

The Holarctic Centipede Subfamily Plutoniuminae
(Chilopoda: Scolopendromorpha: Cryptopidae) (Nomen
Correctum Ex Subfamily Plutoniinae Bollman, 1893)

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ABSTRACT—The Holarctic chilopod subfamily Plutoniuminae Bollman, a corrected name for Plutoniinae, consists of two genera, *Plutonium* Cavanna and *Theatops* Newport, and six species; synapomorphies between them show that the subfamily is a monophyletic group and that the different number of spiracles, 19 pairs in *Plutonium* and 9 pairs in *Theatops*, is only a generic-level character. *Plutonium* and *P. zwierleini* Cavanna occur in Sicily, Sardinia, Napoli and Sorrento provinces in mainland Italy, and Granada Province, Spain. *Theatops erythrocephalus* (C. L. Koch) occurs along the eastern side of the Adriatic Sea in the Balkan Peninsula and in coastal Spain and Portugal. The other four species—*T. posticus* (Say), *T. spinicaudus* (Wood), *T. phanus* Chamberlin, and *T. californiensis* Chamberlin—occur in the United States and northwestern Mexico. *Theatops posticus* occupies a broad area east of the Central Plains from Connecticut and southern New York to the south Florida keys and eastern Texas; an allopatric western population extends from southwestern New Mexico and western Chihuahua to the southern Great Basin, the California desert east of the Sierra Nevada, the Pacific Ocean in Baja California Norte, the Channel Islands off the southern California coast, and the eastern slope of the Coast Range near the latitude of San Francisco Bay. *Theatops spinicaudus* occurs sympatrically with *T. posticus* in two areas of the east; the inner surfaces of its caudal legs possess variable series of ridges and teeth. *Theatops phanus* occurs in epigeal and subterranean environments in southern Texas and extends from east of highway I-35 to west of the Pecos River; the inner surfaces of its caudal legs also possess variable series of ridges and teeth. The distribution of *T. californiensis*, anatomically convergent with *T. erythrocephalus*, is as described previously, but locality information is detailed, as only one site, the type locality, is currently known. Relationships among the plutoniumine species are postulated as $P. zwierleini + (T. spinicaudus + (T. phanus + (T. erythrocephalus + (T. posticus + T. californiensis))))$. The Plutoniuminae and Cryptopinae logically share ancestry, and the Scolopocryptopinae may warrant elevation to family status.

GENERAL INTRODUCTION

Introduction

Among the more readily identified scolopendromorph centipedes in North America and Europe, ones with 21 or 23 pairs of legs and pedal segments, are the representatives of the cryptopid subfamily Plutoniuminae Bollman,¹ a senior subjective synonym of Theatopinae Verhoeff, occasionally misspelled as "Theatopsinae."² Recognizable to the unaided eye by their extremely robust ultimate legs (Fig. 1; see also Attems 1926, Fig. 433, and Shelley 1990a, Fig. 1), they also feature 21 leg pairs, a long caudal segment, roughly twice as long as the penultimate,

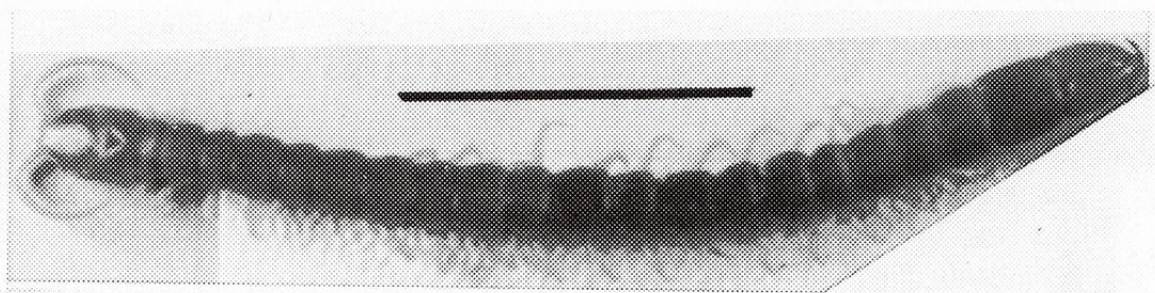


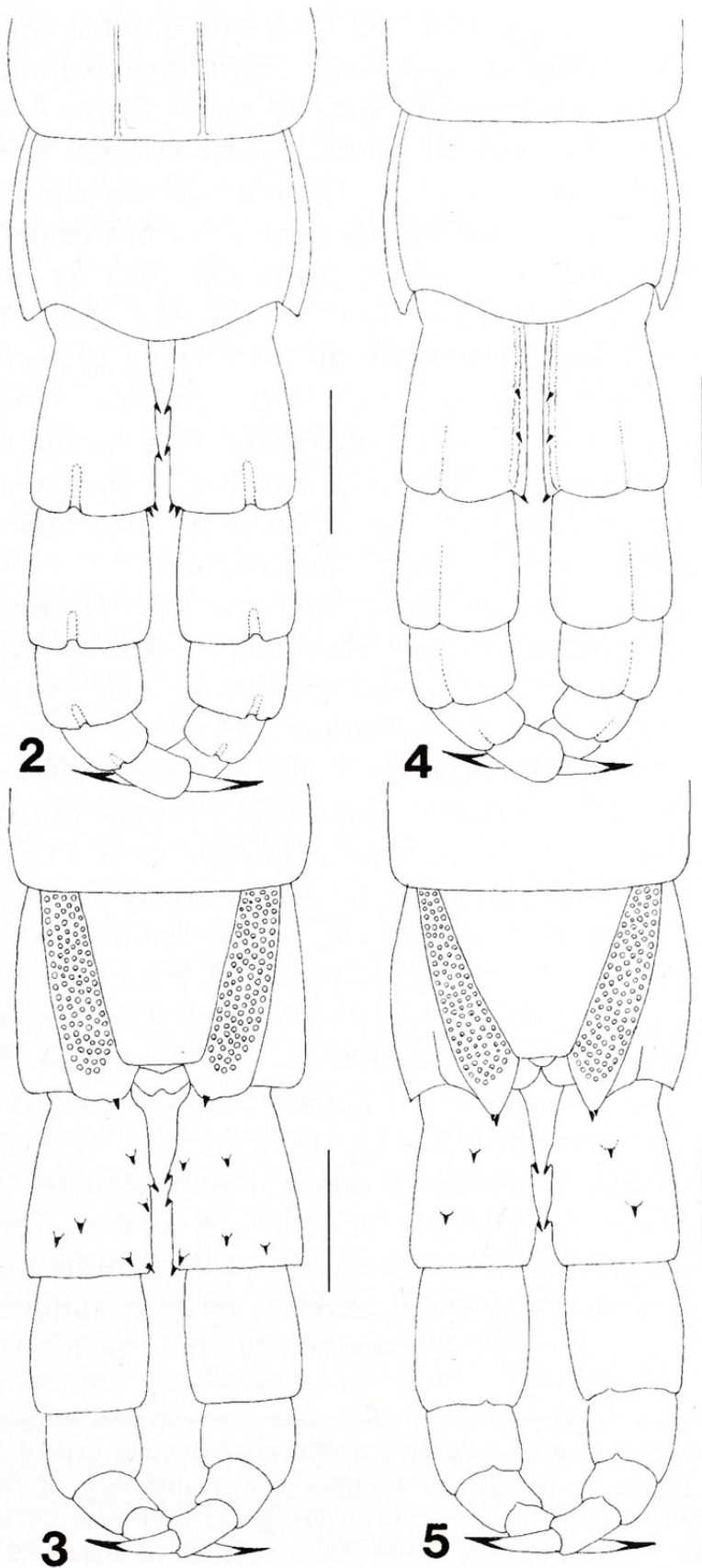
Fig. 1. *Theatops posticus*, dorsal view. Scale line = 1.00 cm.

and pale, lightly pigmented patches in the ocellar positions, lateral to the bases of the antennae. Crabill (1977) referred to the patches as "eyespot," an unfortunate term because these blind chilopods lack photoreceptors. The heavily sclerotized, forcipulate caudal legs are the most visible diagnostic feature, and according to Cloudsley-Thompson (1958) and Manton (1965), function to hold food. The plutoniuminines are thus convergent in this regard with the scolopendrid genus *Cupipes* Kohlrausch (compare Figs. 2-5, with Figs. 6-9).

The Plutoniuminae is comprised of two genera—*Plutonium* Cavanna, monotypic with *P. zwierleini* Cavanna occurring in Spain and mainland Italy, Sicily, and Sardinia, and *Theatops* Newport, with one Palearctic

¹As noted by Würmli (1975), Plutoniinae Bollman (1893) has priority by 13 years over Theatopinae Verhoeff (1906) as the senior name for this family-group taxon. However, Plutoniinae Bollman is preoccupied by the senior homonym, Plutoniinae Cockerell (1893) (Mollusca: Gastropoda), which has priority by one month. Shelley and Backeljau (1995) petitioned the International Commission on Zoological Nomenclature to remove the homonymy but incorrectly believed Plutoniinae Bollman was the older name. By agreement of all parties, Plutoniinae Bollman is being emended to "Plutoniuminae"; this decision will be announced in a forthcoming issue of Bulletin of Zoological Nomenclature. The present contribution is the first taxonomic usage of the corrected name.

²Confusion has existed as to formation of family-group names from genera with the "-ops" suffix, whether the "s" is retained or dropped. The genitive of this ending is "opis", of which the "is" is dropped to form family-group names, so the correct spelling is "Theatopinae" rather than "Theatopsinae."



Figs. 2-5. *Cupipes* spp. 2, ultimate legs and segment of species from Trinidad taken in cargo at Honolulu, Hawaii (NMNH), dorsal view. 3, the same, ventral view. 4, ultimate legs and segment of species from Isle of Palms, Cuba (NMNH), dorsal view. 5, the same, ventral view. Scale lines = 1.00 mm for each figure.

and four Nearctic species. Both the subfamily and the genus *Theatops* thus demonstrate Holarctic/Laurasian distribution patterns, and their biogeographies are intriguing. In addition to the North American/European disjunction in *Theatops*, allopatric populations exist in three species. In Europe, *T. erythrocephalus*³ (C. L. Koch) occurs in Croatia, Montenegro, Bosnia-Herzegovina,⁴ and the Iberian peninsula, thus exhibiting a hiatus of some 992 km (620 mi) that is partly occupied by *P. zwierleini*. In North America, *T. posticus* (Say) occurs east of the Great Plains and in the desert southwest, with an intervening gap of some 1200 km (750 mi) (Shelley 1990a), and *T. spinicaudus* (Wood) occupies two regions in the eastern states segregated by a lacuna ranging from 368-688 km (230-430 mi) (Fig. 31). Because of the extensiveness of past collecting, these lacunae are undoubtedly real and are unlikely to change significantly with future discoveries.

A third genus, *Tonkinodentus* Schileyko (1992), monotypic from Viet Nam, was assigned to the Theatopinae, but the type and only specimen of its species, *Tonkinodentus lestes* Schileyko, is missing the last three leg pairs, the caudalmost of which possesses most of the taxonomically critical characters in this subfamily. This genus occurs some 11,200 km (7,000 mi) east-southeast of the most proximate locality of *Theatops erythrocephalus* in Montenegro and some 11,920 km (7,450 mi) west-southwest of that of *Theatops posticus* in Mexico, and is hence implausible for the Plutoniuminae, which is otherwise geographically coherent. I therefore remove *Tonkinodentus* from the subfamily and leave it unassigned; proper placement awaits the discovery of fresh material, preferably several individuals, possessing all 21 leg pairs. It should be emphasized in this regard that the proposal of a new taxon is a serious action involving the placement of a new entry on the roster of available scientific names. Future students will have to consider this taxon and address shortcomings in the original account, completely rediagnosing it if necessary, and the proliferation of poorly conceived taxa and substandard accounts by past authors is a major reason for the nascency of myriapodology. It is therefore imperative

³Like most chilopods with the *-ops* generic suffix, confusion has existed over the gender of *Theatops* and whether it requires the feminine or masculine form of the species-group name. Thus, Kraepelin (1903) reported *T. erythrocephalus* whereas Attems (1930) cited *T. erythrocephala*. I (Shelley 1987) reviewed this situation in footnote 2 and noted that article 30 (a) (ii) of the 1984 edition of the *International Code of Zoological Nomenclature* supercedes past recommendations and declares that genus-group names ending in *-ops* are to be considered masculine regardless of derivation or treatment by the author.

⁴The countries of Slovenia, Croatia, Macedonia, Bosnia-Herzegovina, Montenegro, and Serbia comprise the former country of Yugoslavia.

that modern myriapod taxonomy be soundly based and not recapitulate this heritage, and the ultimate, and often penultimate, legs hold taxonomic importance in many scolopendromorph genera. The erection of new genera for anatomically incomplete chilopods, taxa that future workers will be compelled to reconceptualize, cannot be too strongly discouraged.

Another intriguing aspect of *Theatops* is the nearly identical external structures of *T. erythrocephalus*, in Europe, and *T. californiensis* Chamberlin, in California and Oregon, which are separated by around 11,520 km (7,200 mi). This resemblance was interpreted as convergence by Shelley (1990a), and it has produced especially similar external anatomies; the species are so nearly identical that confusion reigned for 88 years over the correct name for the latter. Past authors labeled it *T. californiensis* (Chamberlin 1902), *T. erythrocephalus californiensis* (Chamberlin 1911), and *T. erythrocephala* (Attems 1930, Chamberlin 1951a). Crabill (1960) and Kevan (1983) called it *T. californiensis* but suggested synonymy with *T. erythrocephala*. This enigma was resolved by Shelley (1990a), who deduced from variation in southwestern forms of *T. posticus* that *T. californiensis* is a valid species and hence that the name *T. erythrocephalus* applies exclusively to the European representative. Many of the geographically intermediate southwestern variants of *T. posticus* display anatomical conditions that are intermediate between those of its eastern population and *T. californiensis*, showing that these taxa were once united in a single species spanning the breadth of North America through the southern United States and the adjacent part of Mexico (Shelley 1990a). This knowledge indicates that the phenotypic resemblance between *T. californiensis* and *T. erythrocephalus* represents convergence, but it is an especially perfect example with no clear differences in their external anatomies. At present, I can only use geography to distinguish them in the key and assign specific names, and the search for differences requires substantially more critical information as might derive from comparative biochemistry. *Theatops californiensis* and *T. erythrocephalus* are thus prime candidates for investigation by immunological techniques and electrophoresis of haemolymph proteins.

Still another fascinating aspect of *Theatops* is the adaptability of *T. phanus* Chamberlin, which is known only from caves in Sutton and Menard counties, Texas, where it displays troglobitic adaptations. These include pallid color and long, slender appendages, the antennae reaching back to tergites 6-7, instead of to tergites 3-4, the antennomeres being three to five times longer than wide, instead of about twice as long, and the podomeres on the penultimate legs being four to five times longer than wide, as opposed to only two to three times longer (Weaver 1982). Some cave specimens are quite large, and the

anatomical modifications are visibly striking. However, while examining museum collections, I discovered individuals from epigeal populations that lack these features; the relative proportions of their podomeres and antennomeres are similar to those of *T. spinicaudus* and *T. posticus*. These surface forms are geographically proximate to, and clearly conspecific with, cave populations of *T. phanus*, which is consequently a highly variable species demonstrating a level of genetic plasticity that is not apparent in other Nearctic cryptopids. Occasional specimens of *Scolopocryptops sexspinosus* (Say) have been discovered in caves, but they are identical anatomically to epigeal individuals and are not modified by the subterranean environment.

This study of the Plutoniuminae, the first monographic treatment of a supra-generic chilopod taxon since Attems' (1930) ordinal treatise on the Scolopendromorpha, derives from an ongoing survey of North American scolopendromorphs. The discovery of the widespread, anatomically variable southwestern population of *T. posticus* and the resultant deduction of the correct binomial for *T. californiensis* (Shelley 1990a) focused attention on *Theatops* and led to the deletions of *T. spinicaudus* from Hawaii, Mexico, and Canada (Shelley 1990a, 1991). These works indicated that *T. erythrocephalus* should be examined in its proper context, along with the American congeners, and that *P. zwierleini* should be included to consolidate knowledge of the subfamily. The Plutoniuminae is thus one of the few chilopod family-group taxa that is amenable to a modern, all-inclusive treatment, because of its limited composition and occurrence in only two biogeographic regions. Because of the difference in the number of spiracles, Verhoeff (1906, 1907) and Schileyko (1992, 1996) believed that separate families were required for *Plutonium* and *Theatops*, and Schileyko (1996) even suggested that *Plutonium* deserved a separate superfamily as an "absolutely different group." However, most authors, including myself, subscribe to the system originated by Attems (1930), in which *Theatops* and *Plutonium* are assigned to the same subfamily. Such features as the depigmented patches in the ocellar positions, the elongated ultimate tergite, and the heavily sclerotized, forcipulate caudal legs constitute strong synapomorphies that unite *Theatops* and *Plutonium* in a monophyletic group. Although unique to the Scolopendromorpha, the autapomorphic 19 pairs of spiracles in *Plutonium* is only a generic feature; using it as the basis for a separate family or superfamily overemphasizes the character's significance in relation to the several attributes that are shared with *Theatops*, which indicate common ancestry. Consequently, I believe that the present concept of the Plutoniuminae represents a natural assemblage of related taxa.

This contribution presents diagnoses of all components of the Plutoniuminae, complete synonymies at all levels, detailed range descriptions with locality data for each species, and discussions of anatomical variation, ecology, and relationships. Complete citations for all available samples of *T. posticus* and *T. spinicaudus* would be prohibitively long, so these are summarized for certain states as indicated in each account. Acronyms of repositories of preserved study material are as follows:

- AAW—Private collection of A. A. Weaver, Wooster, Ohio.
AMNH—American Museum of Natural History, New York, New York.
ANSP—Academy of Natural Sciences, Philadelphia, Pennsylvania.
AU—Entomology Department, Auburn University, Auburn, Alabama.
CDFA—California Department of Food and Agriculture, Sacramento.
CAS—California Academy of Sciences, San Francisco.
DC—Natural Science Division, Dixie College, St. George, Utah.
EIU—Zoology Department, Eastern Illinois University, Charleston.
FMNH—Field Museum of Natural History, Chicago, Illinois.
FSCA—Florida State Collection of Arthropods, Gainesville.
INHS—Illinois Natural History Survey, Urbana.
LACMNH—Los Angeles County Museum of Natural History, Los Angeles, California.
LEM—Lyman Entomological Museum, MacDonald College, McGill University, Ste. Anne de Bellevue, Québec, Canada.
MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.
MEM—Mississippi Entomological Museum, Mississippi State University, Starkville.
MPM—Milwaukee Public Museum, Milwaukee, Wisconsin.
NCSM—North Carolina State Museum of Natural Sciences, Raleigh.
NHM—The Natural History Museum, London, England.
NMNH—National Museum of Natural History, Smithsonian Institution, Washington, DC.
OPCNM—Organ Pipe Cactus National Monument, Arizona.
SEM—Snow Entomological Museum, University of Kansas, Lawrence.
SREL—Savannah River Ecological Laboratory, Aiken, South Carolina.
SWRS—Southwest Research Station, Portal, Arizona.
TMM—Texas Memorial Museum, University of Texas, Austin.
UAR—University of Arkansas Arthropod Museum, Fayetteville.
UAZ—Entomology Department, University of Arizona, Tucson.
UCB—Essig Museum of Entomology, University of California at Berkeley.
UCD—Bohart Entomological Museum, University of California at Davis.
UCR—Entomology Department, University of California at Riverside.

UCT—Zoology Department, University of Connecticut, Storrs.

UGA—Zoology Department, University of Georgia, Athens.

UL—Biology Department, University of Louisville, Kentucky.

UMMZ—University of Michigan Museum of Zoology, Ann Arbor.

UMO—Enns Entomological Museum, University of Missouri, Columbia.

VMNH—Virginia Museum of Natural History, Martinsville.

WAS—Private collection of W. A. Shear, Hampden-Sydney, Virginia.

WVDA—West Virginia Department of Agriculture, Charleston.

ZMH—Zoologisches Institut und Museum, Universität Hamburg, Germany.

ZMUC—Zoological Museum, University of Copenhagen, Denmark.

LITERATURE REVIEW

The literature of the Plutoniuminae is relatively orderly; difficulties arose primarily from the tendency of early authors to inconsistently cite species under more than one genus, and an erroneous observation by Newport (1844) in his proposal of the oldest genus-group name, *Theatops*. Newport mistook the unpigmented spots in the ocellar positions as eyes, thus stating in the original and subsequent generic accounts (Newport 1844, 1845, 1856) "ocelli distincti." However, he contradicted this statement in the accompanying species accounts with the phrase, "ocellis inconspicuis lateralibus." Confusion thus developed as to whether *Theatops* and its type species, *Cryptops postica* Say, did or did not possess ocelli, which was partly responsible for Wood's proposal (1862) of the genus *Opisthemega*. Because the specimen of *C. postica* on which Newport's proposal was based was sent to him at the NHM by Say, no one else had seen it and could unequivocally resolve the question of eyes. Underwood (1887) reviewed the confusion in footnote 8 and concluded that *Theatops* "may as well be consigned to oblivion" and "at least it is not necessary to include it in future lists." These statements concerned R. I. Pocock, who was at the NHM and in a position to settle the issue by reexamining Say's specimen. He did so; reported (Pocock 1888) that it lacked eyes and that Newport was mistaken; and synonymized *Opisthemega* with *Theatops*. Pocock's analysis was accepted by subsequent authors, and future problems in the Plutoniuminae chiefly involved misidentifications, a few ill-conceived proposals of synonyms, and disagreement about the name and taxonomic status of *T. californiensis*.

