American and/or Mexican/Central American occurrences of widespread South American taxa is explicable primarily by spread onto the “proto-Mexico” part of Euramerica in the late Carboniferous after formation of Western Pangaea (Table 6, Fig. 57), supplemented by recent, northward dispersal from South to Central America after closure of the Panamanian Portal in the Pliocene, ~ 5 ma. However, the question arises as to how southeast Asian occurrences of the primarily Gondwanan taxa in items 2 and 3 can be explained when they are otherwise absent from former Laurasian territory and when no land bridge, like Central America, connected them? The answer is that these taxa had to be fully differentiated and present on the terranes that formed their southeast Asian areas when the latter rifted from Gondwana I. Spirostreptideans are larger and more mobile/vagile than representatives of most southern orders, and their southeast Asian and Indian faunas (Fig. 34) have merged since the latter collided with Asia in the Eocene-Miocene (~ 50 ma). We interpret the western bulge in the southeast Asian spirobolidan area (Fig. 28) as evidence of westward dispersal by this fauna that has not yet merged with the Indian. We reject the alternative, post-collision southeastward dispersal of Indian spirostreptideans, because of insufficient time for such to account for continuous distribution throughout continental southeast Asia, and if even possible, it could not explain occurrences on such islands as Taiwan, the Philippines, and Indonesia, which have been separated from continental Asia by water most of the intervening time. Consequently, we believe that Spirostreptidea were also present on the terranes when they rifted to eventually form southeast Asia. Glomeridesmida, Sphaerotheriida, Siphonophorida, Spirobolida, Spirostreptidea, and Stemmiulida (Fig. 7, 22, 28, 34, 45) must therefore also have originated and fully evolved **before** the terranes that formed their present southeast Asian areas rifted from Gondwana I and began drifting toward Siberia+Kazakhstan+Euramerica, and later Pangaea itself.

After arising, these taxa spread variously through Gondwana I so as to be in territories that became their present areas, but the common denominator is their occurrences in present-day southeast Asia and hence the precursor Gondwana I terranes that formed this area. We agree with Wesener and VandenSpiegel (2009) in that Sphaerotheriida existed in the present areas before the break-up of “Gondwana” and probably arose in “east-Gondwana”; however, this statement implies origin on Gondwana II when it had to be Gondwana I and probably on or near the terranes themselves, and hence far from “proto-South America” that the ordinal dispersion never reached. These authors’ timing of Gondwanan break-up from the mid-Jurassic to mid-Cretaceous, ~ 180-90 ma, pertains to Gondwana II, which illustrates the confusion surrounding the name, “Gondwana.” Sphaerotheriida surely existed on Gondwana II, but they had to arise much earlier to be on the terranes that formed southeast Asia when they rifted beginning in the late Silurian, ~ 415 ma, some 235 my before the dates they cite. Furthermore, while Sphaerotheriida’s age is unknown, it must substantially antedate formation of the terranes to allow time for fully evolved, modern forms to differentiate and spread so as to occupy both Gondwana I and the terranes prior to rifting. According to Metcalf (1998) and Hall (1998, 2009), rifting of the “proto-east/southeast Asia” terranes continued into the Early Devonian, ~ 400 ma, and accretions to Siberia+Kazakhstan/“proto-Laurasia” lasted from the Late Permian (~ 255 ma) to the Early Jurassic (~ 195 ma). We do not know which terrane(s) sphaerotheriidans occupied nor how much of the present area (Fig. 13) represents dispersal subsequent to accretion(s). Assuming minimal dispersal, it seems reasonable to postulate occurrence on early terranes, perhaps that forming South China (Fig. 57), and that the order originated a substantial

time earlier. Not only do Sphaerotheriida have to be at least this old to account for their occurrence on the “proto-southeast Asia” terranes, but so do the other southern/Gondwanan taxa that occupy southeast Asia today and were also present on the terranes – Glomeridesmida, Siphonophorida, Spirobolida, Spirostreptidea, Stemmiulida – and their relictual distributions indicate even greater age for Siphonocryptida and Siphoniulida (Fig. 23). This reasoning, in turn, impacts the age of Diplopoda itself, which necessarily sufficiently antedates subordinate taxa to allow time for the major dichotomies – Penicillata/Chilognatha, Pentazonia/Helminthomorpha, Colobognatha/Eugnatha, and Juliformia/Nematophora/Merocheta – to take place.

While the terranes carrying these taxa were drifting toward Siberia+Kazakhstan+Euramerica, the exclusively Laurasian orders – Glomerida, Platydesmida, Julida, and Callipodida (Fig. 9, 17-21, 26-27, 37-40) – had to be arising and differentiating on Avalonia/Baltica/Euramerica/Siberia+Kazakhstan, to be fully evolved and dispersed at least partly southeastward when the terranes accreted and “proto-southeast Asia” became available for colonization by northern forms. Consistent with their apparently greater ages, as evidenced by higher fragmentation, Glomerida and Platydesmida (Fig. 9, 17) probably reached southeast Asia first and could thus spread onto “proto-Indonesian islands” (Sumatra, Java, Borneo, and Sulawesi for Glomerida; Sumatra and Borneo for Platydesmida) while they were still connected by land to the “proto-Malay Peninsula.” Julida and Callipodida (Fig. 26, 37) arrived later, after the islands were separated by water and unavailable, so the former could not spread beyond present-day Peninsular Malaysia. Consequently, southeast Asia was a “mixing zone” where primarily southern/Gondwanan taxa, imported on the terranes, intermingled with ones that dispersed east/southeastward from distant Laurasian source areas, just as Central America became such in the Pliocene for North and South American taxa dispersing in opposite directions.

ORIGIN OF THE DIPLOPODA

Diplopoda constitute a global arthropod class that ranges from north of the Arctic Circle to southern “mainland” Argentina and subantarctic New Zealand (Table 2). Nineteen ordinal-group taxa are considered here, four of which – Glomerida, Platydesmida, Julida, Callipodida (Fig. 9, 17, 26, 37) – occur exclusively in former Laurasian territory, and seven – Glomeridesmida, Sphaerotheriida, Siphonophorida, Spirobolida, Epinannolenidea, Spirostreptidea, Stemmiulida (Fig. 7, 13, 22, 28, 32, 34, 45) – are Gondwanan except for occupation of parts of Central America/Mexico/US by all but Sphaerotheriida. Other ordinal-group taxa are either widespread (Polyxenida, Polyzoniida, Chordeumatida, Polydesmida [Fig. 3, 20, 41, 46]), restricted and rare (Siphonocryptida, Siphoniulida [Fig. 23]), or miscellaneous (Cambalidea [Fig. 30]). Chilognath taxa are divided between former Laurasian and Gondwanan territories. Merocheta are present in both; one order each of Pentazonia, Colobognatha, Juliformia, and Nematophora is restricted to the former, while two pentazonians, three juliformians, and one order each of Colobognatha and Nematophora are primarily Gondwanan. Neither Gondwana nor Laurasia contained an entire major taxon; all the “multi-ordinal” chilognath groups – Pentazonia, Helminthomorpha, Colobognatha, Eugnatha, Juliformia, and Nematophora – are represented in both areas. Consequently, ancestral stock of these six taxa somehow became established on both Gondwana I and the northern micro-continents, which were thousands of km apart in the Iapetus and Panthalassic Oceans after their formations during breakup of Pannotia. Hypotheses attempting to explain the origin of Diplopoda must therefore account for this fact, northern/Laurasian impression fossils dating back to the late Silurian, and the simultaneous presences

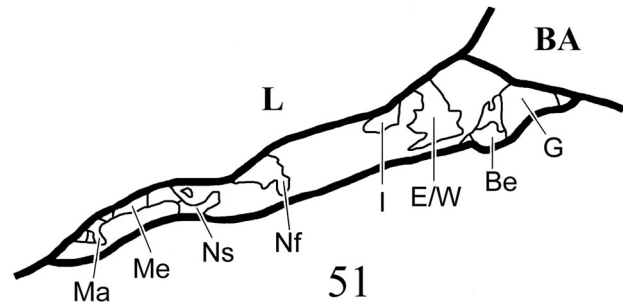


Figure 51. The Avalonia terrane of Gondwana I as it was positioned on Euramerica, after accretions to Baltica and then Laurentia (reproduction of public domain map on <http://en.wikipedia.org/wiki/File:AVALONIA.jpg>). We postulate that the Diplopoda arose on this terrane in the mid-Cambrian, ~ 524 ma, before it rifted from Gondwana I in the Early Ordovician, ~ 480 ma, so the actual site of origin is one of the areas thereon. BA, Baltica; Be, Belgium; E/W, England/Wales; G, Germany; I, Ireland; L, Laurentia; Ma, Massachusetts; Me, Maine; Nf, Newfoundland; NS, Nova Scotia.

of fully evolved Gondwanan orders on Asian terranes *before* they began rifting, also in the late Silurian. Few scenarios can meet such stringent requirements; if a single hypothesis based on documented paleogeographic tectonic events can be formulated, it is probably operative.

In the early Ordovician, ~ 480 ma and 65 my before “proto-southeast Asia” terranes began splitting from Gondwana I in the late Silurian, a rifting took place from its “proto-South America/African” margin (<http://www.scotese.com/earth.htm>; <http://www.uwgb.edu/dutchs/platetec/plhist94.htm#550my>). Avalonia (Fig. 51) detached, drifted northward, and collided with Baltica 30 my later in the late-Ordovician, ~ 450 ma; 10 my later, in the early Silurian (~ 440 ma), the two merged with Laurentia to form “Euramerica.” Today, Avalonia comprises most of England/Wales, southern Ireland, scattered areas in continental Europe, the Avalon peninsula of Newfoundland (hence the name), and parts of Nova Scotia, New Brunswick, and coastal New England.

Gray and Shear (1992), influenced by the earliest body-fossil of a fully evolved helminthomorph, *Archidesmus macnioli* Peach, 1887, in late-Silurian (430-415 ma) deposits in Scotland (Chia and Liu 1959; Hoffman 1963, 1969b; Kraus 1978; Almond 1985; Retallack and Feakes 1987; Robison 1990; Shear and Kukalová-Peck 1990; Engghoff 1990; Shear 1991, 1992, 1994, 1997, 1999; Johnson et al. 1994; Shear et al. 1996, 2009b; Edgecombe 1998; Kime and Golovatch 2000; Retallack 2001; MacNaughton et al. 2002; Wilson 2003, 2006; Wilson and Anderson 2004; Wilson and Hannibal 2005; Shear and Edgecombe 2010; Golovatch and Kime 2010), postulated early Silurian, perhaps even Ordovician, origin for the Diplopoda. Wilson (2006) presented a stratocladogram to superordinal level with the class, represented by Penicillata (and by extension the sister-group Chilognatha), arising about 2/3 of the way through the Ordovician, ~ 460 ma, making Diplopoda the oldest extant class of terrestrial Arthropoda and the second oldest overall after the arachnid order Trigonotarbida, which became extinct around the Permian (Gray and Shear 1992). However, an even earlier origin for Diplopoda is suggested if the track-like fossils in Cambro-Ordovician/Ordovician sediments (Retallack and Feakes 1987, Johnson et al. 1994, Shear 1997, Retallack 2001, MacNaughton et al. 2002, Wilson 2003, Shear et al. 2009b, Shear and Edgecombe 2010) are indeed attributable to penicillates. As non-calcified, soft-bodied organisms, penicillates are unlikely to fossilize, so the oldest are in Cretaceous amber (Nguyen Duy-Jacquemin and Azar 2004, Shear and Edgecombe 2010); however, earlier origin of this subclass is evident. Cladistic principles mandate simultaneous origins of sister-group taxa like Penicillata and Chilognatha, so if the former originated in the Cambro-Ordovician/Ordovician, so did the latter. Minimally, late Silurian origin of Penicillata is appropriate based on the sister-group relationship with Arthropleurida (Kraus and Brauckmann 2003, Wilson and Anderson 2004, Kraus 2005). According to Shear and Edgecombe (2010), no Paleozoic fossil can be confidently assigned to an extant order; most Mesozoic/Cenozoic amber ones can, but not all extant orders are represented in amber. These, and reasonable inferences from the same, show that all supra-ordinal diplopod taxa had evolved by at least the late-Carboniferous, ~ 306 ma, and had existed for ~ 50 my by the time Pangaea began assembling in the Permian. However, the biogeographic information herein, coupled with geologically dated tectonic movements, enable superior, more precise timings. Based on details in the preceding paragraphs, we believe only one scenario exists that plausibly explains the origin and early evolution of the Diplopoda and modern biogeography, bearing in mind the necessity for evolutionary events to precede tangible fossil evidence

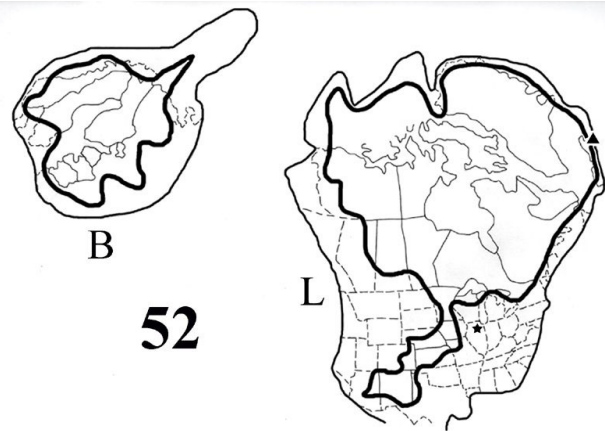


Figure 52. The microcontinents Baltica (left) and Laurentia (right) in the Cambro-Ordovician periods showing approximate positions of modern European countries, Canadian provinces, and US states, adapted from the website of Ron Blakey, Geology Dept., Northern Arizona University, Flagstaff, Arizona, USA (<http://jan.ucc.nau.edu/~rcb7/RCB.html>). The heavy, solid, interior line represents the coast lines with the area inside being above sea level of the Iapetus Ocean; the lighter, solid, outside line is the margins of the continental shelves. Triangle, future location of the Scottish helminthomorph Silurian fossil (uncertain order), *Archidesmus macnioli*; Star, future location of the non-spinose oniscomorph pentazonian Carboniferous fossil in Illinois, USA.

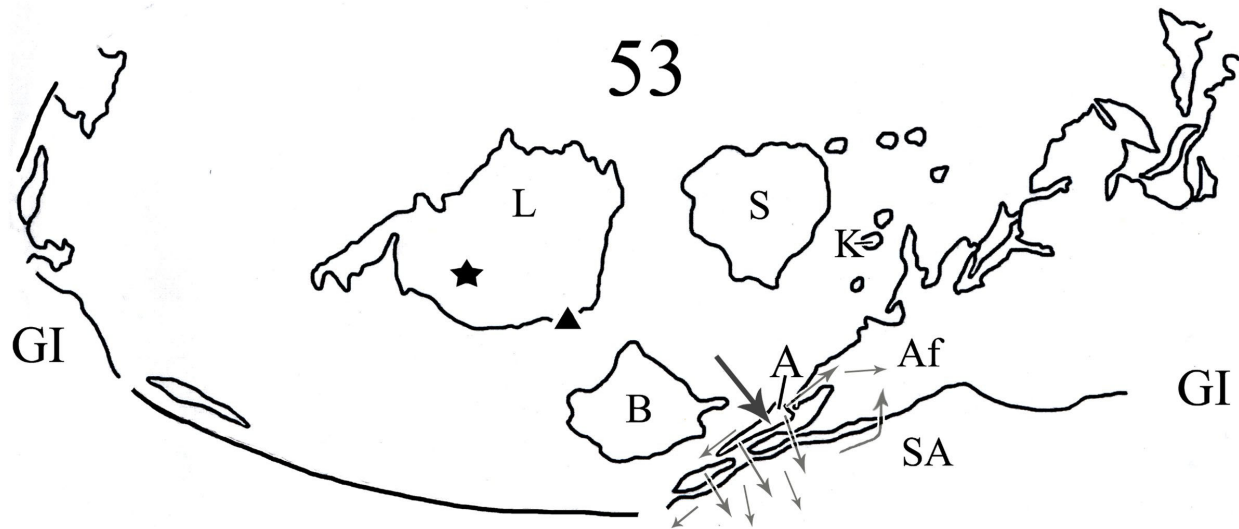


Figure 53. Land areas in the Mid-Cambrian Period, Paleozoic Era, adapted from the website of Ron Blakey, Geology Dept., Northern Arizona University, Flagstaff, Arizona, USA (<http://jan.ucc.nau.edu/~rcb7/RCB.html>), symbols as in Fig. 52. The bold arrow represents emergence of the original ancestor from the Iapetus Ocean onto the Avalonia terrane that is still attached to Gondwana I around 524 ma, and the short, lighter arrows show initial dispersals through Avalonia and onto Gondwana I proper; at this time, other land masses and the rest of Gondwana I were devoid of diplopods. A, Avalonia terrane; Af, “proto-Africa” region of Gondwana I; B, Baltica; GI, Gondwana I; K, Kazakhstan; L, Laurentia; S, Siberia; SA, “proto-South America” region of Gondwana I.

and inferred dispersals. We do not know exactly when the great event happened or the precursor organism involved, but we do know where, because only one ancient land area’s movements cover all the essential requirements.

An Evolutionary Hypothesis. Sometime in the mid-late Cambrian and roughly simultaneous with the invasion of land by higher plants, a multilegged ancestral arthropod, perhaps a somewhat amphibious product of the Cambrian Explosion or a Remipedia-like organism, crawled out of the Iapetus Ocean onto the still-attached Avalonia terrane of Gondwana I and began the evolutionary process that led to the class Diplopoda (Fig. 53). Pisani (2009) suggested that Diplopoda arose ~ 524 ma in the mid-Cambrian, and we accept this date rather than burden the literature with further speculation on timing. Leaving the comforts of aqueous environments for the harsh dryness and fluctuating temperatures of land was a drastic step, so perhaps the driving force was the need to avoid predation (McNamara and Selden 1993). We can only speculate on these matters. However, to allow time for the magnitude of evolution and diversification that was necessary and for ancestral forms to become present on the proper ancient land areas at the proper times, we believe that Diplopoda may have even predated the origin of vascular plants. With the immense totality of these early requirements, origin **no later than the Late Cambrian** seems mandated; anytime later, even at the Cambro-Ordovician boundary, could not produce **both** the diverse totality of the modern fauna **and** its biogeography, as documented herein.

When the ancestor emerged, it found an empty earth; all (sub)surface niches were vacant and available for occupation. As terrestrial plants began to flourish, feeding preferences evolved into those of today. A period of rapid diversification and speciation resulted, as Diplopoda radiated explosively to fill these niches. Wilson (2006) postulated such, and our study supports her hypothesis but at an earlier time, mid-late Cambrian rather than Cambro-Ordovician/early Ordovician. Concurrent with diversification, the ancestral forms dispersed beyond the Avalonia terrane onto Gondwana I itself (Fig. 53), such that when rifting occurred, ~ 480 ma in the early Ordovician, the major dichotomies – Penicillata/Chilognatha, Pentazonia/Helminthomorpha, Colobognatha/Eugnatha, and Juliformia/Nematophora/Merocheta – had taken place along with formations of the orders Polyzoniida, Siphonocryptida, Siphoniulida, and Chordeumatida, plus Polyxenida and Polydesmida, the only components of Penicillata and Merocheta. Ancestral forms of all these taxa spread into adjoining areas of Gondwana I while some remained on, or returned to, Avalonia, such that populations were partitioned when rifting occurred (Fig. 54). Represent-

tatives were left on Gondwana I while others were passively carried by the drifting Avalonia terrane first to Baltica, 30 my later in the late Ordovician (Fig. 55), and then to Euramerica, 10 my later in the early Silurian (Fig. 56). Though not simultaneous, this early vicariance placed ancestral stock of these taxa on both northern and southern land masses; those on the former derived the Northern Hemisphere Paleozoic impression fossils, while those on the latter diversified and spread through Gondwana I, with representatives of Glomeridesmida, Sphaerotheriida, Siphonophorida, Spirobolida, Spirostreptidea, and Stemmiulida, plus Polyxenida and Polydesmida, reaching the “proto-southeast Asia” terranes to be passively transported to Siberia+Kazakhstan when rifting began in the late Silurian. Consequently, two separate diplopod faunas were evolving simultaneously, effectively in “parallel,” between the early Ordovician (~ 480 ma) and the late Carboniferous (~ 306 ma), when Euramerica collided with Gondwana I forming Western Pangaea (Fig. 57). Major lineages, however, had evolved before Avalonia rifted, as Penicillata/Polyxenida, Chilognatha, Pentazonia, Limacomorpha, Oniscomorpha, Helminthomorpha, Colobognatha, Polyzoniida, Siphonocryptida, Eugnatha, Juliformia, Spirostreptida s. l./Cambalidea, Nematophora, Chordeumatida, Merocheta/Polydesmida, and Siphoniulida are either extant or fossilized in both northern and southern regions today. Based on present biogeography and documented paleogeographic events and timings, this is the **only** scenario that leads to ancestral forms in both Laurasian and Gondwanan territories and, ultimately, today’s biogeography. Ecological and morphological objections to this scenario must be reconciled to yield to documented facts and dates of tectonics and geography; presumed rates of anatomical evolution and ecological adaptation must be adjusted to conform to the only paleogeographic possibility. Molecular clock analyses may shed light on the timings of these events, but the late-Silurian (~ 423 ma) origin of Diplopoda derived by such techniques (Pisani et al. 2004) is inoperative because it accounts for the earliest impression fossils but not for the evolution that had to precede them or for today’s biogeography.

Separated from those on Gondwana I, the pentazonians that were transported to Baltica/Laurentia evolved in a different direction. Consequently, Glomerida are strictly Laurasian while Sphaerotheriida and Glomeridesmida are strictly Gondwanan, aside from occurrences of all but Sphaerotheriida in Mexico/Central America. Thus, the non-spinose, volvating (?oniscomorph) pentazonian fossil from the late Carboniferous (~ 306 ma) of Illinois, USA (Fig. 1, 5, 8-9, 52-57; star) (Hannibal and Feldman 1981, Wesener and VandenSpiegel 2009) can only represent a glomeridan or an extinct order, not a sphaerotheriidan. Fig. 9 and 13 show that Glomerida is the only extant pentazonian in North America and that Sphaerotheriida do not occur at or near the site of this fossil, or indeed, anywhere in the Western Hemisphere.

As our model predicts, fewer ordinal taxa are limited to Laurasian territory than Gondwanan, excluding secondary dispersion in Central America. The ancestral stock that dispersed into Gondwana I from Avalonia prior to the latter’s rifting had vastly more area available and a greater number of ecological niches in which to diversify than did those remaining on Avalonia until collision with Baltica ~ 30 my later; furthermore, Gondwanan forms had substantially more time to adapt and diverge. During drifting, the forms on Avalonia were confined to this terrane with its limited area and niches, which were probably fully occupied before rifting began. Little to no ecological selection pressure existed on Avalonia as it drifted, until collisions opened the new lands of first Baltica and then Laurentia for colonization. Consecutive waves of diversification may have followed, but even so, Baltica and Laurentia were small in comparison to Gondwana I and must have contained substantially fewer niches. Consequently, while Avalonia was in transit, Gondwanan forms had a ~ 30 my head start on diversification in addition to far more niches driving the process. With a vastly greater area available for exploration, vastly more niches to fuel diversification, and ~ 30 million more years of time to advance, greater diversification in Gondwana than Laurasia, as reflected by more ordinal taxa, is what would be predicted, and this is indeed the case.