The history of the Plutoniuminae begins with the description of *C. postica* for a specimen from Georgia or east Florida by Say (1821), a binomial subsequently cited by Newport (1844), Kohlrausch (1881), and, in the masculine gender, by Lucas (1840) and Bollman (1893). One of the first dozen or so centipedes to be described from North

America, it became the type species of *Theatops* (Newport 1844), based on the aforementioned specimen from Say. Gervais (1847) placed *Theatops* under *Cryptops*, though indicating that it might refer to a form of *Scolopendra*. Koch (1847) described *C. erythrocephalus* from Pula, Croatia, on the Istrian peninsula, and enhanced the description in an expanded account (1863) with a full-length illustration. He did not connect this centipede with Say's species and said nothing about *Theatops*, if he was even aware of Newport's taxon. Wood (1862) proposed *Opisthemegea* for two ostensibly new species, *O. postica* and *O. spinicauda*, from North Carolina and Illinois, respectively, without designating either as type species. Wood stated that *O. postica* lacked eyes; questioned whether it was identical to Say's species because it agreed with *T. postica* except for the eyes and teeth; and suggested that Newport might be mistaken about the presence of ocelli. However, he followed these accounts with others on *Theatops* and *T. postica* stating, "We have never seen a specimen of this species." Wood (1865) repeated his previous accounts of all these taxa, adding west Pennsylvania to the localities of *O. spinicauda*. Cope (1869) cited *O. postica* from the mountains of southwestern Virginia, misspelling Wood's genus as "*Opisthomega*," and Saussure and Humbert (1872) repeated the previous names and localities.

In the ensuing decade, Latzel (1880) tentatively placed *Theatops* in synonymy under *Scolopendra*. He recognized *Opisthemegea* and transferred Koch's species into this genus, forming the new combination, *O. erythrocephalum*. Kohlrausch (1881) recognized both *Theatops* and *Opisthemegea*; included *postica* under both names and *Cryptops*; cited *erythrocephalus* under *Cryptops* and *Opisthemegea*; but listed *spinicauda* under *Opisthemegea* only. Cavanna (1881) erected *Plutonium* for a new centipede from Sicily, *P. zwierleini*, possessing spiracles on segments 2-20. Meinert (1886) recorded *O. spinicauda* from Acapulco, Mexico; proposed the synonym, *O. insulare*, for specimens ostensibly from Hawaii, then called the Sandwich Islands; and erected *O. crassipes* for specimens from Florida, Virginia, and Kentucky. Though he questioned its distinction from *O. postica*, McNeill (1887, 1888)⁵ recorded *O. crassipes* from Indiana and Escambia County, Florida. In addition to synonymizing *Opisthemegea* with *Theatops*, Pocock (1888) also placed *O. postica* and *O. crassipes* under *T. postica*. The remaining publications of this decade belong to Bollman (1888a-e), who cited the new combination *T. crassipes*, placed *postica* under *Cryptops*, *Theatops*, and *Opisthemegea*, and reported

⁵To conserve space, subsequent publications that merely provide new localities are summarized in the species listings at the conclusion of this section.

several new localities for this species and for *T. spinicaudus*.

In the 1890's, Bollman (1893) established the Plutoniinae and attempted the first general range descriptions for *T. posticus* and *T. spinicauda*,⁶ cited in the ensuing listings. He recorded the latter from the southwestern United States in general, a citation not justified by any collection or previous records and the probable source for future erroneous listings from California and the southwest (Chamberlin 1902, Crabill 1960). Verhoeff (1896) proposed *O. lusitanum* for a centipede from Portugal and attempted to contrast it with *O. erythrocephalus*.

The twentieth century began with the proposal of *T. californiensis* for a form from Quincy, Plumas County, California, by Chamberlin (1902). He also summarized the synonymies and distributions of *T. posticus* and *T. spinicaudus*, largely repeating the ranges reported by Bollman (1893), and provided a key to the then three American species. Kraepelin (1903) assigned Chamberlin's species to synonymy under *T. erythrocephalus* and recorded it from Oregon and California; he also provided a key to *T. posticus*, *T. spinicaudus*, and *T. erythrocephalus*, along with synoptic accounts to these species, *P. zwierleini*, and the genera *Theatops* and *Plutonium*. Other new synonymies proposed by Kraepelin (1903) include *O. insulare* under *T. spinicaudus* and *O. lusitanum* under *T. erythrocephalus*, the last binomial being a new combination. His and subsequent listings of *T. erythrocephalus* from Italy are erroneous and refer instead to *P. zwierleini* (Minelli, *in litt.*), and one also wonders about the source for Kraepelin's record from Oregon. *Theatops californiensis* had only been described the previous year, and Quincy, the only locality Chamberlin (1902) listed, is too distant from Oregon (ca. 224 km [140 mi]) to imply occurrence in that state. I know of no pre-1903 Oregon specimens, and if geographic proximity were the basis for Kraepelin's citation, one would expect him to choose Nevada, since Quincy is only about 80 km (50 mi) from this state. The basis for the sudden Oregon citation is thus a mystery, but it is nevertheless correct as shown by recent samples from Douglas and Josephine counties. Three years later, Verhoeff (1906) proposed the family "Theatopsidae."

In ensuing decades, Chamberlin (1911) reduced his species to a race of *T. erythrocephalus*. Gunthorp (1920) reviewed Wood's papers and authorships, and credited him with *Opisthemea*, *O. postica*, and

⁶Bollman's inconsistencies are noteworthy. He (1888a, c) cited *spinicaudus*, suddenly changing (1893) without explanation to the feminine termination. However, he simultaneously and consistently employed the masculine suffix for *posticus* (1888c-e, 1893), but he suddenly and without explanation cited it (1893) under both *Cryptops* and *Theatops*, whereas he previously (1888c-e) used only the latter genus.

O. spinicauda without alluding to the confusion surrounding *Opisthemega* and *postica* or the synonymy with *Theatops* proposed by Pocock (1888). Attems (1930) published the last comprehensive work on the Scolopendromorpha, recognizing *Plutonium*, *P. zwierleini*, *Theatops*, *T. postica*, *T. erythrocephala*, and *T. spinicauda*. He provided a key to the species of *Theatops* and summarized locality information since Kraepelin's work (1903). Attems (1938) included *T. spinicauda* among the Hawaiian fauna, a record deleted by Shelley (1991). Chamberlin (1951*b*) described the fourth American and fifth total species of *Theatops*, *T. phanus*, from a cave in Sonora County, Texas, and presented a key to species. He recognized only four species, implying that he then considered *T. californiensis* to be a synonym of *T. erythrocephala*. Crabill (1957) reviewed Newport's chilopod genera, credited him with authoring *Theatops*, and indicated that the type species, *C. postica* Say, was fixed by subsequent monotypy. Matic (1960) proposed *T. erythrocephala breuili* for a specimen from a Spanish cave. Crabill (1960) included *Theatops* and Theatopinae in a key to North American scolopendromorph genera, subfamilies, and families, and characterized the ranges of the four North American species. He considered *T. californiensis* to be a species, but suggested that it might be a synonym of *T. erythrocephala*.

In recent years, Würmli (1975) reported authentic localities for *P. zwierleini* and provided a distribution map. In concluding paragraphs, he reviewed the distribution of *T. erythrocephalus*, which he considered as including California and Oregon, thus implying synonymy of *T. californiensis*, placed *T. e. breuili* in synonymy, and noted that Plutoniinae Bollman antedates Theatopidae Verhoeff. Crabill (1977) included *Theatops* and Theatopinae in a key to North American and Mexican cryptopid taxa, and Summers (1979) included *T. posticus*, *T. spinicaudus*, and the Theatopinae in a key and taxonomic listing to centipedes of the north-central United States.

In a definitive text on centipede biology, Lewis (1981) reported the results of Baerg (1924) on the effect of centipede bites, noting that *T. spinicauda* had little to no effect on rats and caused sharp pain in humans that disappeared in 30 minutes. Lewis recognized the subfamily Theatopsinae with *Plutonium*, in Sicily, Sardinia, and Campania, and *Theatops*, in North America, the Mediterranean region, and Hawaii. He noted that *Plutonium* has 19 pairs of spiracles, one each on segments 2-20, or all leg bearing segments except the first and last, instead of the nine pairs typically found in scolopendromorphs with 21 segments. Kevan (1983) reported the northernmost records for *T. postica*, *T. spinicauda*, and *T. californiensis* and questioned whether the last name was a synonym of *T. erythrocephala*. Shelley and Edwards (1987) reported *T. posticus*

statewide from Florida and presented a distribution map, and Shelley (1987) reported general distributions of *T. posticus* and *T. spinicaudus* in North Carolina, showing counties of occurrence on a locality map.

In the latest four papers on the Plutoniuminae, Shelley (1990a, 1991) deleted *T. spinicaudus* from Hawaii, Mexico, and Canada; reported the first Mexican localities for *T. posticus*; demonstrated broad occurrence of this species in the southwestern United States; and deduced that *T. californiensis* is the correct binomial for the congener in northern California and Oregon. Hence, he restricted the name *T. erythrocephalus* to the European species. In a paper on Yugoslavian centipedes Kos (1992) characterized *T. erythrocephalus* as a mediterranean to sub-mediterranean species and recorded it from Croatia, Bosnia-Herzegovina, and Montenegro. Finally, Hoffman (1995) reported *T. posticus* from 14 counties in Virginia. Thus at this writing, plutoniumine species have been reported from the following states in Mexico, counties and states in the United States, and islands and general regions of European countries. The published overall range statements are summarized first for *T. posticus*, *T. spinicaudus*, and *T. californiensis*, and where appropriate, the general range statements for each state are presented first under each state, for the American species, and under each country or island, for the European representatives.

Theatops posticus

USA: General range statements—East of the Mississippi River, north to Virginia, Indiana, and Illinois (Bollman 1893); the eastern United States south of Virginia, Indiana, and Illinois (Chamberlin 1902); sporadic in Utah and Arizona, and ranging from southern Illinois, Ohio, and northern Virginia south to the Gulf States (Crabill 1960); and the eastern United States generally south of the Great Lakes and east of the Central Plains, extending along the Gulf of Mexico to San Patricio County, and inland to Limestone County, Texas (Shelley 1990a).

Indiana—Bloomington, Monroe Co. (McNeill 1887, Bollman 1888e); Dublin, Wayne Co., and Brookville, Franklin Co. (McNeill 1887); New Providence, Clark Co., and Wyandotte, Crawford Co. (Bollman 1888e).

Illinois—Gallatin, Hardin, Pope, Jackson, and Pulaski counties (Summers et al. 1980, 1981).

Ohio—southern Ohio in general (Kevan 1983); southeastern Ohio in general (Williams and Hefner 1928); Vinton, Gallia Co. (Morse 1902).

Virginia—Virginia in general (Underwood 1887); southwestern Virginia in general (Cope 1869); Lee Co. (Meinert 1886); Luray, Page

Co., and Natural Bridge, Rockbridge Co. (Bollman 1888*d*); Albemarle, Alleghany, Botetourt, Buchanan, Floyd, Greenville, Henry, Lee, Montgomery, Page, Patrick, Pittsylvania, Rockbridge, and Rockingham cos. (Hoffman 1995).

Kentucky—Kentucky in general (Underwood 1887, McNeill 1888); Jessamine Co. (Crabill 1955*a*); Bee Spring, Edmonds Co. (Meinert 1886, Crabill 1955*a*); Pine Ridge, Wolfe Co. (Crabill 1955*a*, Branson and Batch 1967); Louisville, Jefferson Co., Campbellsville, Taylor Co., Cumberland Falls State Park, Whitley Co., near Livingston, Rockcastle Co., and near Irvine, Estill Co. (Crabill 1955*a*); and along Red R., Powell Co. (Branson and Batch 1967).

Tennessee—Beaver Cr., Jefferson Co. (Bollman 1888*b*); Mossy Creek, Jefferson Co. (Bollman 1888*c*); Glendale Hills, Davidson Co. (Chamberlin 1918*a*).

Carolina in general without specifying the state (Kraepelin 1903, Attems 1930).

North Carolina—North Carolina in general (Wood 1865, Saussure and Humbert 1872, Kohlrausch 1881, Underwood 1887, Brölemann 1896, Kraepelin 1903); North Carolina in general, but rare in mountains, specific counties shown in Fig. 13 (Shelley 1987); Goldsboro, Wayne Co. (Wood 1862, Bollman 1888*d*, Brimley 1938, Wray 1950, 1967); Hendersonville, Henderson Co., and Duke Forest, Durham Co. (Brimley 1938, Wray 1950, 1967); Greensboro, Guilford Co. (Causey 1940).

South Carolina—Clemson, Pickens Co. (Crabill 1950).

Georgia—Georgia in general (Say 1821, Lucas 1840, Gervais 1847, Saussure and Humbert 1872, Kohlrausch 1881, Pocock 1888, Attems 1930); Macon, Bibb Co. (Bollman 1888*d*); Okefenokee Swamp, Ware Co. (Chamberlin 1918*b*); near Sylvania, Screven Co., Savannah, Chatham Co., and near Pendergrass, Jackson Co. (Chamberlin 1944*a*); and Camilla, Mitchell Co. (Chamberlin 1945).

Florida—Statewide (Shelley and Edwards 1987); Florida in general (Underwood 1887, McNeill 1888, Kraepelin 1903, Attems 1930); East Florida (Say 1821, Lucas 1840, Gervais 1847, Saussure and Humbert 1872, Kohlrausch 1881, Pocock 1888). Jacksonville, Duval Co., and St. Johns River, county uncertain (Meinert 1886); Escambia Co. in general (McNeill 1887); Archbold Biological Station, Lake Placid, Highlands Co., and Gainesville, Alachua Co. (Chamberlin 1951*a*).

Louisiana—Louisiana in general (Brölemann 1896, Attems 1930). Creston, Natchitoches Par. (Chamberlin 1918*b*); Covington, St. Tammany Par. (Viosca 1918).

Texas—Houston, Harris Co. (Chamberlin 1943).

New Mexico—Peloncillo Mountains, Hidalgo Co. (Shelley 1990*a*).

Arizona—Rincon Mountain, Pima Co. (Chamberlin 1944*b*); numerous localities in Coconino, Yavapai, Gila, Maricopa, Graham, Pinal, Yuma, Pima, Santa Cruz, and Cochise cos. (Shelley 1990*a*).

Utah—Washington Co. in general (Chamberlin 1925, Shelley 1990*a*). St. George, Washington Co. (Shelley 1990*a*).

Nevada—Nelson, Clark Co., and Nuclear Testing Site, Pahute Mesa, and Rocky Valley, Nye Co. (Shelley 1990*a*).

California—Santa Cruz Island, Channel Islands National Park, and 48 km (30 mi) SW Palm Desert, Riverside Co. (Shelley 1990*a*).

MEXICO: Chihuahua—51 km (31.8 mi) S Minaca (Shelley 1990*a*).

Sonora—5 km (3.1 mi) NW Huicoche (Shelley 1990*a*).

Baja California Norte—La Turquesa, 23.2 km (14.5 mi) N Ensenada, and 22.4 km (14 mi) S US border (Shelley 1990*a*).

Theatops spinicaudus

General range statements—Southwestern United States in general, north to Chicago, east in Tennessee to the mountains, and north to Allegheny Co., Pennsylvania (Bollman 1893); southwestern United States in general, Tennessee to Pennsylvania (Chamberlin 1902); Hawaiian Islands and southeastern United States (Chamberlin 1920); America north of Mexico (Bücherl 1942); western Pennsylvania to the Gulf Coast west to Missouri and Arkansas (Crabill 1955*b*); Mexico and California without further specification, northern Missouri and Illinois to the Gulf States north through the Carolinas and up the Coastal Plain possibly to southern Pennsylvania (Crabill 1960); the eastern United States generally south of the Great Lakes and east of the Central Plains, being unknown beyond southwestern Arkansas, eastern Oklahoma, and central Iowa (Shelley 1990*a*).

Illinois—Illinois in general (Underwood 1887); southern Illinois (Wood 1862, 1865, Saussure and Humbert 1872, Kohlrausch 1881, Kraepelin 1903, Attems 1930); Chicago and Cook Co. (Wood 1862, 1865, Auerbach 1951*a, b*); Alto Pass, Union Co. (Chamberlin 1944*b*); and Cook, Champaign, McLean, Greene, Union, Gallatin, Johnson, Pope, Union, Jackson, Williamson, Randolph, and Pulaski cos. (Summers et al. 1980, 1981).

Missouri—St. Charles, St. Charles Co. (Chamberlin 1928, Crabill 1955); Libertyville, St. Francois Co. (Chamberlin 1944*b*); Ranken, St. Louis, Chesterfield, and Glencoe, St. Louis Co.; Sullivan, Franklin Co.; and High Ridge and Vaugirard, Jefferson Co. (Crabill 1955*c*).

Arkansas—Near Oliphant, Jackson Co. (Chamberlin 1942); near Hot Springs, Garland Co.; Ben Lomond, Sevier Co.; Mt. Magazine, Logan Co.; Arkadelphia, Clark Co.; and Delight, Pike Co. (Chamberlin

1944b); Little Rock, Pulaski Co., and Ultima Thule, county unknown (Bollman 1888a, 1893); and Arkadelphia and Okolona, Clark Co., and Muddy Fork, county unknown (Bollman 1893).

Pennsylvania—Pennsylvania in general (Underwood 1887); western Pennsylvania (Wood 1862, 1865, Saussure and Humbert 1872, Kevan 1983).

Tennessee—Mossy Cr., Jefferson Co. (Bollman 1888c); Gatlinburg and Great Smoky Mountains National Park, Sevier Co. (Chamberlin 1944b).

North Carolina—North Carolina in general (Brölemann 1896, Kraepelin 1903, Attems 1930); west of the central Piedmont Plateau, specific counties shown in Fig. 13 (Shelley 1987); Mt. Pisgah, Haywood/Buncombe cos. (Wray 1950, 1967).

Georgia—Lula, Hall Co. (Chamberlin 1944a).

Theatops californiensis

General range statement—along the western slope of the Sierra Nevada and Cascade Mountains from Tulare County, California, to Douglas County, Oregon, extending to San Francisco Bay and the Pacific Ocean from Marin to Mendocino cos., California (Shelley 1990a).

California—California in general (Kraepelin 1903, Attems 1930, Crabill 1960); Quincy, Plumas Co. (Chamberlin 1902, Shelley 1990a).

Oregon—Oregon in general (Kraepelin 1903, Chamberlin 1911, Attems 1930, Crabill 1960, Kevan 1983).

Theatops phanus

Texas—Texas in general (Crabill 1960); Sonora, Sutton Co. (Chamberlin 1951b, Reddell 1965, Shelley 1990a); Powell's Cave, Menard Co. (Reddell 1965, Shelley 1990a).

Theatops erythrocephalus

Croatia—Dalmatia (= littoral Croatia) (Kraepelin 1903, Attems 1930). Istrian peninsula in general (Attems 1930), Pula (Koch 1847, 1863, Kohlrausch 1881, Attems 1929). Sipan Island (Shelley 1990a).

Hungary—Hungary in general (Kraepelin 1930); south Hungary (Attems 1930). In modern Europe these reports probably refer to parts of Croatia.

Montenegro—Montenegro in general (Attems 1930).

Spain—Cueva del Cerro de la Pileta (Matic 1960).

Portugal—Portugal in general (Verhoeff 1896, Kraepelin 1903, Attems 1930).

Plutonium zwierleini

Sicily—Sicily in general (Cavanna 1881, Kraepelin 1903, Würmli 1975); Ficuzza and Taormina (Attems 1930).

Sardinia—Sardinia in general (Kraepelin 1903, Attems 1930, Würmli 1975).

Italy—South Italy, Cave of Tirreni and Calabria (Attems 1930); Campania Region (Würmli 1975, Lewis 1981).

TAXONOMIC CHARACTERS

Aside from the segmental spiracles that characterize *Plutonium*, the taxonomic features in the Plutoniuminae are located primarily on the ultimate legs and segment. The dorsal and ventral surfaces are both important in distinguishing species of *Theatops*, and the head and first 20 segments hold little taxonomic utility. The massive caudal legs instantly identify the centipede as a plutoniumine, and if these are lost, *Theatops* can be confused with the species of *Scolopocryptops* Newport that exhibit complete paramedian dorsal sutures. In *Theatops*, tergites 2-20, or every tergite except the first and last, exhibit two such grooves, which lie on both sides of the midline, run the complete length of the plate, and divide it into nearly equal thirds. Three species of *Scolopocryptops* also demonstrate complete paramedian sutures on all except the anteriormost tergites—*S. gracilis* Wood in California, occurring sympatrically with *T. californiensis*; *S. rubiginosus* L. Koch in the midwest, occurring sympatrically with *T. spinicaudus*; and *S. peregrinator* (Crabill) in the northern Appalachians, occurring sympatrically with *T. posticus*. In these areas, care is needed to avoid misidentifying a cryptopid lacking the caudal legs, or the legs and caudal segment, and confusing *Theatops* and *Scolopocryptops*. If such a specimen is found, one should rely on secondary features to distinguish the genera, as listed in Table 1.

Ultimate segment. Dorsal surface. The ultimate/caudal tergite is noticeably longer than the preceding ones and lacks paramedian sutures. It either lacks sutures altogether, as in most specimens of *T. spinicaudus* (Figs. 7-9) (occasional specimens have a short sutural remnant anteriorly), or has a complete or nearly complete one in the midline, as in the other species (Fig. 6). The suture is complete in *T. posticus* and *T. phanus*, running the entire length of the tergite from the anterior to caudal margins; it is rarely complete in *T. californiensis* and *T. erythrocephalus*, as it usually disappears just short of the caudal margin. Thus, in the absence of the caudal legs, the presence or absence of the median suture on the ultimate tergite distinguishes *T. spinicaudus* and *T. posticus* in their areas of overlap in the eastern United States. The latter species was incorrectly illustrated without this suture by Shelley

Table 1. Comparisons of *Theatops* and species of *Scolopocryptops* with complete paramedian sutures.

	<i>Scolopocryptops</i>	<i>Theatops</i>
Ultimate legs	subequal in breadth and degree of sclerotization to other legs, not noticeably enlarged	heavily sclerotized and greatly enlarged, much larger than other legs
Ultimate tergite	subequal in length and with same suture pattern as other tergites	noticeably longer than other tergites, either without sutures or with single one in midline
Caudal coxopleurae	not extended and without spurs	extended and/or with distal spur except in eastern population of <i>T. posticus</i>
Number of segments and leg pairs	23	21
Color	usually orange, reddish-orange, or brown, excepting yellowish variant of <i>S. peregrinator</i>	yellowish
Cephalic plate	depigmented "eyespot" absent	pale, depigmented "eyespot" present
Anteriormost tergites	1st-3rd tergites with incomplete paramedian sutures except in <i>S. gracilis</i>	complete paramedian sutures begin on 2nd tergite

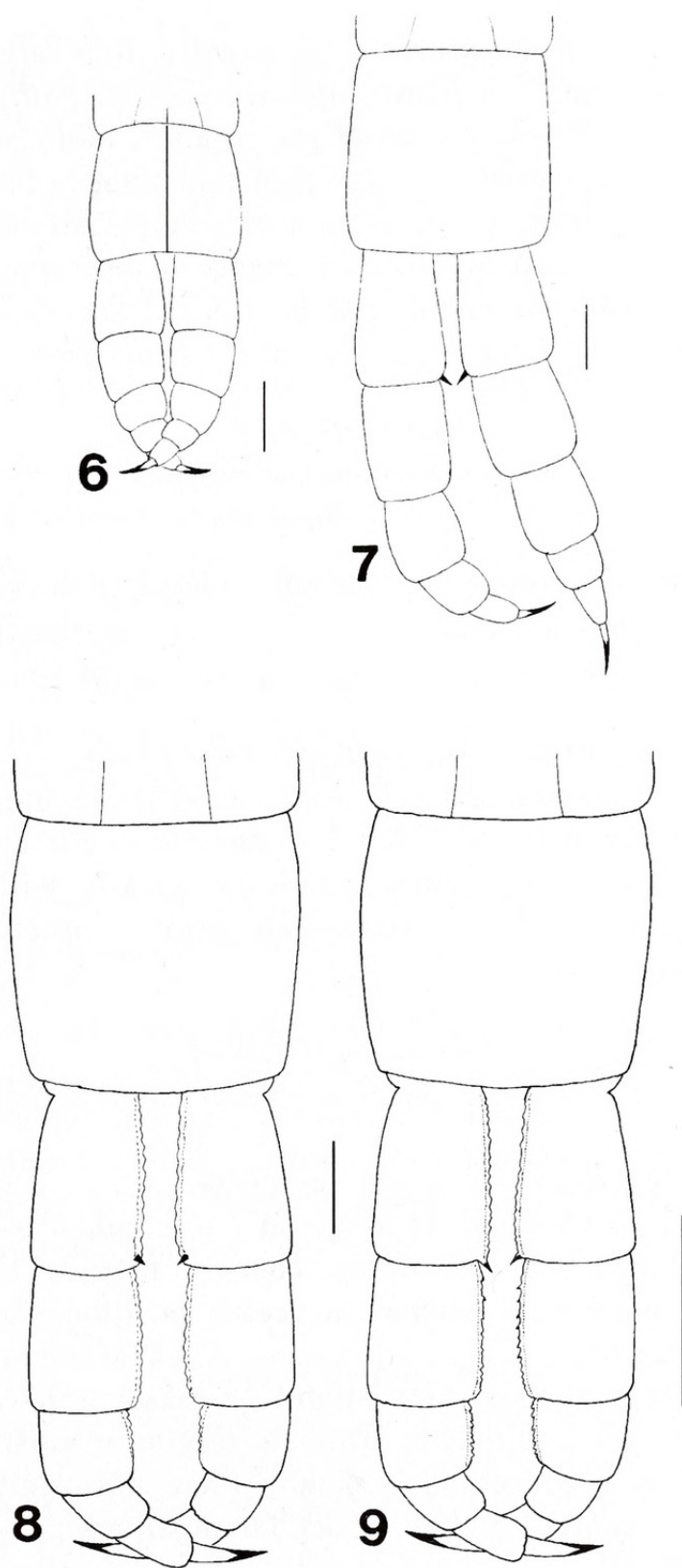
(1987, Fig. 3) and Shelley and Edwards (1987, Fig. 8); the errors were corrected by Shelley (1990a, Fig. 3).

Ventral surface. The caudal coxopleurae, flat, not extended, and apically rounded in the eastern population of *T. posticus* (Shelley 1990a, Fig. 6), are modified to some degree in the other species and most individuals in the southwestern population of *T. posticus*. Conditions vary widely, but the structures are usually elevated, produced slightly beyond the caudal segmental margin, and typically have a variable apical

spur or a black dot; in the residual southwestern intergrades, the structures are elevated and often produced, but lack an apical spur or black dot (Shelley 1990a, Figs. 7-11). The strongest, most pronounced coxopleurae are in *T. californiensis* and *T. erythrocephalus* (Figs. 13-17, 40-41). In the absence of the caudal legs, this coxopleural feature also distinguishes *T. spinicaudus* from *T. posticus* in their areas of sympatry.

Ultimate legs. The robust, heavily sclerotized, forcipulate caudal legs are the most obvious diagnostic trait of the Plutoniuminae and readily identify *Theatops* in the United States. Occasionally distended (Figs. 7, 19), the legs typically extend directly caudad basally then curve towards each other and converge such that the tips either meet or cross. They are believed to hold prey for feeding, and this can probably occur either apically, as the sharply pointed tips could puncture most prey organisms, or basally, with the prey being squeezed or pinched by the legs. The caudal legs are more heavily sclerotized than the tergites or the other appendages, but the inner or medial surfaces in many individuals are particularly hard, much more so than the outer surfaces. Perhaps the caudal legs serve to kill prey by crushing or puncturing as well as to hold it.

The outer surfaces of these legs (dorsal, ventral, and lateral) are usually gently curved to flattened, but the medial surfaces are often strongly flattened, such that there are sharp ventro- and dorsomedial corners that are often elevated above the ventral and dorsal surfaces, forming a ridge. The ridge sometimes points mediad rather than ventrad or dorsad, such that the medial surface is slightly recessed, in some individuals being slightly concave rather than flat. These ridges or corners may be linear or irregularly and lightly scalloped, and are often ornamented with variable teeth or spurs. Ventrally, the number, size, and arrangement of the teeth vary greatly in *T. spinicaudus*, *T. phanus*, and the southwestern population of *T. posticus* (Figs. 19-30, 35-38; Shelley 1990a, Figs. 7-11), whereas there is usually a single distal tooth in *T. californiensis* and *T. erythrocephalus* (Figs. 13-17, 40-41). Dorsally, there is less ornamentation, but occasional individuals show a serrated margin with several fine teeth (Figs. 7-9, 33-34). The distomedial prefemoral spurs in *T. spinicaudus* and *T. phanus* are really at the distal corner of this ridge; consequently, the dorsal surfaces of the legs hold taxonomic utility in distinguishing these species from *T. posticus*, particularly in areas where *T. posticus* and *T. spinicaudus* are sympatric. Although differing in the presence (*T. posticus*) and absence (*T. spinicaudus*) of the median suture on the ultimate tergite, they are most readily distinguished by the presence or absence of the distomedial prefemoral spur. Variation on the ventral surface holds little



Figs. 6-9. Caudal tergite and legs of *T. posticus* and *T. spinicaudus*, dorsal views. 6, *T. posticus* from Jefferson County, Florida. 7-9, *T. spinicaudus* from selected localities. 7, McDowell County, North Carolina. 8, Polk County, Arkansas. 9, Haywood County, North Carolina. Scale lines = 1.00 mm for each figure.

taxonomic utility, but the presence of, usually, four large distal spurs, one on each prefemur and femur, distinguishes *T. californiensis* from *T. posticus* in California; the spurs are smaller, more on the order of teeth, and there are consistently less than four total in the southwestern population of the latter. To be certain of determinations of California material, one should also examine the caudal coxopleurae, which almost always have a sizable terminal spur in *T. californiensis* (Figs. 13-17) and no adornment in *T. posticus* (Shelley 1990a, Figs. 7-11).

TAXONOMY

Order Scolopendromorpha

Key to Families

- With four ocelli on each side of cephalic plate lateral to bases of antennae Scolopendridae Leach
Without ocelli Cryptopidae Kohlrausch

Family Cryptopidae Kohlrausch

Diagnosis (adapted from Hoffman (1982)). Scolopendromorpha with 21 or 23 leg pairs and pedal segments; ocelli absent; tarsi of leg pairs 1-19 single-segmented; sternites usually with median and transverse grooves, without paramedian grooves; intercalary tergites usually strongly developed.

Key to Subfamilies

1. With 23 leg pairs and pedal segments..... Scolopocryptopinae Pocock
With 21 leg pairs and pedal segments..... 2
2. Ultimate legs strongly incrassate and forcipulate; ultimate tergite much longer than preceding; cephalic plate with conspicuous, lightly pigmented patches in ocellar positions lateral to bases of antennae Plutoniuminae Bollman
Ultimate legs at most only slightly crassate, relatively long and slender, not forcipulate; ultimate tergite at most only slightly longer than preceding; cephalic plate uniformly pigmented, without lighter patches in ocellar positions Cryptopinae Kohlrausch

Subfamily Plutoniuminae Bollman (Nomen Correctum)

Plutoniinae Bollman, 1893:165, 168.

Theatopsidae Verhoeff, 1906:432; 1907:253. Ribaut, 1915:338. Attems, 1930:249-250.

Plutoniidae: Verhoeff, 1906:433.

Theatopsini: Attems, 1926:376.

Theatopinae: Bücherl, 1942:325. Matic, 1960:446. Crabill, 1960:9. Summers 1979:696. Summers, Beatty, and Magnuson, 1980:245; 1981:59. Kevan, 1983:2945. Shelley, 1987:505.

Theatopsinae: Lewis, 1981:427. Schileyko, 1992:13.

Components. *Theatops* Newport, 1844, and *Plutonium* Cavanna, 1881. *Tonkinodentus* Schileyko, 1992, assigned to the Theatopinae in its original proposal, is removed from subfamily and left unassigned.

Diagnosis (adapted from Attems 1926). A subfamily of moderate-size to large cryptopids with 21 pairs of legs and pedal segments, color generally yellowish, usually with lighter, pale or unpigmented, patches lateral to bases of antennae in ocellar positions; complete paramedian dorsal sutures present on tergites 2-20 (see Attems 1926, Fig. 433, p. 369); caudal tergite nearly twice as long as penultimate, with or without median suture; ultimate legs short, massive, and forcipulate, heavily sclerotized, basal podomeres nearly as wide as long, with or without dorsal and ventral teeth and spurs.

Distribution. Southern Europe—coastal Croatia and Montenegro, Bosnia-Hercegovina, southern Italy (Campania), Sardinia, Sicily, Spain, and Portugal (Fig. 44); eastern North America generally east of the Central Plains and south of the Great Lakes, from western New England and the vicinity of Chicago, Illinois, to the south Florida Keys and central, southern, and western Texas; and western North America from western Chihuahua and northern Baja California Norte, Mexico, to the southern Basin and Range Province in southern Nevada and southwestern Utah, westward to the Pacific Ocean and southwestern Oregon (Fig. 10).

Genus *Theatops* Newport

Theatops Newport, 1844:409; 1845:60; 1856:60. Wood, 1862:36; 1865:171. Saussure and Humbert, 1872:200. Kohlrausch, 1881:93. McNeill, 1888:16. Pocock, 1888:285, 287; 1895:28. Bollman, 1893:127, 142, 169-170. Brölemann, 1896:50; 1904:244. Kraepelin, 1903:64-65. Verhoeff, 1906:385; 1907:253. Chamberlin, 1911:472. Attems, 1930:250-251. Bücherl, 1942:325-326. Crabill, 1957:345. Matic, 1960:446. Kevan, 1983:2945. Foddai *et al.*, 1995:8.

Opisthemega Wood, 1862:35; 1865:169. Latzel, 1880:145-147. Kohlrausch, 1881:130. Meinert, 1886:207-208. Underwood, 1887:64-65. Daday, 1889:92.

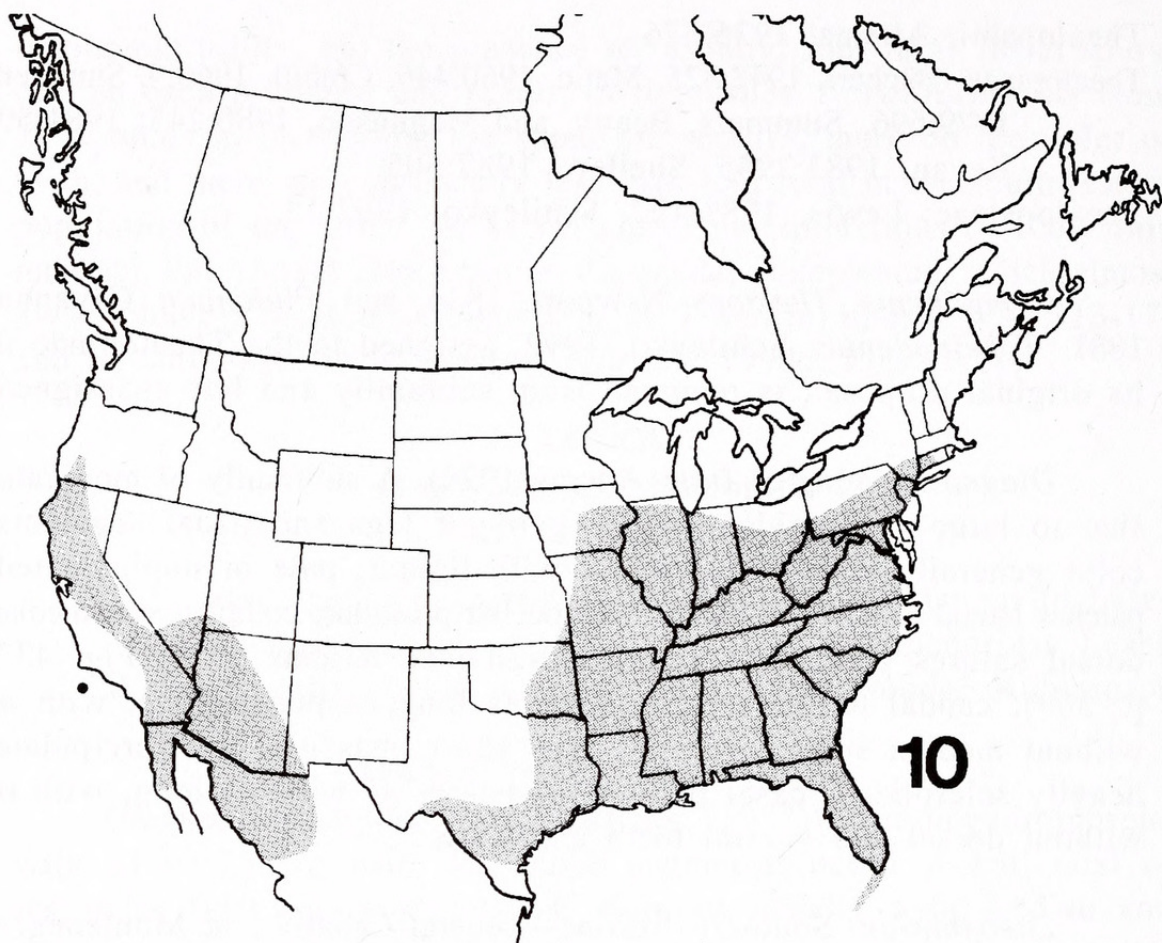


Fig. 10. Approximate probable distributions of *Theatops* and the Plutoniuminae in the Western Hemisphere. A smooth line is drawn around range extremes in all directions.

Opisthomega: Saussure and Humbert, 1872:200. Haase, 1887:78.

Type species. Of *Theatops*, *Cryptops postica* Say, 1821, by subsequent monotypy of Newport (1845). As explained by Crabill (1957), Newport (1844) originally proposed *Theatops* without mention of included species, but the next year, he (Newport 1845) cited *C. postica* under it, thereby fixing this as the type species. *Opisthomega* was proposed for two ostensibly new species, *O. postica* and *O. spinicauda*. Wood (1862) did not designate either as the type species, nor did he (Wood 1865) do so in his work on North American myriapods. No one else has done so either, and this action would be redundant now with *Opisthomega* in synonymy under *Theatops*. According to Article 12(b)(5) of the International Code of Zoological Nomenclature, genus-group names published before 1931 are available if one or more available species-group names are published in combination with it, or clearly included under it, or clearly referred to it by bibliographic reference. As both *postica* and *spinicauda* are valid species-group names, published in accordance with the Code, *Opisthomega* meets the requirements of

this article and is an available genus-group name even though it lacks a type species. It is one of the rare genus-group names lacking a genotype, the only one I know of in myriapods.

Diagnosis. With nine pairs of spiracles, on segments 3, 5, 8, 10, 12, 14, 16, 18, and 20.

Distribution. Coastal Croatia and Montenegro, Bosnia-Herzegovina, Spain, and Portugal; eastern North America from western New England and the vicinity of Chicago, Illinois, to the south Florida Keys and nearly to Corpus Christi, Texas, ranging westward to the eastern border of the Central Plains in Oklahoma and onto the Edwards Plateau in Texas; and western North America from western Chihuahua and southern Sonora, Mexico, to the Pacific Ocean in California and northern Baja California Norte, north to southern Nevada, southwestern Utah, and southwestern Oregon (Fig. 10).

Species. Five, as distinguished in the following key, adapted from those in Attems (1930), Chamberlin (1951*b*), and Weaver (1982).

Remarks. Sutural differences on the ultimate tergite deserve emphasis. Every specimen of *T. posticus* and *T. phanus* that I examined displayed a complete median suture running the entire length of the tergite from the anterior to the posterior edges; conversely nearly every individual of *T. spinicaudus* lacked the suture, but occasional specimens have minute, barely detectable remnants from the anterior margins. For practical purposes, *T. spinicaudus* can be characterized as lacking the suture because these occasional remnants extend no more than 1/32-1/16 of the tergal length. The other species, *T. californiensis* and *T. erythrocephalus*, typically possess incomplete median sutures that extend caudad from the anterior margin but terminate or fade out just before the caudal edge. Rarely in these species does the suture extend the entire length of the tergite.

Key to Species of *Theatops*

1. European species, occurring in Portugal, Spain, Croatia, Bosnia-Herzegovina and Montenegro ... *erythrocephalus* (C. L. Koch)
North American species 2
2. Ultimate prefemora with dorsal distomedial spurs (Figs. 7-9) ... 3
Ultimate prefemora without dorsal spurs (Fig. 6) 4
3. Ultimate tergite with complete longitudinal, midline suture dorsally (Figs. 33-34); central and western Texas *phanus* Chamberlin
Ultimate tergite without midline suture or with only minute remnant anteriorly (Figs. 7-9); eastern United States from northern Illinois and central Iowa to southwestern Arkansas, and from northwestern

- North Carolina, northeastern Tennessee and adjacent periphery of Virginia to central North and South Carolina, and eastcentral and northwestern Alabama..... *spinicaudus* (Wood)
4. Caudal coxopleurae distinctly elongate and apically acuminate, usually with blackened terminal spurs; ventral surfaces of ultimate prefemora and femora usually with one spur each (four spurs total) distal to midlength (Figs. 13-17); Kern County, California, to Douglas County, Oregon *californiensis* Chamberlin
- Caudal coxopleurae at most only slightly prolonged, apically rounded, without blackened spurs; ventral surfaces of ultimate prefemora and femora with or without spurs, rarely with one on each podomere, total almost always less than four (Shelley 1990a, Figs. 6-11); eastern United States from eastern Connecticut to eastern and southern coastal Texas, eastcentral Oklahoma, and south Florida Keys, and western United States and northwestern Mexico from western Chihuahua, southern Sonora, and northern Baja California Norte to southwestern Utah, southern Nevada, and southern California *posticus* (Say)

Theatops posticus (Say)

Figs. 1, 6, 11-12, 18, 32

Cryptops postica Say, 1821:112-113. Newport, 1844:100. Kohlrausch, 1881:130.

Cryptops posticus: Lucas, 1840:547. Bollman, 1893:147-148.

Theatops postica: Newport, 1845:410. Wood, 1862:36-37; 1865:171. Saussure and Humbert, 1872:200. Kohlrausch, 1881:93. Attems, 1930:251. Crabill, 1955:259. Branson and Batch, 1967:83-84. Kevan, 1983:2945.

Cryptops prolonge Gervais, 1847:294.

Opisthomega postica: Wood, 1862:35; 1865:169-170, pl. I., fig. 4. Cope, 1869:179. Kohlrausch, 1881:130.

Opisthomega postica: Saussure and Humbert, 1872:200.