Collisions forming “proto-Laurasia” occurred sequentially, and areas thus became available for colonization in a step-wise fashion; by contrast, Gondwana I was immediately and totally available to the ancestral stock that dispersed onto it from Avalonia. As it constitutes these lands today, Avalonia alone accounts for some presences in England/Wales and other lands that it formed; it collided first with Baltica, in the late Ordovician ~ 450 ma, opening up continental Scandinavia, Poland, and northern European Russia to colonization. Baltica+Avalonia then merged with Laurentia in the early Silurian, ~ 440 ma, forming Euramerica, which opened up Scotland and accounts for the late Silurian, *A. macnioli*, fossil. Formation of Euramerica also allowed ancestral forms into present-day Greenland, Canada west to the Rockies, and the US from the Appalachians to the Great Basin and south to western Texas. The next

event was the collision, ~ 164 my later, of Euramerica with Gondwana in the late Carboniferous, ~ 306 ma, which formed the western half of Pangaea, allowed the Gondwanan and Euramerican faunas to mix, and ended their independent but “parallel” evolutions (Fig. 57). By the Early Triassic, ~ 250 ma, Kazakhstan/Siberia/North China, the last being the first terrane from the “proto-Australia” region of Gondwana I, had joined with the Euramerica part of Pangaea, opening up northern China and central Asia to colonization. Glomerida, Julida, Callipodida, and Chordeumatida (Fig. 9, 12, 26, 27, 37, 40-41, 44) probably spread into central Asia then, as evidenced by “peninsulas” or isolated faunal “islands” there today. By the early Jurassic, ~ 195 ma, Gondwana I terranes forming southcentral and southeast Asia had accreted to Pangaea, thereby opening these areas to the above taxa. Along with Platydesmida (Fig. 17), they spread along the then southern margin of Asia (now the Himalayas after collision with the Indian subcontinent) to the modern Indochina Peninsula, leaving remnants there that are sympatric with fingers/lobes or detached strips of Sphaerotheriida, Siphonophorida, Siphonocryptida, and Spirobolida (Fig. 13, 22, 23, 28) that derive from Gondwana I and represent either presence on that particular terrane or westward dispersal from southeast Asia after later terranes accreted. Additionally in the early Jurassic, Cimmeria (the sliver of land that rifted from northern Gondwana I and formed proto-Turkey, Iran, Afghanistan, Pakistan, etc.) was approaching “proto-Laurasia,” providing a broader west-to-east highway after accretion, though it surely contained Gondwanan diplopods. Consequently, the dispersal of Euramerican forms into southeast Asia had completed by the mid-, if not early-, Jurassic, and they have since intermingled with Gondwanans that were originally transported by the terranes.

Consistent with our evolutionary hypothesis, we believe that some of the Himalayan/Central Asian distributional fingers and remnants of prior faunal linkages date back to the Carboniferous, when the Laurasian part of Pangaea was being assembled by amalgamations of Euramerica, Siberia, Kazakhstan, and rifted Gondwana I terranes, forming, sequentially, north China, south China, Tibet, and southeast Asia proper. Dispersions, primarily from Europe to southeast Asia, occurred along the relatively flat, level, southern margin of the “proto-Asia” part of Laurasia such that after collision with the Indian subcontinent generated the Himalayan orogeny, populations became isolated in valleys and lower elevations where their descendants occur today. The four exclusively northern orders – Glomerida, Platydesmida, Julida, Callipodida – spread from Avalonia/Baltica/Euramerica to southeast Asia, whereas such primarily Gondwanan taxa as Sphaerotheriida and Siphonophorida dispersed from east to west for comparatively short distances along the same pathway, but they have not arrived in Europe, or even the Caspian region, probably because of insufficient time and the now rugged terrain they have to traverse. Consequently, the Himalayan orogeny stopped, or at least interrupted, this natural dispersal pattern on what was, in effect, a well-worn pathway that had been “blazed” by European taxa dispersing in the opposite direction. Gondwanan taxa could not begin spreading into Laurasia until the terranes carrying them accreted to form “proto-southeast Asia”; conversely, the Euramerican taxa had a ~ 150 my head start in dispersing and spread into and across southeastern Asia as accreted terranes became available for colonization. The widespread chilognath taxa – Polyzoniida, Chordeumatida, Polydesmida – with ancestral stock in both Euramerica and Gondwana I, converged on this southern “proto-Asia” margin from both directions, but again, Euramerican forms had substantial lead time and hence dominate this intervening area. Central Asian remnants or continuations of European areas are shown by three of the four exclusively Laurasian taxa – Glomerida, Julida, and Callipodida (Fig. 8-9, 26-27, 37, 39-40) – plus the widespread Chordeumatida (Fig. 41, 44), and the fourth order, Platydesmida (Fig. 17), exhibits a detached area along the southern Caspian Sea. Detached Himalayan areas are exhibited by two Laurasian (Platydesmida and Julida [Fig. 17, 26]), two Gondwanan (Siphonophorida and Siphonocryptida [Fig. 22-23]), and two widespread (Polyzoniida and Chordeumatida [Fig. 20, 41, 44]) orders; and westward pointing fingers/lobes are displayed by the Laurasian Glomerida (Fig. 9) plus the Gondwanan Sphaerotheriida and Spirobolida (Fig. 13, 28). All four Laurasian orders inhabit southeast Asia as well as one or more places in between, but no Gondwanan/southeast Asia taxon (Glomeridesmida, Sphaerotheriida, Siphonophorida, Spirobolida, Spirostreptidea, Stemmiulida [Fig. 7, 13, 28, 34, 45]) occurs anywhere near Europe today.

TAXON ORIGINS AND AGES

Millipeds are low vagility organisms that cannot run, fly, swim, or float. Passive vicariance is operative, as in the “short-term,” they are largely at the mercy of natural forces aside from serendipitous rafting events as may explain cambalidean occurrence in the Hawaiian Islands (Fig. 29-30). However, millipeds are not sessile or immobile. Over thousands, millions, and hundreds of millions of years, generations of millipeds can slowly and steadily spread great distances, as evidenced by the expansive occurrences of the taxa we document. In North America in the past 10,000 years, after retreat of the Tioga maximum of the Wisconsin Glacial Episode, Julida (Parajulidae), Chordeumatida (Caseyidae), Polydesmida (Polydesmidae), and associated higher taxa (Fig. 1, 5, 14, 24-26, 41, 46-47) have spread northward, repopulated the Canadian Shield, and reached at least the latitude of southern Hudson Bay, Ontario, from refugia no closer than the Ohio River region of the US, a distance of ~ 2,000 km (1,250 mi). As noted by Golovatch and Kime (2010), distributions “are rarely static and can be visualized in dynamics like hundreds of ‘ameboid’ patterns, superimposed in the same geographical area, expanding or contracting at different rates.” Depending on the taxon, ancient patterns are masked to varying degrees by subsequent dispersals and extinctions, and one must attempt to distinguish the latter. Smaller scale factors – desertification, climatic changes, availability of calcium to impregnate exoskeletons (Kime and Golovatch 2000), etc. – also impact biogeography as do inherent genetic plasticity and environmental adaptability. Present distributions derive from a host of factors many of which cannot be inferred, leaving overall biogeographic patterns and known timings of paleogeological events as the only measures to apply to questions of ages and dates of origins. High degrees of fragmentation are consistent with age, as sufficient time has elapsed for extinctions to generate range discontinuities; conversely, continuous distributions indicate relative youth and insufficient time for extinctions to manifest themselves geographically. In this section, we discuss each taxon subordinate to Diplopoda to infer where and approximately when it likely originated, summarizing insight from the fossil record, encapsulating that derived from geographic information, and arriving at conclusions on approximate ages. As superordinal relationships in Eugnatha are unresolved – Enghoff’s (1983) cladogram showed an unresolved trichotomy whereas later analyses conflictly resolved Merocheta as sister to both Juliformia (Enghoff 2000) and Nematophora (Sierwald et al. 2003) – we assume that all three taxa arose simultaneously, at the Colobognatha/Eugnatha dichotomy, as did Polydesmida, the only component of Merocheta. First, we review salient aspects of paleogeography and tectonics.

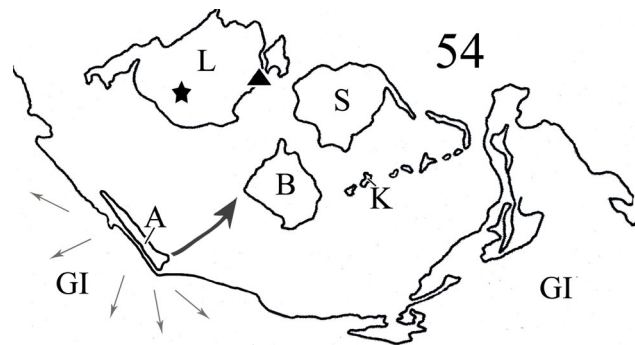


Figure 54. Land areas in the Early Ordovician Period, Paleozoic Era, ~ 480 ma, when the Avalonia terrane rifted from Gondwana I, thereby partitioning ancestral stock between them, and began drifting toward Baltica and passively transporting the forms thereon northward. Adapted from the website of Ron Blakey, Geology Dept., Northern Arizona University, Flagstaff, Arizona, USA (<http://jan.ucc.nau.edu/~rcb7/RCB.html>). The long, curved, bold arrow shows the drift direction of Avalonia, which also partly rotated during the process. The short, lighter arrows represent continued dispersals on Gondwana I; other land masses at this time were devoid of diplopods. Abbreviations and symbols as in Fig. 52-53.

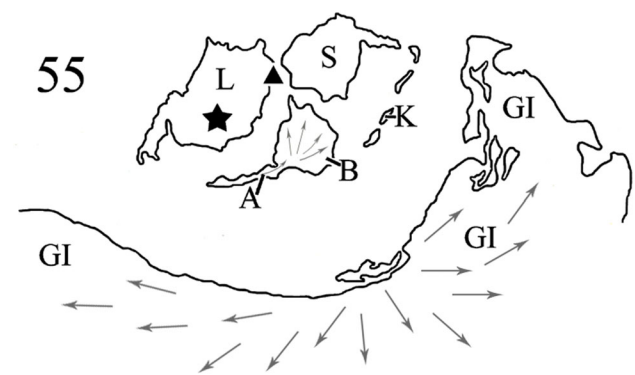


Figure 55. Land areas in the Late Ordovician Period, Paleozoic Era, ~ 450 ma, after Avalonia merged with Baltica, adapted from the website of Ron Blakey, Geology Dept., Northern Arizona University, Flagstaff, Arizona, USA (<http://jan.ucc.nau.edu/~rcb7/RCB.html>). The arrows show dispersals from Avalonia onto Baltica and continued dispersals on Gondwana I; other land masses at this time were devoid of diplopods. Abbreviations and symbols as in Fig. 52-53.

The first rifting of Pangaea, which included most but not all of the existing land masses, occurred in the Late Permian, ~ 255 ma, when Cimmeria split from southern Pangaea (“proto-Gondwana II”) and began drifting toward “proto-Laurasia,” while “proto-southeast Asia” terranes were still drifting northward. Rifting of Pangaea into Laurasia and Gondwana II began in the Late-Jurassic, ~ 152 ma, and Gondwana II split around the Jurassic/Cretaceous boundary, ~ 120 ma, into South America, Africa, Madagascar/India, and Antarctica/Australia/New Zealand. Madagascar/India separated in the mid-Cretaceous, ~ 100 ma, and while India moved toward Laurasia, eventually colliding in the Eocene, ~ 50 ma, and pushing up the Himalayas, Madagascar became locked to the African plate where it has remained. Simultaneously, New Zealand, New Caledonia, and the rest of “Zealandia” separated from Australia/Antarctica and began moving eastward, and Australia/New Guinea and South America rifted from Antarctica around the Eocene/Oligocene boundary, ~ 23 ma, allowing complete oceanic circulation around the latter and consequent cooling and glaciation. To the north, Laurasia began rifting in the Paleocene/Oligocene, when North America/Greenland split from Eurasia. Many more movements and driftings took place in the past and continue today, for example in the Rift Valley, Africa. However, these are the major movements pertaining to the totality of modern diplopod biogeography as depicted herein.

Subclass Penicillata/Order Polyxenida (Fig. 3) – *Fossils*: The oldest definite fossils are from Cretaceous Lebanese amber (Nguyen Duy-Jacquemin and Azar 2004, Shear and Edgecombe 2010). Cockerell (1917) reported *Phryssonotus* (as *Polyxenus*) (Synxenidae) from slightly younger, lower Cretaceous Burmese amber, and true *Polyxenus* is also known from Eocene and Oligocene Baltic amber (Condé 1954b). If it is the true sister-group to Arthropleurida (Kraus and Brauckmann 2003), Penicillata/Polyxenida had to evolve around the same time, in the late Silurian. Wilson (2006) suggested origin “about 2/3 of the way through the Ordovician” ***Geography*:** The widespread occurrences of Penicillata/Polyxenida on all continents except Asia, doubtlessly a sampling artifact, indicate that the subclass and order were fully evolved prior to the splitting of Avalonia from Gondwana I, so as to be partitioned between them. Because of their small sizes and light bodies that lack hardened, calcified exoskeletons, polyxenidans are more susceptible to dispersal by wind and to transportation by birds and other animals (Tajovsky et al. 2001, Golovatch and Kime 2010) than are chilognaths, so distributions may to some degree reflect zoochory. ***Conclusion*:** Both Penicillata and Polyxenida had to arise in the mid-Cambrian (~ 524 ma) soon after the basic class traits evolved so as to occupy both Avalonia and Gondwana I when the former rifted. While they can disperse by other means, neither this possibility nor dispersal through Pangaea after it formed seemingly accounts for their entire ranges. Earliest possible origins, and fully evolved presences on both Avalonia and Gondwana I prior to rifting, are mandated. Even the possibility of extinct penicillate orders does not alter this requirement for either Polyxenida or Penicillata.

Subclass Chilognatha (Fig. 5) – *Fossils*: All Paleozoic fossils are chilognaths, the oldest being from the late Silurian of Scotland, ~ 410 my. ***Geography*:** Their panglobal geography shows that Chilognatha were fully evolved and present on both Avalonia and Gondwana I when they split in the early Ordovician, so as to be partitioned between them. Earlier origin is therefore mandated. ***Conclusion*:** Cladistic principles mandate simultaneous origins of sister-group taxa, so Chilognatha arose simultaneously with Penicillata in the mid-Cambrian (~ 524 ma).

Infraclass Pentazonia (Fig. 6) – *Fossils*: Body fossils of the extinct oniscomorph order Amarynilyspedida exist from the late Silurian, ~ 410 ma (Hoffman 1963, 1969a, c; Enghoff 1990; Gray and Shear 1992; Shear 1999; Wilson and Anderson 2004, Shear and Edgecombe 2010). ***Geography*:** Though discontinuous, Pentazonia’s occurrence on all continents requires their fully evolved presences on both Avalonia and Gondwana I when they split in the early Ordovician, ~ 480 ma, and, consequently, earlier origin. ***Conclusion*:** Wilson (2006) postulated origin “about 1/2 of the way through the Silurian,” ~ 433 ma, but geography (Fig. 6) proves that Pentazonia arose much earlier. We believe it arose in the mid-Cambrian (~ 520 ma) soon after the Penicillata/Chilognatha dichotomy to be fully evolved and present on both Avalonia and Gondwana I when the former rifted.

Superorder Limacomorpha (Fig. 7) – *Fossils*: A limacomorph, “glomeridesmidan-like” fossil was retrieved from early Carboniferous, ~ 350 my, Scottish deposits (Shear 1994). According to Enghoff (1990),

the hypothetical ancestral chilognathan, which lived no later than the early Silurian, ~ 440 ma, resembled Glomeridesmida (Shear 1999, Kime and Golovatch 2000). *Geography*: Today, Limacomorpha are exclusively Gondwanan; their occurrence in Mexico (except the Yucatan)/Central America represents secondary spread from a South American source area. *Conclusion*: The Scottish fossil demonstrates past presence in Laurasian territory, and this plus its present Gondwanan biogeography mandates early Pentazonian dichotomy into Limacomorpha+Oniscomorpha. Limacomorpha had to be fully evolved and present on both Avalonia and Gondwana I prior to rifting, which in turn mandates earlier origin. We therefore postulate Late Cambrian origin (~ 500 ma) and at least one early dichotomy, with ancestral stock transferred to Baltica by Avalonia generating the extinct order.

Order Glomeridesmida (Fig. 7) – *Fossils*: No definite glomeridesmidan fossils, or published inferences from other fossil evidence are available. *Geography*: Glomeridesmida are entirely Gondwanan with secondary northward dispersal in the Western Hemisphere. Occurrences in Indochina, Sumatra/Java, and the Island of Borneo show that it was fully evolved and present on the Gondwana I terranes that formed these areas prior to their rifting in the late Silurian (~ 420 ma); hence Glomeridesmida had to arise earlier. *Conclusion*: Beyond its stated objective, Enghoff's (1990) study and the Scottish fossil show that one or more extinct limacomorph orders existed and that Glomeridesmida should be regarded as the **lone surviving limacomorph component**, not the only one that ever existed. Their absence from Laurasian territory, other than northward dispersal in the Americas, indicates that Glomeridesmida were neither present on Gondwana I nor partitioned when Avalonia split in the early Ordovician. Glomeridesmida thus arose on Gondwana I **after** this rifting but well before the southeast Asia terranes split, to allow sufficient time to disperse into "proto-South America and India" as well as onto the "proto-southeast Asia" terranes to be partitioned by their riftings. We therefore postulate mid-Ordovician origin on Gondwana I, ~ 480 ma, perhaps in the general area of the terranes.

Superorder Oniscomorpha (Fig. 8) – *Fossils*: Body fossils (the extinct order Amynilyspedida) exist in early Silurian deposits of Scotland, ~ 410 ma (Hoffman 1963, 1969a, c; Hannibal and Feldman 1981; Gray and Shear 1992; Shear 1999; Wilson and Anderson 2004, Shear and Edgecombe 2010). *Geography*: Oniscomorpha are present in both former Laurasian and Gondwanan territory. *Conclusion*: With representatives on all continents and major land masses except South America, Oniscomorpha had to be fully evolved and present on both Avalonia and Gondwana I when the former rifted, ~ 480 ma. They were thus passively transported to Baltica, and subsequently Euramerica, with early forms in these regions yielding the Scottish Silurian fossils. As sister-group to Limacomorpha, Oniscomorpha had to also arise in the Late Cambrian, ~ 500 ma.

Order Glomerida (Fig. 9) – *Fossils*: No definite glomeridan fossils exist, but if the order is sister to Amynilyspedida, represented in Scottish Silurian deposits, then it had to arise prior to 410 ma. *Geography*: Like Platydesmida, Julida, and Callipodida (Fig. 17, 26, 37), Glomerida are exclusively Laurasian. The order's fragmented, discontinuous distribution suggests greater age than Julida, whose range is continuous. Geography also shows that the oniscomorph Carboniferous fossil from Illinois, USA, is either a glomeridan or an extinct order, not a sphaerotheriidan, which does not inhabit the Western Hemisphere. *Conclusion*: Being absent from the Southern Hemisphere, Glomerida had to arise either on Avalonia **after** it rifted from Gondwana I in the early Ordovician, on Baltica after collision with Avalonia, or on Laurentia after collision with Baltica+Avalonia. Consequently, their age is ≤ 480 my. We believe the most plausible scenario is mid-Ordovician origin on Baltica after it merged with Avalonia, ~ 448 ma, when the latter's inhabitants were released into a new environment with a host of vacant, available niches to fuel diversification. A substantially greater area and number of niches became available 10 my later, when Avalonia+Baltica merged with Laurentia, and we believe they drove diversification of the North American taxa, *Onomeris*, *Trichomeris*, and *Glomeroides*. During and after this event, the Baltica/European forms dispersed east/southeastward into central Asia, where a remnant exists today, and eventually to southeastern Asia and the area of present-day Asian islands before they were isolated by water. Glomerida and the anatomically similar Sphaerotheriida, passively transported here by the Gondwana I terranes, intermingle in this area. Glomerida were established in North America well before the Cretaceous embayment, which segregated the eastern and western faunas on this continent.

Order Sphaerotheriida (Fig. 13) – *Fossils*: No definite fossils or published inferences from fossil evidence are available. *Geography*: Though absent from South America, Sphaerotheriida are exclusively Gondwanan; their substantial occurrence in Indochina and southeast Asia indicate fully evolved presences on Gondwana I terranes that began rifting in the late Silurian, ~ 415 ma, and formed this area. Earlier Gondwanan origin is therefore mandated, both to fully evolve and for sufficient time to disperse to “proto-Africa, Madagascar, India, and Australia/New Zealand.” *Conclusion*: We postulate mid-Ordovician origin, ~ 475-470 ma and concur with Wesener and VandenSpiegel (2009) that it was in east-Gondwana I, probably near the “proto-southeast Asia” terranes. Sphaerotheriida’s absence from South America indicates that the site was distant from that part of Gondwana I.

Infraclass Helminthomorpha (Fig. 14) – *Fossils*: Most Paleozoic body fossils are helminthomorphs, the oldest being *Archidesmus macnioli* Peach, 1887, from the late Silurian, ~ 410 ma, of Scotland. Wilson (2006) postulated slightly earlier origin, “about 1/4 of the way through the Silurian,” ~ 430 ma. *Geography*: Helminthomorpha occur widely through nearly all of the range of Diplopoda and Chilognatha; fully evolved ancestral forms thus had to exist on both Avalonia and Gondwana I when the former rifted in the early Ordovician, ~ 480 ma, and the taxon thus had to originate earlier. *Conclusion*: Wilson (2006) postulated origin “about 1/4 of the way through the Silurian,” ~ 430 ma, much too late to comply with time constraints. As with Pentazonia, we believe that Helminthomorpha arose in the mid-Cambrian (~ 520 ma) soon after the Penicillata/Chilognatha dichotomy to be fully evolved and present on both Avalonia and Gondwana I when they rifted.

Subterclass Colobognatha (Fig. 15) – *Fossils*: Dzik (1981) considered the Carboniferous fossil, *Pleurojulus*, as the oldest known colobognath; however Wilson and Hannibal (2005) presented strong evidence for a sister-group relationship. From the latter authors’ illustrations and its general facies, the only feature excluding *Pleurojulus* from modern Colobognatha, in our view, are the ocellaria; exoskeletal features match along with apparent concordance in gonopod positions. While the head is not clear, it seems consistent with the triangular/pyriform shape of many modern colobognaths, and *Pleurojulus* also possessed the middorsal suture that persists in Siphonocryptida. *Geography*: From its widespread, but somewhat spotty, occurrence on all continents and major land masses, Colobognatha had to be present on both Avalonia and Gondwana I prior to the former’s rifting in the early Ordovician, ~ 480 ma. Thus it had to originate even earlier. *Conclusion*: Wilson (2006) postulated a late-Silurian origin for Colobognatha, about 7/8 of the way through the period, or ~ 412 ma. It had to be substantially earlier, however, and we postulate mid-Cambrian origin, ~ 518 ma, after major class traits had evolved and the Penicillata/Chilognatha and Pentazonia/Helminthomorpha dichotomies had taken place.