Opisthomega crassipes Meinert, 1886:209. McNeill, 1887:326; 1888:16.

Theatops crassipes: Bollman, 1888b:110.

Theatops posticus: Bollman, 1888c:342; 1888d:346; 1888e:408; 1893:170. Brölemann, 1896:50; 1904:244. Chamberlin, 1902:41; 1918a:23; 1918b:375; 1925:57; 1942:184-185; 1943:97; 1944a:33; 1944b:178; 1945:215; 1951a:33. Kraepelin, 1903:65-66, fig. 25. Williams and Hefner, 1928:137. Brimley, 1938:501, in part. Crabill, 1950:201. Wray, 1950:156, in part; 1967:156, in part. Summers et al., 1980:245; 1981:59. Shelley, 1987:505, figs. 3, 13. Shelley and Edwards, 1987:Fig. 8.

Type specimen. Holotype (NHM) collected by T. Say on an unknown date in the winter of 1818, possibly near Picolata, St. Johns County, Florida. According to Weiss and Ziegler (1931), Say and friends visited Florida in the winter of 1818, traveling overland by carriage to Charleston, then by boat to Savannah, then by smaller boat through the "sea islands" of Georgia. After stopping at Fernandina, on Amelia Island, Florida, they proceeded up the St. Johns River to Picolata, where they disembarked and crossed by foot to St. Augustine to present their papers to the Spanish governor. Because of hostile indians, he advised against traveling farther upriver, so they returned to Picolata, sailed back to the coast and, eventually, Charleston. The type of *C. postica* was collected on this trip somewhere in Georgia or Florida, and although the party stopped repeatedly on the islands of Georgia, including a few days on Cumberland Island, they were ashore for the longest time in the area of Picolata/St. Augustine, the most likely site for the collection. Picolata exists today as a small community on the river along St. Johns County Highway 13, ca. 25.3 km (15.8 mi) west of St. Augustine. According to Underwood (1887) and Pocock (1888), Say sent some or all of the type specimens of his myriapods to Leach in Britain, who deposited them in the NHM, and according to Newport (1845) and Pocock (1888), there was only one specimen of *C. postica* in this shipment, making it the holotype.

Diagnosis. Ultimate tergite with complete, median suture; ultimate legs dorsally without distomedial prefemoral spurs (Fig. 6); ultimate prefemora and femora with or without relatively short, "weak," ventral spurs, when present, usually less than four spurs total or one per podomere; caudal coxopleurae with borders apically rounded, at most only slightly elevated and extended, without apical teeth (Fig. 2; Shelley 1990a, Figs. 5-12).

Variation. The eastern population lacks ventral spurs on the caudal legs, and the coxopleurae are flat and not extended caudad. Variation of the coxopleurae and the ventral surfaces of the ultimate legs in the southwestern population is discussed by Shelley (1990a).

Ecology. In the east, I have found *T. posticus* primarily in moist deciduous litter, occasionally in pine litter, and rarely under rocks and logs (Shelley 1987, 1990a); specimens may also be encountered under large rocks in rather dry sites (Hoffman, *in litt.*). The southwestern population, which inhabits deserts and arid biotopes, has been encountered under rocks, logs, wood debris, and cattle dung (Shelley 1990a). Even the Stanislaus County, California, locality is arid, for it is on the eastern slope of the Coast Range and in the rain shadow of these mountains.

Distribution. *Theatops posticus* consists of allopatric populations in eastern and southwestern North America segregated by around 1200 km (750 miles) (Shelley 1990a, Fig. 3). The eastern population extends, north-south, from eastern Connecticut, the Catskill Mountains of New York, southwestern Pennsylvania, and southern Illinois to the south Florida keys and San Patricio County, Texas, and, east-west, from the Atlantic Ocean to the eastern periphery of the Central Plains in Seminole County, Oklahoma, and Limestone County, Texas. It encompasses all of West Virginia, Kentucky, Tennessee, South Carolina, Georgia, Florida, Alabama, Mississippi, Arkansas, and Louisiana. The southwestern population, centered in the Sonoran Desert, occurs from western Chihuahua, Mexico, to the Channel Islands in the Pacific Ocean off the southern California coast, and from the eastern slope of the Coast Range in

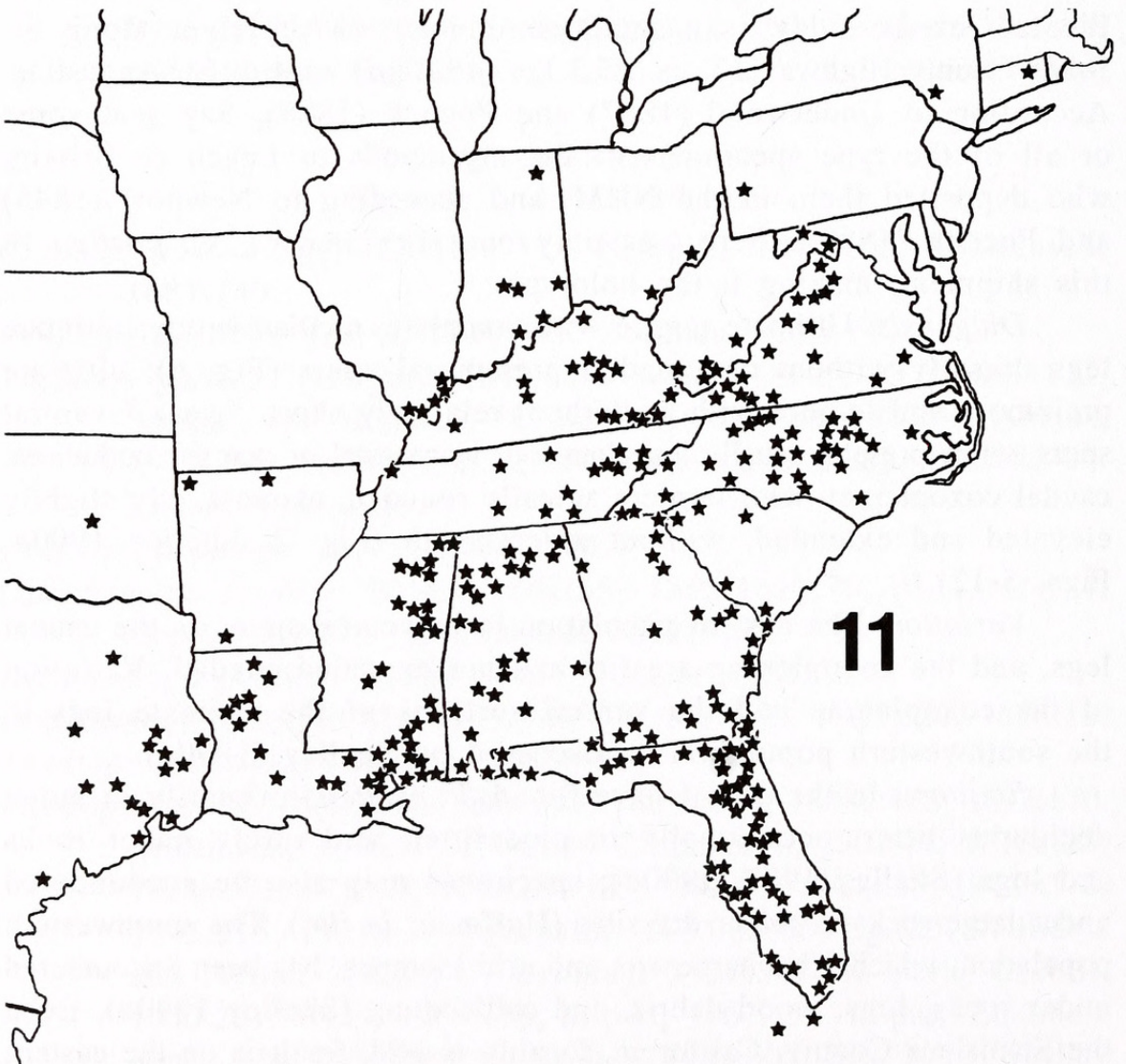


Fig. 11. Distribution of *T. posticus* in eastern North America.

Stanislaus County, California, and the southern Great Basin in southern Nevada and southwestern Utah to southern Sonora and northern Baja California Norte, Mexico. The eastern area represents a slight modification of that showed previously (Shelley 1990a, Fig. 4), which did not include Connecticut and New York (Figs. 11-12), and the Stanislaus County record extends the range significantly northward in western California.

In the following locality listing, general range statements, cited from the literature where appropriate, are presented for each state before detailed data. Counties of occurrence of the eastern population are listed alphabetically for states where the centipede has been taken from five or more counties; full locality data are presented for states where less than five counties are represented. The most peripheral record(s) are cited in detail for states forming range boundaries, even when the centipede is common and only counties are listed. Locality data for the southwestern population presented in Shelley (1990a) are also summarized by county; new sites for this population obtained since that paper was published are detailed.

EASTERN POPULATION

CONNECTICUT: Expected in the western 2/3 of the state, but only one record. *Tolland Co.*, Mansfield, 1 spmn., June 1965, collector unknown (UCT).

NEW YORK: Expected in the southernmost section, south of Catskills, but only one record; may be absent from Long Island. *Sullivan Co.*, 4.8 km (3 mi) N Bruce, 1 spmn., 22 May 1968, S. B. Peck (NCSM).

NEW JERSEY: Expected in the northern 1/3 of state, but no available records.

PENNSYLVANIA: Expected in the east and south, but only one definite record. *Allegheny Co.*, Sewickly, 3 spmn., date unknown, W. L. Walker (NMNH).

INDIANA: Apparently common in the southern third with one northern record, from the northeastern corner, that is somewhat disjunct and needs confirmation. *Brown, Crawford, Franklin, Jefferson, Monroe,* and *Noble* counties (ANSP, NMNH). Northernmost record: *Noble Co.*, Indian Village Lake, 1 spmn., date unknown, B. G. Owens (NMNH).

ILLINOIS: Known only from the southern periphery; the northernmost record is from Pulaski County (Summers et al. 1980). *Gallatin Co.*, Shawneetown, 2 spmn., 23 June 1950, M. W. Sanderson (INHS). *Hardin Co.*, Cave in Rock, 1 spmn., 2 May 1956, L. J. Stannard (INHS). *Pope Co.*, Eddyville, 1 spmn., 1 May 1953, L. J. Stannard (INHS); and 3.2 km (2 mi) N Dixon Springs, 1 spmn., 1 May 1969, collector unknown (EIU). *Johnson Co.*, Bellsmith Springs E of Ozark, 1 spmn., 24 June

1958, H. S. Dybas (FMNH).

MARYLAND: Expected west of Chesapeake Bay, but only one record. *Allegany Co.*, Cumberland, 1 spmn., 29 March 1966, collector unknown (NCSM).

WEST VIRGINIA: Statewide. *Berkeley, Dickenson, Greenbrier, Mercer, Raleigh, and Summers* counties (AAW, NCSM, WAS, WVDA).

VIRGINIA: Expected throughout most of the state except for the eastern shore (Accomack and Northampton counties) and possibly the southeastern corner of the mainland, around Norfolk. *Albemarle, Alleghany, Appomattox, Augusta, Bedford, Botetourt, Buchanan, Dickenson, Fauquier, Floyd, Frederick, Giles, Greenville, Henry, Lee, Madison, Montgomery, Page, Patrick, Pittsylvania, Pulaski, Rappahannock, Rockbridge, Rockingham, and Surry* counties (AMNH, FSCA, LEM, MCZ, NCSM, NMNH, VMNH). Easternmost record: *Surry Co.*, Chipokes Plantation St. Pk., 2 spmns., 12 September 1988, R. M. Shelley (NCSM).

KENTUCKY: Statewide. *Bell, Caldwell, Clark, Edmonson, Estill, Grant, Grayson, Hardin, Harlan, Jefferson, Jessamine, Oldham, Shelby, Todd, and Wolfe* counties (FMNH, INHS, MPM, NCSM, NMNH, TMM, UL, ZMUC).

TENNESSEE: Statewide. *Anderson, Bledsoe, Davidson, Franklin, Hamilton, Jefferson, Knox, Lake, Madison, Marshall, Morgan, Overton, Roane, and Sevier* counties (AMNH, FMNH, FSCA, INHS, MCZ, NCSM, NMNH, TMM).

NORTH CAROLINA: Statewide except for the Outer Banks and the eastern extremity of the mainland; more prominent east of the Blue Ridge Province (Shelley 1987). *Bladen, Burke, Chatham, Cherokee, Clay, Cumberland, Davidson, Durham, Franklin, Gaston, Harnett, Iredell, Jackson, Johnston, Lee, Madison, Pitt, Richmond, Stanly, Stokes, Surry, Wake, Wayne, and Wilkes* counties (FSCA, MCZ, NCSM, NMNH). Easternmost record: *Pitt Co.*, 2.1 km (1.3 mi) W Greenville, along NC hwy. 43, 0.2 km (0.1 mi) W jct. NC hwy 903, 1 spmn., 19 October 1979, R. M. Shelley, P. T. Hertl (NCSM).

SOUTH CAROLINA: Expected statewide, but known from only four counties. *Chester Co.*, 18.6 km (11.6 mi) W Chester, 1 spmn., 30 April 1977, R. M. Shelley (NCSM). *Greenville Co.*, Greenville, 1 spmn., 29 July 1961, S. & D. Mulaik (NMNH). *Aiken Co.*, Savannah River Plant, Sunshine Bay, 16 April 1969, collector unknown (SREL). *Jasper Co.*, Ridgeland, 1 spmn., 6 April 1975, D. Brady (AMNH); and 12.8 km (8 mi) S Hardeeville, along US hwy. 17A, 0.6 km (0.4 mi) W jct. SC hwy. 170, 1 spmn., 9 November 1977, R. M. Shelley (NCSM).

GEORGIA: Statewide. *Bacon, Berrien, Bibb, Camden, Charlton,*

Chatham, Clarke, Decatur, Habersham, Jackson, Jefferson, Jenkins, Lanier, McIntosh, Polk, Rabun, Screven, Thomas, and Ware counties (FMNH, FSCA, MCZ, NCSM, NMNH, UGA).

FLORIDA: Statewide. *Alachua, Baker, Bay, Charlotte, Clay, Collier, Columbia, Dade, Duval, Escambia, Gadsden, Glades, Hamilton, Hernando, Highlands, Hillsborough, Jackson, Jefferson, Lake, Leon, Liberty, Madison, Manatee, Marion, Martin, Monroe, Nassau, Pinellas, Polk, Putnam, Santa Rosa, and Sarasota* counties (AMNH, EIU, FMNH, FSCA, INHS, MCZ, NCSM, NMNH). Southernmost record: *Monroe Co.*, Sugarloaf Key, 1 spmn., March 1898, O. F. Cook (NMNH).

ALABAMA: Statewide. *Baldwin, Butler, Chilton, Choctaw, Clarke, Cullman, Dallas, DeKalb, Lee, Marengo, Marshall, Marion, Mobile, Morgan, Wilcox, and Winston* counties (AU, FMNH, FSCA, NCSM, NMNH).

MISSISSIPPI: Statewide. *Alcorn, Forrest, Hancock, Harrison, Jackson, Jones, Lafayette, Lamar, Lee, Noxubee, Oktibbeha, Pontotoc, Prentiss, Rankin, Scott, Smith, Stone, Tishomingo, Wayne, Webster, and Winston* counties (FMNH, FSCA, INHS, MCZ, MEM, NMNH).

LOUISIANA: Statewide. *East Baton Rouge, Evangeline, Grant, Jefferson, Lincoln, Natchitoches, Orleans, Ouachita, Rapides, St. Tammany, Washington, West Baton Rouge, and Winn* parishes (FMNH, FSCA, MCZ, NMNH).

ARKANSAS: Expected statewide, but known from only three counties. *Baxter Co.*, Lake Norfolk, 1 spmn., 2 August 1952, N. B. Causey (NMNH). *Washington Co.*, locality unknown, 1 spmn., October 1958, G. Ogden (NMNH). *Columbia Co.*, Magnolia, 2 spmns., 24 December 1949, N. B. Causey (NMNH).

OKLAHOMA: Expected in the eastern 1/3 of the state, but only one record. *Seminole Co.*, locality unknown, 5 spmns., May 1931, P. Newport (NMNH).

TEXAS: Expected throughout the forested, eastern 1/4 of the state, generally east of interstate highway 45, extending southward along the coast nearly to Corpus Christi, Nueces County. *Angelina, Brazos, Chambers, Galveston, Harris, Hunt, Jasper, Limestone, Nacogdoches, Sabine, San Patricio, Tyler, Van Zandt, and Walker* counties (AMNH, CAS, FSCA, NMNH). Westernmost records: *Limestone Co.*, Mexia, 1 spmn., 3 December 1961, B. E. Oberholtzer (NMNH) and *Brazos Co.*, 8 km (5 mi) S College Station, 3 spmns., 21 April 1936, L. Hubricht (NMNH). Southernmost record: *San Patricio Co.*, 11.2 km (7 mi) N Sinton, Welder Wildlife Refuge, 1 spmn., 5 July 1965, R. O. Albert (FSCA).

The following literature records of the eastern population are

considered valid and are incorporated into fig. 11.

OHIO: *Gallia Co.*, Vinton (Morse 1902); southeastern Ohio in general (Williams and Hefner 1928). Morse's is the only definite Ohio record, but *T. posticus* probably occurs widely in the southern half of the state.

ILLINOIS: *Jackson* and *Pulaski* cos. (Summers et al., 1980, 1981).

INDIANA: *Wayne Co.*, Dublin (McNeill 1888); *Clark Co.* New Providence (Bollman 1888e).

KENTUCKY: *Jefferson Co.*, Louisville, and *Whitley Co.*, Cumberland Falls St. Pk. (Crabill 1955a); and *Powell Co.*, Middle Fork of Red R. near Slade (Branson and Batch 1967).

NORTH CAROLINA: *Guilford Co.*, Greensboro (Causey 1940); and *Wayne Co.*, Goldsboro (Wood 1862, Bollman 1888d, Brimley 1938, Wray 1950, 1967)).

SOUTH CAROLINA: *Pickens Co.*, Clemson (Crabill 1950).

GEORGIA: *Mitchell Co.*, Camilla (Chamberlin 1945).

LOUISIANA: *St. Helena Par.*, Greenburg (Chamberlin 1942).

SOUTHWESTERN POPULATION

MEXICO:

BAJA CALIFORNIA NORTE, SONORA, and CHIHUAHUA (AMNH, NCSM, NMNH, UCB). Expected in the western periphery of Chihuahua, all but the southern tip of Sonora, and an equivalent distance down the Baja peninsula, including all of Baja California (B. C.) Norte and the northern extremity of B. C. Sur. It is currently unknown from the last state and the southern half of B. C. Norte. New Record: SONORA: 6.4 km (4 mi) SW Los Vidrios, W of Sonoita, 2 spmns., 11 February 1960, V. Roth (AMNH).

USA:

NEW MEXICO: Expected only in the southwestern corner. *Hidalgo County* (NMNH).