Order Platydesmida (Fig. 17) – *Fossils*: Mundel (1981) noted in passing a Carboniferous platydesmidan fossil (also cited by Hannibal (2000)), but it has not been described, studied, or illustrated. Despite the discussion by Hannibal (2000) and its resemblance to *A. macnicoli* (Wilson and Anderson 2004), *Hexecontasoma* appears to us to be a platydesmidan of the long, slender, “andrognathid type” (Shelley et al. 2005, Shear and Marek 2009, Shelley 2010b). *Geography*: Like Glomerida, Julida, and Callipodida (Fig. 9, 26, 37), Platydesmida are exclusively Laurasian and their fragmented, discontinuous distributions suggest greater age than that of Julida, which occurs subcontinuously throughout its range. *Conclusion*: Being absent from the Southern Hemisphere, Platydesmida had to arise **after** Avalonia rifted from Gondwana I in the early Ordovician, ~ 480 ma, either on Avalonia itself, on Baltica after collision with Avalonia, or on Laurentia after collision with Baltica+Avalonia. Consequently, its age is ≤ 480 my. We believe mid-Ordovician origin, ~ 448 ma, on Baltica after collision with Avalonia, is most plausible, after the latter’s occupants were suddenly presented with a new environment and a host of vacant niches to drive diversification. A substantially greater area and number/variety of niches became available around 10 ma later, when Avalonia+Baltica merged with Laurentia forming Euramerica. Platydesmida were established in North America well before the Cretaceous embayment, which segregated the eastern and western faunas on this continent.

Order Polyzoiiida (Fig. 20) – *Fossils*: The only known polyzoiiidan fossil is from Oligocene Baltic amber, ~ 30 ma (Hoffman 1969c). *Geography*: While predominantly Laurasian, Polyzoiiida's occurrences on all continents indicate that fully evolved ancestral forms had to be present on both Avalonia and Gondwana I when the former rifted in the early Ordovician, ~ 480 ma, so the taxon had to originate even earlier. *Conclusion*: We postulate origin in the Late Cambrian, ~ 512-510 ma, after major class traits had evolved, after Penicillata/Chilognatha, Pentazonia/Helminthomorpha, Colobognatha/Eugnatha, and Juliformia/Nematophora/Merocheta dichotomies had taken place, and after Polydesmida, Siphoniulida, and Siphonocryptida had evolved.

Order Siphonophorida (Fig. 22) – *Fossils*: No Paleozoic siphonophoridan fossils are known, but they are frequent occupants of Oligocene-Miocene Dominican amber, around 40-30 ma (Shear 1981, Santiago-Blay and Poiner 1992, Shelley 1996c, plus unpublished samples examined by RMS). *Geography*: Siphonophorida are primarily Gondwanan; Laurasian occurrences are in the Himalayas and southeast Asia, which derive from Gondwana I terranes, and North/Central America, representing secondary dispersal from a South American source area. *Conclusion*: Its exclusive presence in former Gondwanan territory except for the last area shows that Siphonophorida evolved on Gondwana I **after** Avalonia split in the early Ordovician, ~ 480 ma. As it was present on the southeast Asia terranes that began rifting in the late Silurian, we postulate mid-Ordovician origin, ~ 465 ma. The location could have been anywhere on Gondwana I, but dispersal barely nipped “proto-Africa and India,” with only minor occurrences today, and evidently missed “proto-Madagascar,” where siphonophoridans are unknown.

Order Siphonocryptida (Fig. 23) – *Fossils*: No fossils or published inferences from other fossil evidence are available. *Geography*: Because of their rare, spotty, and random occurrences, we conclude that Siphonocryptida, the least widespread order after Siphoniulida, are in a state of decline. While its recent discovery in Nepal (Korsós et al. 2009) suggests occurrence elsewhere in the Old World, its overall biogeography, the only evidence at hand, shows it to be the oldest surviving colobognath taxon. Occurrences in Nepal, Taiwan, and Sumatra/western Malaya clearly derive from “proto-southeast Asia” terranes from Gondwana I that began rifting in the late Silurian, ~ 415 ma. *Conclusion*: Because of the relictual distribution pattern and the presence of the middorsal groove, a plesiomorphic feature (Enghoff and Golovatch 1995) shared with the fossil *Pleurojulus* but absent from other platydesmidans, great age is indicated for Siphonocryptida, but their biogeography is so fragmented as to otherwise lend no clues. We believe that Siphonocryptida date from the earliest days of Chilognatha, Helminthomorpha, and Colobognatha, and that it and Siphoniulida were among the first helminthomorph taxa to evolve and the oldest still extant. We therefore postulate origin in the mid-Cambrian, ~ 516 ma.

Subterclass Eugnatha (Fig. 24) – *Fossils*: While mouthparts and even heads are rarely clearly preserved, apparent eugnathan fossils are available from Paleozoic, Late Silurian sediments, ~ 415 ma. (Hoffman 1963, 1969a, c; Gray and Shear 1992; Shear 1999; Wilson and Anderson 2004, Shear and Edgecombe 2010). *Geography*: Their widespread, continuous occurrences throughout all continents and major land masses are clear evidence that Eugnatha antedate rifting of Avalonia from Gondwana I in the early Ordovician, ~ 480 ma. Thus, they had to originate even earlier. *Conclusion*: Wilson (2006) postulated origin of Eugnatha “about 7/8 of the way through the Silurian,” or about 412 ma. It had to be substantially earlier, however, and we postulate Late Cambrian origin concurrent with Colobognatha, ~ 518 ma, after major class traits had evolved and Penicillata/Chilognatha and Pentazonia/Helminthomorpha dichotomies had taken place.

Superorder Juliformia (Fig. 25) – *Fossils*: Juliformian fossils are available from the Mesozoic (Dzik 1975, Shear et al. 2009b, Shear and Edgecombe 2010) as well as the Permian and Carboniferous, but the oldest date from the early Devonian, ~ 408 ma (Scudder 1878; Fritsch 1899; Hoffman 1963, 1999; Hannibal and Feldmann 1988; Shear et al. 1992; Wilson 2006; Shear and Edgecombe 2010). *Geography*: Their widespread, continuous occurrences throughout all major land masses indicate that Juliformia also antedate rifting of Avalonia from Gondwana I in the early Ordovician and that ancestral forms occupied both land masses. *Conclusion*: Wilson (2006) postulated origin around the Silurian/Devonian boundary, ~ 410-

408 ma, but it clearly was much earlier. Antedating the rifting of Avalonia from Gondwana I pushes the date back to the mid-Cambrian, and we postulate origin around 518 ma.

Order Julida (Fig. 26) – *Fossils*: Impression fossils ≤ 50 my from Eocene/Miocene deposits in Colorado, USA, have been assigned to the North American family Parajulidae (Scudder 1878, Miner 1926, Hoffman 1969c, Hannibal et al. 2004). Additionally, the modern families Julidae and Nemasomatidae are represented in Oligocene Baltic amber, ~ 30 my (Hoffman 1969c). *Geography*: Like Glomerida, Platydesmida, and Callipodida (Fig. 9, 17, 37), Julida are wholly Laurasian; unlike the others, however, their biogeography is primarily continuous. *Conclusion*: Being absent from the Southern Hemisphere, Julida had to arise **after** Avalonia rifted from Gondwana I in the early Ordovician, ~ 480 ma, on either drifting Avalonia itself, on Baltica after collision with Avalonia, or on Laurentia after collision with Baltica+Avalonia. We therefore postulate early Silurian origin and an age of ~ 442 my.

Order Spirobolida (Fig. 28) – *Fossils*: Shear and Edgecombe (2010) suggested that Spirobolida might be the oldest surviving diplopod order because of the ~ 350 my Carboniferous fossils of Xyloiulidae, a presumed spirobolidan (Hoffman 1963, 1969c; Shear 1994, 1997; Hannibal et al. 2004), but we accord this distinction to Polyxenida with Polydesmida being the oldest chilognath. Dzik (1981) inferred ordinal presence on Pangaea because of *Gobiulus sabulosus*, a reasonably modern spirobolidan in Mongolian Cretaceous deposits, ~ 230 ma (Dzik 1975). *Geography*: Spirobolida are Gondwanan but with substantial Laurasian elements in North/Central America and east Asia. *Conclusion*: As with Sphaerotheriida and Siphonophorida (Fig. 13, 22), Spirobolida arose on Gondwana I after rifting of Avalonia in the early Ordovician, ~ 480 ma. The Mongolian fossil plus extant occurrence around Beijing, China, indicate presence on the North China terrane, the first to have rifted from Gondwana I, in the late Silurian ~ 415 ma. It accreted to Siberia in the Late Permian, and Spirobolida thus antedate Spirostreptida (Fig. 29, 34), which do not extend as far northward in east Asia. We therefore postulate origin in the mid-Ordovician and an age of ~ 465 my.

Order Spirostreptida s. l. (Fig. 29) – *Fossils*: Only the cambalidean fossil below is known; no published inferences from other fossil evidence are available. Cook (1895) suggested that the fossil genus *Archicambala* Cook belonged to Spirostreptida: Cambalidae, but Hoffman (1969c) disagreed. *Geography*: Like spirobolidans, Spirostreptida s. l. are Gondwanan but with substantial northern elements in North America and eastern Asia. *Conclusion*: We postulate origin on Gondwana I in the late Cambrian ~ 514 ma, **before** rifting of Avalonia. *Remarks*: From a biogeographic perspective, Spirostreptida s. l., now extinct in Europe, seem heterogeneous above and beyond the anatomical reasons discussed by Shear et al. (2003). We believe the distributions of the component suborders – Cambalidea (Fig. 30), Epinannolenidea (Fig. 32), and Spirostreptida (Fig. 34) – are incongruent to a degree beyond that expected from taxa that are truly closely related, which suggests that elevations to full ordinal statuses are warranted. To occur today in both northern and southern regions, Cambalidea had to be present on both Avalonia and Gondwana I when the former rifted and arise even earlier, whereas the primarily Gondwanan Epinannolenidea and Spirostreptida had to originate after this event from purely southern stock. Detailed anatomical and molecular investigations on these taxa, to determine whether anatomical and/or genetic bases exist for full ordinal statuses, is a fitting subject for future research.

Suborder Cambalidea (Fig. 30-31) – *Fossil*: Mauriès (1992) redescribed *Protosilvestria sculpta*, an Oligocene fossil, ~ 30 my, from Quercy, France. *Geography*: Cambalidea combine Laurasian and Gondwanan elements and seem “biogeographically heterogeneous,” being exclusively Laurasian in the New World and Gondwanan in Asia, Indonesia, Australia/New Guinea, New Caledonia, and New Zealand. Despite their absences from other areas today, fully evolved ancestral cambalideans had to exist on both Avalonia and Gondwana I prior to the former’s rifting, ~ 480 ma, so Cambalidea had to arise even earlier. *Conclusion*: To some degree Cambalidea’s biogeography is more amenable to the Pacifica hypothesis (Jeekel 1985) that we reject than to ours involving Avalonia. Nevertheless, we postulate origin around the late Cambrian, ~ 514 ma, after major class traits had evolved and after the Penicillata/Chilognatha, Pentazonia/Helminthomorpha, Colobognatha/Eugnatha, and Juliformia/Nematophora/Merocheta dichotomies had taken place.

Suborder Epinannolenidea (Fig. 32-33) – *Fossils*: No fossils or published inferences from other fossil evidence are available. *Geography*: Except for the Western Hemisphere, with Laurasian Choctellidae in the southeastern US, Epinannolenidea is exclusively a southern taxon that arose on Gondwana I after Avalonia rifted in the early Ordovician, ~ 480 ma. *Conclusion*: Discounting Choctellidae, whose origin and affinities warrant further investigation, Epinannolenidae's presence in South America, the southern periphery of Africa, and Australia/New Zealand but not southeast Asia indicates that the taxon was not present on the "proto-southeast Asia" Gondwana I terranes that formed this area. However, its presence in the Antilles (excluding Jamaica) shows that it occurred along the Guiana/northern Brazilian margin of "proto-South America" before the "proto-Antillean arc" rifted in the Cretaceous/Paleocene. We therefore postulate origin in the "proto-South American" region of Gondwana I, distant from the area of the "proto-southeast Asia" terranes, around the mid-Ordovician, ~ 470 ma.

Suborder Spirostreptidea (Fig. 34) – *Fossils*: No fossils or published inferences from other fossil evidence are available. *Geography*: The nominate suborder is overwhelmingly Gondwanan but with a substantial Laurasian element in the New World (Golovatch and Kime 2010) that represents secondary dispersal from a South American source area. Evidence for this is shown by the fact that numerous genera inhabit South America, whereas only three – *Isoporostreptus* Silvestri, 1898, *Mayastreptus* Hoffman, 1998, and *Orthoporus* Silvestri, 1897 – occur from Panama northward, and only the last occupies Mexico and the southwestern US (Causey 1975, Hoffman 1999). The taxon's presence in both continental and insular southeast Asia indicates presence on the "proto-southeast Asia" terranes of Gondwana I prior to rifting. The population in Morocco represents northward dispersal of the continuous one in sub-Saharan Africa that was isolated by xerification of the Sahara region, which is also evidenced by the inselberg remnant in the Aïr Mts., Niger. The population in Israel represents expansion of the one in the southwestern Arabian Peninsula (Saudi Arabia and Yemen) through the Jabal Al Hirjaz Mts. (Shelley 2009, Golovatch and Kime 2010) that became isolated by desertification of the Negev region, Israel; the Saudi/Yemenese area was also connected to that in sub-Saharan Africa before the Arabian Peninsula rifted. *Conclusion*: Origin is inferred on Gondwana I after rifting of Avalonia but before the riftings of the "proto-southeast Asia" terranes, which Spirostreptidea had to occupy to be present today in Indochina/Malaysia and western Indonesia. Their absence from northern China, in contrast to Spirobolida, indicate that the taxon was absent from the first, North China, Gondwana I terrane. We therefore postulate origin in the "proto-Africa" area of Gondwana I in the mid-Ordovician, ~ 460 ma.

Superorder Nematophora (Fig. 35) – *Fossils*: Fossils with nematophoran attributes existed in the late Carboniferous, ~ 300 ma (Hannibal 2000, Wilson 2006, Shear and Edgecombe 2010), but Wilson (2006) based her conclusion on *Hexecontasoma*, which we interpret as a slender, andrognathid platydesmidan. Shear et al. (2009b) and Shear and Edgecombe (2010) reported nematophoran fossils from the early Triassic, ~ 248 ma, and the former authors postulated superordinal occurrence in subtropical environments on the eastern edge of Pangaea. *Geography*: Today, Nematophora are represented in both Laurasian and Gondwanan areas, the latter being spottier and more restricted than the former. Fully evolved ancestral forms therefore had to be present on both Avalonia and Gondwana I prior to the former's rifting in the early Ordovician, ~ 480 ma, which mandates even earlier origin. *Conclusion*: We postulate origin in the Avalonia region of Gondwana I in the Late Cambrian, ~ 518 ma.

Order Callipodida (Fig. 37) – *Fossils*: Carboniferous fossils have been assigned to Callipodida but more properly represent an ancestral nematophoran than a modern callipodidan. *Geography*: Like Glomerida, Platydesmida, and Julida (Fig. 9, 17, 26), Callipodida exhibit an exclusively Laurasian distribution pattern. *Conclusion*: Being absent from the Southern Hemisphere, Callipodida had to arise **after** Avalonia rifted from Gondwana I in the early Ordovician, ~ 480 ma, on either Avalonia itself, on Baltica after collision with Avalonia, or on Laurentia after collision with Baltica+Avalonia. We postulate late Ordovician origin and an age of ~ 445 my. Its occurrence in southern China and southeast Asia results from spread into these areas after accretion of the "proto-southeast Asia" Gondwana I terranes. Callipodida lack African representation, in contrast to Glomerida (Fig. 9) and Julida (Fig. 26), which occupy subsimilar

areas in Mediterranean Africa, and also Platydesmida (Fig. 17), which inhabit a corner of Tunisia and Algeria.

Order Chordeumatida (Fig. 41) – *Fossils*: Eocene to Oligocene fossils, ~ 23-35 my, are available in Baltic amber (Hoffman 1969c). *Geography*: Chordeumatida occupy areas that were parts of both Laurasia and Gondwana, the latter being generally spottier and more restricted than the former. *Conclusion*: To be in both areas today, fully evolved ancestral forms had to be present on both Avalonia and Gondwana I prior to the former's rifting in the early Ordovician, ~ 480 ma, thus mandating even earlier origin. The continuity of ranges in North/Central America and northern Eurasia suggests explosive bursts of radiation and speciation from the forms that had been confined to Avalonia for 30 my of drifting, when they gained access to the unoccupied micro-continents of Baltica and Laurentia where all niches were vacant. By contrast, the forms that remained on Gondwana I evolved in different directions while Avalonia drifted. Extinctions have taken place within this fauna such that there are now scattered, relictual, faunal pockets. Chordeumatida present a special situation in that their southeast Asian representatives contain both southern (Metopidiotrichidae) and northern (Vieteumatidae) elements (Shear 2000). For the former to be present, ancestors had to inhabit the "proto-southeast Asia" Gondwana I terranes before they rifted, and the northern forms represent dispersion from Baltica/Euramerica that reached southeast Asia after the terranes carrying Gondwanan forms had accreted. Not only is southeast Asia a mixing zone for southern and northern diplopods in general, but this is true for Chordeumatida itself! Consequently, the order dates back to the earliest days of the class, and we postulate Late Cambrian origin, ~ 512 ma, after major class traits had evolved and after the Penicillata/Chilognatha, Pentazonia/Helminthomorpha, Colobognatha/Eugnatha, and Juliformia/Nematophora/Merocheta dichotomies had taken place.

Order Stemmiulida (Fig. 45) – *Fossils*: No fossils or published inferences from other fossil evidence are available. *Geography*: Like Siphonophorida and Spirostreptidea (Fig. 22, 34), elements in Mexico/Central America indicate spread from South American source areas; otherwise, Stemmiulida are exclusively Gondwanan. Occurrences in central, rather than southern, Africa and northern, rather than southern, South America are *prima facie* evidence of transfer between these areas while the continents were joined, which extended from the very origin of Stemmiulida to the Cretaceous, when they rifted apart on Gondwana II. This reasoning suggests that Stemmiulida should be anticipated in easternmost Brazil, around Recife and in Alagoa, Ceara, Paraiba, Pernambuco, Rio Grande do Norte, and Sergipe states, and possibly also on the Fernando de Noronha archipelago. *Conclusion*: Origin is again inferred on Gondwana I after rifting of Avalonia in the early Ordovician (~ 480 ma) but before "proto-southeast Asia" terranes had split in the late Silurian, ~ 415 ma, as Stemmiulida had to occupy later ones to be present today in Vietnam. We therefore postulate origin in the central "proto-Africa" area of Gondwana I in the mid-Ordovician, ~ 465 ma.

Superorder Merocheta/Order Polydesmida (Fig. 46) – *Fossils*: Late Carboniferous fossils, ~ 306 ma, exist (Wilson 2006, Shear and Edgecombe 2010) as do ones in 30 my Oligocene, Baltic and Dominican amber (Hoffman 1969, Shear 1981, plus unpublished samples examined by RMS). An inclusion in burmite, early Cretaceous amber, is also known (unpublished observation of SIG). *Geography*: Overwhelmingly the most successful (super)order, having diversified and spread through all continents and major land masses, Merocheta/Polydesmida exhibit the largest, most continuous distribution of any ordinal taxa. Many larger polydesmidans are among the most mobile diplopods, so an unknown amount of the distribution may be attributable to recent dispersion; this cannot, however, account for the immensity of the occupied area. Fully evolved, ancestral forms of Merocheta/Polydesmida had to be present on both Avalonia and Gondwana I when the former rifted in the early Ordovician, ~ 480 ma, and the taxa thus had to originate earlier. As with Chordeumatida, southeast Asia was a mixing zone for both northern and southern polydesmidans, the former, exemplified by Polydesmidae (Polydesmidea), dispersing from Baltica/Euramerica, and the latter, exemplified by Paradoxosomatidae (Strongylosomatidea), carried there passively on "proto-southeast Asia" terranes. *Conclusion*: We believe that Polydesmida dates back to the earliest days of the class and postulate mid-Cambrian origin, ~ 518 ma, after major class traits had evolved and after sub-, infra-, and subterclass dichotomies had taken place. Discounting the possibility of

extinct merochetans, Polydesmida and Merocheta arose simultaneously during the Juliformia/Nematomorpha/Merocheta dichotomy.

Helminthomorpha incertae sedis/Order Siphoniulida (Fig. 23) – *Fossils*: No fossils or published inferences from the same are available. *Geography*: The most restricted order geographically, Siphoniulida are known from only two regions, one each in former Gondwanan and Laurasian territories; their Sumatran occurrence derives from “proto-southeast Asia” Gondwana I terranes. We believe that Siphoniulida were fully evolved and present on both Avalonia and Gondwana I when the former rifted in the early Ordovician, ~ 480 ma, and the taxon thus had to originate earlier. Even if future discoveries reveal greater abundance, Siphoniulida are clearly very old and in a state of decline; considering them both “living fossils” and relicts of the Colobognatha/Eugnatha dichotomy seem reasonable, as the ancestral helminthomorph would logically possess features of both component subterclasses. With a rostrate, colobognath head and a rounded, juliformian body, Siphoniulida bridge the somatic anatomical gap between Colobognatha and Eugnatha, suggesting an intermediate phylogenetic position. *Conclusion*: We believe that Siphoniulida date back to the earliest days of the class and evolved subsequent to the Penicillata/Chilognatha and Pentazonia/Helminthomorpha dichotomies. We postulate origin in the mid-Cambrian, ~ 518-517 ma.

Lacking evidence to the contrary, we assume that no extinct penicillate or merochete orders existed, that Polyxenida derived from the first diplopod dichotomy concurrently with Penicillata, and that Polydesmida likewise arose concurrently with Merocheta. The basal dichotomy necessarily antedates all others, and Polyxenida, a highly successful taxon, is thus the “oldest” order. Furthermore, as sister-taxa arise concurrently and assuming a trichotomy among eugnathan superorders, Colobognatha, Eugnatha, Juliformia, Nematophora, and Merocheta arose simultaneously, and Polydesmida is thus the oldest chilognath order. As ancestors had to fully differentiate and be present on **both** Avalonia and Gondwana I proper, we consider the widespread taxa on both Laurasia and Gondwana I to be older than those on either land mass alone, with Siphoniulida followed by Siphonocryptida ranking next oldest after Polydesmida. While Avalonia drifted slowly northward for 30 my, taxa on Gondwana I were free to disperse through the giant land mass and continually evolve/differentiate. We therefore consider exclusively/primarily Gondwanan taxa to be older than exclusively Laurasian ones, which probably arose either after Avalonia collided with Baltica and/or after the subsequent collision of Baltica+Avalonia with Laurentia. Laurasian orders could have evolved earlier, on Avalonia itself prior to collision with Baltica, but we believe its limited size, the finite number of niches on this drifting terrane, and the resultant low selection pressure impeded diversification until collisions with Baltica and Laurentia opened sizeable new and uninhabited areas with wholly vacant niches, sufficient, we believe, to fuel the divergence that had stagnated for 30 my. That this scenario is plausible is shown by the fact that, consistent with the substantially greater available area and time, there are more primarily Gondwanan orders than Laurasians.