ARIZONA: Expected throughout all but the northeastern 1/4 of the state, or most of Navajo and Apache counties. *Cochise*, *Coconino*, *Gila*, *Graham*, *Maricopa*, *Pima*, *Pinal*, *Santa Cruz*, *Yavapai*, and *Yuma* counties (AMNH, CAS, FSCA, NMNH, OPCNM, SWRS, UAZ). New Records: *Coconino Co.*, Schnebly Hill Vista, 1 spmn., 7 October 1987, B. Hebert (LACMNH). *Pima Co.*, Elkhorn Ranch, E slope of Baboquivari Mts., 1 spmn., H. B. Leech, J. W. Green (CAS). *Navajo Co.*, nr. Showlow, 1 spmn., 10 August 1948, G. E. Ball, H. E. Evans (NMNH). *Santa Cruz Co.*, Yane Springs, Sycamore Cyn., 1 spmn., 21 March 1967, V. F. Lee, T. S. Briggs (CAS); and Blanca L. nr. Pena, 1 spmn., 21

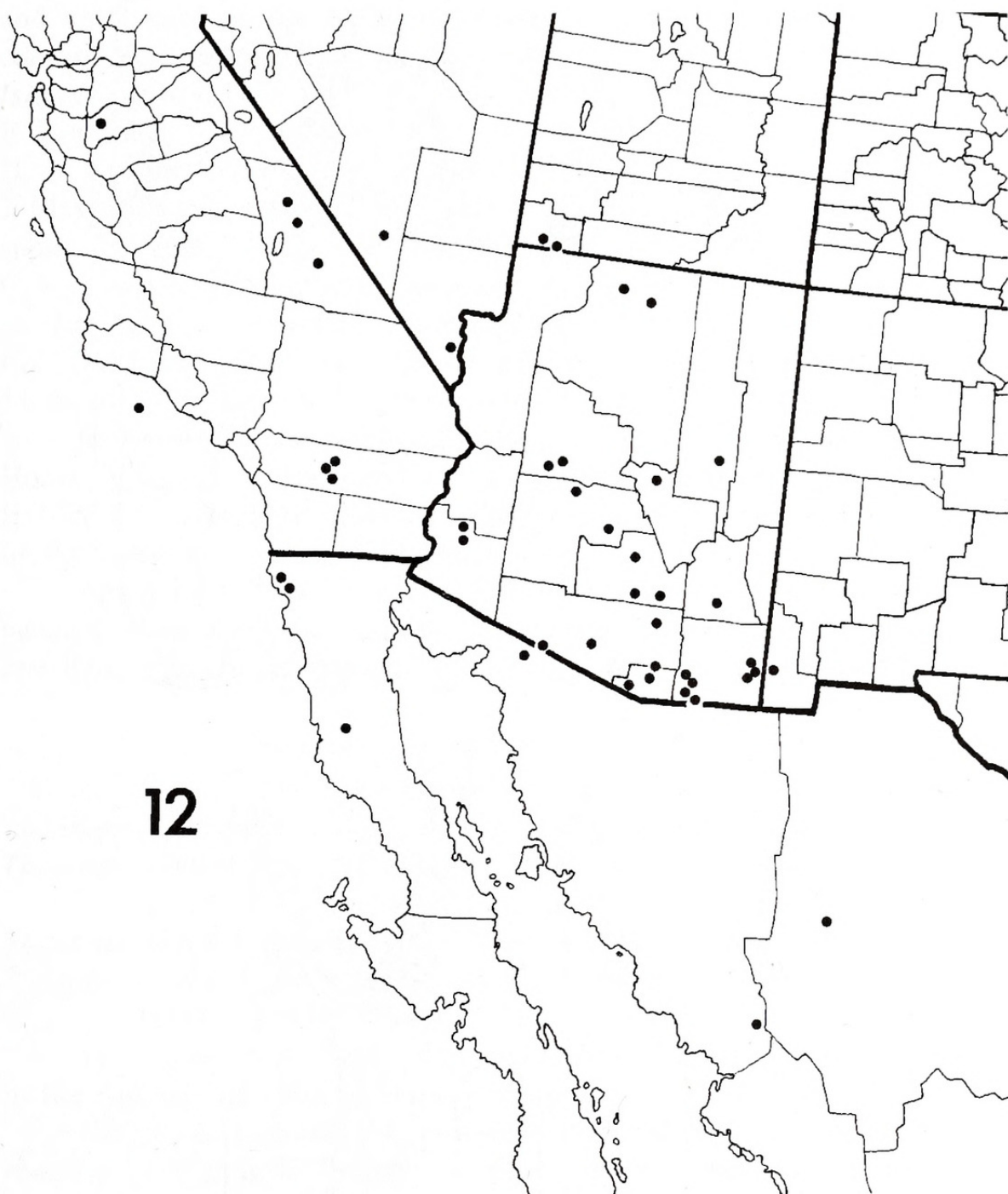


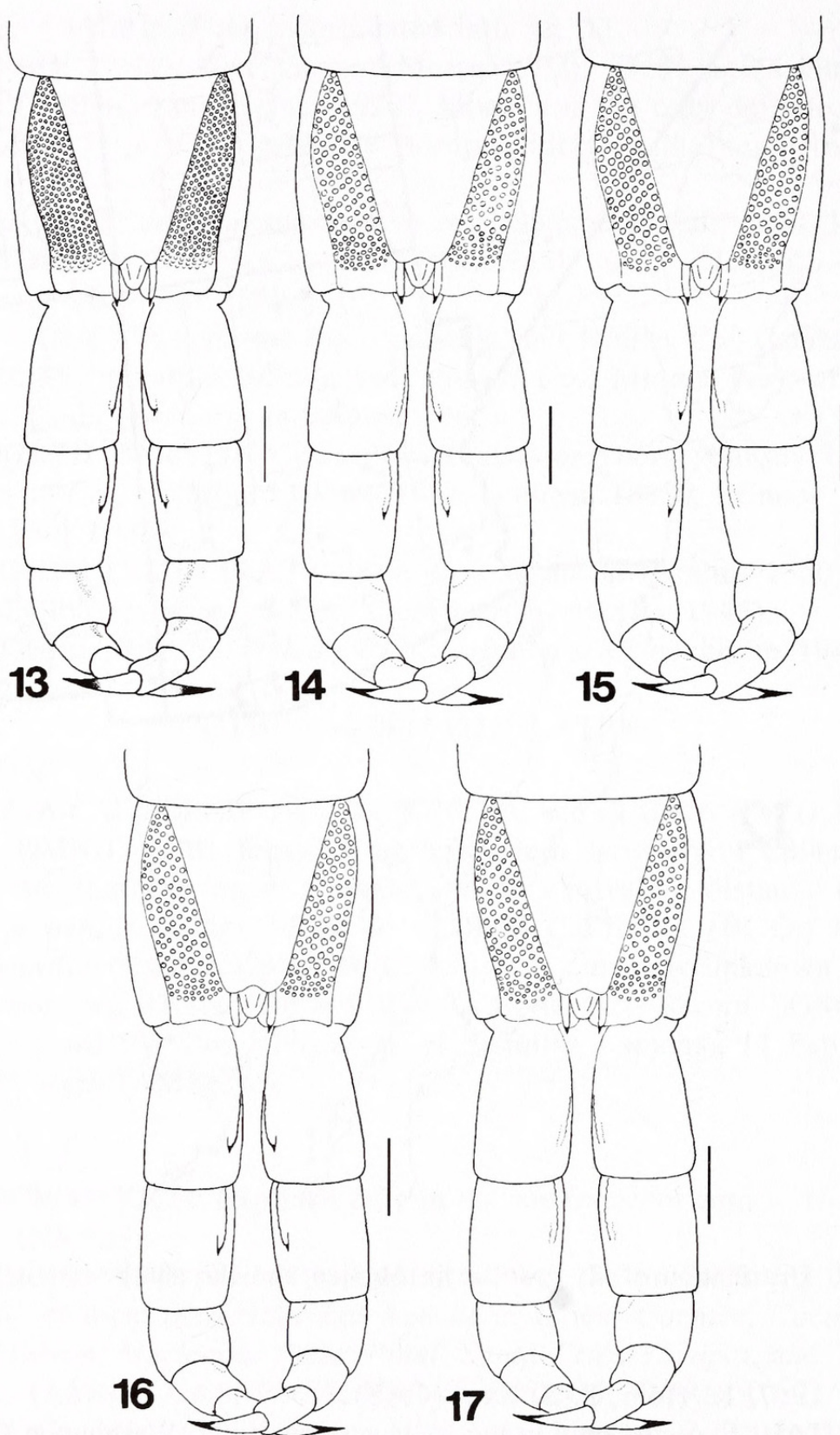
Fig. 12. Distribution of *T. posticus* in Mexico and the southwestern United States.

March 1967, K. Hom, P. S. Sum (CAS).

UTAH: Expected only in the southwestern corner. Washington County (NMNH). New Record: *Washington Co.*, Warner Valley, 1 spmn., 5 April 1975, A. H. Barnum (DC).

NEVADA: Expected only in the southern corner. *Clark* and *Nye* counties (FSCA, NMNH).

CALIFORNIA: Expected in desert areas east of the Sierra Nevada



Figs. 13-17. Variation of the ventral surfaces of the caudal legs and coxopleurae of *T. californiensis* from selected localities. 13, Mariposa County, California. 14, Butte County, California. 15, Tuolumne County, California. 16, El Dorado County, California. 17, Douglas County, Oregon. Scale lines = 1.00 mm for each figure.

and southward to the Mexican border, possibly extending along the coast to Ventura County. *Riverside County* and *Santa Cruz Island, Channel Islands National Park* (UCR). New Records: *Inyo Co.*, 4.8 km (3 mi) E Big Pine, Saline Valley Rd., 1 spmn., 11 June 1967, W. J. Ball, H. E. Evans (NMNH); Saline Valley, Grapevine Rd. Sta. 32, 1 spmn., 7 May 1960, B. Banta (CAS); and 40 km (25 mi) S Saline Valley, 1 spmn, 29 April 1975, A. R. Hardy (CDFA). *Riverside Co.*, Whitewater Cyn., 1 spmn., 15 February 1959, I. Newell (AMNH); and Palm Springs, nr. Taquitz Cyn., 4 spmns., 23 March 1965, D. Yang (CAS). *Stanislaus Co.*, Del Puerto Cyn., ca. 28.8 km (18 mi) W Patterson, 2 spmns., 10-11 April 1990, E. I. Schlinger (UCB).

Remarks. *Theatops posticus* was collected at Appomattox Court House, Virginia, on the very day of the surrender there of Gen. Robert E. Lee's Confederate army, 9 April 1865, by an unknown member of the surrender parties (Shelley 1990b).

Apparently, *T. posticus* and *T. spinicaudus* can occur syntopically, because some preserved samples, ostensibly collected at one place on one date, contain both species.

Theatops californiensis Chamberlin

Figs. 13-18

Theatops californiensis Chamberlin, 1902:41. Kevan, 1983:2945.

Theatops erythrocephalus (nec C. L. Koch): Kraepelin, 1903:66-67, Fig. 26.

Theatops erythrocephalus californiensis: Chamberlin, 1911:472.

Theatops erythrocephala (nec C. L. Koch): Attems, 1930:251-252, Figs. 331-335. Kevan, 1983:2945.

Type specimens. Three syntypes (NMNH) collected by E. Garner in the summer of 1901 at Quincy, Plumas County, California.

Diagnosis. Ultimate tergite usually with incomplete, median suture, running from anterior margin to just short of caudal edge; ultimate legs without dorsal distomedial prefemoral spurs; ultimate prefemora and femora usually with four strong, distinct ventral spurs, one on each podomere, rarely with three or fewer spurs; caudal coxopleurae with medial borders strongly elevated and extended caudad, usually apically acuminate with blackened terminal spurs (Figs. 13-18).

Variation. Occasional exceptions exist to the typical pattern of four ventral spurs, one on each caudal prefemur and femur (Fig. 13). A specimen from Brush Creek, Butte County, California, exhibits three spurs, the right prefemur lacking the structure (Fig. 14). An individual from 19.2 km (12 mi) E Buck Meadows, Tuolumne County, has two spurs, lacking those on the left prefemur and femur (Fig. 15), and

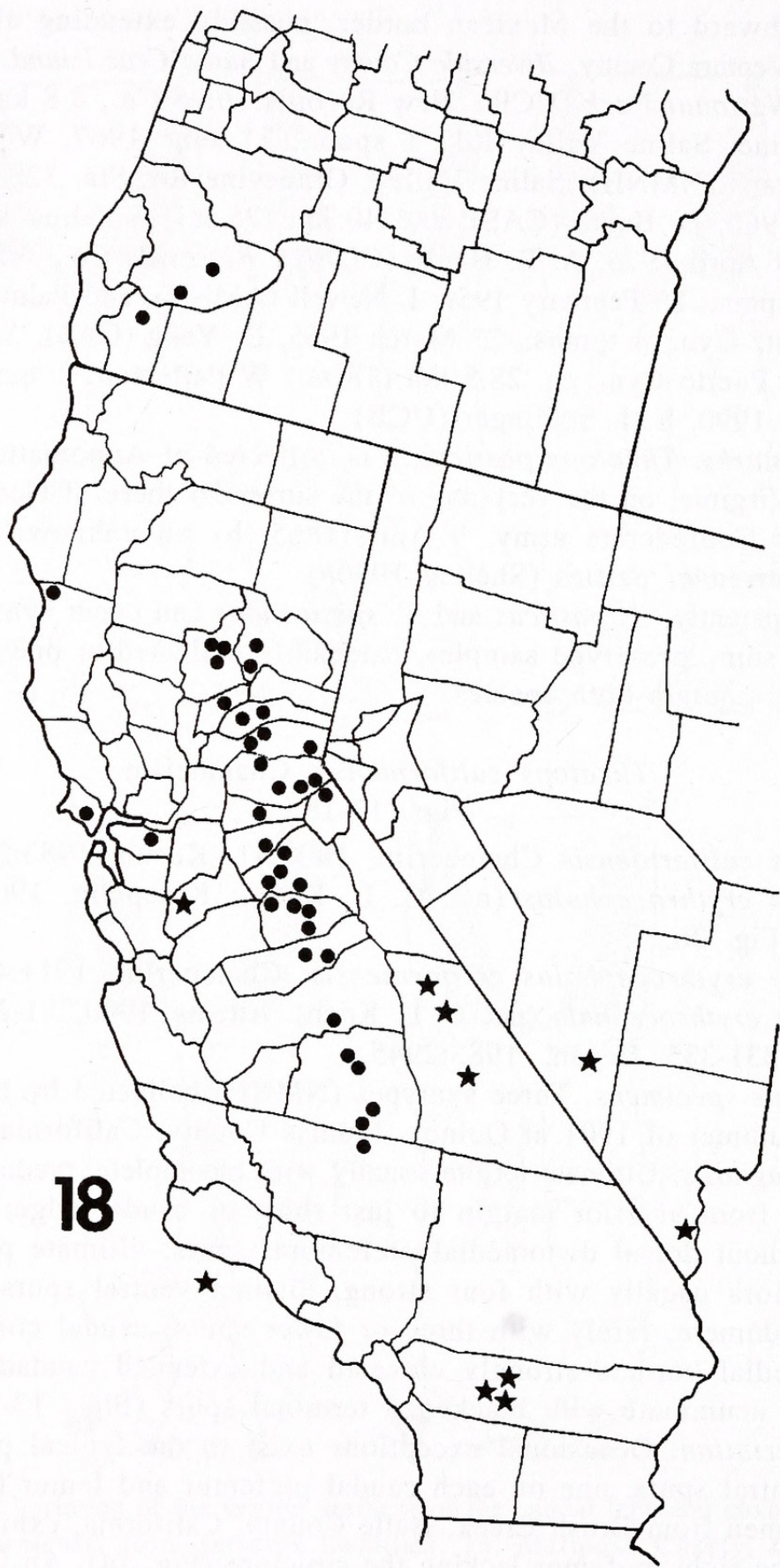


Fig. 18. Distributions of *T. californiensis* (dots) and *T. posticus* (stars) in California, Oregon, and Nevada.

one from 16.8 km (10.5 mi) SW Bucks Lake, Plumas County, lacks spurs on the right leg, which is considerably smaller than the left and apparently regenerating. No individuals are available with only one spur, but four are devoid of the structures, one from Oroville, Butte County, and three from Canyonville, Douglas County, Oregon (Fig. 17). More rarely, a specimen will lack a coxopleural spur, as for example an individual from El Dorado County, which lacks that on the right coxopleura (Fig. 16).

Ecology. Labels with samples indicate that specimens were found under logs and the bark of decaying logs or stumps. Most, however, were encountered in litter, which was my experience during field work in California. In June 1990 and April 1991, I found *T. californiensis* to be abundant in litter in Yosemite Valley, Yosemite National Park, Mariposa County, but I did not find a single specimen under a log.

Distribution. The only specific published locality is the type locality. Several authors have reported this species from California and Oregon in general (Kraepelin 1903, Attems 1930, Crabill 1960, Kevan 1983), but Shelley (1990a, Fig. 4) first delineated regions — along the western slope of the Sierra Nevada and southern Cascade Mountains from Tulare County, California, to Douglas County, Oregon, extending to San Francisco Bay and the Pacific Ocean from Marin to Mendocino counties. The northern limit, in southern Douglas County, Oregon, is unchanged, but I have examined more southerly material from northern Kern County, and the southern limit is thus in this county, in the southern part of the Sequoia National Forest and the Sierra Nevada Mountains. In May 1993, I spent a day searching unsuccessfully for *T. californiensis* in the Toiyabe National Forest, on the eastern side of Lake Tahoe in Nevada. The centipede may eventually be found in this area, but it is currently known only from the California side of the lake. The Oregon localities may be disjunct and represent a small, allopatric, northern population, as there are no records between Josephine County and Mendocino County, California. Because the type locality is the only specific recorded site, I list below all records of *T. californiensis* (Fig. 18).

OREGON: Occurring only in the southwestern interior. *Douglas Co.*, Susan Cr. E of Glide, 1 spmn., 23 July 1962, V. Roth (AMNH); and Canyonville, 3 spmns., 13 February 1946, S. & D. Mulaik (NMNH) and 5 spmns., 12 July 1946, S. & D. Mulaik (NMNH). *Josephine Co.*, 14.4 km (9 mi) W Sunny Valley, 2 spmns., 22 July 1962, V. Roth (AMNH).

CALIFORNIA: Widespread from the northwestern interior to the southern Sierra Nevada, extending primarily along the western slope

of this range and the Cascades, traversing the crest to the vicinity of Lake Tahoe, and expanding westward to San Francisco Bay and northward along the Pacific Ocean. *Mendocino Co.*, 3.2 km (2 mi) W Piercy, 1 spmn., 19 August 1959, W. J. Gertsch, V. Roth (AMNH). *Marin Co.*, Mill Valley, 1 spmn., 28 February 1954, H. B. Leech (CAS) and 1 spmn., 13 November 1958, H. B. Leech (CAS). *Contra Costa Co.*, W of Pittsburg, 1 spmn., 21 March 1957, J. Russell (UCB). *Plumas Co.*, Quincy, 3 spmns., summer 1901, E. Garner (NMNH) and 2 spmns., 7 July 1946, S. & D. Mulaik (NMNH) TYPE LOCALITY; and 16.8 km (10.5 mi) SW Bucks Lake, 1 spmn., 14 September 1983, M. E. Bugler (UCB). *Butte Co.*, 11.2 km (7 mi) E Chico, Bidwell Park, 1 spmn., 2 April 1965, H. B. Leech (CAS), 6.4 km (4 mi) SW Stirling City, Toadtown, 2 spmns., 11 April 1979, C. L. Hogue (LACMNH); Brush Cr., 2 spmns., 30 May 1955, K. W. Haller (AMNH); Forest Ranch, 1 spmn., 27 April 1991, R. M. Shelley (NCSM); and Oroville, 1 spmn., 10 April 1911, collector unknown (NMNH). *Yuba Co.*, Camptonville, 1 spmn., 7 September 1959, V. Roth (AMNH). *Nevada Co.*, Grass Valley, 1 spmn., 12 September 1966, J. S. Buckett, M. R. Gardner (UCD); and 8 km (5 mi) S Washington, 2 spmns., 8 October 1967, V. F. Lee, K. Hom (CAS). *Placer Co.*, E end of Bear Valley, 7 spmns., 1 April and 1 June 1964, P. H. Arnaud (CAS); Colfax, 2 spmns., June 1888, collector unknown (NMNH); Emigrant Gap, 3 spmns., 16 July 1937, R. V. Chamberlin (NMNH); 4.8 km (3 mi) E Auburn, 1 spmn., 28 March 1941, S. & D. Mulaik (NMNH); and 7.5 km (4.7 mi) W Foresthill, 11 spmns., 27 November 1965 and 25 April 1966, H. B. Leech (CAS). *El Dorado Co.*, Lake Tahoe, 25 July 1915, 1 spmn., 25 July 1915, collector unknown (NMNH) and 1 spmn., 11 July 1952, W. J. Gertsch (NMNH); Fallen Leaf Lake, 1 spmn., 9 September 1959, W. J. Gertsch (AMNH); Glen Alpine Springs, 1 spmn., 28 June 1915, collector unknown (NMNH); Echo Pass S Meyers, 1 spmn., 30 June 1955, M. Cazier (AMNH) and 1 spmn., 19 September 1963, W. J. Gertsch (AMNH); Echo Lake, 1 spmn., July 1934, L. W. Saylor (NMNH); Kyburz, 1 spmn., 29 June 1977, C. E. Griswold (UCB); 6.4 km (4 mi) W Kyburz, 2 spmns., 15 September 1959, W. J. Gertsch, V. Roth (AMNH); Pollock Pines, 2 spmns., 14 July 1948, J. W. MacSwain (NMNH); Blodgett For., 20.8 km (13 mi) E Georgetown, 1 spmn., 27 May 1972, J.B. Heppner (FSCA); Garden Valley, 1 spmn., 2 July 1965, S. G. Shepa (LACMNH); and Sly Park, 2 spmns., 6 July 1958, W. J. Gertsch, V. Roth (AMNH). *Amador Co.*, Pine Grove, 1 spmn., 7 July 1958, W. J. Gertsch, V. Roth (AMNH). *Calaveras Co.*, Dorrington, 8 spmns., 12 and 29 September 1952, C. R. Snick (NMNH), 4 spmns., 11 June 1956, H. Ruckes, B. J. Andelson (UCB), 1 spmn., 7 May 1961, W. B. Simonds (CDFA),