Glomeridesmida is the most fragmented Gondwanan taxon, and we therefore consider it to be older than Sphaerotheriida, but they could plausibly be subequal in age. Spirobolida and Spirostreptidea seem close in age, but we consider Spirobolida slightly older because of the number of plausibly spirobolidan Paleozoic fossils and because of the substantially greater northward dispersal it has undergone in both North America and Asia, which indicates more time to spread and, hence, greater age. The inverted triangle on Fig. 28 shows the approximate location of *Gobiulus sabulosus*, the Mongolian spirobolidan fossil (Dzik 1975), that plausibly is this order because of anatomical similarities and the geographic



Figure 56. Land areas in the Early Silurian Period, Paleozoic Era, ~ 440 ma, after Baltica+Avalonia merged with Laurentia to form Euramerica, adapted from the website of Ron Blakey, Geology Dept., Northern Arizona University, Flagstaff, Arizona, USA (<http://jan.ucc.nau.edu/~rcb7/RCB.html>). The arrows show dispersals of forms from Avalonia+Baltica onto Laurentia and continued dispersals on Gondwana I; other land masses at this time were devoid of diplopods. Abbreviations and symbols as in Fig. 52-53.

proximity to modern spirobolidans, which may even be there today, as although arid, the site is in a large, uninvestigated region.

Thus, based on cladistic principles, the necessary sequence of dichotomies, relative continuity versus fragmentation, and presences in Laurasia, Gondwana, or both, we derive the following sequence of relative ordinal ages from oldest to youngest:

Polyxenida > Polydesmida > Siphoniulida > Siphonocryptida > Spirostreptida *s. l.*/Cambalidea > Chordeumatida ≥ Polyzoniida > Glomeridesmida ≥ Sphaerotheriida > Epinannolenidea > Stemmiulida ≈ Siphonophorida > Spirobolida > Spirostreptida > Glomerida ≈ Platydesmida > Callipodida > Julida.

CONCLUSIONS

We know of no way to infer with any degree of accuracy the time required for ancestral forms to diverge to the extents necessary prior to Avalonia's rifting to effect this scenario and ultimately lead to the modern fauna and its biogeography. With the absence, at least at first, of terrestrial predators, and all (sub)surface niches vacant, terrestrial environments and adaptation pressures at that time are incomprehensible now. We do know, however, that the basic diplopodous body plan had to evolve, major lineages had to diverge, and the ordinal taxa Polyxenida, Siphoniulida, Siphonocryptida, Polyzoniida, Cambalidea, Chordeumatida, and Polydesmida arose and became established on both Avalonia and Gondwana I itself **BEFORE** the former rifted and began drifting toward Baltica. If the marine arthropod ancestor that crawled ashore was a burrower and at least partly sclerotized, it surely was not diplopodous, which would not have been advantageous in soft marine sediments. The strong diplosegment condition, with alternate segmental joints rigid and incompressible, logically evolved on land from the need to burrow in comparatively hard, dry, terrestrial soils, and in turn, it compelled additional anatomical changes, for example, relocation of the anterior leg pairs and spiracles on each (diplo)segment. Loss of sclerotization was a major feature of diverging Penicillata, and chilognaths had to subsequently derive pentazonian and helminthomorph body plans with differing modes of spermatophore transfer, and, for the latter, at least two feeding mechanisms, three gonopod positions, and three burrowing mechanisms – bulldozing, wedging, and boring (Hopkin and Read 1992). With the date of Avalonia's rifting fixed by geologists at ~ 480 ma, in the early Ordovician, it is hard to envision **all** this diversification and more taking place in less than the 44 my from a mid-Cambrian origin, even with an accelerated rate of evolution in this Paleozoic period. Based on time constraints and allowing for unknowns, we accept the origination date of Pisani (2009), ~ 524 ma, but this is debatable. For all this evolution and diversification to take place in just 44 my constitutes, in our view, a “**Terrestrial Cambrian Explosion**” that was at least partly contemporaneous with the marine one represented in the Burgess Shale and other stratas; we would even suggest that Diplopoda underwent their own “**mini**” **Cambrian Explosion**. Suffice it to say that documented tectonic events and paleogeological/geographical time constraints mandate Cambrian, not Ordovician, origin, and that evolution, adaptation, radia-



Figure 57. Land areas in the Late Carboniferous Period, Paleozoic Era, ~ 306 ma, after Euramerica (Laurentia+Baltica+Avalonia) merged first with Siberia+Kazakhstan and then with the “proto-South America/Africa” region of Gondwana I, thereby forming Western Pangaea, adapted from the website of Ron Blakey, Geology Dept., Northern Arizona University, Flagstaff, Arizona, USA (<http://jan.ucc.nau.edu/~rcb77/RCB.html>). The arrows show dispersals of forms from the Baltica region of Euramerica onto Siberia+Kazakhstan and from the Laurentia region onto the “proto-South America/Africa” area of Gondwana I and vice versa. By this time, dispersions had extended throughout Gondwana I, and all land masses harbored diplopods; for the first time, separately evolving northern and southern faunas were able to mix, in Western Pangaea. North/South China and southeast Asia terranes, ferrying diplopods, were drifting towards Siberia+Kazakhstan, and Cimmeria had begun rifting. Inverted Triangle, approximate location of *Gobiulus sabulosus*, the Mongolian Cretaceous spirobolidan. Cm, Cimmeria terrane; NC, North China terrane; SC, South China terrane. Other abbreviations and symbols as in Fig. 52-53.

tion, diversification, and speciation necessarily also began then. We therefore consider ~ 524 ma, a mid-Cambrian date ~ 44 my before a documented tectonic event that ancestral millipeds had to exploit, to be a reasonable and possibly even conservative projection.

Paleozoic drift patterns ran primarily from south to north; terranes rifting from both Gondwana I and II drifted north to Baltica/Euramerica/Siberia + Kazakhstania/Pangaea, not vice versa. The northern micro-continents did drift southward and Baltica and Avalonia actually converged, as opposed to Baltica's being stationary, but we know of no evidence of terranes rifting from Baltica, Laurentia, Siberia, or even Laurasia and drifting to and merging with either Gondwana I or II. Consequently, the only tenable evolutionary hypothesis that places ancestral stock on both Gondwana I and a northern micro-continent, so as to derive both northern Paleozoic fossils and today's biogeography, is one beginning in the south, on Gondwana I, with partitionings causing part of this stock to be carried passively northward on small tectonic rafts. Origin on Baltica, Laurentia, Euramerica, or Siberia would not derive the biogeography documented herein because ancestral forms would not have arrived on Gondwana I in time for the southern orders to evolve and disperse to the "proto-southeast Asia" terranes before they rifted so as to even arrive in that area, and Sphaerotheriida, the lone Gondwanan order that has not dispersed northward, would not exist. Skeptics may argue that southeast Asian presences of the predominantly Gondwanan taxa Glomeridesmida, Siphonophorida, Spirobolida, Spirostreptidea, and Stemmiulida (Fig. 7, 22, 28, 34-35) could result from southeastward dispersion from a Baltica/Laurentia/Euramerica source area. Our rebuttal is that (a) all are absent from modern Europe, and (b) such dispersal somehow occurred without leaving evidence in the form of detached remnants around the Caspian Sea and/or in central Asia/Nepal, as happened in all taxa that clearly dispersed in this manner – Glomerida, Platydesmida, Polyzoniida, Julida, Callipodida, and Chordeumatida (Fig. 9, 17, 20, 26, 37, 40-41, 44). Furthermore, origin on a northern micro-continent would not insert millipeds into Gondwana I until collision with Euramerica in the late Carboniferous (~ 306 ma), thus delaying or averting evolution of the southern orders and resulting in a substantially different global fauna and biogeography from that documented herein. Carboniferous origins for Gondwanan taxa, if even possible, would be after all terranes had rifted and transport to southeast Asia would be precluded. Because of time constraints, we contend that our hypothesis is the **only** one that is operative, places ancestral stock on **both** Gondwana I and northern micro-continents in a timely fashion, allows formation of Paleozoic fossils, allows time for the 16 modern orders to evolve, and enables modern biogeographic patterns to develop. The only question for debate is how much time was needed prior to Avalonia's rifting in the early Ordovician for a marine ancestor to emerge from the sea on or around Avalonia, evolve, adapt, radiate, differentiate, disperse to the extents necessary, and position descendants/ancestral stock on both Avalonia and Gondwana I so populations would be properly partitioned when rifting occurred. Given the enormity of what had to take place, origin surely antedated even the Cambro-Ordovician boundary that Wilson (2006) postulated, and to us, the ~ 44 my from a mid-Cambrian origin, ~ 524 ma, constitutes a reasonable time frame given the explosive nature of Cambrian events.

Our maps show that, consistent with a Gondwanan origin, Diplopoda remain predominantly Gondwanan today; only four of the 16 orders – Glomerida, Platydesmida, Julida, and Callipodida – are primarily Laurasian. As with the class itself, all extant ordinal taxa are substantially older than previously realized, with Polyxenida, Siphoniulida, Siphonocryptida, Polyzoniida, Chordeumatida, and Polydesmida, a roster including both relictual and widespread modern taxa, also dating back to the Cambrian and the earliest days of the class. Those that thrive today – Polyxenida, Spirobolida, Spirostreptidea, Chordeumatida, and Polydesmida – are not "younger," as one might expect, but simply more successful, Polydesmida being tops in this regard. Siphoniulida are nearing extinction with Siphonocryptida second and Glomeridesmida, the lone surviving limacomorph, being third in this category but not next in relative age. Of the taxa considered here, Callipodida and Julida seem to be the "youngest," and the latter demonstrates high biogeographic continuity, some of which surely results from its adaptability and relative motility.

"Species swarms" have been documented for Madeira and the Canary and Cape Verde Islands, and one may exist for Spirostreptidea/Spirostreptidae/*Globanus* on São Tomé and Príncipe. All these islands are in the Atlantic Ocean, and though rarely identified as such, the phenomenon also exists on ones in the Pacific, for example *Nannolene* Bollman, 1887, comprising ± 15 species on Kauai, Lanai, Maui, Molokai, and Oahu, Hawaiian Islands, USA (Silvestri 1904; Nishida 1994, 2002), and possibly Rhinocricidae

(Spirobolida), comprising ~ 27 species in Fiji (Chamberlin 1920, Marek et al. 2003). Enghoff (1982) defined an insular “species swarm” as a species group that includes “all descendants of a single ancestral, immigrant species”; they develop when a generic representative somehow reaches a largely pristine island with a depauperate fauna and then rapidly and explosively radiates, speciates, and penetrates the many vacant niches. Insular “species swarms” warrant intensive study by diplopodologists because, beyond naming and describing numerous new species, they exemplify in a microcosm the incomprehensibly more complex situation that occurred ~ 524 ma in the mid-Cambrian, when a multilegged ancestor crawled ashore on/near the Avalonia sector of Gondwana I and **every** (sub)surface niche was vacant and available for occupation. During the subsequent eons of time, this process has reprised over and over including twice in the Ordovician (450-440 ma), when stock on Avalonia, progeny from the original radiation that had been passively transported northward, was released into the unoccupied microcontinents of Baltica and then Laurentia, where they became ancestral to subsequent speciations and radiations. It also occurred when at least the first few “proto-east/southeast Asia” terranes accreted to Siberia + Kazakhstania + Euramerica, and the Gondwana I forms that were ferried were released into the largely or entirely vacant environments on these lands. Man could never study phenomena as large and complex as these on such gargantuan areas, but a minute speck like São Tomé or Madeira is a manageable microcosm in which to attempt to grasp a process that is fundamental to the class. In a very real sense, the largest “species swarm” in the Diplopoda is Diplopoda itself, as all of the estimated 80,000+ extant species (Adis 2002, Shelley 2003a) descended from this one, multilegged, Cambrian ancestor. When the ancestors of the glomeridan and julidan swarms reached their Macaronesian islands, they radiated and speciated explosively through these limited areas, thereby providing small-scale examples of the evolutionary phenomena that Diplopoda itself, and multiple subordinate taxa, experienced on vastly greater scales from the mid-Cambrian to perhaps the late Devonian, ~ 524-370 ma. The best way to gain insight into ancient events is to study small-scale examples from the recent past that, indeed, continue in the present.

Finally, we emphasize that we could not have deduced our hypothesis with all the movements and timings without the maps and their inherent biogeographical information. Fossils alone could never generate such insights and indeed have not done so. A “total evidence” approach, integrating fossil and biogeographical knowledge with documented paleogeographic events and tectonic drift patterns, is necessary to derive a complete picture and enable plausible inferences into early evolutionary events. For such to happen, biogeography and detailed mappings must be accorded high priority, which had not been done on a meaningful scale for a class that workers agreed, with little substantiation, was “biogeographically significant.” This statement is true and is now authenticated. We encourage present colleagues and future workers to map taxon distributions regardless of how minor they may seem and to continually augment this contribution as additional biogeographic data enable clearer inferences into the past. Much greater emphasis is warranted on biogeography in taxonomic research on the Diplopoda. It should be routinely addressed with at least one or more spot maps in all generic-level systematic works.

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Table 1. Countries, Dependencies, and Major Islands Lacking Indigenous Milliped Records (listed alphabetically with countries in each world region preceding dependencies)**North America**

None, but only the introduced species, *Cylindroiulus caeruleocinctus* (Wood, 1864) (Julida: Julidae) is known from the Canadian prov. of Prince Edward Island (Kevan 1983; Shelley 1988, 2002b).

Central America

None.

South America

Chilean “mainland” and islands south of Isla Grande de Chiloé – no samples known.

Argentina/Chile – Isla Grande de Tierra del Fuego – no samples known.

Caribbean Islands

Turks and Caicos – no samples known.

Anguilla (UK) – no samples known.

Aruba (Netherlands) – no samples known.

Aves I. (Venezuela) – no samples known.

Bonaire (Netherlands) – no samples known.

Cayos de Albuquerque (Colombia) - no samples known.

Cayos Miskitos (Nicaragua) - no samples known.

Courtown Cays (Colombia) - no samples known.

Culebra I. (USA, Puerto Rico) - no samples known.

Curaçao (Netherlands) – no samples known.

Descheo I. (USA, Puerto Rico) - no samples known.

Dog I. (UK) - no samples known.

East, Middle, North, and Southwest Cays (Colombia) - no samples known.

Isla de San Andrés (Colombia) - no samples known.

Isla del Maíz Grande (Nicaragua) - no samples known.

Isla del Maíz Pequeña (Nicaragua) - no samples known.

Isla la Tortuga (Venezuela) - no samples known.

Isla Orchila (Venezuela) - no samples known.

Islas de Aves (Venezuela) - no samples known.

Islas de la Bahía (Honduras) - no samples known.

Islas los Monjes (Venezuela) - no samples known.

Islas los Roques (Venezuela) - no samples known.

Islas Santarilla [Swan Is.] (Honduras) - no samples known.

La Blanquilla (Venezuela) - no samples known.

Los Hermanos (Venezuela) - no samples known.

Los Testigos (Venezuela) - no samples known.

Mona I. (USA, Puerto Rico) - no samples known.

Montserrat (UK) – no samples known.

Morant Cays (Jamaica) - no samples known.

Pedro Cays (Jamaica) - no samples known.

Saba (Netherlands) – no samples known.

St. Barthélemy (France) – no samples known.

St. Martin/St. Maarten (France/Netherlands) – no samples known.

Sombrera I. (UK) - no samples known.

Turnette Is. (Belize) - no samples known.

Vieques I. (USA, Puerto Rico) - no samples known.

Africa and Associated Islands

Egypt (including the Sinai Peninsula) – Only introduced millipeds seem to have been recorded from Egypt (Akkari et al. 2010a) unless the enigmatic *Lysiopetalum plicatum* Guérin, 1837, reported from Egypt in general by Gervais (1847) and Porat (1876), refers to perhaps an indigenous julid (Julida). It probably is not a representative of Callipodida, which is absent from Africa (Shear et al. 2003, Stoev et al. 2008, herein), and the name appears to be a *nomen dubium*.

Mauritania – no samples known.

Western Sahara (Morocco) – no samples known.

Europe

Vatican City – no samples known (M. Zapparoli, pers. comm. to RMS).

Asia – Middle East

Bahrain – no samples known.

Kuwait – no samples known.

Oman – no samples known.

Qatar – no samples known.

United Arab Emirates – no samples known.

Palestinian National Authority, Gaza Strip – no samples known.

Asia – Continental

None

Asia – East Indies

None

Australia and New Zealand

None

Antarctica and Associated Islands (Adelaide Is., Biscoe Is., Palmer Archipelago, South Orkney Is., South Sandwich Is., South Shetland Is.) – No native or introduced millipeds have ever been recorded from this region of the world.

Arctic Ocean Islands – No native or introduced millipeds have ever been recorded from these islands, which lie well north of the Arctic Circle and have too cold a climate for millipeds to survive there.

Canadian Islands - Baffin, Banks, Bathurst, Borden, Bylot, Cornwallis, Devon, Ellesmere, King William, Mackenzie King, Parry Is., Prince of Wales, Prince Patrick, Queen Elizabeth Is., Somerset, Sverdrup Is., Victoria – no samples known.

Norwegian Islands – Jan Mayen, Svalbard – no samples known.

Russian Islands – Anjou Is., Franz Josef Land, Lyakhov Is., New Siberian Is., North Land Is., Novaya Zemlya, Wrangel – no samples known.

Atlantic Ocean Islands

Ascension I. (UK) – ?only introduced species known?

Bouvet I. (Norway) – no samples known.

Falkland Is. (UK) - ?no samples known?

Faroe Is. (Denmark) – only introduced species known (Hammer and Henricksen 1930).

Greenland (Denmark) (H. Enghoff, pers. comm. to RMS) – no samples known.

Martin Vaz Is. (Brazil) – no samples known.

Sable I. (Canada, Nova Scotia) – only introduced species known (Shelley 1988).

South Georgia I. (UK) – no samples known.

St. Helena (UK) – Only introduced species known other than the presumed indigenous polyzoniidan (Hoffman 1977b).

Trinidad I. (Brazil) – no samples known.

Tristan da Cunha Is. (UK) – no samples known (Jeekel 1954), only introduced species expected.

Bering Sea Islands

Little Diomed I., Nunivak I., St. Matthew Is., and the Pribilof Is. (USA: Alaska) – no samples known. The climate and winters are too harsh for millipeds to survive here.

Ostrov Ratmanova [Big Diomed I.] (Russia) – no samples known. The climate and winters are too harsh for millipeds to survive here.

Coral Sea Islands

Ball's Pyramid I. (Australia) – no samples known.

Coral Sea Is. Territory (Australia) - no samples known.

Îles Chesterfield (France) - no samples known.

East China Sea Islands

Cheju Do (South Korea) – samples exist, but apparently no published records.

Indian Ocean Islands

Agalega Is. (Mauritius) - no samples known.

- Andaman Is. (India) - no samples known.
Ashmore Is. (Australia) – no samples known, only introduced species expected.
Bassas da India (France) - no samples known, only introduced species expected.
Cartier I. (Australia) - no samples known, only introduced species expected.
Chagos Is. (UK) - no samples known, only introduced species expected.
Christmas I. (Australia) - no samples known, only introduced species expected.
Cocos (Keeling) Is. (Australia) - no samples known, only introduced species expected.
Crozet I. (France) - no samples known, only introduced species expected.
Diego Garcia I. (UK) – only introduced species known.
Île Europa (France) - no samples known, only introduced species expected.
Kerguelen I. (France) - no samples known, only introduced species expected.
Lakshadweep Is. (India) - no samples known.
McDonald Is. (Australia) - no samples known, only introduced species expected.
Nicobar Is. (India) - no samples known.
Prince Edward I. (Republic of South Africa) - no samples known, only introduced species expected.
Shag I. (Australia) - no samples known, only introduced species expected.
Tromelin I. (France) - no samples known, only introduced species expected.

Mediterranean Islands

- Isole Pelagie (Italy) - no samples known.
Pantelleria I. (Italy) - no samples known.

Pacific Ocean Islands (Oceania)

- Cook Is. – only introduced species known.
Independent State of Samoa Is. – only introduced species known.
Niue – only introduced species known.
Republic of Kiribati – only introduced species known.
Republic of Nauru – only introduced species known.
Tuvalu – only introduced species known.
Afognak and Shuyak Is. (USA, Alaska, Kodiak Archipelago) – No samples are known from these islands that are proximate to the location, in the Pleistocene, of the Bering Land Bridge. However, as all Alaskan millipeds occur in temperate rainforests, and all of Shuyak and the northern half of Afognak contain virgin, uncut, old growth, and biologically unexplored rainforest, they could harbor diverse faunas.
Aleutian Is. (USA, Alaska) – These grassy, windswept islands in the North Pacific Ocean lack the humus and litter layers necessary to support indigenous millipeds. One or two introduced species may exist in inhabited communities, but no such millipeds are known elsewhere in Alaska, and no Aleutian samples are available.
American Samoa (USA) – only introduced species known.
Antipodes Is. (New Zealand) - no samples known.
Baker I. (USA) – no samples known, only introduced species expected.
Bounty Is. (New Zealand) - no samples known, only introduced species expected.
Clipperton I. (France) – no samples known, only introduced species expected.
Daito Is. (Japan) - no samples known, only introduced species expected.
Ducie I. (UK) – no samples known, only introduced species expected.
French Polynesia (France) – only introduced species known.
Henderson I. (UK) – only introduced species known.
Howland I. (USA) – no samples known, only introduced species expected.
Isla de Malpelo (Colombia) – no samples known.
Isla de Pascua [Easter I.] (Chile) – only introduced species known.
Isla San Ambrosio (Chile) – no samples known.
Isla San Felix (Chile) – no samples known.
Islas Revillagigedo (Mexico) – no samples known.
Johnston I. (USA) – no samples known, only introduced species expected.
Kermadec Is. (New Zealand) – only introduced species known (Johns 1976).
Komandorskiye Ostrova [Commander Islands] (Russia) – no samples known.

- Line Is. (USA) – no samples known, only introduced species expected.
Lôtô I. (Iwo Jima, Japan) – no samples known, only introduced species expected.
Minami Tori Shima (Japan) - no samples known.
Norfolk I. (Australia) - no samples known.
Oeno I. (UK) – no samples known, only introduced species expected.
Palmyra I. (USA) – only introduced species known, only introduced species expected.
Phillip I. (Australia) - no samples known.
Pitcairn I. (UK) – only introduced species known.
Volcano Is. (Japan) - no samples known.
Wake I. (USA) – no samples known, only introduced species expected.
Wallis and Futuna (France) – only introduced species known.