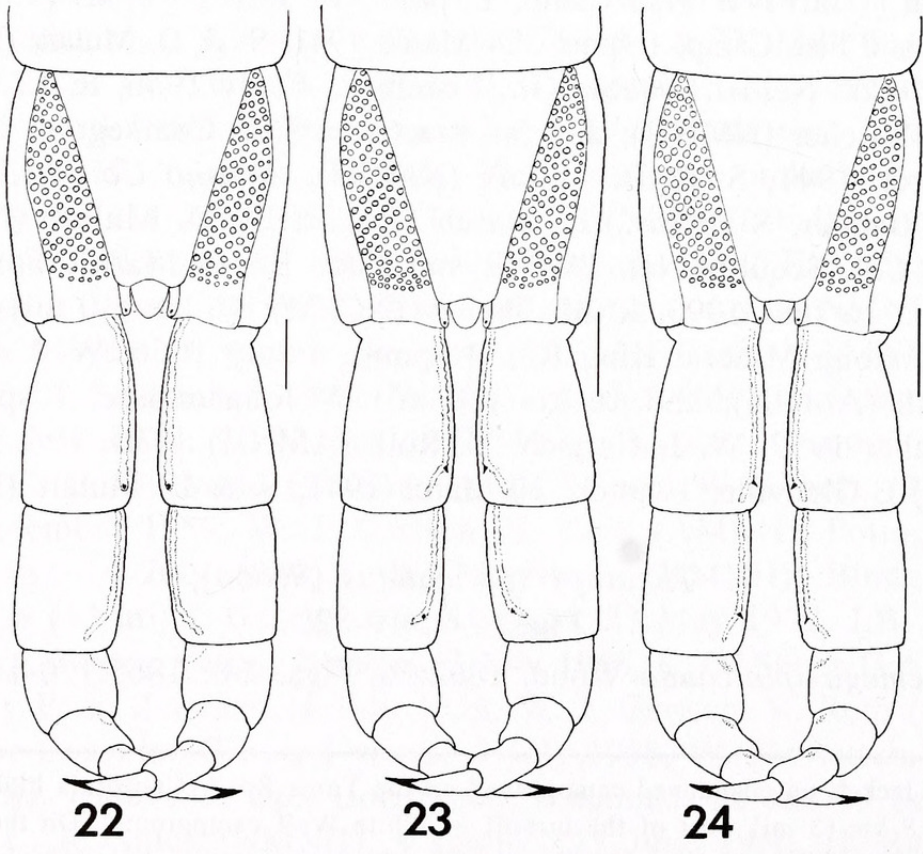
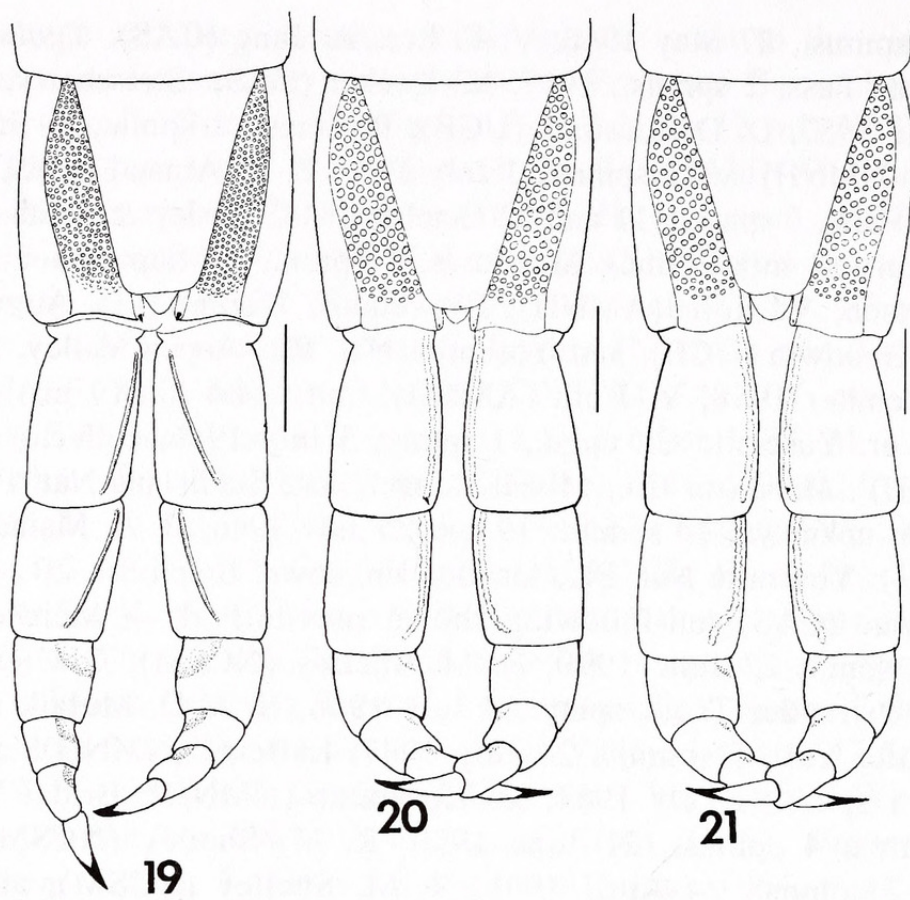
and 5 spmns., 27 May 1966, V. F. Lee, A. Jung (CAS). *Tuolumne Co.*, Emigrant Pass, 2 spmns., 1937, M. Bocker (CAS); Strawberry, 1 spmn., 15 June 1957, D. D. Linsdale (UCB); Pinecrest, 1 spmn., 29 June 1946, Pearce (NMNH) and 2 spmns., 1 July 1947, P. H. Arnaud (CAS, NMNH); Twain Harte, 2 spmns., 11 and 22 October 1948, Linsley & Smith (NMNH); 19.2 km (12 mi) E Buck Meadows, 1 spmn., 11 September 1959, W. J. Gertsch, V. Roth (AMNH); Groveland, 1 spmn., 15 August 1957, R. H. Goodwin (UCB); and Yosemite Nat. Pk., Aspen Valley, 2 spmns., 4 September 1958, V. Roth (AMNH), and "14.4 km (9 mi) E Smoky Jack," nr. Yosemite Cr. cpgd., 1 spmn., 5 July 1946, collector unknown (AMNH)⁷. *Mariposa Co.*, Miami Ranger Sta., Stanislaus Nat. For., exact location unknown, 10 spmns., 19 and 25 July 1946, B. A. Maina (FMNH, NMNH); Yosemite Nat. Pk., location unknown, 6 spmns., 20 May 1934, O. Bryant (CAS) and following known sites in Park — Merced Sequoia Gr., 1 spmn., 22 June 1990, R. M. Shelley (NCSM); Glacier Pt. Rd., along Ostrander Tr., 1 spmn., 4 July 1946, S. & D. Mulaik (NMNH); Yosemite Val., 5 spmns., 24 July 1947, Lafferty (NMNH); nr. Vernal Falls, 1 spmn., 1 July 1964, M. Kosztarab (NMNH); Bridal Veil Falls pkg. area, 4 spmns., 21 June 1990, R. M. Shelley (NCSM); Happy Isles, 2 spmns., 24 April 1991, R. M. Shelley (NCSM); and Mirror Lake Loop Tr., 1 spmn., 22 June 1990, R. M. Shelley (NCSM) — 11.2 km (7 mi) NW Fish Camp, 1 spmn., 16 July 1946, H. P. Chandler (CAS); and Fish Camp, 1 spmn., 24 March 1941, S. & D. Mulaik (NMNH). *Madera Co.*, Nelder Sequoia Gr., 2 spmns., 4 July 1946, R. L. Usinger, T. O. Thatcher (NMNH); and 9.6 km (6 mi) NE Coarsegold, 1 spmn., 24 March 1941, S. & D. Mulaik (NMNH). *Fresno Co.*, 11.2 km (7 mi) N Badger, 8 spmns., 23 March 1941, S. & D. Mulaik (NMNH). *Tulare Co.*, Sequoia Nat. Pk., Crystal Cave Rd. at Marble Fork Cyn., 1 spmn., 16 June 1990, R. M. Shelley (NCSM); 16 km (10 mi) E Three Rivers, along Mineral King Rd., 1 spmn., 4 July 1956, W. J. Gertsch, V. Roth (AMNH); and 16 km (10 mi) W Johnsondale, 1 spmn., 15 September 1959, W. J. Gertsch, V. Roth (AMNH). *Kern Co.*, 17.6 km (11 mi) E Glenville, 1 spmn., 19 March 1941, S. & D. Mulaik (NMNH).

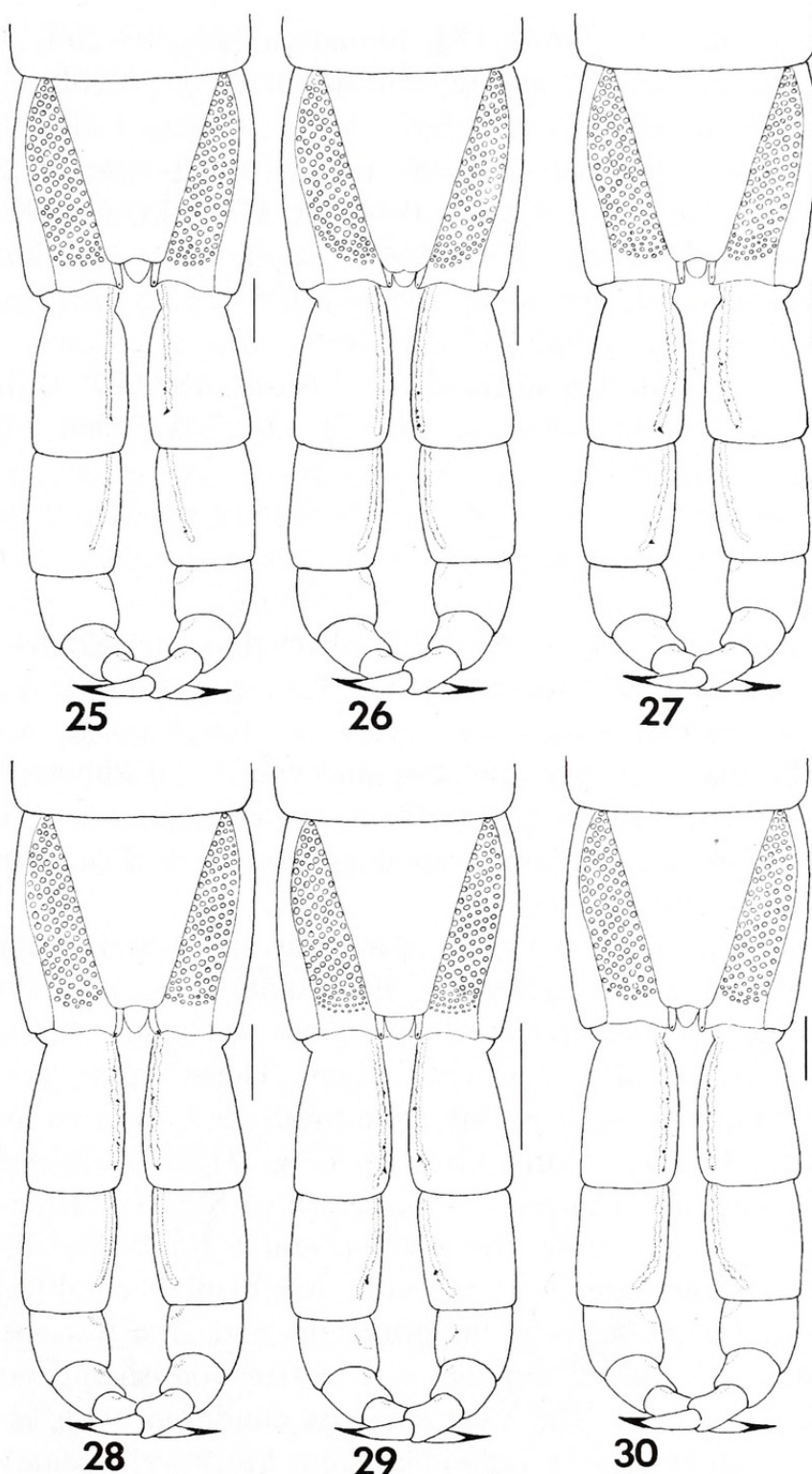
Theatops spinicaudus (Wood)

Figs. 7-9, 19-32

Opisthemega spinicauda Wood, 1862:36, Figs. 7-8; 1865:170-171, Figs.

⁷Smoky Jack is an abandoned campground on the Tioga Road (California highway 120) about 4.8 km (3 mi) west of the turnoff to White Wolf campground. On the highway that existed in 1946, 14.4 km (9 mi) east of Smoky Jack would be near today's Yosemite Creek Campground.





Figs. 19-30. Variation of the ventral surfaces of the caudal legs and coxae of *T. spinicaudus* from selected localities. 19, McDowell County, North Carolina. 20, Union County, Illinois. 21, Stone County, Missouri. 22, Pike County, Arkansas. 23, Lee County, Alabama. 24, Cobb County, Georgia. 25, Cleveland County, North Carolina. 26, Wilkes County, North Carolina. 27, Graham County, North Carolina. 28, Polk County, Arkansas. 29, Edgefield County, South Carolina. 30, Montgomery County, North Carolina. Scale lines = 1.00 mm for each figure.

8-11. Kohlrausch, 1881:130. Meinert, 1886:208-209.

Opisthomega spinicauda: Saussure and Humbert, 1872:200.

Opisthomega insulare Meinert, 1886:209-210. Haase, 1887:79.

Theatops spinicaudus: Bollman, 1888a:6; 1888c:341. Chamberlin, 1902:41; 1920:10; 1928:153. 1942:185; 1944a:33; 1944b:177-178. Kraepelin, 1903:65. Brölemann, 1904:244. Crabill, 1950:201; 1955b:39. Summers, 1979, Figs. 7-8. Shelley, 1987:505-506, Figs. 4, 13. Summers et al., 1980:245; 1981:59.

Theatops spinicauda: Bollman, 1893:170. Pocock, 1895:28. Brölemann, 1896:50-51. Attems, 1930:253. Bücherl, 1942:326. Crabill, 1955c:157. Kevan, 1983:2945.

Theatops posticus (nec Say): Brimley, 1938:50, in part. Wray, 1950:156, in part; 1967:156, in part.

Type specimens. Neotype (NMNH) collected by an unknown person on an unknown date in Chicago, Cook County, Illinois. A vial at the ANSP, supposedly containing a paratype taken by R. Kennicott in southern Illinois, is empty, and the holotype is not known to exist.

Diagnosis. Ultimate tergite without median suture or with only minute vestige anteriad; ultimate legs dorsally with a distomedial spur on each prefemur (Figs. 7-9).

Variation. I examined over 250 specimens and observed unreported variation along the inner surfaces of the caudal legs. This surface is generally flattened, particularly on the prefemur and femur, thus forming a ridge along its dorsal and ventral edges. These ridges are highly variable, and the dorsal surfaces vary from unadorned, as in an individual from McDowell County, North Carolina (Fig. 7), to scalloped, as in a specimen from Polk County, Arkansas (Fig. 8), to scalloped with minute teeth, as in one from Haywood County, North Carolina (Fig. 9). The ventral ridges are more variable and display conditions with one or more small, fine teeth on the prefemora and, in a few specimens, the femora. Moreover, these teeth also vary in size from sharply acuminate spurs to minute denticles. The most common condition, with no ventral spurs or teeth is shown by an individual from McDowell County, North Carolina (Fig. 19); eleven variants are depicted in Figures 20-30. This variation does not conform to an observable geographic pattern; it occurs sporadically in both areas occupied by *T. spinicaudus*. The medial borders of the caudal coxopleurae are slightly elevated and prolonged caudad, but there is a darkly pigmented subapical spot and a suggestion of a tooth on nearly all specimens. Individuals from McDowell County, North Carolina, and Polk County, Arkansas, have two distinct teeth at this position (Figs. 19, 28), those in the former being larger and

resembling the conditions in *T. californiensis* and *T. erythrocephalus* (compare Fig. 19 with Figs. 13 and 40).

Ecology. As with *T. posticus*, *T. spinicaudus* occurs primarily in moist deciduous litter. It is occasionally found in predominantly pine litter, and rarely under logs, loose wood debris, and large rocks.

Distribution. As shown in Fig. 32, the distribution of *T. spinicaudus* is more restricted than that of the eastern population of *T. posticus*, and the available records cluster into two segregated areas: the southern Blue Ridge Province of North Carolina and the southern periphery of Virginia, extending eastward and southward into the Piedmont Plateau and Fall Zone of the Carolinas, Georgia, and Alabama, and westward onto the Cumberland Plateau of Tennessee and Alabama; and from the Central Lowlands of northeastern Illinois and central Iowa southwestward to the Ozark and Ouachita provinces of southwestern Arkansas and eastern Oklahoma, extending onto the Coastal Plain in southeastern Arkansas (Fig. 31). Specimens were examined as follows; counties are listed alphabetically for states where the species is known from more than five counties, and complete data are provided for states where *T. spinicaudus* is known from five or fewer counties. Each state listing begins with a general description of anticipated occurrence.

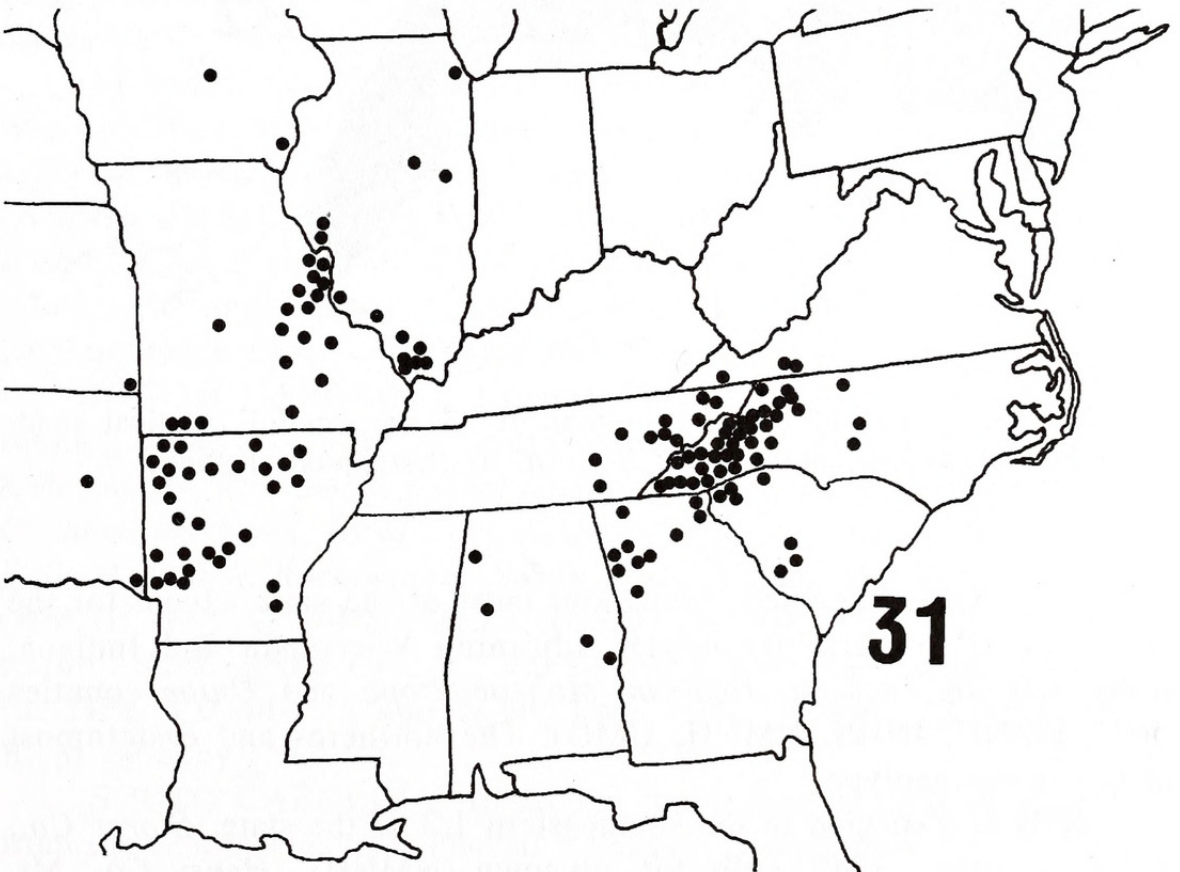


Fig. 31. Distribution of *T. spinicaudus*.

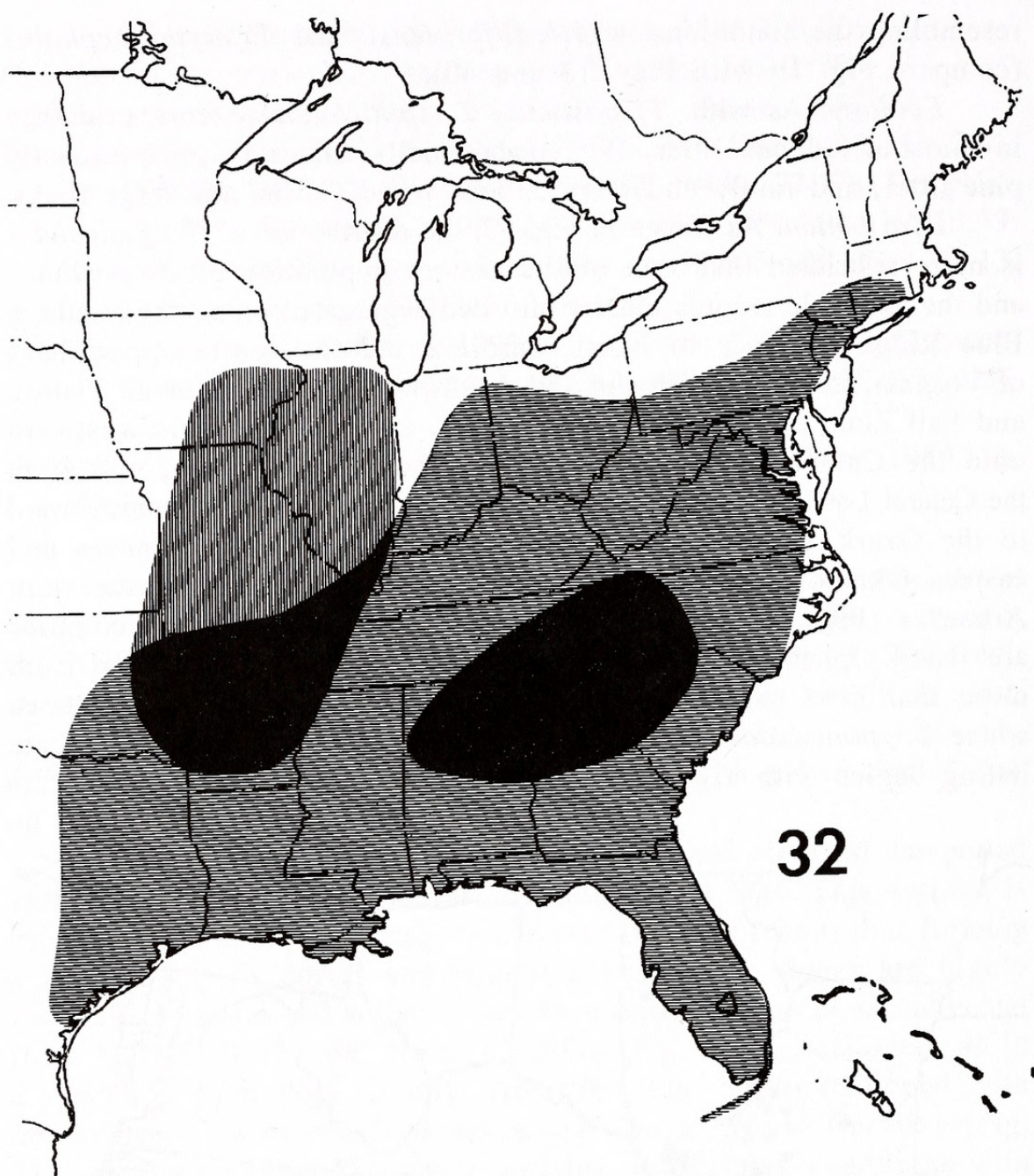


Fig. 32. Comparison of the distributions of *T. spinicaudus* (vertical shading) and the eastern population of *T. posticus* (horizontal shading).