Sea of Japan Islands

- Oki Guntô (Japan) - no samples known.
Tsushima I. (Japan) - no samples known.

South China Sea Islands

- Paracel Is. (China, Vietnam) - no samples known.
Spratly Is. (Brunei, China, Malaya [Sabah], Philippines, Taiwan, Vietnam) – no samples known.
Tungsha Tao [Pratas I.] (China) - no samples known.

Table 2. Milliped extremes.

Northernmost millipeds in Eurasia and the World – *Proteroiulus fuscus* (Am Stein, 1857) (Julida: Blaniulidae), southern Yamal Peninsula, Russia, and *Angarozonium amurense* (Gerstfeldt, 1859) (Polyzoniida: Polyzoniidae), Yana River, Yakutia, Russia, latitude about 67° 30' 40"N, north of the Arctic Circle (Golovatch 1992a, Kime and Golovatch 2000, Mikhaljova and Marusik 2004, Mikhaljova 2004, Golovatch and Kime 2010).

Northernmost millipeds in North America and the Western Hemisphere – *Litiulus alaskanus* Cook, 1904 (Julida: Parajulidae) and *Scytonotus insulanus* Attems, 1931 (Polydesmida: Polydesmidae) from USA, Alaska, Yakutat Bay, lat. 59° 32' 49"N (Cook 1904; Shelley 1990a, 1993c).

Southernmost milliped in South America and the Western Hemisphere – *Propolyxenus patagonicus* (Silvestri, 1903) (Polyxenida: Polyxenidae), Argentina, Santa Cruz Prov., Santa Cruz River, around 50°S (Mauriès 1998). Apparently, this record is unsubstantiated and lacks a voucher specimen in the MNHN (Nguyen Duy-Jacquemin, in litt. to SIG).

Southernmost chilognaths in South America and the Western Hemisphere – *Anaulacodesmus lacustris* and *Monenchodesmus inermis nahuelhuapiensis*, both by Schubart, 1954 (Polydesmida: Dalodesmidae), and *Argentocricus* sp. (Spirobolida: Rhinocricidae), Parque Nacional Alerces, Chubut Prov., Argentina, lat. ~ 42° 48' 27" S, new record herein).

Southernmost milliped and chilognath in subantarctic New Zealand and the World – *Notonaia campbellensis* Johns, 1970 (Polydesmida: Dalodesmidae), several localities on Campbell Island, lat. ~52° 36' 18"S (Johns 1964, 1970)

Highest altitudinal millipeds in the World – Unidentified, 5,300 m (17,384'), Nepal; *Nepalmatoiulus ivanloebli* Enghoff, 1987 (Julida: Julidae), eastcentral Nepal north of Kathmandu, towards Gosainkund, 4,800 m (17,744') (Enghoff 1987, Beron 2008, Golovatch and Kime 2010)

Lowest altitudinal milliped in the World – *Tetrarthrosoma syriacum* (Humbert and Saussure, 1869) (Polydesmida: Paradoxosomatidae), West Bank and Jordan, Dead Sea vicinity, -422 m (-1,385') (Schubart 1934b, Hoffman and Lohmander 1968, Tabacaru 1995, Shelley 2009).

Table 3. Ordinal occurrences by geographical regions and biogeographical realms.

- Polyxenida (Fig. 3) – **Regions:** North America, Mexico/Central America (possibly excluding the Yucatan Peninsula), Caribbean Islands, South America, Atlantic Ocean Islands, Africa-Mediterranean, Africa-SubSahara, Indian Ocean Islands, Europe, Asia-Middle East (northern), Asia-Continental, Asia-Islands, Australia/New Zealand, Oceania. **Realms:** All (inhabited realms).
- Glomeridesmida (Fig. 7) – **Regions:** Mexico/Central America (excluding the Yucatan Peninsula), Caribbean Islands, South America, Asia-Continental, Asia-Islands, Oceania (western). **Realms:** Neotropical, Indo-Malay.
- Glomerida (Fig. 9) – **Regions:** North America, Mexico/Central America (northern and excluding the Yucatan Peninsula), Atlantic Ocean Islands, Europe, Asia-Middle East (northern, eastern), Asia-Continental, Asia-Islands. **Realms:** Nearctic, Neotropical (northern), Palearctic, Indo-Malay, Australasian (western).
- Sphaerotheriida (Fig. 13) – **Regions:** Africa-SubSahara (southern), Indian Ocean Islands, Asia-Continental, Asia-Islands, Australia/New Zealand. **Realms:** Afrotropical (southern), Indo-Malay, Australasian.
- Platydesmida (Fig. 17) – **Regions:** North America, Mexico/Central America, Europe, Africa-Mediterranean, Asia-Middle East (northern), Asia-Continental, Asia-Islands. **Realms:** Nearctic, Neotropical, Palearctic, Indo-Malay.
- Polyzoniida (Fig. 20) – **Regions:** North America, Mexico/Central America, South America, Atlantic Ocean Islands, Africa-SubSahara (primarily southern), Indian Ocean Islands, Europe, Asia-Middle East (northern), Asia-Continental, Asia-Islands, Australia/New Zealand, Oceania. **Realms:** All.
- Siphonophorida (Fig. 22) – **Regions:** North America, Mexico/Central America, Caribbean Islands, South America, Africa-SubSahara (southern), Indian Ocean Islands, Asia-Continental, Asia-Islands, Australia/New Zealand, Oceania. **Realms:** All.
- Siphonocryptida (Fig. 23) – **Regions:** Atlantic Ocean Islands, Asia-Continental, Asia-Islands. **Realms:** Palearctic, Indo-Malay.
- Julida (Fig. 26) – **Regions:** North America, Mexico/Central America (northern), Atlantic Ocean Islands, Europe, Africa-Mediterranean, Asia-Middle East, Asia-Continental, Asia-Islands. **Realms:** Nearctic, Neotropical (northern), Palearctic, Indo-Malay.
- Spirobolida (Fig. 28) – **Regions:** North America, Mexico/Central America, Caribbean Islands, South America, Africa-SubSahara, Indian Ocean Islands, Asia-Continental, Asia-Islands, Australia/New Zealand, Oceania. **Realms:** All.
- Spirostreptida (*sensu lato*) (Fig. 29) – **Regions:** North America, Mexico/Central America, Caribbean Islands, South America, Atlantic Ocean Islands, Africa-Mediterranean (western), Africa-SubSahara, Indian Ocean Islands, Asia-Middle East, Asia-Continental, Asia-Islands, Australia/New Zealand, Oceania (western). **Realms:** All.
- Cambalidea (Fig. 30) – **Regions:** North America, Mexico/Central America (northern), Asia-Continental, Asia-Islands, Australia/New Zealand, Oceania (western). **Realms:** Nearctic, Neotropical, Palearctic (southern), Indo-Malay, Australasian, Oceania (western).
- Epinannolenidea – **Regions:** North America, Mexico/Central America (southern), Caribbean Islands, South America, Atlantic Ocean Islands, Africa-SubSahara (southern), Australia/New Zealand. **Realms:** Nearctic, Neotropical, Afrotropical (southern), Australasian.
- Spirostreptidea (Fig. 34) – **Regions:** North America, Mexico/Central America, Caribbean Islands, South America, Atlantic Ocean Islands, Africa-Mediterranean (western), Africa-SubSahara, Indian Ocean Islands, Asia-Middle East, Asia-Continental, Asia-Islands. **Realms:** Nearctic, Neotropical, Palearctic (North Africa), Afrotropical, Indo-Malay.
- Callipodida (Fig. 37) – **Regions:** North America, Mexico/Central America (northern), Europe, Asia-Middle East (northern), Asia-Continental. **Realms:** Nearctic, Palearctic, Indo-Malay.
- Chordeumatida (Fig. 41) – **Regions:** North America, Mexico/Central America, South America (southwestern), Atlantic Ocean Islands, Indian Ocean Islands (Madagascar), Europe, Asia-Middle East (northern), Asia Continental, Asia-Islands, Australia/New Zealand. **Realms:** Nearctic, Neotropical, Palearctic, Afrotropical (Madagascar), Indo-Malay, Australasian.

Stemmiulida (Fig. 45) – **Regions:** Mexico/Central America, Caribbean Islands, South America, Africa-SubSahara, Asia-Continental, Asia-Islands. **Realms:** Neotropical, Afrotropical, Indo-Malay, Australasian.

Polydesmida (Fig. 46) – **Regions:** North America, Mexico/Central America, Caribbean Islands, South America, Atlantic Ocean Islands, Africa-Mediterranean, Africa-SubSahara, Indian Ocean Islands, Europe, Asia-Middle East, Asia-Continental, Asia-Islands, Australia/New Zealand, Oceania. **Realms:** All.

Siphoniulida (Fig. 23) – **Regions:** Mexico/Central America (northern), Asia-Islands (only from original discovery in 1888, 122 years ago). **Realms:** Neotropical (northern), Indo-Malay (only from original discovery).

Notes: (1) There are no exclusively Holarctic diplopod orders and none that are endemic to a single area or biogeographical realm. Glomerida, Platydesmida, Julida, and Callipodida (Fig. 9, 17, 26, 30) are **primarily** Holarctic, but the first three nip the northern extremity of the Neotropics, and all occur well southward into the Indo-Malay Realm.

(2) Siphoniulida is the only order occurring in both two areas (Mexico/Central America, Asia-Islands) and two realms (Neotropical, Indo-Malay). Siphonocryptida occurs in three areas (Atlantic Ocean Islands, Asia Continental [Nepal, Peninsular Malaysia], and Asia-Islands [Taiwan, Sumatra]) but only two realms (Palearctic, Indo-Malay).

(3) Six orders occur in all inhabited biogeographical realms – Polyxenida, Polyzoniida, Siphonophorida, Spirobolida, Spirostreptida *s. l.*, and Polydesmida.

(4) Polyxenida, Polyzoniida (including the possible introduction on St. Helena) and Polydesmida are the only orders occurring in all geographical areas.

Table 4. Ordinal Inhabitants per Biogeographical Realm.

- Nearctic** – 14 ordinal taxa (11 orders): Polyxenida, Glomerida, Platydesmida, Polyzoniida, Siphonophorida, Julida, Spirobolida, Spirostreptida *s. l.*, Cambalidea, Epinannolenidea, Spirostreptidea, Callipodida, Chordeumatida, Polydesmida.
- Neotropical** – 16 ordinal taxa (13 orders): Polyxenida, Glomeridesmida, Glomerida (northern), Platydesmida (northern), Polyzoniida, Siphonophorida, Julida (northern), Spirobolida, Spirostreptida *s. l.*, Cambalidea (northern), Epinannolenidea, Spirostreptidea, Chordeumatida, Stemmiulida, Polydesmida, Siphoniulida.
- Afrotropical** – 11 ordinal taxa (9 orders): Polyxenida, Sphaerotheriida (southern), Polyzoniida (southern), Siphonophorida (southern), Spirobolida, Spirostreptida *s. l.*, Epinannolenidea (southern), Spirostreptidea, Chordeumatida (Madagascar), Stemmiulida, Polydesmida.
- Paleartic** – 13 ordinal taxa (11 orders): Polyxenida, Glomerida, Platydesmida, Polyzoniida, Siphonocryptida, Julida, Spirobolida (eastern, China), Spirostreptida *s. l.*, Cambalidea (Iran, southern China), Spirostreptidea (Morocco, Israel), Callipodida, Chordeumatida, Polydesmida.
- Indo-Malay** – 18 ordinal taxa (16 orders): Polyxenida, Glomeridesmida, Glomerida, Sphaerotheriida, Platydesmida, Polyzoniida, Siphonophorida, Siphonocryptida, Julida, Spirobolida, Spirostreptida *s. l.*, Cambalidea, Spirostreptidea, Callipodida, Chordeumatida, Stemmiulida, Polydesmida, Siphoniulida.
- Australasian** – 13 ordinal taxa (10 orders): Polyxenida, Glomerida, Sphaerotheriida, Polyzoniida, Siphonophorida, Spirobolida, Spirostreptida *s. l.*, Cambalidea, Epinannolenidea, Spirostreptidea, Chordeumatida, Stemmiulida, Polydesmida.
- Oceania** – 5 ordinal taxa and orders: Polyxenida, Glomeridesmida, Polyzoniida, Siphonophorida, Polydesmida.

Table 5. Ordinal Occurrences per Geographical Area.

- North America (Canada, United States)** – 14 ordinal taxa (11 orders): Polyxenida, Glomerida, Platydesmida, Polyzoniida, Siphonophorida (southwestern), Julida, Spirobolida, Spirostreptida *s. l.*, Cambalidea, Epinannolenidea, Spirostreptidea (southwestern), Callipodida, Chordeumatida, Polydesmida.
- Mexico/Central America** – 17 ordinal taxa (14 orders): Polyxenida, Glomeridesmida, Glomerida, Platydesmida, Polyzoniida, Siphonophorida, Julida (northern), Spirobolida, Spirostreptida *s. l.*, Cambalidea, Epinannolenidea, Spirostreptidea, Callipodida (northern), Chordeumatida, Stemmiulida, Polydesmida, Siphoniulida (restricted).
- Caribbean Islands** – 9 ordinal taxa (6 orders): Polyxenida, Glomeridesmida, Siphonophorida, Spirobolida, Spirostreptida *s. l.*, Epinannolenidea, Spirostreptidea, Stemmiulida, Polydesmida.
- South America** – 11 ordinal taxa (9 orders): Polyxenida, Glomeridesmida, Polyzoniida, Siphonophorida, Spirobolida, Spirostreptida *s. l.*, Epinannolenidea, Spirostreptidea, Chordeumatida (southwestern), Stemmiulida, Polydesmida.
- Atlantic Islands** – 10 ordinal taxa (8 orders): Polyxenida, Glomerida, Polyzoniida, Siphonocryptida, Julida, Spirostreptida *s. l.*, Epinannolenidea, Spirostreptidea, Chordeumatida, Polydesmida.
- Africa-Mediterranean** – 8 ordinal taxa (7 orders): Polyxenida, Glomerida, Platydesmida, Julida, Spirostreptida *s. l.*, Spirostreptidea (northwestern), Chordeumatida, Polydesmida.
- Africa-Sub-Saharan** – 10 ordinal taxa (8 orders): Polyxenida, Sphaerotheriida (southern), Polyzoniida (primarily southern), Siphonophorida (southern), Spirobolida, Spirostreptida *s. l.*, Epinannolenidea (southern), Spirostreptidea, Stemmiulida, Polydesmida.
- Madagascar and Indian Ocean Islands (except Sri Lanka)** – 9 ordinal taxa (8 orders): Polyxenida, Sphaerotheriida, Polyzoniida, Siphonophorida, Spirobolida, Spirostreptida *s. l.*, Spirostreptidea, Chordeumatida (Madagascar), Polydesmida.
- Europe** – 8 ordinal taxa and orders: Polyxenida, Glomerida, Platydesmida, Polyzoniida, Julida, Callipodida, Chordeumatida, Polydesmida.
- Asia-Middle East (Cyprus, Turkey and Arabian Peninsula)** – 10 ordinal taxa (9 orders): Polyxenida, Glomerida, Platydesmida, Polyzoniida, Julida, Spirostreptida *s. l.*, Spirostreptidea, Callipodida, Chordeumatida, Polydesmida.
- Asia-Continental** – 17 ordinal taxa (15 orders): Polyxenida, Glomeridesmida, Glomerida, Sphaerotheriida, Platydesmida, Polyzoniida, Siphonophorida, Siphonocryptida, Julida, Spirobolida, Spirostreptida *s. l.*, Cambalidea, Spirostreptidea, Callipodida, Chordeumatida, Stemmiulida, Polydesmida. Missing only Siphoniulida.
- Asia-Islands** – 17 ordinal taxa (15 orders): Polyxenida, Glomeridesmida, Glomerida, Sphaerotheriida, Platydesmida, Polyzoniida, Siphonophorida, Siphonocryptida, Julida, Spirobolida, Spirostreptida *s. l.*, Cambalidea, Spirostreptidea, Chordeumatida, Stemmiulida, Polydesmida, Siphoniulida. Missing only Callipodida.
- Australia and New Zealand** – 10 ordinal taxa (8 orders): Polyxenida, Sphaerotheriida, Polyzoniida, Siphonophorida, Spirobolida, Spirostreptida *s. l.*, Cambalidea, Epinannolenidea, Chordeumatida, Polydesmida.
- Oceania** – 6 ordinal taxa and orders: Polyxenida, Glomeridesmida, Polyzoniida, Siphonophorida, Spirobolida, Polydesmida.

Table 6. Events and Approximate Dates in Early Diplopod Evolution.

Era, Period	Approximate Date (ma)	Major Events	Major Land Forms	Major Results and Consequences
Paleozoic, Mid-Cambrian	>524	Origin from marine ancestor on or near Avalonia terrane of Gondwana I	Gondwana I (incl. Avalonia), Baltica, Laurentia, Siberia, Kazakhstania	Evolution begins, as ancestral form(s) crawl onto Avalonia, disperse onto Gondwana I proper, and radiate explosively into the empty terrestrial environments in the absence of predators and with all niches vacant and unoccupied.
Paleozoic, Mid-Cambrian - Early Ordovician	524 – 480	Class traits evolve; major divergences/dichotomies take place	Gondwana I (incl. Avalonia), Baltica, Laurentia, Siberia, Kazakhstania	Penicillata/Chilognatha, Pentazonia/Helminthomorpha, Colobognatha/Eugnatha, Julida/Nematophora/Merocheta diverge; Polyxenida, Siphoniulida, Siphonocryptida, Polyzoniida, Spirostreptida <i>s.l.</i> /Cambalidea, Chordeumatida, Polydesmida arise and spread between Avalonia and Gondwana I proper.
Paleozoic, Early Ordovician	480	Avalonia rifts from Gondwana I and begins drifting northward towards Baltica,	Gondwana I, Avalonia, Baltica, Laurentia, Siberia, Kazakhstania	Ancestral populations of Pentazonia, Colobognatha, Eugnatha, and Nematophora are partitioned between Avalonia and Gondwana I, as are ones of the existing ordinal taxa: Polyxenida, Polyzoniida, Siphonocryptida, Cambalidea, Chordeumatida, Polydesmida, Siphoniulida.
Paleozoic, Ordovician	480-450	Avalonia and Baltica converge	Gondwana I, Laurentia, Siberia, Kazakhstania; Avalonia; Baltica	Glomeridesmida, Sphaerotheriida, Siphonophorida, Spirobolida, Epinannolenidea, Spirostreptidea, Stemmiulida arise and disperse on Gondwana I; partitioned Gondwanan populations of Polyxenida, Polyzoniida, Siphonocryptida, Cambalidea, Chordeumatida, Polydesmida, Siphoniulida evolve and disperse farther; little to no divergence, dispersal, or advancement among forms on Avalonia
Paleozoic, Late Ordovician	450	Avalonia collides with Baltica	Gondwana I, Avalonia + Baltica, Laurentia, Siberia, Kazakhstania	Forms confined to drifting Avalonia terrane for 30 my disperse into Baltica and radiate explosively into the empty terrestrial environments with all niches vacant; probable burst of evolution and origins of Glomerida, Platydesmida, Julida, Callipodida; divergences and dispersals continue among forms on Gondwana I.
Paleozoic, Early Silurian	440	Baltica + Avalonia collides with Laurentia forming Euramerica	Gondwana I, Euramerica, Siberia, Kazakhstania	Forms on Baltica + Avalonia disperse onto Laurentia, again radiating explosively into the new land with empty terrestrial environments and all niches vacant; probable second burst of evolution further differentiating Glomerida, Platydesmida, Julida, Callipodida, and possibly also Cambalidea and Polydesmida; divergences and dispersals continue on Gondwana I.

Table 6. Continued

Era, Period	Approximate Date (ma)	Major Events	Major Land Forms	Major Results and Consequences
Paleozoic, Late Silurian	415	North China terrane rifts from Gondwana I	Gondwana I, Euramerica, Siberia, Kazakhstania, N China terrane	Gondwana I spirobolidans partitioned, those on N China terrane begin transit to Siberia (+ Kazakhstania); forms on Euramerica differentiate and disperse farther into it; dispersals and differentiations continue on Gondwana I; <i>Archidesmus macnioli</i> fossilizes in "proto-Scotland."
Paleozoic, Early Devonian	400	Kazakhstania grows; S China and SE Asia terranes rift from Gondwana I	Euramerica, Siberia, Kazakhstania, Gondwana I, N and S China terranes, SE Asia terranes	Spirobolidans on N China terrane continue passive transit northward; dispersions continue on Euramerica and Gondwana I.
Paleozoic, Late Devonian	370	Siberia and Kazakhstania merge; Proto- and Paleotethys oceans filled with drifting Gondwana I terranes	Euramerica, Siberia + Kazakhstania, Gondwana I, N and S China terranes, SE Asia terranes	Spirobolidans on N China terrane continue passive transit northward; dispersions continue on Euramerica and Gondwana I.
Paleozoic, Early Carboniferous	356	Euramerica merges with Siberia + Kazakhstania; N China terrane continues to drift northward; S China and SE Asia terranes in transit	Euramerica + Siberia + Kazakhstania, Gondwana I, N and S China terranes, SE Asia terranes.	Forms on Euramerica released into Siberia + Kazakhstania; spirobolidans on N China terrane continue passive transit northward; dispersions continue on Euramerica and Gondwana I.
Paleozoic, Late Carboniferous	306	Euramerica + Siberia + Kazakhstania collides with "proto-Colombia/Venezuela" margin of "proto-South America/Africa" area of Gondwana I forming western half of Pangaea	West Pangaea, N. and S. China terranes, other Southeast Asia terranes	Forms evolving on Euramerica and Gondwana I mix for first time; Glomeridesmida, Siphonophorida, Spirobolida, Spirostreptidea, Stemmiulida spread directly into "proto-Mexico from "proto-South America" and then to "proto-southwestern US"; Illinois pentazonian fossilizes; dispersions continue on Euramerica and Gondwana I.
Paleozoic, Early Permian	270	Gondwana I terranes drift closer to Siberia + Kazakhstania part of West Pangaea	West Pangaea, N and S China terranes, SE Asia terranes	Continued north and south dispersals in West Pangaea by Glomeridesmida, Siphonophorida, Spirobolida, Spirostreptidea, Stemmiulida; continued dispersals elsewhere on West Pangaea and "proto-Gondwana II."

Table 6. Continued

Era, Period	Approximate Date (ma)	Major Events	Major Land Forms	Major Results and Consequences
Paleozoic, Late Permian	255	N China terrane merges with Siberia + Kazakhstania part of West Pangaea; S China and SE Asia terranes continue drifting; Cimmeria begins to rift from Gondwana II part of Pangaea	West Pangaea + N China; S China and SE Asia terranes; Cimmeria	Spirobolidans on N China terrane released into Siberia + Kazakhstania; continued north/south dispersals in Mexican part of West Pangaea; continued dispersals on rest of West Pangaea and "proto-Gondwana II."
Mesozoic, Early Triassic	250	Pangaea/Laurasia a nearly completely assembled; S China, Indochina/Malay terranes nearly merged with "proto-Laurasia"; other SE Asia terranes approaching; Cimmeria drifting	Pangaea; S China, Indochina/Malay, SE Asia terranes; Cimmeria	Glomerida, Platydesmida, Julida, Callipodida begin dispersing east/southeastward along southern margin of accreted terranes; continued dispersals on West Pangaea and "proto-Gondwana II"; continued north/south dispersals in Mexico part of West Pangaea.
Mesozoic, Late Triassic	220	S China terrane merges with Eurasia part of "proto-Laurasia"; SE Asia terranes and Cimmeria approach latter.	Pangaea, SE Asia terranes, Cimmeria	Forms on Euramerica continue dispersing southeastward, spread into newly accreted S China and mix with Gondwana I inhabitants that disperse outward; continued dispersal on "proto-Gondwana II"; continued north/south dispersals in "proto-Mexico" part of West Pangaea.
Mesozoic, Early Jurassic	195	SE Asia terranes accrete to "proto-Laurasia," Pangaea now fully assembled; Cimmeria begins merging with southwestern border of "proto-Laurasia".	Pangaea, Cimmeria	Forms on Euramerica continue spreading and now disperse into SE Asia and "proto-western Indonesian islands," mix with Gondwana I inhabitants that begin dispersing north/northwestward.

Table 6. Continued

Era, Period	Approximate Date (ma)	Major Events	Major Land Forms	Major Results and Consequences
Mesozoic, Late Jurassic	152	Pangaea rifts into Laurasia + Gondwana II; Central America begins to form on southern border of Mexico; Cimmeria continues merging with Laurasia	Laurasia, Gondwana II	"Proto-Mexican" forms of Siphonophorida, Spirobolida, Spirostreptidea, Glomeridesmida, Stemmiulida disperse southward into "proto-Central America."
Mesozoic, Late Cretaceous	94	India separates from Madagascar; embayment divides North American part of Laurasia; Cimmeria completely merged with Laurasia	Laurasia, western North America, Africa, India, Madagascar, South America + Antarctica + Australia + New Zealand	Glomerida, Platydesmida, Julida, Callipodida on North America partitioned into separate eastern and western populations; continued southeast and northwestward dispersals in SE Asia; continued dispersals on Gondwana II fragments; formerly continuous European/North African populations of Glomerida, Platydesmida, Julida, and Chordeumatida partitioned; continuous stemmiulid fauna through west Africa and eastern Brazil partitioned; continuous faunas of India and Madagascar partitioned; <i>Gobiulus sabulosus</i> fossilizes in present-day Mongolia.
Mesozoic/Cretaceous-Cenozoic/Paleocene	66	India drifts northward; Madagascar locks to African plate; North American embayment begins closing in north; Laurasia rifts into North America + Greenland and Eurasia; "proto-Antilles" rift from South America, begin drifting northward and fragmenting	North America, Eurasia, Africa, India, Madagascar, South America + Antarctica + Australia + New Zealand, "proto-Antilles."	Formerly continuous North American/European populations of Glomerida, Platydesmida, Julida, Cambalidea, Chordeumatida, Polydesmida partitioned, Cambalidea becoming extinct in Europe by Oligocene; South American populations of Glomeridesmida, Siphonophorida, Spirobolida, Epinannolenidea, Spirostreptidea, Stemmiulida, and Polydesmida partitioned between South America and "proto-Antilles."

Table 6. Continued

Era, Period	Approximate Date (ma)	Major Events	Major Land Forms	Major Results and Consequences
Cenozoic, Eocene	50	India collides with Eurasia, Himalayan Orogeny begins; Australia + New Guinea split from South America + Antarctica; North American embayment fully closed; "proto-Antilles" continue drifting northward and fragmenting	North America, Eurasia + India, Africa, Madagascar, New Zealand, Australia + New Guinea, South America + Antarctica	Julida and Callipodida begin dispersing into and filling void in central North America caused by Cretaceous embayment, generating continuous faunas of today and spreading southward into Mexico/northern Central America; Glomerida, Platydesmida, Polyzoniida, Julida, Cambalidea, Chordeumatida, Polydesmida spread southward into Mexico/Central America; continuous fauna between Australia and Antarctica broken.
Cenozoic, Late Miocene	14	Central America nearly formed; Antilles in place; Arabian peninsula begins rifting from Africa; SE Asia islands isolated by water; North America essentially complete except for Florida; South America separates from Antarctica	North/"proto-Central America, Antilles, South America, Eurasia incl. India, Africa/Arabia, Madagascar, Australia + New Guinea, New Zealand, Antarctica	Continued dispersals southward of Glomeridesmida, Siphonophorida, Spirobolida, Spirostreptida, Stemmiulida, Polydesmida in Central America; Antarctica freezes and glaciates, eradicating all diplopods thereon.

APPENDIX: New records impacting ordinal distributions.

For those in the US, complete locality and sampling data are provided for states with six or fewer counties; counties alone are listed for states with more than six counties. In some cases, numbers of each sex were counted and are provided; in others, total numbers of individuals are given after repositories; in still others sexes and numbers of individuals were not counted or are irrelevant. Missing sample data were not provided on vial labels.

POLYXENIDA: POLYXENIDAE***Polyxenus* spp.**

NORTH AMERICA: USA: ALABAMA: *Jackson Co.*, Princeton, 29 October 1960, H. R. Steeves (FSCA). *Shelby Co.*, Calera, 18 June 1959, W. Suter (FMNH). ARIZONA: *Coconino Co.*, Grand Canyon National Park, South Rim, 14 October 1985, M.W. Sanderson (NCSM). *Pima Co.*, along Little Rollito Cr., 24 August 1986, C.A. Olson (UAIC); and Organ Pipe Cactus National Monument, along Alamo Cr., 28 November 1987, C.A. Olson (UAIC). *Pinal Co.*, Peppersauce Canyon, Santa (Sta.) Catalina Mts., 24 February 1988, C.A. Olson (UAIC). ARKANSAS: *Stone Co.*, Blanchard Spgs., 12 November 1966, P.H. Freytag (FSCA). CALIFORNIA: *Alameda, Contra Costa, Humboldt, Los Angeles, Marin, Mendocino, Napa, Nevada, Orange, Plumas, Riverside, San Francisco, San Joaquin, San Luis Obispo, San Mateo, Santa Barbara, Santa Clara, Shasta, Solano, Sonoma, Tehama, Trinity, and Ventura cos.* (AMNH, CSCA, FSCA, LACM, EMEC, UCDC, USNM). COLORADO: *El Paso Co.*, Ute Pass, 15 January 1981, B. Reid (USNM). *Larimer Co.*, Ft. Collins, below Horsetooth Res., 7 November 1980, T.A. Woolley (NCSM); and along Poudre R. off CO hwy. 14, Young Gulch, 16 March 1991, C.R. Nelson (BYUC). CONNECTICUT: *Fairfield Co.*, Stamford, July 1952, W.W. Cantelo (USNM). *New Haven Co.*, Woodbridge, 3 December 1934, A. Barter (PMNH) and 11 May 1961, C.L. Remington (PMNH); and Mt. Carmel, 11 January and 11 October 1941, W.M. Summersby (MCZC, USNM). DELAWARE: *Sussex Co.*, Bethel, M. Creary (UDDC). **New State Record.** DISTRICT OF COLUMBIA: *Rock Creek Park*, 7 December 1913, R.C. Shannon (USNM). GEORGIA: *Camden Co.*, Cumberland Island National Seashore, under boards on beach, 22 September 1976, R.E. Woodruff (FSCA). *Dougherty Co.*, 24 km (15 mi) W Albany, Talasse Swamp, 28 March 1964, C. Johnson, J. Fowler (FMNH). *Glynn Co.*, Jekyll I., 18 August 1965, W. Suter (FMNH). *Muscogee Co.*, Columbus, 20 August 1948, L.W. Cunningham (USNM) **New State Record.** ILLINOIS: *Jersey Co.*, Grafton, 30 September 1943, M.W. Sanderson (USNM). KANSAS: *Lyon Co.*, Emporia, Emporia State Univ., 1986, C. Prophet (NCSM) **New State Record.** LOUISIANA: *Calcasieu Par.*, 5 January 1966, M. Kordish (FSCA). *East Baton Rouge Par.*, Baton Rouge, 4 October 1963, N. Hepburn (FSCA). *West Feliciano Par.*, Starhill, 4 September 1963, N. Hepburn (FSCA) **New State Record.** MARYLAND: *Montgomery Co.*, Plummer's I., 20 July 1902, H.S. Barber (USNM). *Prince Georges Co.*, Cheverly, 28 November 1991, W.E. Steiner, J.M. Swearingen (USNM). *Talbot Co.*, Jefferson I., 29 April 1980, A.K. Johnson (TMMC). MISSISSIPPI: *Hancock Co.*, St. Louis Bayou N of Jourdan R., 18 December 1982, M.W. LaSalle (NCSM). *Franklin Co.*, along tributary of McGehee Cr., 27 July 1992, R.L. Brown, T.L. Schiefer (MEMU). *Jackson Co.*, Ocean Springs, 1 October 1958 (FSCA). *Oktibbeha Co.*, 12.8 km (8 mi) NE Starkville, 11 August 1981, P.R. Miller (MEMU); and Noxubee National Wildlife Refuge, 7 July 1982, R.L. Brown (MEMU). *Pontotoc Co.*, 1.6 km (1 mi) SE Ecu, 10 October 1980, G.L. Snodgrass (MEMU). MONTANA: *Lake Co.*, 13.8 km (8.6 mi) S Flathead Lake Biological Station, along MT hwy. 35, 3 June 1996, C.R. Nelson (BYUC). *Missoula Co.*, Missoula, 21 March 1978, D. Peressini (MTEC). NEBRASKA: *Dawes Co.*, Thompson Res. near Chadron, 28 August 1987, H.R. Lawson (NCSM); and E. Chadron, 330 Beaver Valley Rd., 5 May 2005, H.R. Lawson (NCSM) **New State Record.** NEW MEXICO: *Bernalillo Co.*, Alameda, 1 October 2002, C.S. Crawford (NCSM). *Los Alamos Co.*, White Rock, 2 March 1994, D. Fagerlund (NCSM). *Taos Co.*, Taos, 2 March 1995, D. Fagerlund (NCSM) **New State Record.** NEW YORK: *Monroe Co.*, Rochester, 24 August 1970, W.B. Muchmore (WASC). *Ontario Co.*, 6.4 km (4 mi) NW Naples, 19 June 1971, W.B. Muchmore (WASC). *Tompkins Co.*, Ithaca, 3 October 1975, T.L. McCabe (NCSM). *Wayne Co.*, Marion, 15 May 1955, R.L. Hoffman (USNM). NORTH CAROLINA: *Dare Co.*, Salvo, Cape Hatteras National Seashore, 13 July 1982, T.J. Spillman (USNM). OHIO: *Ottawa Co.*, Middle and South Bass Islands, 18 and 27 June 1968, A.A. Weaver (NCSM); Gibraltar I., Put-in Bay, 15 July 1965 and 28 June 1971, A.A. Weaver (NCSM). OREGON: *Benton, Clackamas, Clatsop, Columbia,*

Coos, Curry, Douglas, Jackson, Lane, Lincoln, Linn, Polk, Wallowa, and Yamhill cos. (AMNH, FMNH, FSCA, UCDC, USNM, WASC, WSUC). PENNSYLVANIA: *Center Co.*, State College, 17 September 1952, S.W. Frost (PSUC). RHODE ISLAND: *Washington Co.*, Shannock, 1 February 1971, A.G. Olavallee (UGCA) **New State Record**. SOUTH CAROLINA: *Aiken Co.*, jct. I-20 and SC hwy. 230, 9 October 1975, D.P. Wojcik (FSCA). TENNESSEE: *Fentress Co.*, Cumberland Mts., near Wilder, 22 July 1956, Lackey (FMNH). *Scott Co.*, 1.6 km (1 mi) S New River, 20 December 1964, H.S. Dybas (FMNH). TEXAS: *Cameron Co.*, Brownsville, H.S. Barber (USNM) and 21 December 1937, Reagan (USNM). *Garza Co.*, 6.4 km (4 mi) ENE Justiceburg, Rowland (WASC). *Kendall Co.*, 16 km (10 mi) N Boerne, 1 April 1965, J.R. Reddell (FSCA). *Travis Co.*, Austin, Brackenridge Field Lab., 14 June 1991, C.R. Nelson (BYUC). UTAH: *Cache Co.*, Logan Canyon, 2 November 1968, G.F. Knowlton (USNM); and Providence, 1 June 1970, G.F. Knowlton (WASC). *Davis Co.*, Kaysville, 9 April 1970, G.F. Knowlton (USNM). *Salt Lake Co.*, Salt Lake City, Ft. Douglas, 12 July 1951, Y.M. Wang (USNM) **New State Record**. VIRGINIA: *Amherst Co.*, Blue Ridge Pkwy., Otter Cr., 18 October 1965, J. and W. Ivie (AMNH) **New State Record**. WASHINGTON: *Benton, Chelan, Clallam, Cowlitz, Island, King, Kittitas, Klickitat, Mason, Pierce, Skagit, Skamania, Snohomish, and Whatcom cos.* (UWBM, WSUC). WEST VIRGINIA: *Mercer Co.*, Brunch Creek Falls, 27 February 1972, W.A. Shear (WASC). *Summers Co.*, Bluestone, 17 June 1966, W.A. Shear (WASC) **New State Record**.

OCEANIA: USA: HAWAII: *Oahu*, Waikakaleia Gulch, 10 November 1952 (USNM).

GLOMERIDESMIDA: GLOMERIDESMIDAE

Glomeridesmus sp.

LESSER ANTILLES: DOMINICA: Long Diton, 17 June 1911 (AMNH-3). TRINIDAD and TOBAGO: *Tobago*, Bloody Bay, 7 July 1999, R.M. Shelley (NCSM-2); and English Bay, 9 July 1999, R.M. Shelley (NCSM-1) **New Island Record**. *Trinidad, St. George Co.*, Arima, 16 July 1969, L.N. Sorkin (AMNH); and Tamana Hall, February 1971, J.A.L. Cooke (AMNH-1).

MEXICO: TABASCO: Teapa, Las Grutas de Cocona, 11 August 1948, Goodnights (AMNH-1). VERACRUZ, 6.4 km (4 mi) N Catemacu, 28 August 1970, E. and J. Fisher (LACM-1); and 12.8 km (8 mi) N Santecompan, 29 August 1970, E. and J. Fisher (LACM-1).

CENTRAL AMERICA: COSTA RICA: Las Cruces, F, 7 July 1977, E.A. Sugden (UCDC).

SOUTH AMERICA: BOLIVIA: SANTA CRUZ: Buena Vista (17° 27'S, 63° 40'W), 350m, F, 18 July 1993, P.S. Ward (UCDC) **New Country Record and Southernmost Record of the Genus, Family, Order, and Infraclass in the New World**. BRAZIL: PARÁ: Ilha de Mosquito, 20 June 1974, R.T. Schuh (AMNH-6). COLOMBIA: AMAZONAS: 2 km (1.3 mi) N Leticia, along rd. to lakes behind airport, 10 July 1977, R.M. Shelley (NCSM-1). CUNDINARMARCA: Anolaima, 15 July 1967, P. Wygodzinsky (AMNH-1). VALLE, El Saladito and 5 km (3.1 mi) W Delfino, 26 and 29 August 1967, P. Wygodzinsky (AMNH-2). ECUADOR: COTOPAXI: NW slope Mt. Cotopaxi, 26 July-5 August 1969, P. and B. Wygodzinsky (AMNH-1). PERU: HUANUCO: 20 km (32 mi) NE Huanuco, Carpish Mts., F, 28 December 1954, E.S. Ross, E.I. Schlinger (CASC); and confluence of Rios Pachitea and Luillapichta, F, juv., 24 January – 13 February 1975, C.A. Toft (UCDC). LORETO: 80 km (50 mi) upstream from Benjamin Constant, Brazil, along trail from Yagua village, 21 July 1977, R.M. Shelley (NCSM-1). **New Country Record for Genus, Family, and Order**.

ASIA: MALAYSIA: EASTERN MALAYSIA: SARAWAK: Gunung Mulu National Park, Manday Cv., 13 May 1978 and 22 December 1980, P.J. Chapman (VMNH-3), and Leopard Cv., 18 December 1980 (VMNH-1). INDONESIA: JAVA: Tjibodes (6°46'54"S, 107°30'17"E, NNW of Bandung), juv., August 1921, Dammerman (AMNH).

OCEANIA: FIJI: VITI LEVU: Nandarivatu, berlese of elfin forest litter, 1100m, 16-20 August 1978, S. and J. Peck (FMNH-5) **New Country and Island Record**.

Termitodesmus sp.

ASIA: VIETNAM: DONG NAI: Cat Tien National Park, termite nest, F, May 2008, A. Anichkin (ZMUM).

GLOMERIDA: GLOMERIDAE***Onomeris* spp.**

NORTH AMERICA: USA: ALABAMA: *Bibb, Blount, Bullock, Calhoun, Cherokee, Chilton, Choctaw, Clarke, Clay, Cleburne, Colbert, Conecuh, Coosa, Covington, Crenshaw, Cullman, Dale, Elmore, Franklin, Henry, Jackson, Jefferson, Lauderdale, Lee, Lowndes, Madison, Marshall, Mobile, Monroe, Morgan, Pike, Randolph, Shelby, St. Clair, Sumter, Talladega, Tallapoosa, Tuscaloosa, Walker, and Wilcox* cos. (FSCA, MCZC, SMNH, USNM, VMNH) **New State Record.** FLORIDA: *Jackson Co.*, Florida Caverns State Park, MM, FF, juvs., 27 May 1958, 14 April 1960, 31 July 1960, 21 April 1967, N.B. Causey, H.V. Weems, L. Hubricht, P.C. Drummond (FSCA). *Liberty Co.*, Torreya State Park, MM, FF, juvs., 21 and 24 - 25 January 1965, N.B. Causey, H.V. Weems (FSCA, VMNH). **New State Record.** GEORGIA: *Baldwin, Chatham, Dade, Dawson, Decatur, DeKalb, Effingham, Floyd, Gilmer, Gordon, Jasper, Laurens, Lincoln, Meriwether, Monroe, Pickens, Rabun, Richmond, Talbot, Taliaferro, Towns, Upson, Walker, Washington, White, and Wilkinson* cos. (AMNH, FSCA, MCZC, NCSM, USNM, VMNH). KENTUCKY: *Anderson, Barren, Edmonson, Jackson, Meade, Menifee, Mercer, Metcalf, and Warren* cos. (FSCA, VMNH). MISSISSIPPI: *Choctaw, Clarke, Forrest, Harrison, Itawamba, Jackson, Jasper, Lamar, Lauderdale, Stone, Tishomingo, and Wayne* cos. (FSCA, NCSM, USNM, VMNH). NORTH CAROLINA: *Graham, Haywood, Jackson, Macon, Madison, Swain, and Transylvania* cos. (AMNH, MCPM, NCSM, USNM, SIUC, VMNH). SOUTH CAROLINA: *Aiken, Beaufort, Charleston, Edgefield, Jasper, Oconee, and Saluda* cos. (NCSM, VMNH). TENNESSEE: *Anderson, Blount, Campbell, Cocke, Coffee, DeKalb, Franklin, Greene, Grundy, Hamilton, Hardin, Hawkins, Knox, Lincoln, Loudon, Macon, Marion, Meigs, Monroe, Morgan, Polk, Roane, Scott, Sevier, Smith, Trousdale, and White* cos. (FMNH, FSCA, VMNH). **New State Record.** VIRGINIA: *Dickenson Co.*, 8 km (5 mi) W Haysi, along Crane's Nest Branch Creek, MM, FF, juvs., 11 and 21 April 1962, R.L. Hoffman (VMNH); and 5.6 km (3.5 mi) SE Clintwood, MM, FF, 8 May 1975, L. Hubricht (VMNH). *Lee Co.*, Cudjo's Cv., 23 and 29 June 1950, A. Fowler, R.L. Hoffman (VMNH-2); and Cave Hollow, M, 14 November 1967, T.C. Barr (FSCA). **New State Record.**

***Glomeroides primus* (Silvestri, 1929)**

NORTH AMERICA: USA: CALIFORNIA: *Contra Costa Co.*, Redwood Park, MM, FF, juvs., 18 and 28 May 1953, R.O. Schuster, E.E. Gilbert (FSCA, USNM); and *Morega Redwoods*, end of Linehurst Rd., 2M, 26 May 1985, T.S. Briggs, T. Ohumi (CASC). *Santa Cruz Co.*, Ben Lomond, MM, FF, 21 June 1953, C. D. MacNeill (FSCA); and *Santa Cruz, City Cv.*, M, 31 January 1960, collector unknown (FSCA).

***Glomeroides ?promiscus* Causey, 1964**

MEXICO: TAMAULIPAS: *Sótano de Gómez Farias*, 5 km (3.1 mi) E Gómez Farias, M, 3F, 6 December 1964, T. Raines (TMMC). *Sótano de El Naranjo*, Gómez Farias, F, 23 October 1971, T. Raines (TMMC). *Sótano de Tres Manantiales*, 15 km (9.4 mi) SW Gómez Farias, M, January 1972, W. Russell (TMMC). *Cueva del Rio Frio*, F, 18 April 1965, J. Fish, J.R. Reddell (TMMC). *Mine Cv.*, *Rancho del Cielo*, F, and unnamed caves #3 and #7, 2F, 3 June 1964, J.R. Reddell, D. McKenzie, L. Manila (TMMC).

***Glomeroides* spp.**

MEXICO: SAN LUIS POTOSÍ: *Sótano de Tlamaya*, 2M, 2 July 1965, T. Raines, J. Fish (TMMC). *Sótano de Quita*, 10 km (6.3 mi) S Aquismon, M, January 1974, P. Strickland (TMMC).