ILLINOIS: Expected throughout most of the state except for the northern and eastern peripheries adjoining Wisconsin and Indiana. Cook, Greene, Jackson, Johnson, Monroe, Pope, and Union counties (EIU, FMNH, INHS, NMNH, UMO). The northern- and easternmost record is the neotype.

IOWA: Expected in the southeastern 1/3 of the state. Storey Co., Ames, 1 spmn., 1949, collector unknown (NMNH). Henry Co., Mt. Pleasant, 2 spmns., date and collector unknown (NMNH).

MISSOURI: Expected statewide except for the northwestern corner. *Barry, Camden, Oregon, Reynolds, Shannon, St. Charles, St. Louis, Stone,* and *Wayne* counties (EIU, FSCA, INHS, NMNH, UMO).

ARKANSAS: Expected statewide except for the southern tier of counties. *Baxter, Benton, Carroll, Clark, Cleburne, Drew, Franklin, Garland, Hot Spring, Howard, Independence, Jackson, Lawrence, Lincoln, Madison, Montgomery, Pike, Polk, Pulaski, Saline, Searcy, Stone, Washington,* and *Yell* counties (CAS, FSCA, INHS, MCZ, MPM, NMNH, UAAM, UGA). Southernmost record: *Drew Co.*, locality unknown, 6 spmns., 22 July, 21 August, and 5 November 1990, L. Thompson (UAR).

KANSAS: Expected only in the southeastern corner. *Cherokee Co.*, 9.6 km (6 mi) E Baxter Springs, 1 spmn., 7 April 1955, R. W. Frederickson (SEM).

OKLAHOMA: Expected in the eastern periphery. *Muskogee Co.*, locality unknown, 2 spmns., April 1957, H. Gibson (FSCA).

VIRGINIA: Expected only in the southern fringe of the Blue Ridge Province and possibly to the west in the Ridge and Valley Province. *Scott Co.*, 2.4 km (1.5 mi) E Shelleys, 1 spmn., 2 May 1989, C. A. Pague (VMNH). *Carroll Co.*, New River Trail St. Pk., nr end of VA hwy. 737, 3.2 km (2 mi) NNE Fries, 1 spmn., 18 September 1988, R. L. Hoffman (VMNH); and 2.4 km (1.5 mi) NNW Lambsburg, along Stewart's Cr., 1 spmn., 23 May 1993, R. L. Hoffman (VMNH).

TENNESSEE: Expected in the eastern 1/4 of the state, extending westward onto the Cumberland Plateau. *Greene, Hamilton, Hawkins, Jefferson, Knox, Morgan, Sevier, Unicoi, Warren,* and *Washington* counties (AMNH, FMNH, MCZ, NMNH, TMM, UMMZ). Westernmost record: *Warren Co.*, S slope of Cardwell Mtn., exact location unknown but probably in southeastern corner of county SE of McMinnville, 1 spmn., 27 September 1958, T. C. Barr (NMNH).

NORTH CAROLINA: Common in the mountains and foothills, ranging eastward into the central Piedmont Plateau (Shelley 1987). *Ashe, Avery, Buncombe, Burke, Caldwell, Cherokee, Cleveland, Gaston, Graham, Haywood, Henderson, Jackson, Macon, Mitchell, Montgomery, Polk, Randolph, Rockingham, Swain, Transylvania,* and *Wilkes* counties (AMNH, FSCA, INHS, MCZ, NCSM, NMNH, TMM). Easternmost record: *Rockingham Co.*, 7.7 km (4.8 mi) SW Wentworth, along co. rd. 2192, 1.0 mi (1.6 km) N NC hwy. 704, 1 spmn., 18 April 1973, R. M. Shelley (NCSM).

SOUTH CAROLINA: Expected in the western half of the state, from the central Piedmont Plateau westward. *Spartanburg Co.*, Landrum, 3 spmns., 4 August 1910, R. V. Chamberlin (NMNH). *Pickens Co.*, Table Rock St. Pk., 1 spmn., 12 August 1976, R. M. Shelley (NCSM);

and Clemson, 1 spmn., 23 May 1962, J. A. Payne (NMNH). *Oconee Co.*, 27.2 km (17 mi) S Highlands, NC, along SC hwy. 28, 1 spmn., 3 June 1931, S. & D. Mulaik (NMNH); and Seneca, 4 spmns., 2 August 1910, R. V. Chamberlin (NMNH). *Newberry Co.*, 15 km (9.4 mi) NW Newberry, along SC hwy. 32, 1 spmn., 5 August 1976, R. M. Shelley (NCSM). *Saluda Co.*, 8.5 km (5.3 mi) NE Saluda, along SC hwy. 39, 1.4 km (0.9 mi) N jct. SC hwy. 450, 1 spmn., 4 May 1977, R. M. Shelley (NCSM). *Edgefield Co.*, ca. 14.4 km (9 mi) N of Edgefield, along US hwy. 378, 1 spmn., 13 June 1958, collector unknown (FSCA).

GEORGIA: The northern half of the state, from the Fall Zone northward. *Bartow, Cobb, Coweta, Fulton, Habersham, Hall, Haralson, Murray, Polk, and Rabun* counties (FSCA, MEM, NCSM, MNMH, ZMUC). Southernmost record: *Coweta Co.*, locality unknown, 2 spmns., date and collector unknown (ZMUC).

ALABAMA: Expected in the eastern part of state south to the Fall Zone, with one segregated record from western Alabama near the western terminus of the Cumberland Plateau. *DeKalb Co.*, DeSoto St. Pk., 1 spmn., 5 September 1966, F. A. Coyle (NCSM). *Tallapoosa Co.*, Dadeville, 1 spmn., 13 July 1900, W. R. Maxon (NMNH). Southernmost record: *Lee Co.*, Auburn, 1 spmn., April 1896, collector unknown (NMNH) and 1 spmn., 14 June 1959, collector unknown (FSCA). Westernmost record: *Marion Co.*, Hamilton, bank of Buttahatchee R., 1 spmn., 18 June 1958, collector unknown (FSCA).

The following literature records are considered valid and are incorporated into Fig. 31.

ILLINOIS: *McLean, Champaign, Randolph, Williamson, Gallatin, and Pulaski* cos., (Summers et al. 1980, 1981).

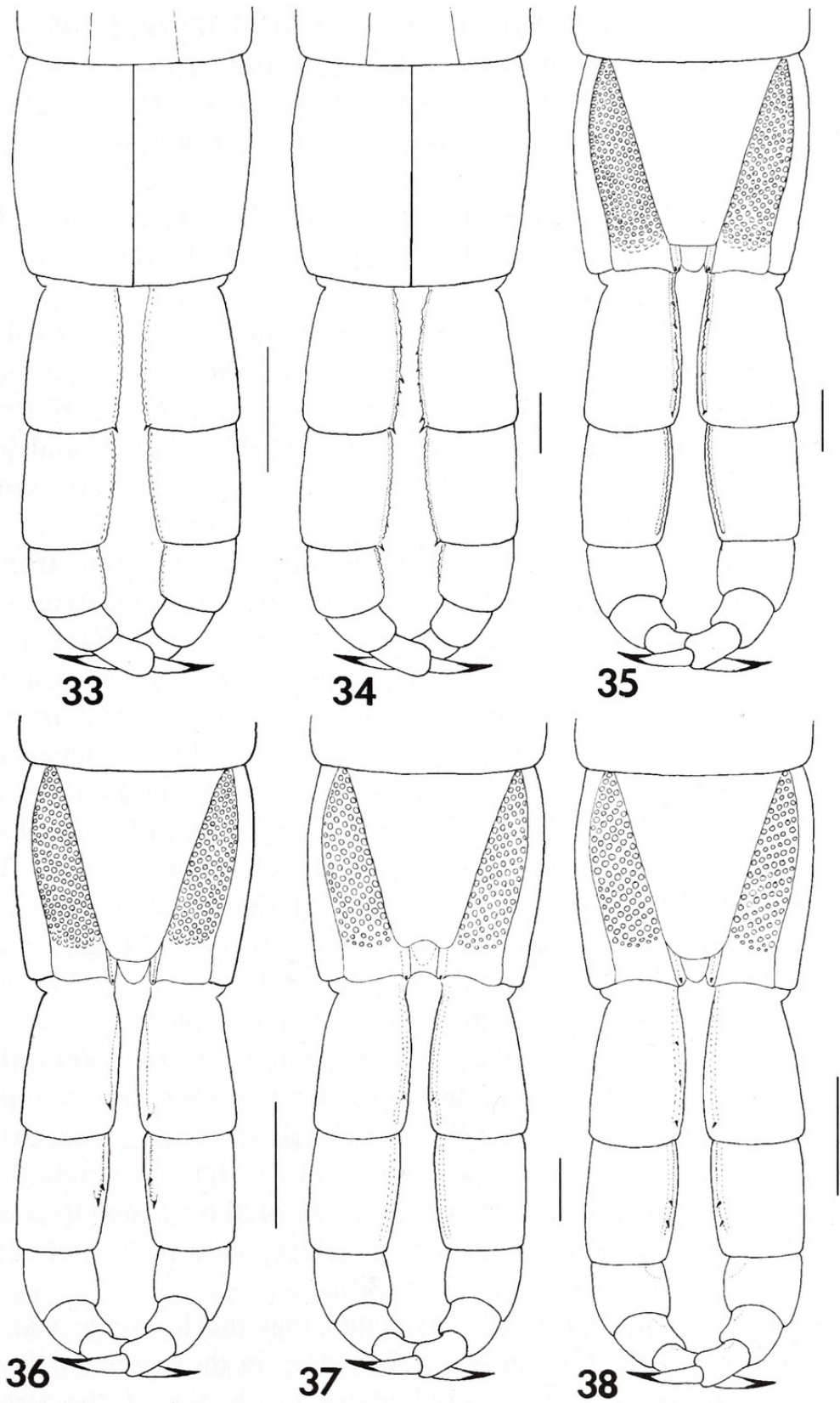
MISSOURI: *St. Francois Co.*, Libertyville (Chamberlin 1944b). *Franklin Co.*, Sullivan; and *Jefferson Co.*, High Ridge and Vaugirard (Crabill 1955c).

ARKANSAS: *Sevier Co.*, Ben Lomond; and *Logan Co.*, Mt. Magazine (Chamberlin 1944b).

NORTH CAROLINA: *Haywood/Buncombe* cos., Mt. Pisgah (Wray 1950, 1967).

Remarks. *Theatops spinicaudus* does not occur near Pennsylvania, so past records from this state in general, none from specific sites or counties (Wood 1862, 1865; Saussure and Humbert 1872, Underwood 1887, Bollman 1893, Kevan 1983), represent misidentifications of *T. posticus*.

Theatops phanus Chamberlin
Figs. 33-39



Figs. 33-38. Variation of the caudal legs and segment of *T. phanus* from selected localities. 33-34, dorsal views. 33, Atascosa County, Texas. 34, Menard County, Texas. 35-38, ventral views. 35, Menard County, Texas. 36, Atascosa County, Texas. 37, Williamson County, Texas. 38, Jim Wells County, Texas. Scale lines = 1.00 mm for each figure.

Theatops phanus Chamberlin, 1951b:101. Reddell, 1965:166.

Theatops spinicauda (nec Wood): Reddell, 1965:166.

Type specimen. Holotype (NMNH) taken by G. G. Stevenson, 16 April 1926, from an unnamed cave on his ranch near Sonora, Sutton County, Texas.

Diagnosis. Ultimate tergite with complete median suture; ultimate legs dorsally with a distomedial spur on each prefemur (Figs. 33-34).

Variation. The most striking variation in *T. phanus* involves its adaptability to subterranean environments and the differences between individuals from cave and epigeal environments. Most of the cave specimens that I examined were quite large, much longer and broader than the surface specimens from Atascosa and Jim Wells counties, which were small and similar in size to individuals of *T. posticus* from southwestern deserts. Cave individuals also display troglomorphic modifications like pallid color and longer, narrower appendages. Their antennae extend backwards to tergites 6-7; the antennomeres are three to five times longer than wide; and the podomeres on the penultimate legs are four to five times longer than wide. By contrast in epigeal specimens, the antennae reach back only to tergites 3-4; the antennomeres are approximately twice as long as wide; and the podomeres on the penultimate legs are only two to three times longer than wide. In both cave and surface specimens, the dorsal and ventral edges (ridges) of the flattened inner (medial) surfaces of the ultimate legs vary as in *T. spinicaudus*. The dorsal edge varies from wavy and lightly scalloped to highly irregular with variably minute teeth (Figs. 33-34), and on the left prefemur of the individual from Menard County, the distalmost tooth is almost as long as the adjacent spur (Fig. 34). Ventrally, all specimens show at least one tooth on each prefemur (examples of variation depicted in Figs. 35-38) and epigeal specimens from Atascosa and Jim Wells counties also have teeth on the femora (Figs. 36, 38). As with *T. spinicaudus*, the medial borders of the coxopleurae exhibit subapical pigmented spots, which are developed into teeth on the individual from Williamson County (Fig. 37).

Ecology. Chamberlin (1951b) stated that the holotype was found beneath a stone on the bottom of the first drop in the cave, and Reddell's specimens (1965) were discovered along the banks of the stream in Powell's Cave, Menard County. Because previous cave specimens display elongated legs and antennae, classical adaptations to subterranean life, *T. phanus* was thought to be exclusively troglomorphic, but the epigeal specimens in Atascosa and Jim Wells counties lack these modifications. The Terrell County cave specimen was found on silt 60 m (200 ft.)

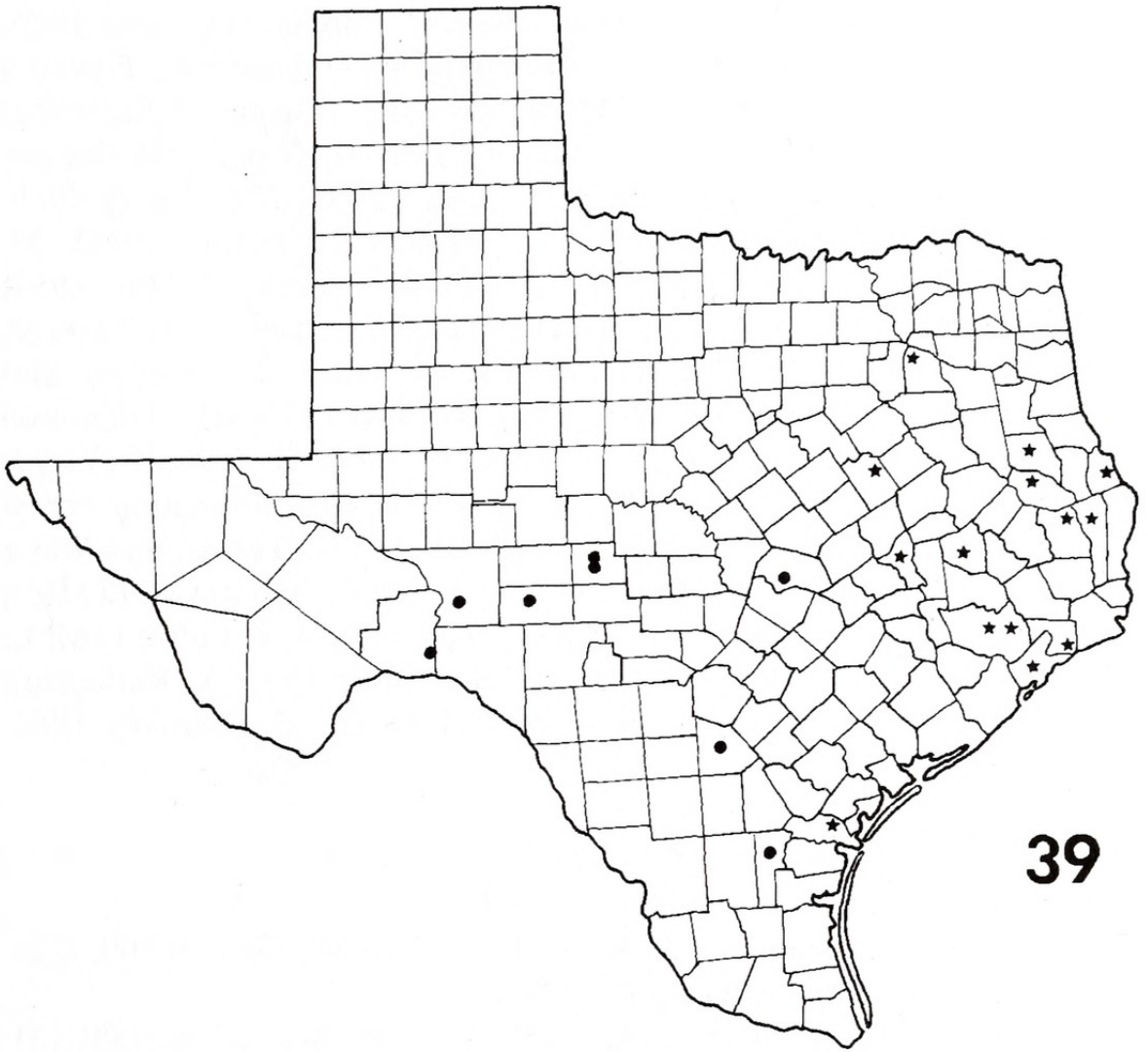


Fig. 39. Distributions of *T. phanus* (dots) and *T. posticus* (stars) in Texas.

from the entrance; other vial labels lack habitat data.

Distribution. No distributional information has been published for *T. phanus*. Crabill (1960) merely listed Texas without specification, and the only published record in addition to the type locality is Powell's Cave, Menard County (Reddell 1965, Shelley 1990a). The species occurs in south Texas from Menard and Williamson to Jim Wells counties, suggesting general occurrence in this region of the state; it ranges westward onto the Edward's Plateau and may extend southward to near the Rio Grande (Fig. 39). Specimens were examined as follows; the exact locations of 0-9 well in Crockett County and caves in Bexar, Burnet, Menard, Travis, and Williamson counties are unknown.

TEXAS: *Terrell Co.*, Longley Cv., 4.8 km (3 mi) W Val Verde co. line, 1 spmn., date unknown, J. Reddell, W. Russell (NMNH). *Crockett Co.*, 0-9 well, 1 spmn., 31 July 1988, G. Veni, A. Cobb, J. Ivy (TMM) and 1 spmn; 15 August 1992, C. Savvas (TMM). *Sutton*

Co., nr. Sonora, cave on Stevenson's Ranch, 1 spmn., 16 April 1926, G. G. Stephenson (NMNH) TYPE LOCALITY. *Menard Co.*, Powell's Cv., 1 spmn., date and collector unknown (NMNH), 2 spmns., 7 September 1964, J. Reddell, D. McKenzie, B. Russell (NMNH), 1 spmn., 25 October 1980, J. Reddell, D. McKenzie (TMM), and 1 spmn., 28 January 1989, W. Steele (TMM); Silver Mine Cv., 1 spmn., 23 January 1982, M. Minton (TMM); 8 km (5 mi) NW Menard, 1 spmn., 5 May 1957, S. Fowler (AAW). *Burnet Co.*, Simons Water Cv., Lost Falls Passage, 1 spmn., 3 August 1991, M. Warton (TMM). *Travis Co.*, Ceiling Slot Cv., 1 spmn., 31 March 1991, J. Reddell, M. Reyes (TMM). *Williamson Co.* Inner Space Caverns, 1 spmn., October 1966, B. Russell (TMM) and 1 spmn., 22 December 1968, W. Elliott (TMM); Formation Forest Cv., 1 spmn., 31 March 1993, J. Reddell, M. Reyes (TMM); and Water Tower Cv., 1 spmn., 15 May 1993, J. Reddell, M. Reyes (TMM). *Bexar Co.*, Robber Baron Cv., 1 spmn., 19 June 1993, J. Loftin (TMM). *Atascosa Co.*, Jourdanton, 1 spmn., 27 November 1935, S. Rutherford (NMNH). *Jim Wells Co.*, Alice airport, 1 spmn., 3 February 1962, R. O. Albert (NMNH).

Theatops erythrocephalus (C. L. Koch)

Figs. 40-41

Cryptops erythrocephalus C. L. Koch, 1847:173-174; 1863:99-100, Figs. 221a,b. Kohlrausch, 1881:130.