PLATYDESMIDA: ANDROGNATHIDAE***Andrognathus corticarius* Cope, 1869**

NORTH AMERICA: USA: ALABAMA: *Barbour Co.*, 4.3 km (2.7 mi) S Eufaula, along US hwy. 431, 0.8 km (0.5 mi) S jct. AL hwy. 30, 29 April 1983, R.M. Shelley (NCSM-2). *Clay Co.*, Talladega National Forest, 10 April 1965 (FSCA-5). *Coosa Co.*, 9.6 km (6 mi) S Sylacauga, 18 September 1959, H.R. Steeves (FSCA-6). *DeKalb Co.*, Ft. Payne, DeSoto Falls, 28 June 1966, A.A. Weaver (NCSM-1). *Etowah Co.*, Gadsden, Nocaluca Falls, 1958, N.B. Causey (FSCA-1). *Lee Co.*, Auburn, 19 January 1937, C.F. Baker (USNM-10); and 4.8 km (3 mi) N Auburn, along AL hwy. 143 at Saugahatchee Cr., April 1973, T. French

(AUEM-2). *St. Clair Co.*, 5.2 km (3.2 mi) E Springville, 3 July 1974, L. Hubricht (VMNH-3). *Tuscaloosa Co.*, 2.7 km (1.7 mi) W Peterson, 23 June 1959, W.T. Keeton, B.D. Valentine, Lund (VMNH-1). **FLORIDA:** *Gadsden Co.*, Quincy, 3-6 October 1928, O.F. Cook (USNM, VMNH). *Liberty Co.*, Torreya State Park, 31 March 1964, A.A. Weaver (NCSM-3). **First Definite State Record.** **GEORGIA:** *Fulton Co.*, Fort McPherson, 9 December 1943, D.E. Beck (USNM). *Hall Co.*, Gainesville (USNM). *Haralson Co.*, Tallapoosa, 29 July 1910, R. V. Chamberlin (USNM-1). *Polk Co.*, Cave Spring, 1958, N.B. Causey (FSCA-1). *Stephens Co.*, Toccoa Lake, 10 October 1928, ?O.F. Cook (USNM-1). **SOUTH CAROLINA:** *Chesterfield Co.*, Cheraw State Park, 5 November 1979, J.F. Cornell (NCSM-1). *Oconee Co.*, along SC hwy. 28 12.8 km (8 mi) S Highlands, NC, 30 August 1961, S. and D. Mulaik (USNM-1). **TENNESSEE:** *Blount Co.*, Great Smoky Mountains National Park, Elkmont, 11 May 1922, G.G. Ainslie (USNM-3) and Cade's Cove, 18 June 1976, R.M. Shelley (NCSM-1). *Hamblen Co.*, Russellville, 8 August 1910 (USNM-1). *Jefferson Co.*, along US hwy. 41, 23 June 1958, L. Hubricht (UCDC-10). *Sevier Co.*, Gatlinburg, 24 July 1947 (AMNH). *Washington Co.*, Johnson City, 9 August 1910 (USNM-1). **VIRGINIA:** *Augusta Co.*, 8 km (5 mi) W Newport, 16 June 1962 (CMNH-12). *Campbell Co.*, Brookneal, 28 August 1949, L. Hubricht (VMNH-5). *Floyd Co.*, 3.2 km (2 mi) S Copper Valley, along VA hwy. 787, 14 October 1962, R.L. Hoffman (VMNH-2). *Montgomery Co.*, Blacksburg, May 1953 and October 1954, R.L. Hoffman (VMNH-5). *Pulaski Co.*, 16 km (10 mi) NE Pulaski, June 1963, L. Hubricht (VMNH-1). *Roanoke Co.*, Poor Mtn. S of Roanoke, 3 September 1949, L. Hubricht (VMNH). *Washington Co.*, 3.2 km (2 mi) E Mendota, along VA hwy. 620, 8 August–2 December 1997 (VMNH-1); and 4.8 km (3 mi) NE Mendota, 31 July 1965, R.L. Hoffman, Brownell (VMNH-1). **WEST VIRGINIA:** *Kanawha Co.*, 0.8 km (0.5 mi) E Crown Hill, 17 May 1958, L. Hubricht (VMNH-1); and S of Hudnall, 17 May 1958, L. Hubricht (VMNH). *Mercer Co.*, 0.8 km (0.5 mi) NE Athens, 7 July 1968, N. Price (MCZC-1). *Summers Co.*, S of Hinton, 16 June 1956, L. Hubricht (VMNH-1).

***Gosodesmus claremontus* Chamberlin, 1922**

NORTH AMERICA: **USA:** **CALIFORNIA:** *Del Norte, El Dorado, Fresno, Humboldt, Kern, Los Angeles, Madera, Mariposa, Mendocino, Monterey, Orange, Plumas, San Bernardino, San Diego, San Joaquin, Santa Barbara, Santa Clara, Santa Cruz, Shasta, Stanislaus, and Tulare cos.* (AMNH, CASC, EMEC, FSCA, LACM, NCSM, UAIC, UCDC, UCRC, USNM). **OREGON:** *Benton Co.*, McDonald State Forest, 10 November 1984, K.W. Radtke (AMNH-1). *Curry Co.*, Redwood Park, Myrtle Grove, 23 May 1957, B. Malkin (USNM-1). *Josephine Co.*, Oregon Caves National Monument, 11 June 1991, R.M. Shelley (NCSM-1); and 8 km (5 mi) N Rand, Rainey Falls Trail along Graves Creek, 11 June 1991, R.M. Shelley (NCSM-1).

?*Ischnocybe* spp.

NORTH AMERICA: **USA:** **CALIFORNIA:** *Humboldt Co.*, 3.6 km (2 mi) N Mendocino Co. line, Avenue of Giants, F, 14 September 1971, V.D. Roth (AMNH). *Plumas Co.*, 22.4 km (14 mi) up N Fork Feather R. from Belden, M, F **paratypes**, 25 December 1922, H.S. Barber (FSCA); and 14.4 km (9 mi) SE Quincy, rest area on CA hwy 70, 7 December 1986, Akre, Garnett (WSUC-1). *Sonoma Co.*, 25 August 1961, N.G. Fry (BMNH-1). **OREGON:** *Curry Co.*, 1.6 km (1 mi) N Sixes, 30 September 1959, V.D. Roth (AMNH-4); and 3.2 km (2 mi) N Brookings, 31 September 1959, V.D. Roth (AMNH-4). *Douglas Co.*, 1.6 km (1 mi) S Reedsport, 30 September 1959, V.D. Roth (AMNH-1). **IDAHO:** *Clearwater Co.*, Elk Creek Falls Recreation Area E of Bovill, 8 August 1991, R.M. Shelley (NCSM-1). *Idaho Co.*, along Orogrande Cr., 30 August 1933, M.H. Hatch (FSCA-4); and 5.3 km (3.3 mi) ESE Lowell Bridge, along Selway R., 17 May 1975, F.W. Grimm (CMNC-5). *Latah Co.*, Moscow, 20 April 1951, E.F. Dailey (UWBM-1); and 6.4 km (4 mi) N, 12.8 km (8 mi) E Harvard, Bank's Gulch, F, 16 September 1978, A.K. Johnson (NCSM).

***Dolistenus ?savii* Fanzago, 1874**

ASIA: **TURKEY:** Yalova, 6 May 1947 (VMNH-3).

***Fioria tuberculata* Silvestri, 1898**

EUROPE: **ITALY:** Sanctuario di Savona, 1 October 1959, C.A.W. Jeekel (VMNH-4).

***Plutodesmus typhlus* (Daday, 1889)**

EUROPE: GREECE: PELEPONNESUS: Lakonia Prefecture, 12 km (7.5 mi) W Spárti, 1 October 1962 (VMNH-1).

PLATYDESMIDA: PLATYDESMIDAE***Platydesmus* sp.**

CENTRAL AMERICA: BELIZE: CAYO: 22.8 km (14.3 mi) SE Belmopan, 6 August 1993, W. D. Shepard (BYUC). **New Country Record for the Order, Family, and genus.**

***Corcyrozonium ?typhlum* (Daday, 1889)**

ASIA: GEORGIA: AJARIA: Kintrish Nature Reserve near Zeraboseli, M, 2F, October 1981, S.I. Golovatch (ZMUM).

POLYZONIDA: HIRUDISOMATIDAE**Unknown genus and species**

ASIA: CHINA: SICHUAN: 5 December 1928, D.C. Graham (VMNH-2).

POLYZONIDA: SIPHONOTIDAE***Burinia* sp.**

AFRICA: REPUBLIC OF SOUTH AFRICA: MPUMALANGA: Barberton and Graskop, M, F, March 1960, R.F. Lawrence (NMSA). KWAZULU-NATAL: Mtunzini, 29 July 2002, Z. Korsós (NCSM-8)

Unknown genus and species – possibly *Rhinotus purpureus* (Pocock, 1894)

MADAGASCAR: TOAMASINA: Mahavelona (=Foulpointe) (17°40'S, 49°31'S), M, October 1994, A. Pauly (RMCA).

SIPHONOPHORIDA: SIPHONORHINIDAE**Unknown genus and species**

ASIA: INDIA: ASSAM: 4 km (4 mi) N Cherrapiniji, 1376 m, 3 October 1961, E.S.Ross, D.Q. Cavagnaro (CASC). **New State Record.**

JULIDA: NEMASOMATIDAE***Thalassisobates littoralis* (Silvestri, 1903)**

NORTH AMERICA: UNITED STATES: MASSACHUSETTS: County Unknown, Vineyard Sound, in dead eel grass at high water mark, 2M, 1883 (PMNH). CONNECTICUT: New Haven Co., Savin Rock, F, 1 June 1874, A.E. Verrill (PMNH); 3.2 km (2 mi) SW Guilford, Joshua Cove, 2M, FF, juv., 2 May 1964, C.J. and B.V. Durden (TMMC); and Leetes I., Guilford, Yale Field Station, M, 30 September 1973, J. Slade (PMNH).

JULIDA: JULIDAE

ASIA/MIDDLE EAST: IRAQ: KURDISTAN: Sersang, 3 juvs., 20 June 1952, N.A. Weber (USNM); and Dahk, Zawita, F, 20 March 1951, N.A. Weber (USNM).

JULIDA: PARAJULIDAE

NORTH AMERICA: MEXICO: BAJA CALIFORNIA NORTE: Sierra Juarez, Little Cantillas Canyon, 3F, 20 March 1967, J. Powell (EMEC).

SPIROBOLIDA: SPIROBOLIDEA: ATOPETHOLIDAE***Comanchelus hubrichti* Hoffman and Orcutt, 1960**

NORTH AMERICA: USA: TEXAS: Lampasas Co., E of Bend, along co. rd. 335 at Farm Market rd. 580, 2F, 6 March 2010, M.B. Connior (NCSM).

SPIROBOLIDA: SPIROBOLIDEA: RHINOCRICIDAE***Argentocricus* sp.**

SOUTH AMERICA: ARGENTINA: CHUBUT: Parque Nacional los Alerces, W of Esquel, La Balsa, 9-11 December 1961, H.C. Happer (VMNH-5) **Southernmost Record of Genus, Family, Order, and Subclass in the Western Hemisphere.**

SPIROBOLIDA: SPIROBOLIDEA: SPIROBOLIDAE***Tylobolus uncigerus* (Wood, 1864)**

NORTH AMERICA: USA: WASHINGTON: Skamania Co., Spring Creek National Fish Hatchery, 1.6 km (1 mi) W White Salmon R., 16 June 2000, W.P. Leonard (NCSM-1).

SPIROBOLIDA: TRIGONIULIDEA: PACHYBOLIDAE***Xenobolus* sp.**

ASIA: INDIA: WEST BENGAL: Birbhum Dist., Burdwan, Howrah, July 1994, S. Brakat (VMNH).

SPIROBOLIDA: SUBORDER and FAMILY UNCERTAIN**?*Amblybolus* sp.**

AFRICA: EQUATORIAL GUINEA: BOKO: Moca (3°21'46"N, 8°39'52"E), 5F, 2 juvs., 1-11 October 1998, M. Boko, D.K. Dabney, R.C. Drewes, L. Henwood, M.P. Ndung, R.W. Tomos, D. Ubick, J.V. Vindum (CASC); and Pico Basilé (3°37'38"N, 8°48'15"E), 3F, juv., 29 September 1998, D.K. Dabney, D. Ubick (CASC) **New Island Record for Genus and Order.**

SPIROSTREPTIDA: CAMBALIDEA: CAMBALIDAE***Cambala annulata* (Say, 1821)**

NORTH AMERICA: USA: FLORIDA: Liberty Co., Torreya State Park, MM, FF, 24 January 1965, N.B. Causey (FSCA). *OHIO:* Wayne Co., Wooster, 2F, 31 May 1963, W.A. Shear (WASC). *PENNSYLVANIA:* Montgomery Co., Bryn Mawr, MM, FF, October 1952, N.B. Causey (FSCA).

***Cambala minor* Bollman, 1888**

NORTH AMERICA: USA: OHIO: Montgomery Co., Dayton, 3F, 4 April 1969, G.A. Coovert (DMNH). *Preble Co.,* Hueston Woods, F, 16 April 1969, G.A. Coovert (DMNH).

***Cambala ?speobia* (Chamberlin, 1952)**

NORTH AMERICA: **USA:** **COLORADO:** *Douglas Co.*, 32 km (20 mi) W Sedalia, MM, FF, juvs., 6 August 1941, S. and D. Mulaik (AMNH). *Fremont Co.*, Wet Mtns., Station 42, 7,500', MM, FF, 10 October 1964, B. Banta (CASC). **NEW MEXICO:** *Eddy Co.*, Two Snakes Cv., F, 9 February 1992, D. Pate (TMMC). *Grant Co.*, Black Mtns., Iron Cr. Forest Camp, MM, FF, 31 August 1952, B. Malkin (USNM). *Guadalupe Co.*, 22.4 km (14 mi) E Santa Rosa, F, 20 May 1993, D. Sissom (NCSM). *San Miguel Co.*, Las Vegas High School, F, Baker, Schwarz (USNM). *Torrance Co.*, Osha Peak, Manzano Mtns., 5M, 6F, 29 August 1991, C.S. Crawford (NCSM). **OKLAHOMA:** *Murray Co.*, Bitter Enders Cv., August 1985, A. Grubbs (TMMC).

***Cambala ?washingtonensis* Causey, 1954**

NORTH AMERICA: **USA:** **IDAHO:** *Adams Co.*, 9.6 km (6 mi) S Pollock, MM, FF, 6 June 1993, R.M. Shelley (NCSM). *Idaho Co.*, White Bird and 2.6-6.6 km (1.6-4.1 mi) S White Bird, MM, FF, 4-5 May 1975, F.W. Grimm (CMNC). *Nez Perce Co.*, Arrow Junction, FF, 12 October 1964, R.L. Westcott (UCDC); and 4.8 km (3 mi) S Juliaetta, M, F, 17 October 1964, R.L. Westcott (UCDC). **WASHINGTON:** *Asotin Co.*, Grande Ronde R., 0.5 km (0.3 mi) W confluence of Snake R., 5F, 3 May 1975, F.W. Grimm (CMNC); Snake R. Gorge, 9.3 km (5.8 mi) N Grande Ronde R., MM, FF, F.W. Grimm (CMNC); and along WA hwy. 129, 4 km (2.5 mi) NE Grande Ronde R., M, 17 April 1985, R.S. Zack (WSUC). *Garfield Co.*, along Snake R. near Lower Granite Dam, 6 February 1986, R.S. Zack (WSUC); and 0.5 mi downstream from Lower Granite Dam, 8 February 1991, R.S. Zack (WSUC). *Whitman Co.*, 12.8 km (8 mi) SW Colfax, Steptoe Canyon., MM, FF, 27 April 1985, R.S. Zack (WSUC) and 2M, F, 5 June 1993, R.M. Shelley, R.S. Zack (NCSM).

***Tridere* sp.**

NORTH AMERICA: **USA:** **CALIFORNIA:** *San Diego Co.*, Banner Grade, M, 15 February 1979, D.K. Faulkner (SDMC). **MEXICO:** **BAJA CALIFORNIA NORTE:** ca 51-55 km (31.9-34.4 mi) W Mexicali, 8M, 21F, 1-3 March 1992, D.B. Weissman, V.F. Lee (CASC, NCSM). **New Country and State Record.**

***Chiraziulus ?kaiseri* Mauriès, 1983**

ASIA: **IRAN:** **KERMANSHAH:** 8 km (5 mi) E Qasr-e-Shirin, F, 14 April 1966, J. Neal (USNM). **New Provincial Record.**

Unidentified Cambalidae

NORTH AMERICA: **USA:** **CALIFORNIA:** *Alameda, Colusa, Contra Costa, Del Norte, El Dorado, Glenn, Humboldt, Kern, Los Angeles, Monterey, Napa, Orange, Plumas, Riverside, Sacramento, San Bernardino, San Diego, San Luis Obispo, Santa Barbara, Shasta, Solano, Stanislaus, Tehama, Trinity, Yolo, and Yuba cos.* (AMNH, CASC, CSCA, FSCA, LACM, MHNG, NCSM, EMEC, UCDC, UNMC, USNM); **ISLAND RECORDS:** *Los Angeles Co.*, Catalina I., S of Avalon, 2M, F, 20 August 1927 (USNM). *Santa Barbara Co.*, Channel Islands National Park, Santa Cruz I., September 1903 (USNM-1). **OREGON:** *Clatsop Co.*, Young R. falls near Olney, F, 4 June 1991, R.M. Shelley (NCSM). *Curry Co.*, Pistol R., 7 July 1951, B. Malkin (USNM); and Loeb State Park, MM, FF, 23 May 1957, B. Malkin (FSCA). *Jackson Co.*, 32 km (20 mi) E Ashland, Hyatt Lake, F, April 1947, V. Thatcher (USNM). *Lincoln Co.*, Waldport, MM, FF, 14 March 1937, J.C. Chamberlin (USNM); and near Otis, Three Rocks, MM, FF, 3 May 1942, J.C. Chamberlin (USNM). **WASHINGTON:** *Pacific Co.*, Nahcotta, MM, FF, 10 July 1954 (USNM); and Ocean Park, 2M, 22 July 1955 (USNM).

Unidentified Cambalidae

ASIA: **LAOS:** **VIENTIANE:** *Saysamboun Dist.*, military controlled area, grassy hills, 2F, 14 November 1999, R.J. Timmins (NCSM). **MALAYSIA:** **SARAWAK:** Gunung Mulu National Park, Green Cv., 4 March 1978, P.J. Chapman (VMNH-1) **New State Record.** **PHILIPPINES:** **LUZON:** northern part, 1 May 1981, W.L. Brown (VMNH-2) **New Island and Country Record.**

SPIROSTREPTIDA: EPINANNOLENIDEA: CHOCTELLIDAE***Choctella cumminsi* Chamberlin, 1918**

NORTH AMERICA: USA: ALABAMA: *Jackson Co.*, 2.4-5.6 km (1.5-3.5 mi) NW Stevenson, 9 May 1954 and 20 June 1957, L. Hubricht (USNM); 12.8 km (8 mi) W Stevenson, SW slope of Little Coon Mtn., 9 April 1966, J.E. and M.R. Cooper (NCSM); Russell Cave National Monument, 29 June 1966, A.A. Weaver (NCSM-4); and 7.2 km (4.5 mi) NE Woodville, 9 May 1954, L. Hubricht (USNM). *Madison Co.*, Huntsville, Monte Sano State Park, 8 May 1954, L. Hubricht (USNM), 4-8 April 1967, S.B. Peck (FSCA), and 2M, 2F, 27 May 1980, R.M. Shelley (NCSM); outside Scott Cv., exact location unknown, M, 20 June 1959, H.R. Steeves (FSCA); 6.4 km (4 mi) SE Huntsville, 8 May 1954, L. Hubricht (USNM); and Keel Mtn. S of Gurley, 9 May 1954, L. Hubricht (USNM). *Marshall Co.*, 2.4 km (1.5 mi) S Guntersville, 8 May 1954, L. Hubricht (USNM); and Grant, Cathedral Caverns, 27 June 1966, A.A. Weaver (USNM-1). TENNESSEE: *Davidson, DeKalb, Franklin, Grundy, Marshall, Maury, Rutherford, Smith, Van Buren, Warren, and Wilson cos.* (FSCA, NCSM, USNM).

***Choctella hubrichti* Hoffman, 1965**

NORTH AMERICA: USA: ALABAMA: *Shelby Co.*, Oak Mountain State Park, MM, 2F, 22 May 1980, R.M. Shelley (NCSM). *St. Clair Co.*, Odenville, F, 28 June 1997, M. Busse (NCSM).

SPIROSTREPTIDA: SPIROSTREPTIDEA: SPIROSTREPTIDAE***Globanus ?integer* (Karsch, 1884)**

ATLANTIC ISLANDS: GULF OF GUINEA: SÃO TOMÉ and PRINCIPE: SÃO TOMÉ: Nova Moca (0°17'25.8"N, 6°37'58.1"E), 920m, 3M, 19F, juv., 27 February 2010, R.C. Drewes (CASC).

***Globanus ?marginescaber* (Karsch, 1884)**

ATLANTIC ISLANDS: GULF OF GUINEA: SÃO TOMÉ and PRINCIPE: SÃO TOMÉ: Morro Provaz Ridge (0°17'20"N, 6°35'50.9"E), 3M, 8F, 2 juvs., March 2010, R.C. Drewes (CASC). PRINCIPE: Slopes of Pico Papagaio (1°37'10"N, 7°23'28"E), 2M, 7F, 8 March 2010, R.C. Drewes (CASC). E side, road to Infante Henrique (1°36'2.4"N, 7°24'56"E), 6M, 14F, 9 March 2010, R.C. Drewes (CASC). Bela Vista (1°37'10.8"N, 7°24'49.7"E), 13M, 15F, juv., 11 March 2010, R.C. Drewes (CASC).

Globanus n. sp.

ATLANTIC ISLANDS: GULF OF GUINEA: SÃO TOMÉ and PRINCIPE: SÃO TOMÉ: Morro Provaz Ridge, headwaters Rio do Oro (0°17'3.8"N, 6°35'57.5"E), M, 6F, 3 March 2010, R.C. Drewes (CASC). Morro Provaz Ridge, en route Lagoa Amelia (0°16'58.5"N, 6°35'12.5"E), 2M, 7F, 5 March 2010, R.C. Drewes (CASC).

***Orthoporus ornatus* (Girard, 1853)**

NORTH AMERICA: MEXICO: CHIHUAHUA: 64 km (40 mi) S Hidalgo del Parral, MM, FF, 4 August 1962, A.S. Lockley (LACM); 15.5 km (9.7 mi) W Cuauhtemoc, near Casa Colorado, M, Liner, Johnson, Chaney (NCSM); 22.2 km (13.9 mi) SSW Ciudad Camargo, MM, FF, 20 July 1973, Liner, Johnson, Chaney (NCSM). COAHUILA: Monclora and 60.8 km (38 mi) S Monclora, 3M, juv., 23 July 1974, Liner, Johnson, Chaney (NCSM). SONORA: 11.2 km (7 mi) SW Narca, F, 8 July 1965, D.E. Harvey (LACM); 14.4 km (9 mi) SW Agua Prieta, F, 9 July 1965, D.E. Harvey (LACM); 9.4 km (5.9 mi) N Los Pocitas, 22 July 1963 (LACM); and 5.0 km (3.1 mi) NW Huicoche, F, 13 July 1989, S. Prchal (NCSM).

***Archispirostreptus syriacus* (Saussure, 1859)**

ASIA-MIDDLE EAST: ISRAEL: Jerusalem, old Hebrew Cemetery on Mt. of Olives, March 1965, I. Brown (VMNH-18). Kfar Shmuel, M, 2F, juv., 1-15 March 1968, S. Blenzynski (USNM). LEBANON: Beirut, Rue de Paris, Ghazzara Bldg., MM, FF, 15 December 1964, L. Brown (VMNH) **New Country Record for Species, Genus, Family, Suborder, and Order.**

***Orthoporus cavicollis* (Karsch, 1881)**

LESSER ANTILLES: US VIRGIN ISLANDS: ST. THOMAS: Mountaintop, F, 14 August 1988, R.M. Shelley (NCSM).

Unknown Spirostreptidae

NORTH AMERICA: MEXICO: CAMPECHE: Edzna, 2F, 12 January 1966, G.E. Ball, D.R. Whitehead (VMNH) **New State Record for Family and Order.**

CENTRAL AMERICA: BELIZE: ORANGE WALK: M, 2F, summer 1957, E. Willis (VMNH) **New Country Record for Family and Order.** **EL SALVADOR: SAN SALVADOR:** Quezaltepeque, M, 6 July 1963, M. Irwin, D.Q. Cavagnaro (CASC).

LESSER ANTILLES: TRINIDAD AND TOBAGO: TOBAGO: St. Georgia-St. Mary, 0.8-1.6 km (0.6-1.0 mi) NW Hillsborough, 21 December 1978, A.L. Braswell, D.L. Stephan (NCSM); and St. John, Charlotteville, 3M, FF, 16-21 December 1978, A.L. Braswell, D.L. Stephan (NCSM).

AFRICA: BOTSWANA: NGAMILAND: between Maun and Xaxaba, MM, FF, 30 December 1983, J.L. Meinshull (VMNH) **New Country Record for Family, Suborder, Order, and Subclass.** **CENTRAL AFRICAN REPUBLIC:** Dzhanga-Sangha (Dense Forest) Reserve, November 1996 (VMNH-8). **GAMBIA:** N Bank of Gambia R., Kerewan, F, August 1986, C.J. Rushkin-Bell (VMNH) **New Country Record.**

SPIROSTREPTIDEA: HARPAGOPHORIDAE

ASIA: CAMBODIA: MONDOLKIRI: *Pichrada Dist.*, Phnom Nam Lyr Wildlife Sanctuary, M, 4F, June 2000, B.L. Stuart (NCSM) **New Country Record.** **NEPAL: GANDA KI:** S Slope Mt. Annapurna, between Lumbe and Khare, 14 December 1973, J. Martens (VMNH-2). **TAIWAN: KAOHSIUNG:** Liougui township, Mt. Wugong, F, 24 September 2005, M.H. Hsu (NSSU) **New Country Record**

SPIROSTREPTIDEA: ODONTOPTYGIDAE***Peridontopyge rubescens* Attems, 1927**

AFRICA: GAMBIA: N Bank Gambia R., Kerewan, August 1986, C.J. Rushkin-Bell (VMNH); and S Bank Gambia R., Latrikunda, September 1986, C.J. Rushkin-Bell (VMNH-3) **New Country Record.**

***Peridontopyge spinosissima* (Silvestri, 1897)**

AFRICA: GAMBIA: N Bank Gambia R., Kerewan, August 1986, C.J. Rushkin-Bell (VMNH) **New Country Record.**

***Syndesmogenus caboverdus* (Pierrard, 1987)**

ATLANTIC ISLANDS: CAPE VERDE ISLANDS: *Brava Region, Nova Sintra I.*, Santa Barbara, September 15 (VMNH).

Unidentified Odontopygidae

AFRICA: EQUATORIAL GUINEA: BIOKO: Moca (3°21'46"N, 8°39'52"E), F, 3-6 October 1998, D.K. Dabney, D. Ubick (CASC); and 3.5 km (5.6 mi) N Luba (3°28'54"N, 8°34'58"E), 2M, 13 October 1989, D.K. Dabney, D. Ubick (CASC) **New Island Record for Family and Order.**

CALLIPODIDA: SCHIZOPETALIDAE: TYNOMMATINAE***Tynomma magnum* Buckett and Gardner, 1969**

NORTH AMERICA: USA: CALIFORNIA: *San Luis Obispo Co.*, Cambria, M, 23 June 1952, M. Cazier, R. Schrammel, W.J. Gertsch (AMNH) and 7F, 7 February 1967, V. Roth (AMNH).

CHORDEUMATIDA: CASEYIDAE***Opciona columbiana* Chamberlin, 1951**

NORTH AMERICA: USA: ALASKA: *Prince of Wales/Outer Ketchikan Borough (Bor.)*, Prince of Wales I., Exchange Cove Campground (56°12'38.2"N, 133°04'14.3"W), M, 2 juvs., 15 August 2007, R.M. Shelley, M.F. Medrano, K. Ovaska (NCSM).

CANADA: BRITISH COLUMBIA: *Saturna I.*, Lyell Cr. M, 11 November 2004, K. Ovaska (NCSM).

?*Underwoodia tida* Chamberlin, 1925

NORTH AMERICA: CANADA: BRITISH COLUMBIA: Terrace, 5F, 10 August 1988, S. and J. Peck (NCSM). Prince George, Meadow Park, Boiler Cr., 3F, juv., 12 August 1988, S. and J. Peck (NCSM).

CHORDEUMATIDA: CLEIDOGONIDAE***Cleidogona atropos* Shear, 1972**

NORTH AMERICA: USA: MARYLAND: *Talbot Co.*, St. Michaels, M, 16 February 1992, W.E. Steiner, J.M. Swearingen (USNM).

***Cleidogona australis* Loomis, 1966**

NORTH AMERICA: FLORIDA: *Highlands Co.*, Parker Islands, 2F, April 1956, C.C. Hoff (AMNH).

***Cleidogona bacillipus* (Chamberlin and Mulaik, 1941)**

NORTH AMERICA: USA: TEXAS: *Hidalgo Co.*, Edinburgh, M, August 1956, S. and D. Mulaik (USNM).

***Cleidogona major* Cook and Collins, 1895**

NORTH AMERICA: USA: SOUTH CAROLINA: *Horry Co.*, Myrtle Beach State Park, M, 14 December 1967, W. Ivie (AMNH).

***Cleidogona* spp.**

NORTH AMERICA: USA: DELAWARE: *New Castle Co.*, Brandywine Cr. off DE hwy. 92, F, 21 April 1998, R.M. Shelley (NCSM) **New State Record for Genus, Family, and Order.** FLORIDA: *Volusia Co.*, Orange City, F, 21 January 1988, D.T. Corey (NCSM). LOUISIANA: *Tangipahoa Par.*, near Robert, F, 26 October 1976, J.E. and M.R. Cooper (NCSM). NORTH CAROLINA: *Brunswick Co.*, 16.6 km (10.4 mi) N, 7.2 km (4.5 mi) SSW Shallotte, 2F, 4 August 1972, R.M. Shelley (NCSM); and 25.9 km (16.2 mi) N Bolivia, ravine on Cape Fear R., F, 16 October 1979, R.M. Shelley, P.T. Hertl (NCSM). *Carteret Co.*, 8 km (5 mi) WSW Newport, Croatan National Forest, F, 25 March 1975, M.R. Cooper (NCSM); 16 km (10 mi) WSW Newport, Croatan National Forest, 30 June 1975, R.M. Shelley, J.C. Clamp (NCSM); and Bogue Banks, Roosevelt Natural Area E of Salterpath, F, 7 October 1975, M.R. Cooper (NCSM). *Dare Co.*, Buxton, Cape Hatteras National Seashore, F, 19 November 1980, D.L. Stephan (NCSM); and 0.6 km (0.4 mi) SSE Buxton, F, 12 August 1984, D.L. Stephan (NCSM). TEXAS: *Hardin Co.*, Lumberton, Wier Woods Nature Reserve, F, 11 October 2001, R.M. Shelley (NCSM). *Newton Co.*, 19.2 km (12 mi) NE Newton, Wild Azalea Trail, F, 7 October 2004, R.M. Shelley (NCSM). MEXICO: DURANGO: 24 km (15 mi) W El Salto, mixed oak and Douglas Fir litter, F, 6 August 1964, E.E. Lindquist (CNCI) **New State Record for Genus, Family, and Order.** JALISCO: 20.8 km (13 mi) W Atenquique, M, F, 10-18 September 1971, A. Newton (VMNH). **New State Record for Genus and Family.**

***Dybasia divergens* (Loomis, 1964)**

CENTRAL AMERICA: PANAMA: CHIRIQUI: Bocas de Toro, cloud forest litter, 2F, 9 June 1995, R. Anderson (NCSM).

Genus and species unknown

CENTRAL AMERICA: BELIZE: ORANGE WALK: Rio Bravo Conservation Area, M, 3F, 25 April-5 May 1996, C.E. Carlton (NCSM) **New Country Record for Family and Order.**

CHORDEUMATIDA: CONOTYLIDAE***Austrotyla borealis* Shear, 1971**

NORTH AMERICA: CANADA: ALBERTA: Jasper National Park, 46.7 km (29.2 mi) SE Jasper (town), along hwy. 93, 2F, 9 May 1979, B.D. Ainscough (RBCM).

***Austrotyla montivaga* (Loomis, 1943)**

NORTH AMERICA: USA: ARIZONA: Cochise Co., Chiricahua Mts., Upper Cave Cr., F, 29 October 1963, V.D. Roth (USNM), San Mateo Cliffs, M, F, 6 October 1972, V.D. Roth (SWRS), and Barefoot Meadow, M, 2F, 28 July 1963, V.D. Roth (SWRS). Santa Cruz Co., Santa Catalina Mts., Marshall Gulch, F, 1 August 1959, F.G. Werner (UAIC).

***Brunsonia albertana* (Chamberlin, 1920)**

NORTH AMERICA: CANADA: ALBERTA: Jasper National Park, Mt. Edith Cavell Lodge, confluence Athabasca and Rocky Rs., MM, FF, 13-24 August 1965, J. and W. Ivie (AMNH), and Jasper (town), juv. M, 30 September 1973, B. Wright (NSMC); and Bow R. at Baker Cr., 4 juvs., 26 August 1965, J. and W. Ivie (AMNH). BRITISH COLUMBIA: Prince George, Meadow Park, 2M, 4F, 12 August 1988, S. and J. Peck (NCSM). Tupper, F, 5 September 1968, J. and W. Ivie (AMNH).

***Brunsonia atrolineata* (Bollman, 1893)**

NORTH AMERICA: CANADA: BRITISH COLUMBIA: 128 km (80 mi) W Dawson Creek, Pine Pass, M, F, 1 August 1969, E. Thorn (RBCM). East Kootenays, Moyle Mtn. summit, F, 16 July 1959, H.B. Leech (CASC).

***Conotyla blakei* (Verhoeff, 1932).**

NORTH AMERICA: USA: NEW HAMPSHIRE: Coos Co., 0.6 km (0.4 mi) S Jefferson Notch, M, 5F, 20 May 1984, A. Newton, M. Thayer (MCZC). NEW JERSEY: Hunterdon Co., Lambertville, M, 5 May 1953, W. Ivie (AMNH) **New State Record for Species, Genus, and Family.**

***Idagoga lehmanensis* Shear, 2007.**

NORTH AMERICA: USA: NEVADA: White Pine Co., N Snake Range, headwaters of Deadman's Cr., F, 4 August 1987, W.L. Pratt (NCSM).

CHORDEUMATIDA: TRICHOPETALIDAE***Trichopetalum lunatum* Harger, 1872.**

NORTH AMERICA: CANADA: NOVA SCOTIA: Inverness, MacFarlane Woods, 2F, 31 July 1986, B. Wright, A. Wilson (NSMC).

USA: CONNECTICUT: New Haven Co., 3.2 km (2 mi) N Northford, MM, FF, 25 April 1964, C. Durden (PMNH); and West Rock Ridge, MM, FF, 26 April 1964, C. Durden (PMNH). MAINE: Oxford Co., Norway, MM, FF, 22 July 1872 (PMNH) **New State Record for Species, Genus, and Family.** MASSACHUSETTS: Norfolk Co., Wellesley, M, 18 May 1913 (USNM). NEW HAMPSHIRE: Carroll Co., Union, F (ZSMC). Coos Co., 0.6 km (0.4 mi) S Jefferson Notch, M, 5F, 20 May 1984, A. Newton, M. Thayer (MCZC).

CHORDEUMATIDA: EUDIGONIDAE***Eudigona* sp.**

SOUTH AMERICA: CHILE: ISLA GRANDE DEL CHILOÉ: 2 km (1.3 mi) N Puente Rio Pulo, 9 February 2001, T. Cekhalovich (VMNH).

STEMMIULIDA: STEMMIULIDAE***Stemmiulus* spp.**

SOUTH AMERICA: PERU: HUANUCO: Tingo Maria National Park, Monson Valley, 2F, 23 September 1954, E.I. Schlinger, E.S. Ross (CASC) **New Country Record and Southernmost for Genus, Family, and Order in New World.** LORETO: Yagua Village on Javari R. ca 80 km (50 mi) upstream from Benjamin Constant, Brazil, F, 18 July 1977, R.M. Shelley (NCSM). **BRAZIL:** AMAZONAS: off Javari R. ca 83 km (51.9 mi) upstream from Benjamin Constant, F, 19 July 1977, R.M. Shelley (NCSM).

AFRICA: EQUATORIAL GUINEA: BIOKO: Pico Basilé (3° 37' 38"N, 8° 48' 15"E), 2F, 28 September 1998, D.K. Dabney, D. Ubick (CASC). **New Island Record for the Genus, Family, and Order.**

ASIA: INDIA: MAHARASHTRA: Mahabaleshwar, F, 13 February 1962, E.S. Ross, D. Cavagnaro (CASC) **New State Record for Genus, Family, and Order.** TAMIL NADU: below Kodaikanal (10° 15'N, 77° 03'E), F, 3 October 1989, V. and B. Roth (CASC); and Tirunelveli Dist., F, juvs., 27 March 1962 (CASC). VIETNAM: VINPHU: Ba Vi Mtns. N of Hanoi, F, April 1986, S.I. Golovatch (ZMUM). **New Provincial Record for Genus, Family, and Order.**

POLYDESMIDA: CHELODESMIDAE: PREPODESMINAE***Diaphorodesmus* sp.**

AFRICA: EQUATORIAL GUINEA: BIOKO: Pico Basilé (3° 41' 44"N, 8° 52' 17"E), M, 4F, 17 October 1998, M. Boko, D.K. Dabney, L. Henwood, R.W. Tomos, D. Ubick, J.V. Vindum (CASC) **New Island Record for Genus, Subfamily, Family, Suborder, and Order.**

***Prepodesmus* sp. (*ornatus* group)**

AFRICA: EQUATORIAL GUINEA: BIOKO: 8 km (5.6 mi) N Luba (3° 27' 56"N, 8° 29' 42"E), 2F, 14 October 1998, M. Boko, D.K. Dabney, R.W. Tomos, D. Ubick, J.V. Vindum (CASC); and Punta Beecrof (3° 43' 18"N, 8° 39' 41"E), F, 18 October 1998, D.K. Dabney, D. Ubick (CASC). **New Island Record for Genus.**

***Paracordyloporus porati* (Carl 1905)**

AFRICA: EQUATORIAL GUINEA: BIOKO: Pico Basilé (3° 41' 44"N, 8° 52' 17"E), 5M, 3F, 17 October 1998, D.K. Dabney, D. Ubick, M. Boko, L. Henwood, R.W. Tomos, J.V. Vindum (CASC) **New Island Record for Species and Genus.**

POLYDESMIDA: DALODESMIDAE***Anaulacodesmus lacustris* Schubart, 1954**

SOUTH AMERICA: ARGENTINA: NEUQUÉN: Parque Nacional Nahuel Huapi, 9 km (5.6 mi) NNW Angostura, 3M, 2F, 2 juvs., 21 February 1999, S.L. Heydon, J.M. Ledford (CASC). RIO NEGRO: Parque Nacional Nahuel Huapi, Puerto Blest, M, juv., S.L. Heydon, J.M. Ledford (CASC).

***Monenchodesmus inermis nahuelapensis* Schubart, 1954**

SOUTH AMERICA: ARGENTINA: NEUQUÉN: Parque Nacional Nahuel Huapi, 9 km (5.6 mi) NNW Angostura, M, 21 February 1999, S.L. Heydon, J.M. Ledford (CASC).

Genus and species unknown.

SOUTH AMERICA: ARGENTINA: BUENOS AIRES: Sierra de la Ventana, 30 September 1975, L.A. Pereira (VMNH). CHILE: ISLA GRANDE DE CHILOÉ: 2 km (1.3 mi) N Puente, Rio Pualeta, 9 February 2001, T. Cekhalovic (VMNH-2).

POLYDESMIDA: HAPLODESMIDAE**Unknown Genus and species**

AUSTRALIA: NORTHERN TERRITORY: 51.2 km (32 mi) NW Katherine, 4M, 3F, 26 October 1962, E.S. Ross, D.Q. Cavagnaro (CASC). **First definite diplopod locality from Northern Territory.**

POLYDESMIDA: OXYDESMIDAE: OXYDESMINAE***Coromus* sp.**

AFRICA: EQUATORIAL GUINEA: BIOKO: 8 km (5.6 mi) N Luba (3° 27' 56"N, 8° 29' 42"E), M, 14 October 1998, M. Boko, D.K. Dabney, R.W. Tomos, D. Ubick, J.V. Vindum (CASC); and Pico Basilé (3° 41' 44"N, 8° 52' 17"E), 2M, F, 17 October 1998, M. Boko, D.K. Dabney, L. Henwood, R.W. Tomos, D. Ubick, J.V. Vindum (CASC) **New Island Record for Genus, Subfamily, and Family.**

POLYDESMIDA: PARADOXOSOMATIDAE***Tetrarthrosoma syriacum* (Humbert and Saussure, 1869)**

ASIA/MIDDLE EAST: ISRAEL: Kfar Shmuel, 4M, 2F, April 1968, S. Blenzynski (USNM).

Unidentified Genus and Species.

AUSTRALIA: NORTHERN TERRITORY: Darwin, 10 March 1961, J.L. and M.K. Gressitt (BPBM); and 50 km (31.2 mi) SE Darwin, Berry Springs, 12 March 1961, J.L. and M.K. Gressitt (BPBM) **First definite diplopod locality from Northern Territory.**

Eviulisomatini*, New genus near *Scolodesmus

AFRICA: EQUATORIAL GUINEA: BIOKO: 8 km (5.6 mi) N Luba (3° 27' 56"N, 8° 29' 42"E), MM, FF, 12-14 October 1998, M. Boko, D.K. Dabney, R.W. Tomos, D. Ubick, J.V. Vindum (CASC); Pico Basilé (3° 41' 44"N, 8° 52' 17"E), 2M, F, 27-29 September 1998, M. Boko, D.K. Dabney, L. Henwood, R.W. Tomos, D. Ubick, J.V. Vindum (CASC); and Moca (3° 21' 46"N, 8° 39' 52"E), M, F, 4-9 October 1998, M. Boko, D.K. Dabney, L. Henwood, R.W. Tomos, D. Ubick, J.V. Vindum (CASC) **New Island Record for Tribe, Subfamily, and Family.**

POLYDESMIDA: POLYDESMIDAE***Scytonotus insulanus* Attems, 1931.**

NORTH AMERICA: USA: ALASKA, Skagway/Hoonah/Angoon Bor., Gustavus, along Rink Cr. Rd., 7.8 km (4.9 mi) E Gustavus Rd. (58° 26' 18.7"N, 135° 40' 06.6"W), F, 5 September 2006, R.M. Shelley (NCSM). *Prince of Wales/Outer Ketchikan Bor.*, Prince of Wales I., Tongass National Forest, along Forest Service Rd. 21, 5.6 km (3.5 mi) E Hydaburg Rd. (55°, 20', 31.6"N, 132°, 47', 14.4"W), 2F, 12 August 2007, R.M. Shelley, M.F. Medrano, K. Ovaska (NCSM). *Wrangel/Petersburgh Bor.*, Kupreanof I., Lindenbergh, Omer's Slough, F, 29 August 1951, B. Malkin (USNM). *Sitka Bor.*, Sitka, F, Harriman Exp. (USNM). *Juneau Bor.*, Juneau, F, 28 April 1945, J.C. Chamberlin (USNM).

***Scytonotus piger* Chamberlin, 1910.**

NORTH AMERICA: CANADA: BRITISH COLUMBIA: W Kootenays, rest area on hwy. 3 between Salmo and Creston (49, 4.13'N, 117°, 14.9'W), M, 2F, 22 September 2007, K. Ovaska, L. Sopuck (NCSM) **New Country and Provincial Record for Species.**

USA: IDAHO: Bonner Co., 7.2 km (4.5 mi) NE Hope, 3M, juv., 5 October 2002, W.P. Leonard, J. Bawah (NCSM). *Fremont Co.*, 14.4 km (9 mi) N Ashton, juv., 10 August 1959, C.C. Hoff (AMNH). *Kootenai Co.*, E side Hayden Lake, 4F, 25 March 1959, F.C. Raney (FSCA). **MONTANA: Sanders Co.,**

Skeleton Cr., juv., 13 October 2006, P. Hendricks (NCSM); Saddle Cr., M, F, 13 October 2006, S. Lenard (NCSM); and Devil Gap, Marten Cr., M, 13 October 2006, P. Hendricks (NCSM). WYOMING: Teton Co., 5.4 km (3.4 mi) W Wilson, along WY hwy. 22, F, 14 June 1994, R.M. Shelley (NCSM); 14.4 km (9 mi) W Jackson, juv., 5 August 1959, C.C. Hoff (AMNH); and Grand Teton National Park, juv., 3 August 1958, D.C. Lowrie (AMNH).

POLYDESMIDA: PYRGODESMIDAE

Stylodesmus cf. horridus Cook, 1895.

AFRICA: EQUATORIAL GUINEA: BIOKO: Moca (3° 22' 0"N, 8° 39' 57"E), F, 3-10 October 1998, M. Boko, D.K. Dabney, R.C. Drewes, L. Henwood, M.P. Ndung, R.W. Tomos, D. Ubick, J.V. Vindum (CASC). **New Island Record for Species, Genus, and Family.**

POLYDESMIDA: XYSTODESMIDAE

Apheloria virginiensis corrugata (Wood, 1864).

NORTH AMERICA: USA: DELAWARE: Newcastle Co., White Clay Creek State Park (39° 42' 54.6"N, 75° 45' 37.5"W), 2M, 3F, 9 May 2007, R.M. Shelley (NCSM). **New State Record for Subspecies, Species, Genus, and Family.**

Rhysodesmus sp.

NORTH AMERICA: MEXICO: CHIHUAHUA: Santo Nino, M, 2F, 26 July 1968, T.A. Sears, R.C. Gardner, C.C. Glaser (UCDC) **New State Record for Genus and Family.** COAHUILA: 9.6 km (6 mi) E San Antonio de las Alazanas, 3M, F, 21 October 1965, G.E. Ball, D.R. Whitehead (VMNH). DURANGO: 10 km (6.3 mi) W El Salto, M, F, 1 July 1964, J.E.H. Martin (CNCI) **New State Record for Genus and Family.** JALISCO: Chamela Biological Station, MM, FF, 20-21 July 1984, J.T. Doyen (EMEC); and Sierra de Manaretta, M, 18 August 1985, J.T. Doyen (EMEC). SINALOA: El Palmito, M, 2 July 1964, J.E.H. Martin (CNCI); 3.2 km (2 mi) SE Elota, 4M, 4F, 2 August 1966, J.S. Buckett, M.R. Gardner (UCDC); and 6.9 km (4.3 mi) S Durango border on Hwy. 40, tropical forest near waterfall, 2M, 13 July 2008, M.F. Medrano (NCSM) **New State Record for Genus and Family.** ZACATECAS: 20.8 km (13 mi) W Milpillas, M, 10 July 1954, R.H. Brewer (CASC) **New State Record for Genus and Family.**