Opisthemega erythrocephalum: Latzel, 1880:147-149. Kohlrausch. 1881:131. Latzel, 1880:147-148. Daday, 1889:92.

Opisthemega lusitanum Verhoeff, 1896:78-79.

Theatops erythrocephalus: Kraepelin, 1903:66-67, Fig. 26. Attems, 1929:299. Verhoeff, 1941:figs. 89-90.

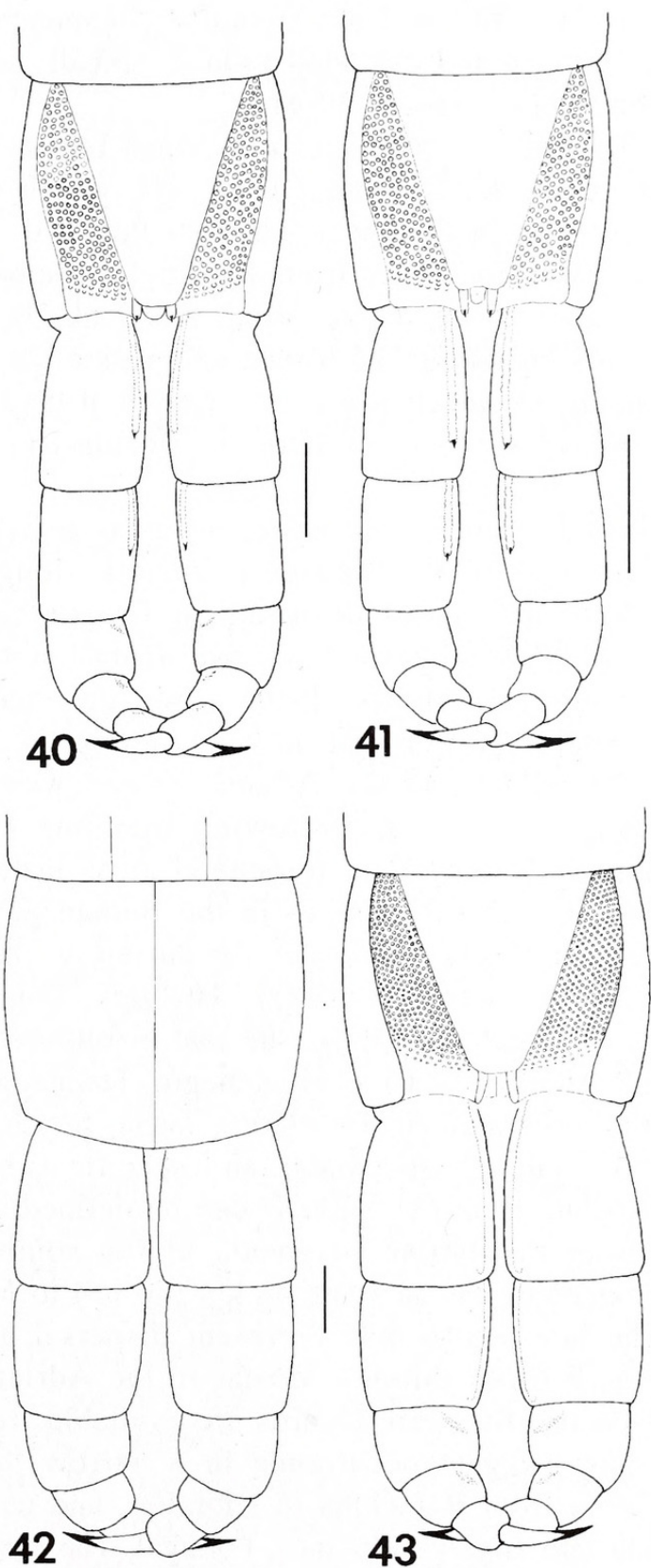
Theatops erythrocephala: Attems, 1930:251-252, Figs. 4, 27, 32, 331-335; 1959:319. Foddai *et al.*, 1995:8.

Theathops erythrocephalus breuili Matic 1960:446-447, Figs. 7-8.

Theatops erythrocephala erythrocephala: Matic, 1960:447.

Type specimen. Most of Koch's centipede types are deposited in the NHM, but that of *C. erythrocephalus* is not labeled as such (Minelli, *in litt.*) and could not be located by the curator. According to Koch (1847) the type was collected by Prof. Dr. V. Siebold at Pula on the Istrian peninsula, Croatia.

Diagnosis. Ultimate tergite usually with incomplete median suture, running from anterior margin to just short of caudal edge; ultimate legs without dorsal distomedial prefemoral spurs; ultimate prefemora and femora usually with four strong, distinct ventral spurs, one on



Figs. 40-43. Variation of the ventral surfaces of the caudal legs and segment of *T. erythrocephalus*. 40, specimen from Sipan Island, Croatia. 41, specimen from Portugal, locality unknown. 42-43, caudal segment and legs of a specimen of *P. zwierleini* from Sardinia. 42, dorsal view. 43, ventral view. Scale lines = 1.00 mm for each figure.

each podomere, rarely with fewer spurs; caudal coxopleurae with medial borders strongly elevated and extended caudad, apically acuminate with blackened subapical spurs (Figs. 40-41).

Variation. The NCSM specimen from Sipan Island, Croatia, lacks the ventral spur on the left prefemur (Fig. 40), which contrasts with the normal condition as in the specimen from Portugal (Fig. 41). One caudal leg on a ZMH specimen from Rijeka (= Fiume), Croatia, is much smaller, appears to be regenerating, and lacks both spurs.

Ecology. To my knowledge, no habitat information has been published on *T. erythrocephalus*. However, Kos (1992) records it from mediterranean and submediterranean districts in Croatia, Bosnia-Herzegovina, and Montenegro.

Distribution. European, occurring in two areas segregated by some 992 km (620 mi), one in the Balkan Peninsula along the Adriatic Sea, extending from the Istrian peninsula of Croatia to the southern coastal extremity of Montenegro below Lake Scutari and probably also into Albania, including offshore islands along the coast of Croatia, and the other in Spain and Portugal, probably along the Mediterranean Coast south of Barcelona and the Atlantic Ocean west of the Strait of Gibraltar (Figs. 44, 45). The following literature records cannot be placed today because they refer to general areas instead of specific sites and because of political changes in the Balkan peninsula during the First and Second World Wars and the currently chaotic situation in this war-torn region: Kraepelin (1903)—Hungary, Dalmatia (southern coastal Croatia), Portugal, and Italy, the last erroneously referring to *P. zwierleini*; and Attems (1930) -- Montenegro, Dalmatia, "Kroatisches Litorale" (roughly equivalent to Dalmatia), Istria, South Hungary, and Portugal. However, enough specimens and specific literature records exist that the distribution in the Balkans can be defined as the Adriatic coastal region from the Istrian peninsula to the southern extremity of Montenegro, extending inland some 48 km (30 mi) to Mostar, Bosnia-Herzegovina. The last record may represent dispersal up the Neretva River Valley, which flows through Mostar to the Adriatic Sea. Fewer specimens and specific literature records are available from the Iberian Peninsula, but they suggest occurrence in a narrow band along the Mediterranean Coast from Barcelona to Gibraltar, and continuing along the Atlantic Ocean into Algarve Province, Portugal. The available evidence thus indicates a primarily coastal distribution for *T. erythrocephalus* in both the Balkan and Iberian peninsulas, and the question mark in Figure 44 is placed in southern Portugal because of the known coastal records in Spain. The specimens examined, and literature and other records, are as follows; where the name of a city has changed from that in the

literature or on the vial label, the modern name is cited first with the older equivalent in parentheses:

CROATIA: Istrian Peninsula, Rijeka (=Fiume), 2 spms., 1897, collector unknown (ZMH). Sipan Island, Luka, 1 spmn., date and collector unknown (NCSM). Dalmatia, locality unspecified, 1 spmn., 1 January 1899, collector unknown (ZMH).

BOSNIA-HERCEGOVINA: Exact locality unknown, 3 spms., 1903, collector unknown (ZMH).

MONTENEGRO: Bar (=Antivari), 2 spms., date and collector unknown (MCZ).

SPAIN: *Barcelona Prov.*, Barcelona, 3 spms., October 1927, collector unknown (ZMH).

PORTUGAL: Province and locality unspecified, 2 spms., 30 January 1900, collector unknown (ZMH) and 2 spms., date unknown, K. W. Verhoeff (MCZ).

The following literature records are incorporated into Figures 44 and 45.

CROATIA: Velebit Mtns., Senj (=Zengg) (Attems 1929). Istrian Peninsula: Pula (Attems 1929) TYPE LOCALITY. Dalmatia: Zadar (=Zara) (Attems 1929); Kali (a community on Pashan Island directly west of Zadar) (=Kali Pecina) (Attems 1959); Dugi Island (=Isola Grossa, the outermost island in the Adriatic Sea due west of Zadar), Dubrovnik (=Ragusa), Lapad (a town in the metropolitan area of Dubrovnik, at the tip of its peninsula), and Pridvorje, ca. 24 km (15 mi) SE Dubrovnik, below Zupski Bay (Attems 1929).

BOSNIA-HERCEGOVINA: Trebinje (a town below Mostar and ENE of Dubrovnik) (Attems 1929); along the Trebisinca River (a river just inside Bosnia-Herzegovina border that flows through Trebinje and parallel to the border) (=Vodena Dolina am Popovo Polje) (Attems 1959); Diklici (a community near Trebinje on the Trebesinca River) (=Pecina bei Diklici) (Attems 1959); Mostar (Attems 1929); Konjsko (a small town just SE of Trebinje) (Attems 1929); Prenj (a community just inside the Bosnia-Herzegovina border south of Mostar) (Attems 1929); Plasa, exact location unknown (Attems 1929); and Mljet (=Meleda) Island (Attems 1929, 1959).

MONTENEGRO: Hercegnovi (=Castelnuovo) (Attems 1959); Kotor (on south end of Kotorski Bay) (=Cattaro), Njegos (a small community slightly north of Kotor), Virpazar (on the western shore of the northern end of Lake Scutari), Cetinje, Titograd (=Podgorica), and Ulcinj (=Dulcigno) (Attems 1929).

SPAIN: *Alicante Prov.*, Denia, ca. 72 km (45 mi) NE Alicante, Cueva de la Punta de Benimaquia (Ribaut 1915), *Valencia Prov.*, Gandia,

ca. 60.8 km (38 mi) SSE Valencia, Cueva Negra de Palma (Ribaut 1915). *Malaga Prov.*, Cueva del Cerro de la Pileta, nr. Ronda, nearest town Benaolan, ca 100 km (62.5 mi) NNE Gibraltar (Matic 1960, Würmli 1975).

The following unpublished records were communicated by A. Minelli and are incorporated into Figures 44 and 45.

CROATIA: Krk Island.

SPAIN: *Granada Prov.*, Sierra Nevada and Capileira de Poqueira (possibly referring to a small town on the southern slope of the Sierra Nevada).

Deleted records. The following literature records are deleted. Minelli (1991) does not include *T. erythrocephalus* in his list of centipedes in northeastern Italy and does not anticipate its discovery at Trieste; a voucher specimen has never been located, and an old Trieste label could refer to a site in Istria (Minelli, *in litt.*). Foddai *et al.* (1995) list *T. erythrocephalus* as a questionable inhabitant of northern Italy and state that its presence should be confirmed. Kos (1992) does not record *T. erythrocephalus* from Slovenia, and this location, some 128 km (80 mi) inland, is implausible for the species.

ITALY: *Trieste Prov.*, Trieste (Attems 1929).

SLOVENIA: near Brestanica (=Bucerca-Hohle bei Reichenburg, Sudsteiermark (Attems, 1959)).

Genus *Plutonium* Cavanna

Plutonium Cavanna, 1881:169. Kraepelin, 1903:67. Verhoeff, 1907:253.

Attems, 1930:253. Foddai *et al.*, 1995:8.

Type species. *P. zwierleini* Cavanna, 1881, by monotypy.

Diagnosis. With 19 pairs of spiracles, on segments 2-20.

Distribution. Known from Granada Province, Spain, and the following regions of Italy: Sicily, southeastern Sardinia, and coastal Campania, particularly the Sorrento Peninsula (Fig. 44) (Würmli 1975, Foddai *et al.* 1995).

Species. One.

Remarks. A check of Attems (1930) and subsequent publications reveals that *Plutonium* and *Tonkinodentus* are the only known cryptopid genera that are absent from the Western Hemisphere and that the family Cryptopidae is primarily an "American," New World, taxon.

Plutonium zwierleini Cavanna

Figs. 42-43

Plutonium zwierleini Cavanna, 1881:169-170, Figs. 1-7. Kraepelin, 1903:67-68, Fig. 27.



Fig. 44. Distributions of *T. erythrocephalus* (stars) and *P. zwierleini* (dots). Some symbols of *T. erythrocephalus* in Croatia and Montenegro denote more than one locality; the site in Portugal is unknown and indicated by the question mark.

Plutonium zwierleinii: Verhoeff, 1906:387. Attems, 1926:Fig. 433; 1930:253-254, Figs. 336-338. Foddai *et al.*, 1995:8.

Type specimen. Neotype (ZMH) collected by G. A. Markens, 16 May 1898, at Palermo, Sicily, Italy. The holotype is not known to exist; it is not housed at either museum in Florence, Italy, the Museo Zoologico de La Specola (Zoological Museum of Florence University) or the Istituto Sperimentale per la Zoologia Agraria (Minelli, *in litt.*). According to Cavanna (1881), the holotype was collected in 1878 at an unspecified location, probably in Sicily, by Dom. Eq. Zwierlein.

Diagnosis. With the character of the genus (Figs. 42-43).

Variation. The few specimens that I examined agree with the description by Cavanna (1881). Würmli (1975) also does not indicate significant variation.

Ecology. According to Würmli (1975) and Minelli and Iovane (1987), *P. zwierleini* occurs from 0-900 m (0-2,952 ft.) in seashore environments and woodlands; it is usually encountered under large rocks or small stones, where soil moisture is preserved.



Fig. 45. Distribution of *T. erythrocephalus* in the Balkan Peninsula.

Distribution. Same as that of the genus (Fig. 44). Würmli (1975) discusses the authentic localities and erroneous ones reported by previous authors. In addition to the neotype, specimens were examined as follows:

ITALY: *Salerno Prov.*, Salerno, 1 spmn., 1928, collector unknown (ZMUC). *Sardinia*, Assuni, 1 spmn., 30 June 1911, N. L. H. Krausse (NMNH); and Lanusei, 1 spmn., 23 October 1899, collector unknown (ZMH).

The following localities were communicated by the indicated colleague and are incorporated into Figure 44.

ITALY: *Napoli Prov.*, Sorrento. *Sicily*, San Cataldo, ca. 6.4 km (4 mi) W Caltanissetta (H. Enghoff).

SPAIN: *Granada Prov.*, Orgiva (A. Minelli).

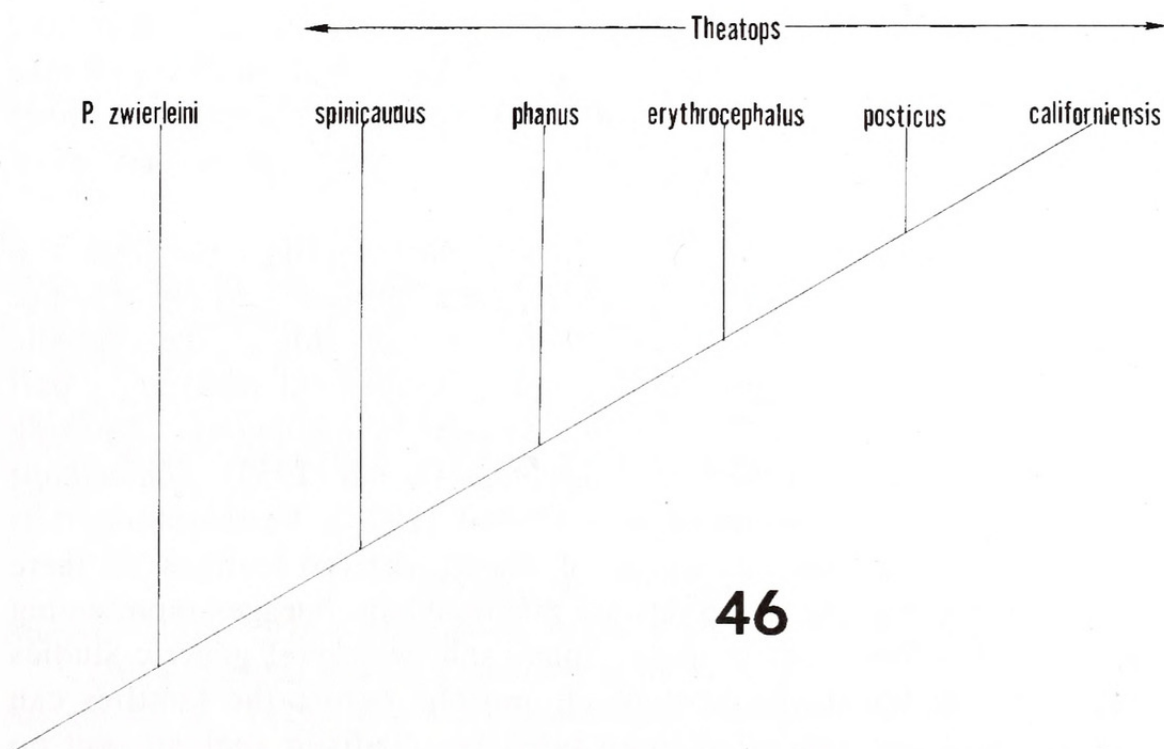
Remarks. The ultimate legs and segment of the examined specimens

of *P. zwierleini* are identical to those in the eastern population of *T. posticus* (compare Figs. 6 and 42 and Fig. 43 with Fig. 6 in Shelley (1990a)). The legs lack dorsal or ventral spurs, and the segment possesses a complete median dorsal suture and has rounded, nonextended coxopleurae. The only detectable distinction between *P. zwierleini* and eastern forms of *T. posticus* is the different number of spiracles.

RELATIONSHIPS

In assessing relationships among the plutoniumine taxa, *P. zwierleini* is obviously the sister-group to the five species of *Theatops*. Within the latter, *T. spinicaudus*, which is unique in lacking a median suture on the ultimate tergite, is the sister-group to the other four species. *Theatops phanus*, with the dorsal prefemoral spur, is then sister to the three species lacking this structure, and because *T. posticus* and *T. californiensis* were once geographic races of a single species, as shown by the residual intergrade specimens in the southwestern deserts (Shelley, 1990a), *T. erythrocephalus* is sister to its American counterparts (Fig. 44). Most of these proposed lineages cannot now be defined by autapomorphies, and comparative biochemical investigations may be necessary to elucidate such characters because of the high degree of phenotypic similarity among the members of this subfamily.

Their Holarctic distributions indicate a Laurasian origin for both the subfamily and the genus *Theatops*. Aside from *Plutonium* and *Theatops*,



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Fig. 46. Relationships in the Plutoniuminae.

the only European cryptopid genus is *Cryptops* Leach (Cryptopinae), which also has 21 leg pairs and pedal segments, with slightly enlarged caudal legs. The Cryptopinae, a global taxon, also is indigenous to the Nearctic, whereas the other cryptopid subfamily, the Scolopocryptopinae, with narrow caudal legs and 23 leg pairs and pedal segments, is primarily a New World group with minor representation along the western Pacific Rim from Japan to New Guinea (Attems 1930). The Plutoniuminae and Cryptopinae therefore logically share ancestry and may antedate the Scolopocryptopinae, whose concentration in the Americas suggests a post-Laurasian origin. Its diversity and abundance in North and South America probably reflect considerable northward and southward dispersal after closure of the Panamanian portal, and the occurrence of *Scolopocryptops* Newport in Japan, Korea, and China surely represents a Pleistocene invasion of Asia via the Bering Land Bridge. However, this genus and the subfamily also occur in the Philippines, Viet Nam, New Guinea, Sulawesi, and the Sunda and Fiji Islands (Attems 1930, Schileyko 1995), and their existences in these areas, if native and not the result of introductions, hardly represent trans-Beringian dispersal. With this circum-Pacific distribution, the Scolopocryptopinae may be a chilopod analog to the diplopod family Cambalidae (order Spirostreptida), whose biogeography was attributed to the lost continent "Pacifica" by Jeekel (1985). Not nearly enough is known about scolopocryptopine biogeography to further explore this possibility, but it raises questions about the composition of the Cryptopidae, because an independent biogeography for the Scolopocryptopinae implies a different origin and phylogeny. This in turn implies that concordance with the Cryptopinae and Plutoniuminae in the absence of ocelli represents convergence rather than shared ancestry; consequently, the Scolopocryptopinae may merit separate family status.

The prevailing concept of the Scolopendromorpha recognizes two families, Scolopendridae and Cryptopidae, based primarily on the presence and absence, respectively, of four ocelli on each side of the cephalic plate. Schileyko (1992) proposed a new arrangement derived in part from that of Haase (1887), but this system is incomplete, omitting at least three cryptopid genera, *Dinocryptops* Crabill (1953), *Thalkethops* Crabill (1960), and *Ectonocryptops* Crabill (1977). Furthermore, it is not based on a rigorous assessment of shared, derived features, so there is no assurance that the groupings are monophyletic lineages representing true lines of affinity. Many more alpha- and beta-level generic studies must be conducted in the Scolopendromorpha before the families can be reappraised and subjected to an intensive cladistic analysis, but no longer should the present division, based primarily on the presence or

absence of eyes, be uncritically accepted.

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